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Nonpollen palynomorphs: Indicators of salinity and environmental change in the Caspian–Black Sea–Mediterranean corridor

P.J. Mudie*
Geological Survey Canada Atlantic, Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada

S.A.G. Leroy†
Institute for the Environment, Brunel University, Uxbridge UB8 3PH, West London, UK

F. Marret†
Department of Geography, Liverpool University, Liverpool L69 7ZT, UK

N. Gerasimenko†
National Taras Shevchenko University of Kyiv, Earth Sciences and Geomorphology Department, Kyiv, GSP 680, Ukraine

S.E.A. Kholeif†
National Institute of Oceanography and Fisheries Egypt, Qayed Bay, Alexandria, Egypt

T. Sapelko†
Institute of Limnology, Russian Academy of Sciences, St. Petersburg 196105, Russian Federation

M. Filipova-Marinova†
Museum of Natural History, 41 Maria Louisa Blvd., 9000 Varna, Bulgaria

ABSTRACT

Previous palynological studies of the Caspian–Black Sea–Mediterranean corridor primarily focused on pollen and spores for paleoecological and chronostratigraphic studies. Until recently, there has been less emphasis on the nonpollen palynomorphs, such as dinoflagellate cysts, algal and fungal spores, and animal remains. New studies of nonpollen palynomorphs in land-locked seas, estuaries, and lakes reported here indicate that they are important markers of salinity, nutrient loading, and human activity, including ballast discharge, farming, and soil erosion. We describe the nonoxidative laboratory processing methods necessary to extract nonpollen palynomorphs from marine- and brackish-water sediment samples. We list 48 nonpollen palynomorphs taxa from 37 surface sediments (including the past millennium) for cores

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*Corresponding author, mudiep@ns.sympatico.ca.
†Leroy—suzanne.leroy@brunel.ac.uk; Marret—marret@liv.ca.uk; Gerasimenko—geras@gu.kiev.ua; Kholeif—Suzan_Kholeif@yahoo.com; Sapelko—tsapelko@mail.ru; Filipova-Marinova—marianafilipova@yahoo.com.

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along the salinity gradient from <16‰ off the Danube Delta to >39‰ in the Aegean, Mediterranean, and Red Seas, for two Crimean saline lakes, the Caspian and Aral Seas, and for lakes in Iran and Kazakhstan. The main nonpollen palynomorphs taxa are illustrated and listed systematically to provide a baseline for future collaborative studies among Black Sea corridor palynologists. We outline the biological affinities of some nonpollen palynomorphs and discuss the initial results of the study in terms of what nonpollen palynomorphs may reveal about the history of the salinity in the Black Sea corridor and the impact of humans on soil erosion, plankton production, and harmful algal blooms.

INTRODUCTION

Most previous palynological studies (e.g., Traverse, 1974, 1978; Rossignol-Strick, 1995; Aksu et al., 1995; Mudie et al., 2002; Filipova-Marinova and Christova, 2004) of the Black Sea and Eastern Mediterranean Sea focus on the study of pollen and spores for interpretation of climate change, because these terrestrial palynomorphs are continuously present throughout the Pliocene to Holocene sediments. However, there are many other kinds of palynomorphs in addition to pollen. These nonpollen palynomorphs (or NPM, nonpollen microfossils) include dinoflagellate cysts, various types of algal and fungal spores, zooplankton egg capsules, and other animal remains like the organic linings of small foraminifera (Van Geel, 2001). Nonpollen palynomorphs have often been discarded by Quaternary palynologists because of a lack of knowledge concerning their ecological and biological affinities; recently, however, new projects have focused on them because they contribute a wealth of information about paleoecological conditions, fires, and human land use (van Geel, 2006). Moreover, nonpollen palynomorphs are the focus of industry research on processes of black shale formation in anoxic basins, like the present Black Sea. Knowledge of nonpollen palynomorphs therefore represents a rich mine of information that should be better exploited, both for the completeness of Pleistocene and Holocene geological studies and for benefit of industry exploration. This research could represent a minimal effort to make the most use of the time already devoted to sampling, extracting, and counting the slides for pollen and spores. Furthermore, new studies of nonpollen palynomorphs in lakes and estuaries have shown that they are important markers of salinity, while others are more sensitive to nutrient loading and human activity (e.g., Brenner, 2001, 2006). In this paper, we document the most frequent nonpollen palynomorphs present in the surface samples from cores along the salinity gradient from <16‰ off the Danube Delta to >39‰ in the Aegean and Mediterranean Seas, in parts of the Caspian and Aral Seas, and in some saline or brackish-water coastal lakes adjoining the seas, and we also discuss what they might tell us about the history of the Caspian–Black Sea–Mediterranean corridor (abbreviated here as the Black Sea Corridor; Fig. 1).

The main categories of nonpollen palynomorphs that have been reported in studies of Holocene sediments of the Black Sea corridor are dinoflagellate cysts (= dinocysts), including organic linings of calcareous cysts, and various types of algae, including unicellular and colonial chlorophytes, cyanobacteria, filamentous zygnemataceans, and desmids. Also present are fungal spores and remains of fungal hyphae and fruiting bodies, zooplankton and insect skeletal remains, organic linings of small foraminifera and ostracods, scolecodonts (an old term for the mouthparts of marine worms), and other still unidentified forms known under the general name of incertae sedis or acritarchs. In some of the inland lakes and in the Nile Delta, filamentous cyanobacteria are found in the sediment deposits. In this paper, we present the initial results of studies made by members of the International Geological Correlation Programme (IGCP) 521 WG2 (Palynology), with the intent of stimulating further inputs from other palynologists working on nonpollen palynomorphs of the Caspian and Aral Seas, saline ponds (liman-lagoons), and other coastal environments of the Black Sea, Eastern Mediterranean, and the Nile Delta. At this early stage of our studies, we will simply demonstrate the existence of various nonpollen palynomorphs in the very large range of environments making up the Black Sea corridor, and discuss possible trends in relative abundances that seem to distinguish inland lakes with very unstable salinities from the continuously hypersaline Aegean and Levantine Seas. Key nonpollen palynomorphs taxa are illustrated, and where possible, we link their fossil names to modern life forms.

At present, there is no standard application of terms describing salinity zones along the gradient from pure water (lacking any mineral salt) to brine ponds encrusted in sodium chloride (Fig. 2). For the purposes of this paper, therefore, we have adopted the terminology long used by scientists studying the benthic fauna of the Black Sea corridor (see Yanko-Hombach, 2007), but with a slight modification to accommodate the greater range of our salinity spectrum above 38‰. This terminology is also similar to that used in marine botany textbooks (e.g., Dawes, 1998). Figure 2A shows the salinity scale and the corresponding terminology for the planktonic nonpollen palynomorphs of the Black Sea corridor. The Yanko-Hombach scale for Black Sea corridor benthos is presented for comparison up to its maximum reported value (40‰). The accompanying map (Fig. 2B) shows the geographical distribution of the fresh to saline surface waters above the halocline at ~100 m depth. In the strongly stratified waters of the Black Sea corridor, the bottom water below ~200 m water depth is ~10‰ more saline than the surface layer. Bottom water in the brackish Black Sea is ~24‰ (brackish–semimarine), and it is in the normal marine range (~29‰–34‰) below the semimarine (~21‰–24‰) surface water of the Marmara Sea.

For comparison with our studies, the salinity ranges commonly used in coastal northwestern Europe and the Baltic Sea (Denys and de Wolf, 1999) are also presented. The salinity scale (Fig. 2A) shows that there is a much broader salinity range known as "brackish" in Europe (3‰–18‰–28‰) than in the Black Sea region (3‰–5‰–12‰), but there is close agreement in the definition of "freshwater" as less than 0.5‰. The misuse of the term "freshwater" for salinities less than 3‰–5‰ by sedimentologists and archaeologists (Turney and Brown, 2007) is unfortunate and confusing because permanent human habitation and irrigation in the Holocene Black Sea brackish lake would have been constrained by access to potable freshwater (<1‰), as discussed by Mudie et al. (2002, 2004).

PREVIOUS STUDIES

So far, most nonpollen palynomorphs studies have concentrated on peat (e.g., van Geel, 2001). From there, in the last decades, they have expanded to lake sediment. In Europe, a working group, ACCROTELM (Abrupt Climate Changes Recorded over the European Land Mass), has aimed to identify and publish on nonpollen palynomorphs of peat and lakes (www2.glos.ac.uk/accrotelm/micproto.html). Much less work has been concerned with nonpollen palynomorphs of estuaries, closed seas, and open seas (Leroy, 1992; Matthiessen and Brenner, 1996; Brenner, 2001; Kholeif, 2004; Mudie et al., 2010). In the Black Sea corridor, several studies have been made of dinoflagellate cysts (dinocysts) and some of the acritarchs, starting with Wall et al. (1973) and Roman (1974). Traverse (1974, 1978) looked at dinocysts, acritarchs, fungal spores, and microforaminifera in Pliocene–Holocene Deep Sea Drilling Program (DSDP) cores. Mudie et al. (2001, 2002) studied the dinocysts, acritarchs, colonial algae, and fungal spores in the Black, Marmara, and Aegean Seas, while Filipova-Marinova and Christova (2004) and Atanassova (2005) reported on some Black Sea dinocysts, *Cymatiosphaera* and *Pediastrum.* Marinova and Atanassova (2006) described the nonpollen palynomorphs in a core from brackish (2‰–4‰) Lake Durankulak on the coast of northeastern Bulgaria. Hiscott et al. (2007) showed the Holocene history of microforaminiferal linings and *Pediastrum* in a core from the southwestern Black Sea shelf. Marret et al. (2004) and Leroy et al. (2007) reported on Caspian Sea dinocysts and other nonpollen palynomorphs, and Kazancı et al. (2004) listed various nonpollen palynomorphs from the coastal lagoon of Anzaleh (SW Caspian). Leroy et al. (2006) and

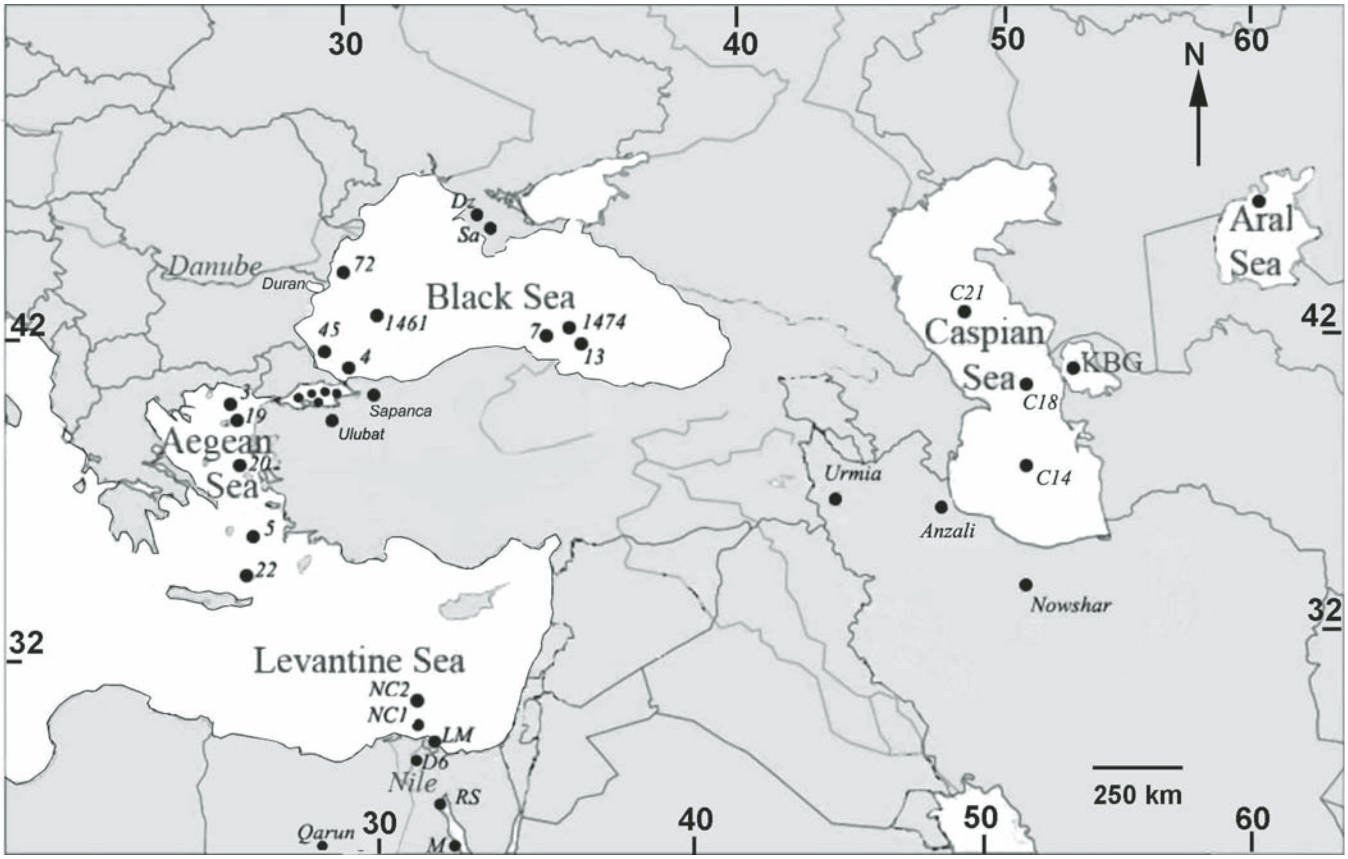

Figure 1. Regional map of the Caspian–Black Sea–Mediterranean corridor showing locations of the core sites used in this study. KBG—Kara-Bogaz Gol.

Sorrel et al. (2006) also documented the dinocysts and other nonpollen palynomorphs from the Kara-Bogaz Gol and the Aral Sea, respectively, and Leroy et al. (2009) studied the nonpollen palynomorphs in Lake Sapanca east of the Marmara Sea. Giralt et al. (2004) reported on nonpollen palynomorphs in Lake Issyk-Kul, Kyrgyzstan. For the Aegean region, there is a report on the use of microforaminifera as an index of carbonate dissolution (Kotthof et al., 2008), and Aksu et al. (1995, 1999) and Zonneveld et al. (2001) studied dinocysts as indices of bottom-water oxidation and as markers of plankton production and export to organic-rich sapropel sediments. The late Pleistocene–Holocene history of dinocysts in Nile cone sediments was documented by Kholeif and Mudie (2009), and initial studies of dinocysts and nonpollen palynomorphs on the inner Egyptian Shelf were reported by Marret et al. (2008).

The main results from the pioneer studies of Wall et al. (1973) was a succession of dinoflagellate assemblages from one dominated by *Spiniferites cruciformis* and *Pyxidinopsis psilata*

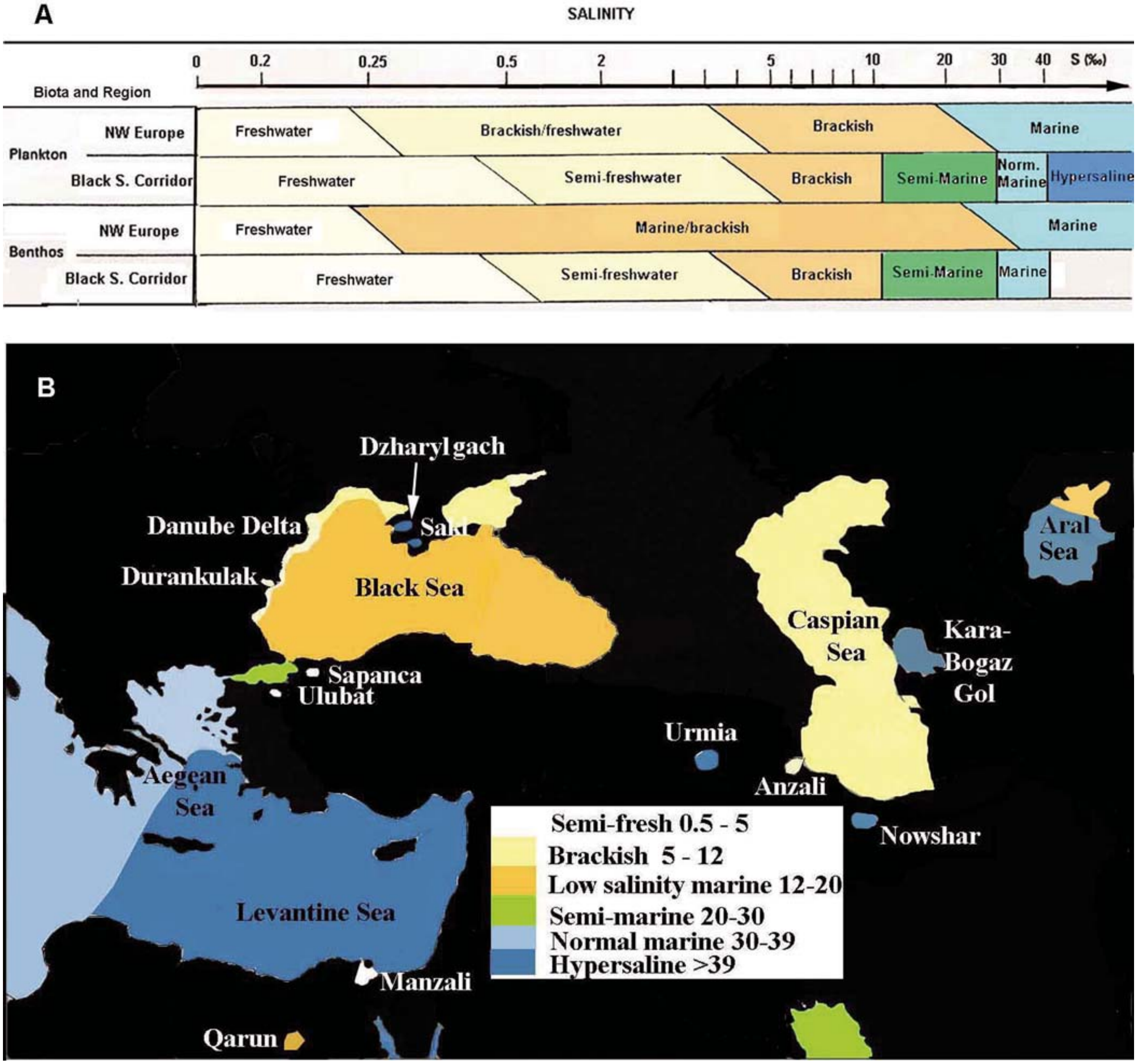

Figure 2. Range of salinity in the Black Sea corridor. (A) Salinity scale showing the ranges of paleosalinity categories used for the Black Sea versus northwest Europe and the Baltic Sea (modified from Denys and de Wolf, 1999). (B) Map of the surface salinity in the study region; Aral Sea is presently hypersaline but was brackish for most of the past millennium.

(*Tectatodinium psilatum*), which they thought marked very low salinity, to a *Lingulodinium* assemblage, which they interpreted as indicating marine conditions at ca. 7 ka. This *Lingulodinium* cyst assemblage was followed by a peak of what they called an acritarch, *Cymatiosphaera globosa*, which they also attributed to marine influence. However, this interpretation was made just 5 yr after the link was established between living dinoflagellate plankton populations and fossil dinoflagellate cysts, and 2 yr after the biological link was made between *Cymatiosphaera* and the resting spore (phycoma) of the Chlorophyte alga *Pterosperma* (Martin, 1993). Since that time, laboratory cultures and more detailed ecological studies have shown that both these organisms, *Lingulodinium* and *Pterosperma*, respond to nutrient enrichment and water turbulence as much as to salinity. For example, Dale (1996) summarized the basic elements of the dinocyst salinity signal for the Baltic and Black Sea as consisting of: (1) coastal/neritic cyst species tolerating a broad range from normal marine (~35‰) to reduced marine conditions of ~20‰; (2) assemblages of *Operculodinium centrocarpum* and small *Spiniferites* spp. with reduced processes in salinities below 3‰; and (3) in the Black Sea, *Pyxidinopsis psilata* marking the interval 3‰–10‰, and above 7‰, an increase in abundance of *Lingulodinium machaerophorum*. Brenner (2001), however, found that in the entrance of the Baltic Sea and in the North Sea, there was a change from *O. centrocarpum* assemblages dominating below 15‰ to *L. machaerophorum* assemblages that may have been triggered by nutrient enrichment and by sensitivity to summer sea-surface temperature above 10 °C rather than just salinity. Similarly, Brenner (2001) found that the occurrence and abundance of *P. psilata* cysts in annual varves of Baltic Sea sediment is controlled by additional, as yet unknown, factors other than salinity.

Consequently, simple conclusions about a marine index of salinity or a sea-level change from increases in *Lingulodinium* and *Pterosperma*, are not justified, and the trophic conditions of the waters must also be considered, in addition to stratification versus turbulence, nutritional requirements of associated heterotrophic species, and biological growth strategies (opportunistic r-type versus conservative K-type), as outlined for dinoflagellates by Taylor (1987). The terminology for trophic levels that we use in this paper is based on chlorophyll *a* (chl-a) values for the modern waters, as measured by satellite observations in June 1997 (Fig. 3) and the Aegean Sea trophic status classification of Ignatiades (2005). The succession of dominant nonpollen palynomorphs groups in the Black Sea cores studied by Wall and Dale (1974) looks more like a shift in phytoplankton from populations that characterize stenohaline oligotrophic conditions (e.g., *Spiniferites cruciformis* assemblages, according to Kouli et al., 2001) to a dominance of euryhaline opportunistic autotrophs such as *L. machaerophorum*, and followed by heterotrophs that characterize turbid nutrient- and diatom-rich water. Interpretation of the near-surface decline in *Lingulodinium* and *Cymatiosphaera* as a salinity decrease over the past 3 k.y. also disagrees with the occurrence of the exclusively marine coccolith *Emiliania huxleyii* in the Black Sea during this time (Marret et al., 2009). Studies of the carotenoid pigment isorerenieratene as a marker of stratification intensity, and δD records of C_{37}

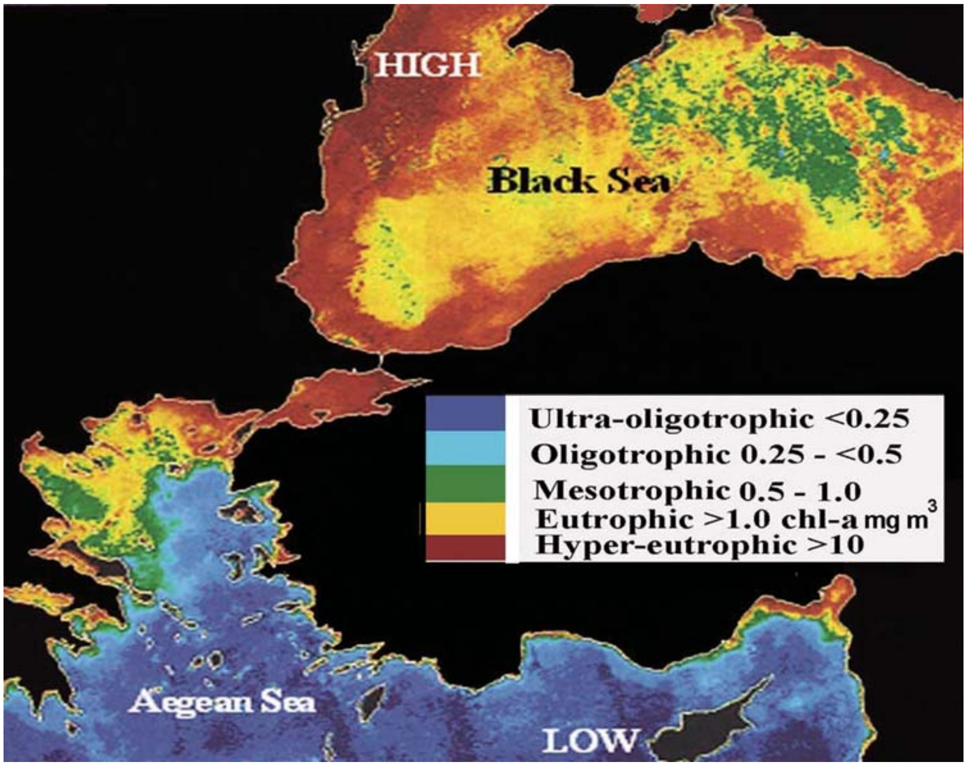

Figure 3. Distribution of trophic status categories for waters in the western study region, based on June 1997 values of chlorophyll a (in mg m^3) and the classification of Ignatiades (2005).

alkenones produced by haptophyte algae as a marker of surface salinity (van der Meer et al., 2008), however, suggest that a gradual increase in stratification and a 6‰ decline in salinity has occurred in the Black Sea over the past 2.7 k.y. This trend would be expected to favor the dominance of *Lingulodinium*, as evident from core-top assemblages off the Crimean Peninsula (Anna Gapanova, Odessa National University, 2009, personal commun.), where *L. machaerophorum* constitutes ~50%–90% of the core-top dinocyst assemblages.

Alfred Traverse (1974, 1978) worked mainly on core cutter samples from DSDP cores back to the Miocene, and, therefore, his sampling intervals were more than a meter wide, providing no details for the late Pleistocene–Holocene. However, the long DSDP records do show the persistent presence of acritarchs, with fluctuations in their abundance that Traverse interpreted as indicating increased marine influence from sea-level changes. He devised a marine influence index (MI), calculated as

$$\text{MI} = (\text{dinocysts} + \text{acritarchs})/(\text{dinocysts} + \text{acritarchs} + \text{pollen}).$$

Traverse was convinced that a high MI marked a sea-level transgression phase. It was a good idea, but the lack of correspondence with his marine dinocyst record reveals that it was not a very solidly based index because he did not know that some dinocysts and most acritarchs are fresh- and brackish-water species that respond to nutrient loading and temperature more than salinity or sea level. Beginning in 1992 (Leroy, 1992; Aksu et al., 1995), there has been a resurgence of interest in the study of nonpollen palynomorphs in the Black Sea corridor—mainly focused in dinocyst assemblages in the Marmara, Black, and Caspian Seas, as cited previously, but recently also including a wider range of nonpollen palynomorphs in the Nile Delta and cone, Red Sea coast, and Egyptian desert, and in the saline mountain lakes of northern Iran and Kyrgyzstan (see Fig. 2B; Table 1, and its references).

LABORATORY PROCESSING METHODS AND SYSTEMATICS

The palynological processing methods used by members of IGCP 521 for past studies include the acetolysis-KOH methods recommended by the ACCROTELM group, the cold HCl-HF digestion method preferred for marine sediments (Marret, 1993), and heavy liquid separation. Dale (1976) noted that hot HCl has an adverse effect on some dinocysts, and processing using only sonification and sieving is the best method when possible (although gypsum deposits or fluoride precipitate may necessitate HCl usage). In the past 30 yr, there have also been important advances in our knowledge about the preservation potential of brackish-water and marine nonpollen palynomorphs that must be considered when selecting a processing method (Versteegh and Blokker, 2004; Zonneveld et al., 2008). Although the walls of dinocysts and acritarchs are similar to pollen, they are not made of sporopollenin, which is very oxidation resistant. The walls of organic dinocysts and chlorophyte phycomata are composed of more labile substances, produced by either the formation of linear carbon chains forming algaenans in the Chlorophytes, or by another pathway producing the aromatic wall chemistry of the Dinophyta. Versteegh and Blokker (2004) listed the biomolecular chemistry and resistance to acetolysis for a large number of algae that produce nonpollen palynomorphs. Postmortem polymerization of lipids is known to lead to fatty acid–based molecules in the walls of Eocene dinocysts, and there is still an important need for elucidating the chemical differences between the macromolecules produced by the living algae and their fossilized remains.

To extract the full range of the nonpollen palynomorphs, strong oxidants like acetolysis and hot 10% KOH cannot be used. Figure 4 shows the recovery of dinocysts and selected algal nonpollen palynomorphs from five Black Sea cores when different processing methods are used. The low recovery of dinocysts in cores 72 and 1461 (probably also in Lake Durankulak, Table 1) reflects processing with the traditional KOH and acetolysis methods of Faegri and Iversen or Birks (Bryant and Wrenn, 1998) in contrast to the other samples that were processed by sieving, followed by chemical digestion with cold 10% HCL and warm 52% HF (e.g., Mudie et al., 2004). Other new methods use only sodium hexametaphosphate $(\text{NaPO}_3)_6$, as described by Riding and Kyffin-Hughes (2006), or dilute KOH (Bryant and Wrenn, 1998). Extraction using heavy liquid separation (e.g., Wood et al., 1996) is satisfactory in preventing oxidation damage of thin-walled palynomorphs, but it needs careful application to avoid loss of specimens by settling after coagulation of clumped grains. Hot HCl followed by cadmium-iodide heavy liquid separation was used to process the Crimean lake samples reported in this study.

Zonneveld (2001) studied dinocysts in the western Levantine Sea and derived an index of oxidation sensitivity, showing that the most sensitive group is the protoperidinioid taxa. Cysts of heterotrophic, diatom-eating protoperidinioids are important markers of productivity in the Black Sea, but they are usually destroyed when acetolysis is used for processing (Marret, 1993). In contrast, *L. machaerophorum* is a moderately oxidation-resistant taxon, so when acetolysis is used, inevitably this species appears in relatively high numbers, inflating its importance as an ecological marker. The Zonneveld oxidation index ranks organic-walled dinocysts as follows:

(1) extremely sensitive: *Protoperidinium* spp., e.g., *Brigantedinium*, *Quinquecuspis* (formerly *Multispinula), Echinidinium*;

(2) moderately sensitive: *Operculodinium centrocarpum, Spiniferites* species;

(3) moderately resistant: *Impagidinium, Nematosphaeropsis*; and

(4) resistant: *Lingulodinium, Operculodinium israelianum, Polysphaeridium*.

The systematics used for the nonpollen palynomorphs are given in the following sections that describe the individual groups. Mainly, we followed the systematics used by Fensome et al. (1990) for acritarchs and prasinophytes, the dinocyst

TABLE 1. OCCURRENCES OF NONPOLLEN PALYNOMORPHS (NPP) AND CORRESPONDING SURFACE-WATER SALINITIES (IN PARTS PER THOUSAND, ppt) OF LATE HOLOCENE SEDIMENTS (LAST 2–3 KA) FOR VARIOUS LACUSTRINE TO MARINE ENVIRONMENTS IN THE STUDY REGION

	EGYPT (1, 2)					**NILE (3)**		**AEGEAN SEA (4)**				
Core/Sample number:	**Qarun**	**Del 6**	**Manz**	**Hama**	**Red S**	**NC-1**	**NC2**	**22**	**G5**	**20**	**19**	**3**
Surface salinity (ppt):	**11**	**low**	**3**	**41.4**	**42**	**38**	**39**	**39.5**	**39.3**	**39.1**	**38.4**	**34**
Pollen-Spores/g ×1000	80.1	70.5	+	20	A	8.69	24.3	0.11	0.06	0.21	1.23	0.37
Dinocysts/g ×1000	0	0	0	C	C	7.232	6.221	0.12	0.13	0.37	0.16	0.37
Acritarch types:												
Leiosphere/Acritarch-8 Trav.	0	0	0	0	C	+	+	0	0	0	0	0
Chomotriletes minor	C	0	0	0	R	C	C	0	0	0	0	0
Cymatiosphaera spp.	C	0	0	C	R	**O**	**O**	0	0	0	0	0
Heaxasterias problematica	0	0	0	0	0	0	0	0	0	0	0	0
Micrhystridium	**O**	0	0	R	R	+	0	0	0	0	0	0
Pseudoschizaea rubinus.	0	0		0	0	0	0	0	0	0	0	0
Pseudoschizaea sp.	0	0	+	0	+	+	0	0	0	0	0	0
Pterospermopsis sp.	0	0	0	0	+	0	0	0	0	0	0	0
Sigmopollis spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiosperma corbiferum	0	0	0	0	0	0	0	0	0	0	0	0
Tasmanites	**O**	0	0	0	C	0	0	0	0	0	0	0
Colonial algae	0	0	0	C	0	**O**	0	0	0	**O**	0	0
Botryococcus species	0	0	0	0	0	0	0	0	0	0	0	0
Pediastrum simplex	+	0	+	C	R	R	0	0	0	0	0	0
Pediastrum boryanum	0	0	C	C	0	0	0	0	0	0	0	0
Cyanobacteria	0	0	0	0	0	0	0	0	0	0	0	0
Anaboena	0	0	0	0	0	0	0	0	0	0	0	0
Zygnemataceae	0	+	++	0	0	R	R	0	0	0	0	0
Fungal spores	0	+	0	**O**	C	**O**	**O**	0	0	R	0	C
Glomus-type	A	0	0	C	R	C	**O**	0	0	0	0	0
Neurospora	0	0	0	0	0	0	0	0	0	0	0	0
Sporormiella/Sordaria	0	0	0	0	0	0	0	0	0	0	0	0
Tetraploa	0	0	+	0	0	0	0	0	0	0	0	0
Thecaphora	0	0	0	0	0	0	0	0	0	0	0	0
Fungal hyphae	C	0	0	C	0	C	0	0	0	0	0	0
Fruiting bodies, germlings	**O**	0	0	0	0	0	0	0	0	0	0	0
Microforaminifera	R	0	A	C	C	C	C	C	R	C	R	C
Tintinnids	0	0	0	0	0	+	R	0	0	0	0	0
Thecamoebians	0	+	+	0	+	0	0	0	0	0	0	0
Centropyxis **species**	0	0	0	0	0	0	0	0	0	0	0	0
cf. copepod eggs	0	+	0	0	C	C	A	+	0	0	0	0
Rotifers	0	0	0	0	0	0	0	0	0	0	0	0
Scolecodonts	0	0	0	0	+	0	0	0	0	0	0	0
Artemia salina	0	0	**0**	C	C	C	**O**	0	0	0	0	0
Other animals	0	0	0	0	0	+	+	0	0	0	0	0
Ostracod lining/jaw	0	0	0	0	0	R	0	0	0	0	0	0
Taxon diversity	**10**	**5**	**8**	**12**	**17**	**19**	**12**	**4**	**3**	**5**	**3**	**4**

Note: +—present; R—rare (<5%), O—occasional (6%–15%), C—common (16%–30%), A—abundant (>30%). Data sources for the sites, which are shown on Figure 1, are as follows. 1—Qarun Lake, Fayoum Depression: Kholief et al. (2007); Hamata mangrove swamp: Kholeif (2007); Suez tidal flat: Kholeif (2004). 2—Nile Delta site 6 and Manzala lagoon site 8: Leroy (1992). 3—Nile cone cores NC-1 and NC-2, Kholeif and Mudie (2009). 4—Aegean Sea sites 3–22 and G5, Marmara sites 2–12, and Black Sea sites 4–13: Mudie et al. (2002, 2004). 5—MAR02-45: Marret et al. (2009). 6—Sites 72 and 1461 of Roman (1974); site 1474 of Wall and Dale (1974). 7—Lake Dzarylgach: Sapelko and Subetto (2007). 8—Lake Saki: Gerasimenko and Subetto (2007). 9—Caspian Sea: Marret et al. (2004). 10—Leroy et al. (2007). 11—Lake Anzaleh (Anz.): Kazanci et al. (2004). 12—Kara-Bogaz Gol (KBG): Leroy et al. (2006). Iran: 13—Nowshahr: Ramezani et al. (2008). 14—Lake Urmia: Djamali et al. (2008); Aral: Sorrel et al. (2006); Issyk-Kul (IssK): Giralt et al. (2004). KYRG—Kyrgyzstan.

(*continued*)

TABLE 1. (*continued*)

	MARMARA SEA (4, 16, 17)							**BLACK SEA (4, 5 ,6, 7)**						
Core/Sample number:	**2**	**12**	**5**	**11**	**9**	**Sapa**	**Dura**	**4**	**72***	**1461***	**45**	**13**	**7**	**1474+**
Surface salinity (ppt):	**24**	**23**	**22**	**22**	**20.1**	**0.5**	**3**	**17.6**	**15**	**17**	**18**	**22**	**22**	**22**
Pollen-Spores/g ×1000	5.8	3.2	2.73	5.78	3.89	A	20	3.11	0.15	6	5.96	55.94	42	160
Dinocysts/g ×1000	2.7	2.53	6.09	7.87	2.33	R	R	2.97	0.5	0.12	3.99	2.07	12	2–62.0
Acritarch types:														
Leiosphere/Acritarch-8 Trav.	0	0	0	0	0	0	0	C	+	0	R	A	A	+
Chomotriletes minor	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cymatiosphaera spp.	0	**O**	0	0	0	0	0	0	+	**O**	R	C	A	A
Heaxasterias problematica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrhystridium	0	0	0	0	0	0	C	0	0	0	0	0	0	0
Pseudoschizaea rubinus.	8	0	0	**O**	R	0	0	**O**	0	0	A	A	A	0
Pseudoschizaea sp.	0	0	0	0	0	+	0	0	0	0	**O**	0	0	0
Pterospermopsis sp.	0	0	0	0	0	0	0	0	+	0	+	0	0	0
Sigmopollis spp.	0	0	**O**	**O**	R	0	+	C	0	0	C	A	A	0
Radiosperma corbiferum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tasmanites	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colonial algae	0	**O**	0	0	0	+	A	0	R	R	R	A	A	C
Botryococcus species	0	0	0	0	0	0	R	0	0	0	0	0	0	0
Pediastrum simplex	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Pediastrum boryanum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C**yanobacteria**	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anaboena	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Zygnemataceae	0	0	0	0	0	+	R	0	0	0	0	0	0	0
Fungal spores	R	A	A	C	C	0	C	C	+	+	C	A	A	C
Glomus-type	0	0	0	0	0	+	**O**	0	0	0	+	0	0	0
Neurospora	0	0	0	0	0	0	R	0	0	0	0	0	0	0
Sporormiella/Sordaria	R	0	0	0	0	+	C	0	0	0	R	0	0	0
Tetraploa	0	0	0	0	0	+	R	0	0	0	0	0	0	0
Thecaphora	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Fungal hyphae	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Fruiting bodies, germlings	0	0	0	0	0	0	0	0	++	0	0	0	0	0
Microforaminifera	R	A	0	A	A	+	0	C	0	0	A	0	0	0
Tintinnids	0	0	0	0	0	0	0	C	0	0	0	0	0	0
Thecamoebians	0	0	0	0	0	+	0	0	0	0	R	0	0	0
Centropyxis **species**	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cf. copepod eggs	A	0	0	0	0	0	0	0	0	0	**O**	0	0	0
Rotifers	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Scolecodonts	R	0	0	0	0	0	0	0	0	0	0	0	0	0
Artemia salina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other animals	0	0	0	0	0	0	0	0	0	0	R	0	0	0
Ostracod lining/jaw	0	0	0	0	0	+	0	0	0	0	**O**	0	0	0
Taxon diversity	**8**	**6**	**4**	**6**	**4**	**19**	**12**	**5**	**9**	**5**	**17**	**8**	**8**	**6**

Note: +—present; R—rare (<5%), O—occasional (6%–15%), C—common (16%–30%), A—abundant (>30%). Data sources for the sites, which are shown on Figure 1, are as follows. 1—Qarun Lake, Fayoum Depression: Kholief et al. (2007); Hamata mangrove swamp: Kholeif (2007); Suez tidal flat: Kholeif (2004). 2—Nile Delta site 6 and Manzala lagoon site 8: Leroy (1992). 3—Nile cone cores NC-1 and NC-2, Kholeif and Mudie (2009). 4—Aegean Sea sites 3–22 and G5, Marmara sites 2–12, and Black Sea sites 4–13: Mudie et al. (2002, 2004). 5—MAR02-45: Marret et al. (2009). 6—Sites 72 and 1461 of Roman (1974); site 1474 of Wall and Dale (1974). 7—Lake Dzarylgach: Sapelko and Subetto (2007). 8—Lake Saki: Gerasimenko and Subetto (2007). 9—Caspian Sea: Marret et al. (2004). 10—Leroy et al. (2007). 11—Lake Anzaleh (Anz.): Kazanci et al. (2004). 12—Kara-Bogaz Gol (KBG): Leroy et al. (2006). Iran: 13—Nowshahr: Ramezani et al. (2008). 14—Lake Urmia: Djamali et al. (2008); Aral: Sorrel et al. (2006); Issyk-Kul (IssK): Giralt et al. (2004). KYRG—Kyrgyzstan.

(*continued*)

TABLE 1. (*continued*)

	CRIMEA (8, 9)		**CASPIAN (10, 11, 12, 13)**				**ARAL**	**IRAN (14, 15)**		**KYRG**
Core/Sample number:	**Saki**	**Dzar**	**C21**	**C14**	**Anz.**	**KGB**	**Aral***	**Nows**	**Urm**	**IssK***
Surface salinity (ppt):	**>40**	**100**	**13**	**13**	**2–9**	**20–60**	**10**	**low**	**200**	**6**
Pollen-Spores/g ×1000	A	2	15	10	50	2.–12	10.0–43	VA	5	34
Dinocysts/g ×1000	0	0	5	5	15	2.–18	2.0–10	0	+	0
Acritarch types:										
Leiosphere/Acritarch-8 Trav.	0	0	A	0	0	0	A	0	0	0
Chomotriletes minor	0	0	0	0	0	0	0	0	0	0
Cymatiosphaera spp.	0	0	0	0	0	0	A	0	0	0
Heaxasterias problematica	0	0	0	0	0	0	R	0	0	0
Micrhystridium	A	+	0	0	0	0	C	0	0	0
Pseudoschizaea rubinus.	0	0	0	0	0	0	0	0	0	0
Pseudoschizaea sp.	R	0	0	R	0	0	0	0	0	0
Pterospermopsis sp.	0	0	A	**O**	0	0	0	0	0	0
Sigmopollis spp.	0	0	0	0	0	0	0	0	0	0
Radiosperma corbiferum	0	0	0	**O**	0	0	**O**	0	0	0
Tasmanites	0	0	0	0	0	0	0	0	0	0
Colonial algae	0	+	A	0	0	0	R	0	0	++
Botryococcus species	0	0	0	+	R	R-C	A	0	0	A
Pediastrum simplex	0	0	0	+	R-O	0	+	0	0	0
Pediastrum boryanum	0	0	0	0	0	0	0	0	0	R
Cyanobacteria	0	0	0	0	0	0	0	0	0	+
Anaboena	0	0	A	0	O-A	+	0	0	0	R
Zygnemataceae	0	0	0	+	R-C	0	0	**O**	0	++
Fungal spores	**O**	R	0	0	R	0	0	C	0	R-C
Glomus-type	R	**0**	0	0	0	0	0	0	0	R
Neurospora	0	0	0	0	0	0	0	0	0	0
Sporormiella/Sordaria	0	0	0	0	0	0	0	0	0	0
Tetraploa	0	0	0	0	0	0	0	**O**	0	0
Thecaphora	0	0	0	0	0	0	0	0	0	R
Fungal hyphae	0	0	0	0	0	0	0	0	0	0
Fruiting bodies, germlings	0	0	0	0	0	0	0	0	0	0
Microforaminifera	0	R	0	0	0	R	0	0	0	R
Tintinnids	0	0	0	0	0	0	**O**	0	0	0
Thecamoebians	0	0	0	0	0	0	0	R	0	+
Centropyxis **species**	0	0	0	0	0	0	0	**O**	0	0
cf. copepod eggs	0	0	0	0	0	0	0	0	0	0
Rotifers	0	0	0	0	R	0	0	0	0	0
Scolecodonts	0	0	0	0	**O**	0	0	0	0	0
Artemia salina	**O**	0	0	0	0	0	0	0	0	0
Other animals	0	+	0	0	R	0	0	0	0	+
Ostracod lining/jaw	R	+	0	0	+	0	0	0	0	+
Taxon diversity	**7**	**7**	**6**	**8**	**11**	**5**	**10**	**6**	**2**	**13**

Note: +—present; R—rare (<5%), O—occasional (6%–15%), C—common (16%–30%), A—abundant (>30%). Data sources for the sites, which are shown on Figure 1, are as follows. 1—Qarun Lake, Fayoum Depression: Kholief et al. (2007); Hamata mangrove swamp: Kholeif (2007); Suez tidal flat: Kholeif (2004). 2—Nile Delta site 6 and Manzala lagoon site 8: Leroy (1992). 3—Nile cone cores NC-1 and NC-2, Kholeif and Mudie (2009). 4—Aegean Sea sites 3–22 and G5, Marmara sites 2–12, and Black Sea sites 4–13: Mudie et al. (2002, 2004). 5—MAR02-45: Marret et al. (2009). 6—Sites 72 and 1461 of Roman (1974); site 1474 of Wall and Dale (1974). 7—Lake Dzarylgach: Sapelko and Subetto (2007). 8—Lake Saki: Gerasimenko and Subetto (2007). 9—Caspian Sea: Marret et al. (2004). 10—Leroy et al. (2007). 11—Lake Anzaleh (Anz.): Kazanci et al. (2004). 12—Kara-Bogaz Gol (KBG): Leroy et al. (2006). Iran: 13—Nowshahr: Ramezani et al. (2008). 14—Lake Urmia: Djamali et al. (2008); Aral: Sorrel et al. (2006); Issyk-Kul (IssK): Giralt et al. (2004). KYRG—Kyrgyzstan.

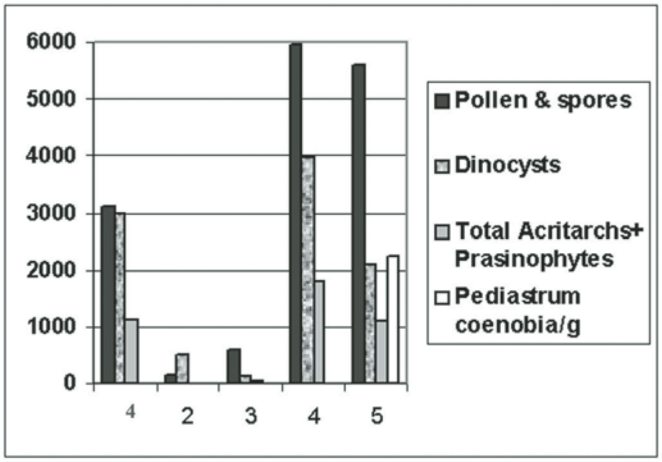

Figure 4. Recovery of pollen, dinocysts, acritarchs + prasinophytes, and colonial algae in Black Sea core using acetolysis (samples 72, 1461) versus hydrochloric + hydrofluoric acid (all others) for processing.

systematics of Fensome and Williams (2004) and Marret and Zonneveld (2003), and the fossil fungal spore studies of Kalgutkar and Jansonius (2000) and van Geel (2006).

RESULTS

Figure 1 shows the sites for which nonpollen palynomorphs have been reported for late Holocene and modern (surface) sediments in the Black Sea corridor, and Table 1 shows the corresponding salinity of the surface water at each site. Because sedimentation rates vary widely among the sites, the table shows all the nonpollen palynomorphs reported for the sites for the historical time interval covering approximately the past 2000 yr. Table 2 is a list of the taxa and their known or presumed biological affinity. The following sections provide an overview of our current knowledge about the biology and ecology of the main nonpollen palynomorphs that have been reported for the surface and latest Holocene sediments the Black Sea corridor.

Dinoflagellate Cysts

Dinoflagellate cysts are the most common nonpollen palynomorphs throughout the regions of the Black Sea corridor that have been continuously connected to the Mediterranean Sea over the past 2000 yr or longer, but they are absent in the hypersaline intermittently connected or isolated coastal lagoons of the Crimean Peninsula (e.g., Lakes Saki and Dzharylgach). Dinocysts are also absent from late Holocene sediments of both the low- and high-salinity mountain lakes studied in Iran and the brackish lake in Kyrgyzstan (Table 1), although *Spiniferites belerius* was found in a short interval of penultimate glacial sediment in the presently hypersaline Lake Urmia (Djamali et al., 2008). However, dinocysts are common in the brackish to hypersaline Caspian, Kara-Bogaz Gol, and Aral Seas, where some species are endemic (Marret et al., 2004). Two taxa (*Spiniferites* and *Lingulodinium machaerophorum*) are reported for the low salinity (2‰–4‰) Lake Durankulak-3 (Marinova and Atanassova, 2006), and *Spiniferites cruciformis, Impagidinium caspienense*, *Caspidinium rugosum*, and *Brigantedinium* are present in the oligotrophic freshwater of Lake Sapanca.

The most familiar group of dinocysts consists of the spiny gonyaulacoid, autotrophic cysts (Plate 1, figs. 9–10, 13–15, and 17–20) that may be slightly sensitive to oxidation, but usually some are recovered even after acetolysis. With HF processing, however, a much wider range of dinocysts is obtained, particularly including thin-walled "round brown" protoperidinioids (Plate 1, figs. 2–6, 8, 12, and 16) and polykrikoids (Plate 1, fig. 7), which are facultative or obligate heterotrophs (often diatom-eating) and flourish in eutrophic water, along with thin-walled toxic gymnodinioid species such as *Gymnodinium catenatum* (Plate 1, fig. 1). Some gonyaulacoids also proliferate with increased nutrients, including *Alexandrium* and *Lingulodinium*. Laboratory experiments of Lewis and Hallett (1997) show that *Lingulodinium* populations respond more to nutrients and low turbulence than to salinity—they are extremely euryhaline. These authors also reported that cyst populations of the autotroph *Lingulodinium machaerophorum* respond first to a temperature increase for breaking winter dormancy. Subsequently, the flagellated theca-stage cells need strong stratification for their growth in the photic zone because they are not powerful swimmers. If the photic zone is enriched with nutrients, then red tide population explosions follow, and many resting stage cysts are formed. Therefore, blooms of *Lingulodinium* cysts may indicate water-column stratification and nutrient enrichment more strongly than either salinity or sea level.

Principal component analysis of dinocyst core-top data from the Black Sea to Eastern Mediterranean (Mudie et al., 2004) shows two main components: (1) a group of stenohaline halophilic autotrophic species associated with the clear, oligotrophic Aegean Sea waters, and (2) heterotrophic protoperidinioids that are euryhaline and most closely linked with eutrophic surface waters in the Black Sea corridor. It is notable that in this analysis, *L. machaerophorum* is aligned with the heterotrophic protoperidinioids, suggesting a strong link with high nutrient levels, and explaining the weak correlation of process length and paleosalinity measured by Mudie et al. (2001). Using a larger global data set, however, Mertens et al. (2009) showed that the length and number of processes in *L. machaerophorum* are also strongly positively correlated with both temperature and salinity at 30 m water depth, possibly related to the sinking rates of the cysts under varying conditions of turbulent mixing versus stratification.

Acritarchs and Prasinophytes

The term Acritarcha is an artificial category that refers to all small (5–249 μm) microfossils of unknown and varied biological affinities, having a single or multiple-layered organic

TABLE 2. LIST OF TAXA MENTIONED IN THE TEXT, WITH GENERIC AND SPECIFIC NAMES AND COMPLETE AUTHORSHIPS OF GENERIC AND SPECIFIC NAMES WHERE KNOWN

PHYTOPLANKTON SPORES AND PLANT REMAINS

Acritarcha
Beringiella Bujak, 1984
Chomotriletes minor (Kedves) Pocock, 1970
Chromotriletes Naumova, 1939
Chromotriletes rubinus (Christopher, 1976) Fensome et al., 1990
Concentricystes Rossignol, 1962 *ex* Jansonius and Hills, 1976 emend. Jiabo, 1978 (misspelled as *Concentricystis*) (taxonomic senior synonym = *Chromotriletes*)
Concentricystes rubinus. Rossignol, 1962 *ex* Jansonius and Hills, 1976
Concentricystes rubinus Rossignol, 1962 (*partim*), p. 134, pl. 2, figs. 5, 6 (*nomen nudum*)
Copepod egg-type of *Cobricosphaeridum* Harland and Sarjeant, 1970 emend Head et al., 2003
Halodinium Bujak, 1984
Leiosphaera Eisenack, 1938 (junior synonym for *Tasmanites* Newton, 1875)
Leiosphaeridia Eisenack, 1958
Micrhystridium Deflandre, 1937
Micrhystridium cf. *braunii*-type of Sorrel et al., 2006
Micrhystridium. cf*. M. asagaiense* Takahashi, 1964
Micrhystridium minus Takahashi, 1964
?Micrhystridium spinuliferum Takahashi, 1964
Multiplicisphaeridium Staplin, 1961
cf. *Multiplicisphaeridium* sp. of Struthers, 1996
Nonpollen palynomorph (NPP) “Type 115” of Pals et al. (1980).
Pacillina Cleve, 1899
Palaeostomocystis Deflandre, 1937
Paleostomocystis = Beringiella Bujak, 1984
Pseudoschizaea Thiergart and Frantz *ex* R. Potonié emend. Christopher, 1976
Pseudoschizaea rubina Rossignol *ex* Christopher, 1976
Pseudoschizaea circula (Wolff), emend. Christopher, 1976
Sigmopollis Hedlund, 1965
Sigmopollis carbonis Hedlund, 1965
Sigmopollis hispidus Hedlund, 1965 = “Type 128” of van Geel, Hallewas & Pals, 1983
Sigmopollis psilatus Piel, 1971
Sphaeropsis, illustrated by Reid and John (1978)
Sporites circulus Wolff, 1934 (*partim*)
Tasmanites Newton, 1875

Chlorococcales
Botryococcus Kützing
Botryococcus braunii Kützing, 1849
Pediastrum F.J.F. Meyen, 1829
Pediastrum boryanum (Turpin 1828) Meneghini, 1840
Pediastrum duplex Meyen, 1929
Pediastrum kawraiskyi Schmidle, 1897
Pediastrum F.J.F. Meyen, 1829
Pediastrum simplex Meyen, 1829
Pediastrum kawraiskyi Schmidle, 1897
Tetraedron Kuetzing, 1845

Cynanobacteria
Anabaena St. Vincent, 1886, *ex* Bornet and Flahault, 1886
Gloeocapsomorpha Zalesskij, 1918
Gloeotrichia J. Agardh *ex* Bornet et Flahault, 1887
Rivularia [Roth] Agardh *ex* Bornet et Flahault, 1887

Dinoflagellata
Alexandrium Halim, 1960
Alexandrium monilatum (Howell) F.J.R. Taylor, 1979
Alexandrium tamarense (Lebour, 1925) Balech, 1985 cyst type
Brigantedinium simplex (Wall, 1965) Reid, 1977 = cyst of *Protoperidinium conicoides* (Paulsen) Balech
Brigantedinium spp. Reid, 1977 *ex* Lentin et Williams, 1993 = *Protoperidinium* spp.
Caspidinium rugosum Marret in Marret et al., 2004
Dubridinium caperatum Reid, 1977
Echinidinium transparantum Zonneveld, 1997
Gonyaulax apiculata (Penard, 1891) Entz, 1904
Gymnodinium catenatum Graham, 1943 cyst form
Gymnodinium fuscum (Ehrenberg) F. Stein, 1878
Gymnodinium mikimotoi Miyake et Kominami *ex* Oda, 1935
Gymnodinium nolleri Ellegaard & Moestrup, 1999
Gymnodinium uberrimum (G.J. Allmann, 1854) Kofoid & Swezey, 1921
Gyrodinium aureolum Hurlburt, 1957
Impagidinium caspienense Marret in Marret et al., 2004
Imagidinium aculeatum (Wall, 1967) Lentin and Williams, 1981
Impagidinium patulum (Wall, 1967) Stover and Evitt, 1978
Impagidinium sphaericum (Wall, 1967) Lentin and Williams, 1981
Impagidinium strialatum (Wall, 1967) Stover and Evitt, 1978
Islandinium minutum (Harland et Reid in Harland et al., 1980) Head et al., 2001
Lingulodinium machaerophorum (Deflandre et Cookson, 1955) Wall, 1967 = *Lingulodinium polyedrum* (Stein) J.D. Dodge, 1989
Lingulodinium machaerophorum forms with short club-shaped processes (vars. A–D of Marret et al., 2004)
Nematosphaeropsis labyrinthus (Ostenfeld, 1903) Reid, 1974
Operculodinium centrocarpum sensu Wall and Dale, 1966 = cyst of *Protoceratium reticulatum* (Claparède et Lachmann) Bütschli, 1885
Operculodinium israelianum (Rossignol, 1962) Wall, 1967
Peridinium Ehrenberg 1830 cyst type
Peridinium ponticum Wall and Dale, 1973
Polykrikos Bütschli, 1873
Polykrikos kofoidii Chatton, 1914 cyst form
Polysphaeridium zoharyi (Rossignol, 1962) Bujak et al., 1980 = *Pyrodinium bahamense*
Protoperidinium americanum (Gran et Braarud, 1935) Balech, 1974
Pyxidinopsis psilata Wall and Dale, 1973
Pyxidinopsis reticulata (McMinn et Sun, 1994) Marret et de Vernal, 1997
Quinquecuspis Reid, 1976
Quinquecuspis concreta (Reid) Harland, 1977
Scrippsiella sensu Head et al., 2006
Selenopemphix nephroides (Benedek, 1972) Bujak in Bujak et al., 1980, Benedek et Sarjeant, 1981 = cyst of *Protoperidinium subinerme* (Paulsen) Loeblich III, 1970
Spiniferites Mantell, 1850
Spiniferites belerius Reid, 1974
Spiniferites bentorii (Rossignol, 1964) Wall and Dale, 1970
Spiniferites cruciformis Wall and Dale, 1973
Spiniferites cruciformis morphotype C of Marret in Marret et al., 2004
Spiniferites hyperacanthus (Deflandre et Cookson, 1955) Cookson et Eisenack, 1974
Spiniferites inaequalis Wall and Dale, 1973
Spiniferites mirabilis (Rossignol, 1967) Sarjeant, 1970
Stelladinium stellatum (Wall and Dale, 1968) Reid, 1977

(*continued*)

TABLE 2. (*continued*)

PHYTOPLANKTON SPORES AND PLANT REMAINS (continued)

Prasinophyta
Cymatiosphaera O. Wetzel, 1933 (syn. *Pterosperma* Pouchet, 1893 [Parke et al., 1978] phycoma)
Cymatiosphaera globulosa Takahashi, 1964 (= *Pterosperma* sp. phycoma)
Hexasterias problematica Cleve, 1900 (syn. *Polyasterias problematica* Meunier, 1910)
Leiosphaeridia Eisenack, 1958
Pterosperma Pouchet, 1893
Tasmanites Newton, 1875

Zygnematales
Zygnemataceae
Mougeotia C.A. Agardh, 1824
Spirogyra Link in C.G. Nees, 1820
Zygnema C.A. Agardh
Desmidiaceae (sometimes classified in a separate order, **Desmidiales**)
Cosmarium Ralfs, 1848

FUNGI

Alternaria Nees, 1817 *ex* Fries, 1821 conidium
Callimothalus Dilcher, 1965 type of fruiting body
Chaetomium Kunze, 1817 ascospore
Coniochaeta ligniaria (Greville) Cooke ascospore
Gaeumannomyces Arx & D.L. Olivier; fungal germling similar to hyphopodium of *Gaeumannomyces* sp. illustrated by Head (1992)
Glomus L.R. and C. Tulasne, 1845 chlamydospore type
cf. *Monosporisporites* van der Hammen, 1954 emend. Kalgutkar and Jansonius, 2000

Sorosporidium Rudolphi, 1829 type of spore mass illustrated by Kholeif (2004)
(syn. Papulosporonites subcircularis Chandra, Saxena & Setty, 1984 type of spore mass)
Sporormiella Ellis et Everhart, 1892
Tetraploa Berkeley and Broome, 1850
Thecaphora Fingerh., 1836
Tilletia L.-R. Tulasne and C. Tulasne, 1847 type of teliospores
cf. "Type 729" spore of van Geel, Hallewas and Pals, 1983
Valsaria Ces. and de Not. ascospore

ANIMAL REMAINS

Annelida

Polychaeta Grube, 1850

Arthropoda
1. Insecta
Chironomidae (nonbiting midges)
"NPP 219" of Van Geel et al. (1989), for the mentum of a Chironomid simulid black fly
2. Cladocera
Exoskeletal parts (probably the first thoracic antennae, 150 µm long) of a juvenile cladoceran
3. Crustacea Brunnich, 1772
Branchiopoda
Artemia salina (Linnaeus, 1758): brine shrimp
Copepoda: copepod egg capsule with fibrous outer wall
Ostracoda Latreille, 1802 (ostracodes; ostracods; seed shrimp)
Leptocythere Sars, 1925

Chaetognatha (Leuckart, 1854) Hyman, 1959, chaetognaths

Platyhelminthes Minot, 1876, flatworms

Turbellaria Ehrenberg, 1831, flatworms, planarians
Neorhabdocoela Meixner, 1938, microturbellarians

Protista
1. Protozoa
Ciliophora Doflein, 1901
Tintinnida Kofoid and Campbell, 1929
"ELENO-2" of van Waveren, 1993
Fusopsis A. Meunier, 1919 lorica type
Pacillina cyst with fimbricated outer wall of Kunz-Pirrung (1998)
Tintinnopsis Stein, 1867
Rhizopoda Foraminiferida (planktonic and benthic foraminifera)
Arcellinida (Arcellaceans): testate amoebae such as *Arcella* Ehrenberg, 1832

2. Protozoa Incertae Sedis
Radiosperma corbiferum Meunier 1910 (= Sternhaarstatoplast of Hensen, 1887)

Rotifera
Filinia longiseta (Ehrenberg, 1834)
Tardigrada J.A.E. Goeze, 1773
Macrobiotus Schultze, 1834
Macrobiotus hufelandi C.A.S. Schultze, 1834 = egg-type of Jankovska (2007, personal commun.)

Note: Further information on the taxonomy and nomenclature of many of the taxa can be found in Fensome et al. (1990).

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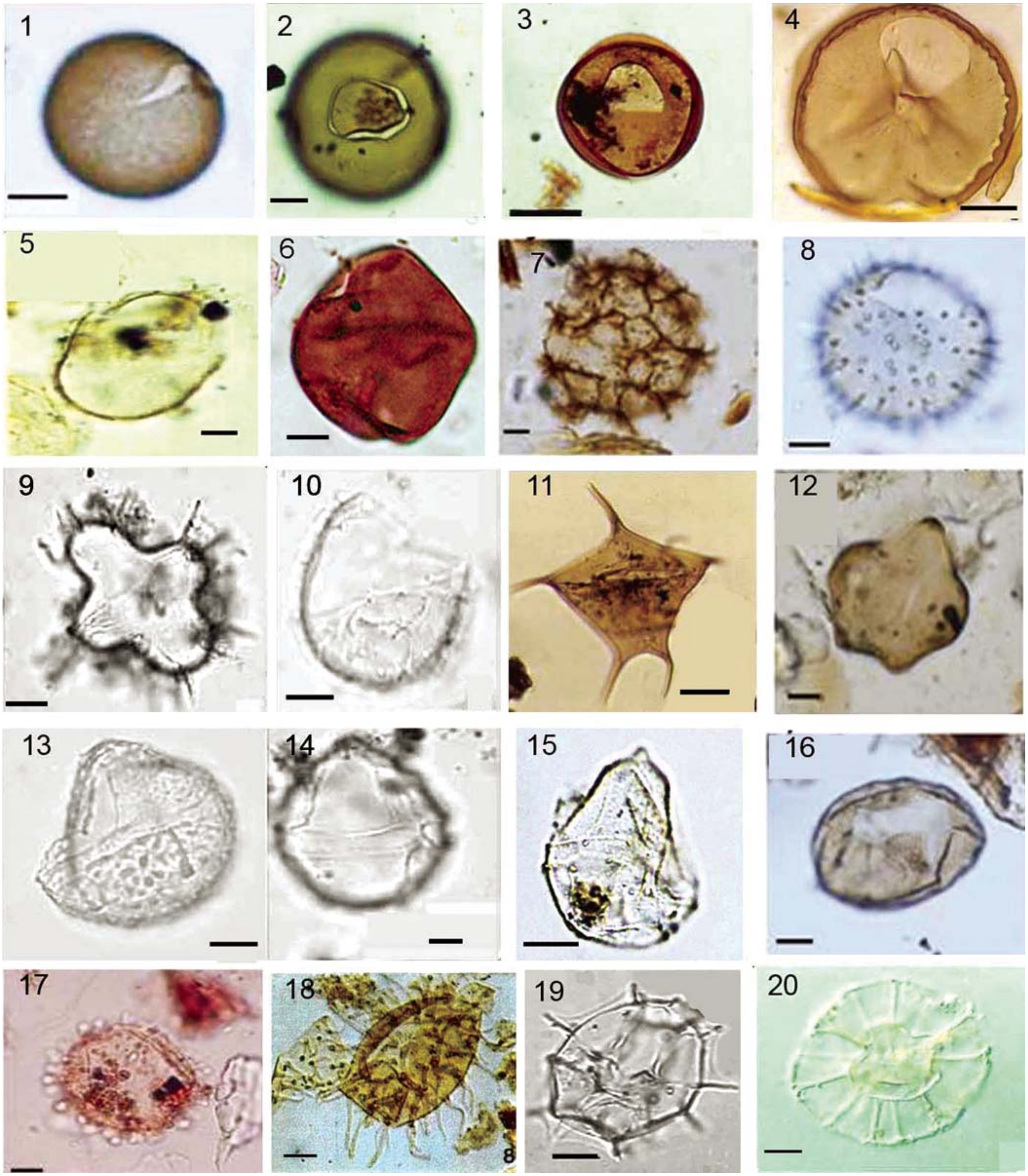
Plate 1. Light microscope photographs of various ecologically diagnostic dinocysts in the Black Sea corridor. Scale bar is 10 µm. Letters in parentheses are the initials of contributing authors other than P.J. Mudie. Figures 1, 5. Introduced potentially toxic species. (1) *Gymnodinium catenatum* (F.M.); (5) *Alexandrium* cyst form (S.E.A.K.). Figures 2–4, 6, 8, 11–12, and 16. Thin-walled cysts of heterotrophic protoperidinioids. (2) *Brigantedinium* sp.; (3) *Peridinium ponticum*; (4) *Selenopemphix nephroides*; (6) *Quinquecuspis concreta*; (8) *Echinidinium transparentum* (F.M.); (11) *Stelladinium* cf. *robustum*; (12) *Quinquecuspis concreta*; (16) *Quinquecuspis* sp. Figure 7. Oxidation sensitive polykrikoid *Polykrikos kofoidii* (F.M.). Figure 9. *Spiniferites cruciformis* form 4 (F.M.) first described in the Black Sea early Holocene sediment, but later found common in surface sediment of the Caspian Sea. Figures 10, 17, and 18. *Lingulodinium machaerophorum*; (10) Caspian Sea morphotype (F.M.); (17) form with clavate spines common in low-salinity waters (F.M.); (18) long-spine form usually only in fully marine environments. Figures 13, 14. Caspian Sea endemics. (13) *Caspidinium rugosum* (F.M.); (14) *Impagidinium caspienense* (F.M.). Figure 15. Exclusively freshwater species *Gonyaulax apiculata*. Figures 19, 20. Exclusively marine species. (19) *Impagidinium aculeatum* from Nile cone (S.E.A.K.); and (20) *Nematosphaeropsis labyrinthus* from Aegean Sea.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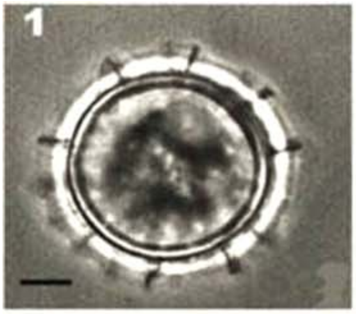
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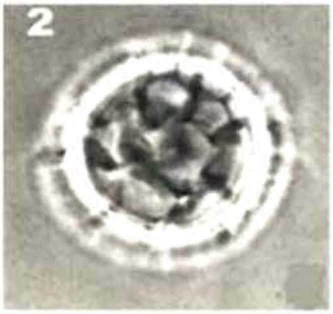
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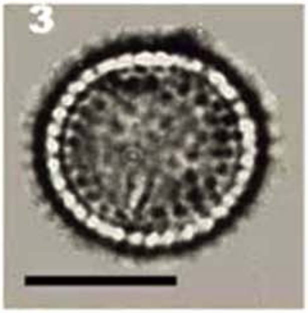
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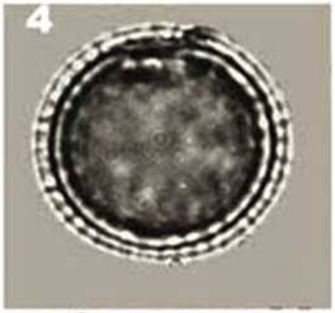
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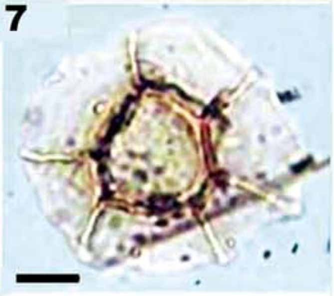
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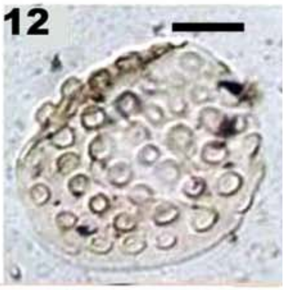
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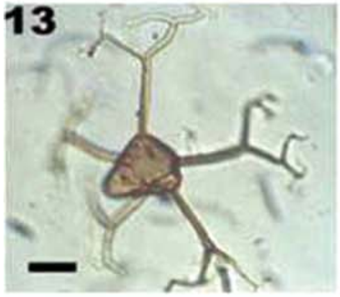
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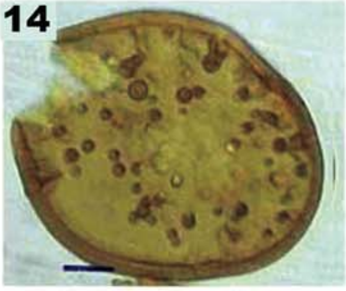
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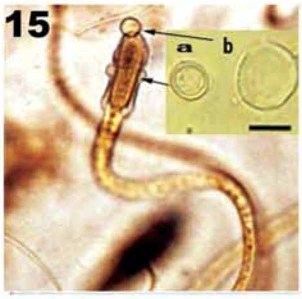
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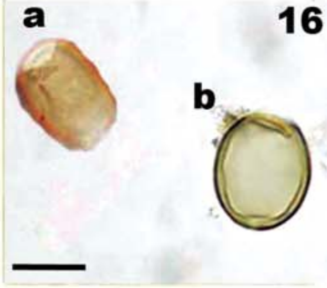
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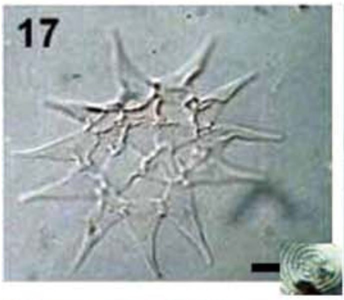
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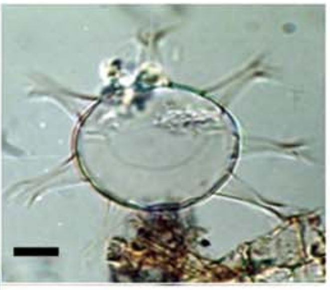

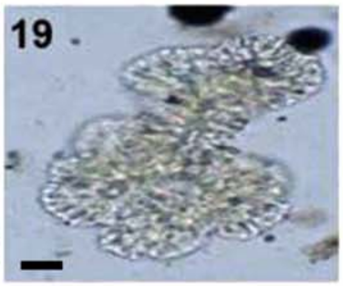
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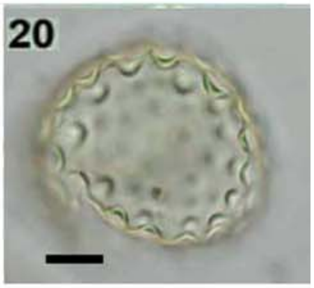
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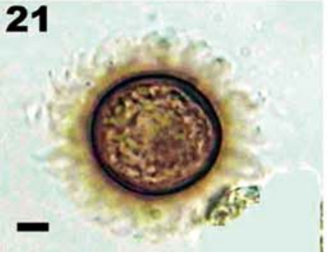
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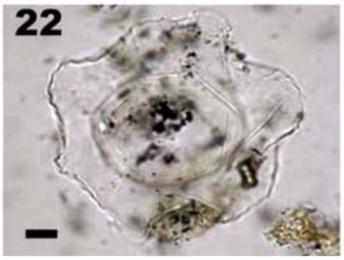
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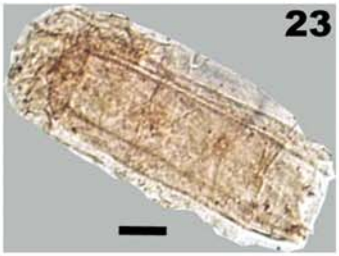
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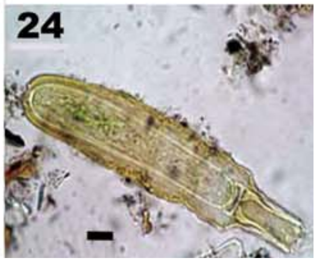
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wall surrounding a vesicle with variable ornamentation, and opening by a slit-like or irregular rupture or by a circular pylome (Martin, 1993). A good example of this is found in *Sigmopollis* (Plate 2, figs. 5 and 6). A comparison of various phenetic classifications of this artificial group is given by Strother (1996). We include the category here because of its long-standing use in geology and because of its use in Traverse's marine index. However, it is likely that in the future, the term acritarch will be replaced by nonpollen palynomorphs for studies of Pleistocene–Holocene sediments.

Prasinophytes and acritarchs, together with dinocysts, are sometimes referred to as organic-walled microphytoplankton (Playford, 2003). However, it has been shown that prasinophyte phycomata are the fossilized cyst-like nonmotile stage of Prasinophyceae (= Micromonadophyceae), which is the oldest group of the green algae (Chlorophyta). The life cycle of some living prasinophytes, e.g., *Pterosperma and Pachysphaera*, consists of a unicellular motile stage with scale-covered flagella, and a nonmotile floating resting stage called a phycoma (Fig. 5A). The fossil genera *Cymatiosphaera* (Plate 2, figs. 1 and 2) and *Tasmanites* (Plate 2, fig. 14) are believed to be the phycomata of *Pterosperma* and *Pachysphaera*, respectively (Martin, 1993).

A classification of the phylum Prasinophyta is given by Tomas (1993) and by Guy-Olsen (1996), who lists four orders and eight Holocene families of these mainly oceanic planktonic and benthic microalgae. Plate 2 illustrates the main prasinophytes (figs. 1, 2, and 8) and similar nonpollen palynomorphs in the Black Sea corridor cores. Notably, most of these occur in both the brackish to hypersaline Aral Sea (Sorrel et al., 2006), with a fluctuating salinity of ~6‰–15‰ to >100‰ and a history of strong pollution over the past 1000 yr (Aladin and Potts, 1992), and in Lake Issyk-Kul, a slightly brackish (6‰), oligotrophic lake in Kyrgyzstan (Giralt et al., 2004). Modern prasinophytes are regarded as primarily marine, but they also live in brackish and freshwater, and their fossils are associated with lagoonal or deltaic environs. They are most abundant in cold waters, with high nutrients being more important than temperature or salinity, according to Batten (1996). The data for the Black Sea corridor show that *Pterosperma* (*Cymatiosphaera*) dominates only

Plate 2. Light microscope photographs of acritarchs, colonial algae, and zygnemataceans, and scanning electron microscope (SEM) photographs of colonial alga. Scale bar is 10 µm. Letters in parentheses are the initials of contributing authors other than P.J. Mudie. Figures 1, 2. *Cymatiosphaera* sp., Mackenzie Delta. (1) Midfocus; (2) high focus. Figures 3, 4. *Micrhystridium* cf. *ariakense*; Fink Cove coastal pond, Nova Scotia. (3) High focus on dense covering of short spines; (4) mid focus. Figure 5. *Sigmopollis sigmoides*, Mackenzie Delta; high focus on characteristic sigmoid suture. Figures 6, 8, 9, and 11–13. Black Sea core M02-45, 30 cm. (6) *Sigmopollis* sp., Black Sea M02-45, 30 cm; (7) *Pterospermella*, Red Sea (S.E.A.K.); (8) *Micrhystridium* cf. *ariakense*, Black Sea; (9) *Pseudoschizaea rubina*, with irregular polar ornament (details inset); (10) Black Sea core M18 *Pseudoschizaea circula*, with linear polar ornament. Figures 11–13, 17, and 19, from Mar02-45, SW Black Sea shelf. (11) *Spirogyra* zygospore; (12) *Zygnema*-type spore, excysted and partly folded to show projections on inner wall corresponding to surface depressions, 480 cm; (13) *Multiplicasphaeridium*-type acritarch. Figure 14. *Tasmanites*, Nile cone (S.E.A.K.). Figure 15. *Gloeotrichia* filament with terminal heterocyst and lateral akinetospores (P.A. Siver, http://www-cyanosite.bio.purdue.edu/images/lgimages/GLOET1.JPG); (15A–15B) *Gloetrichia*-type akinetospores from Lake Saki (NG). Figure 16. *Anabaena* heterocysts from Caspian Sea (S.A.G.L.); (16A) GS18-481-3(20); (16B) CS102-37(1). Figure 17. *Pediastrum simplex*, Egyptian shelf, showing the large size and open structure of most colonies (S.E.A.K.). Figure 18. *Hexasterias problematica* Black Sea core M18. Figure 19. *Botryococcus braunii*, Black Sea core Mar02-45, 590 cm. Figure 20. *Zygnema* spore Lake Ulubat 9/1 (S.A.G.L.). Figure 21. Stenoblast, Hamata mangrove swamp, Red Sea (S.E.A.K.). Figure 22. *Radiosperma,* SA03K7-300/1 (S.A.G.L.). Figure 23. *Gloeotrichia* filament, Black Sea Mar02-45. Figure 24. *Gloeotrichia* filament with endocyst, SA03k71-1 (S.A.G.L.).

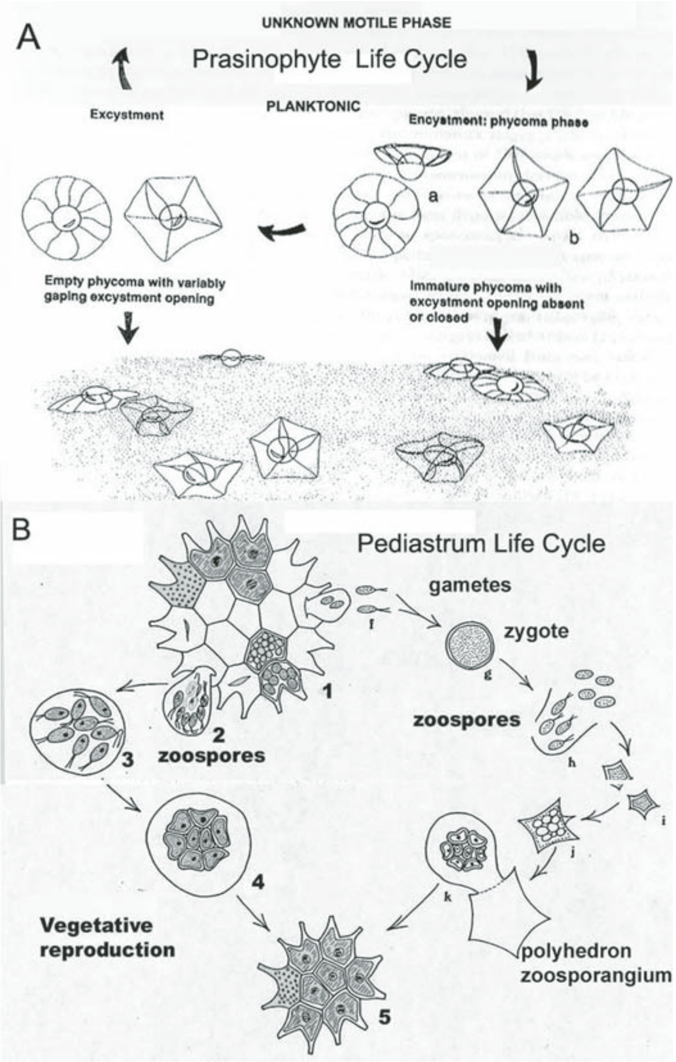


Figure 5. Life cycles of algal nonpollen palynomorphs: (A) *Pterosperma* (from Martin, 1993); and (B) *Pediastrum boryanum* (from Batten, 1996). Stages: 1—coenobium; 2–5—asexual reproduction stages: 2, 3—release of vesicle with zooids, 4—new coenobium forming within vesicle, 5—release of coenobium, 5f–5k—sexual reproduction stages.

in the lower-salinity eutrophic waters, and it is absent in the oligotrophic marine–hypersaline Aegean waters. In contrast, *Pterospermella* (Plate 1, fig. 7) is only reported for the hypersaline Red Sea, and the small spiny acritarch *Micrhystridium* (Plate 2, figs. 3, 4, and 8) was found only in the Red Sea, the hypersaline Crimean liman-lagoons, and, as *Micrhystridium braunii*–type, in the Aral Sea. The acritarch *Polyasterias problematica* is found in the Caspian and Aral Seas (as *Hexasterias problematica*; Sorrel et al., 2006); it is usually considered as a brackish to marine organism, but appears to be euryhaline (Matthiessen et al., 2000; Sorrel et al., 2006). The acritarch *Radiosperma corbiferum* was present mostly in the brackish intervals of the Aral Sea (rare and possibly reworked in the hypersaline intervals) and in the modern sediments of the freshwater Lake Sapanca east of the Marmara Sea (Leroy and Albay, 2010). The biological affinity of this nonpollen palynomorphs is unknown; a morphologically similar organism in the plankton of the Gulf of St. Lawrence, Canada (Bérard-Therriault et al., 1999, their plate 149b), is listed as *Protiste* sp. 2, in the group Protiste incertains (Uncertain Protists). Brenner (2001) reported that an apparently similar morphotype *Radiosperma* cf. *corbiferum* has a widespread distribution ranging from low-salinity Arctic estuaries to upwelling marine waters off Peru.

Colonial Algae

The colonial algae are unicellular Chlorophyceans that form colonies (coenobia) from a number of cells linked together and arranged in a specific pattern. In *Pediastrum* (Plate 2, figs. 17 and 18), the colonies have a fixed number of cells, the coenobia are flattened, and reproduction is by means of biflagellated cells, either aggregated within a vesicle that is liberated from the parent colony cell, or during sexual reproduction, and they are briefly free-swimming (Fig. 3B). In *Botryococcus*, the colonies range from small (~30 µm) subspherical clumps of cells (Plate 2, fig. 19), embedded in an oil-rich matrix, to relatively large (~140 µm) grape- or mulberry-like (botryoidal) groupings held together by gelatinous fibers or membranes (Batten and Grenfell, 1996).

In the Black Sea corridor, the distribution of the colonial algae *Pediastrum* and *Botryococcus* shows the same trend as for *Pterosperma* (*Cymatiosphaera*). These nonpollen palynomorphs are abundant in parts of the Black Sea, sparse in the Marmara Sea, and almost absent in the Aegean and Levantine Seas, but they reappear in the Nile Delta and on the Egyptian shelf. These colonial algae are commonly considered to be indicators of river-water inflow (e.g., Head, 1992, and references therein). However, they also appear in sediments of the Aral Sea and the hypersaline Kara-Bogaz Gol of the Caspian Sea, and *Botryococcus braunii* ha been found in plankton surveys of the Aral Sea (Piontkovski and Elmuratov, 2008). Detailed studies of surface sediment samples in the Baltic Sea show that *Pediastrum boryanum* and *P. kawraisky* are dominant in salinities from 6‰ to 8‰ (full range is 5‰–9‰), while *P. simplex* and *P. duplex* occur in salinities of less than 3‰–5‰ (Matthiessen and Brenner, 1996). The Baltic study also shows that *Botryococcus* cf. *braunii* tolerates salinities up to 8‰. Zalessky (1926) reported that large botryoidal colonies of *B. braunii* occurred in the freshwater Russian Lake Beloë, while those in the brackish water (4‰) of Lake Balkash (Kyrgyzstan) were closely packed and globular. Growth of *Botryococcus* may be favored by seasonally cold, oligohaline conditions (Batten and Grenfell, 1996), in either eutrophic shallow or deep oligotrophic lakes (Chmura et al., 2006); in contrast, blooms of *Pediastrum* in the Canadian Great Lakes are triggered by excess phosphate loading (Nicholls, 1997).

Zygnematales

The Zygnematales are charophycean green algae that reproduce by conjugation to produce resting spores or zygotes with a sporopollenin-like cell wall. This order includes unbranched filamentous green algae of the families Zygnemataceae and single-celled Desmidiaceae (sometimes classified in a separate order Desmidiales). Modern Zygnemataceae typically live in shallow, stagnant freshwater lakes, ponds, or in wet soil (Van Geel, 2001) and produce spores in the spring when conditions are warm. In late Holocene sediments of the Black Sea corridor, zygospores known to be formed by Zygnematacean algae have been found only in low-salinity lakes or freshwater lakes. These include *Spirogyra*, which was found in Lake Durankulak (Marinova and Atanossova, 2006), the montane inland Lake Izzyk-Kul, Lake Sapanca, and Lake Manzala of the Nile Delta. Zygospores of *Spirogyra* and the Zygnematacean genera *Mougetia* and *Debarya* were also found in sediments of the Nile Delta (Leroy, 1992). *Zygnema* spores (Plate 2, fig. 20) are common in the polluted, freshwater Lake Ulubat south of the Marmara Sea (Fig. 1).

Pseudoschizaea rubina (Plate 2, fig. 9) may be a zygospore of the zygnematacean alga *Debarya* (Grenfell, 1995), although this relationship has not been confirmed by laboratory cultures, and it is often simply grouped with the acritarchs, as in Tables 1 and 2. This sphaeromorphitic acritarch, with distinctive concentric markings on both hemispheres of its dorsoventrally flattened vesicle, was first described as *Sporites circulus* in Pliocene brown coals, and then as *Concentricystes rubinus* in marine sediments off Israel. *Pseudoschizaea rubinus* is distinguished from the similar species *Pseudoschizaea circula* by an irregular, maze-like polar complex up to one quarter of the vesicle diameter (Christopher, 1976). *Concentricystes* s.l. is usually considered to be a freshwater alga because of its association with wadi or river terrace deposits (Christopher, 1976), and some species, including *P. circula*, have only been recorded from terrestrial or fluvial environments. However, both *P. circula* and *P. rubina* are occasionally present in the late Holocene marine sediments of the Black Sea but are absent from the early Holocene brackish-water sediments. *Pseudoschizaea circula* is rare in the hypersaline Lake Saki, and unspecified *Pseudoschizaea* species have been found in the Nile Delta, Red Sea, and Aral Sea.

Desmids are most common in oligotrophic freshwater lakes and ponds, but some species e.g., *Closterium aciculare*, mark eutrophic conditions (Graham and Wilcox, 2000). Desmid zygotes *Coelastrum* and *Mougeotia* occur in Lake Durankulak (Marinova and Atanassova, 2006), but in the Black Sea, *Mougeotia and Closterium* have been reported only for mid-Holocene sediments (Mudie et al., 2010), although they are markers of river transport to modern sediments in the Beaufort Sea (Matthiessen et al., 2000). Zygotes of *Tetraedon* and *Coelastrum* are sporadically abundant in the freshwater Lake Sapanca.

Cyanobacteria

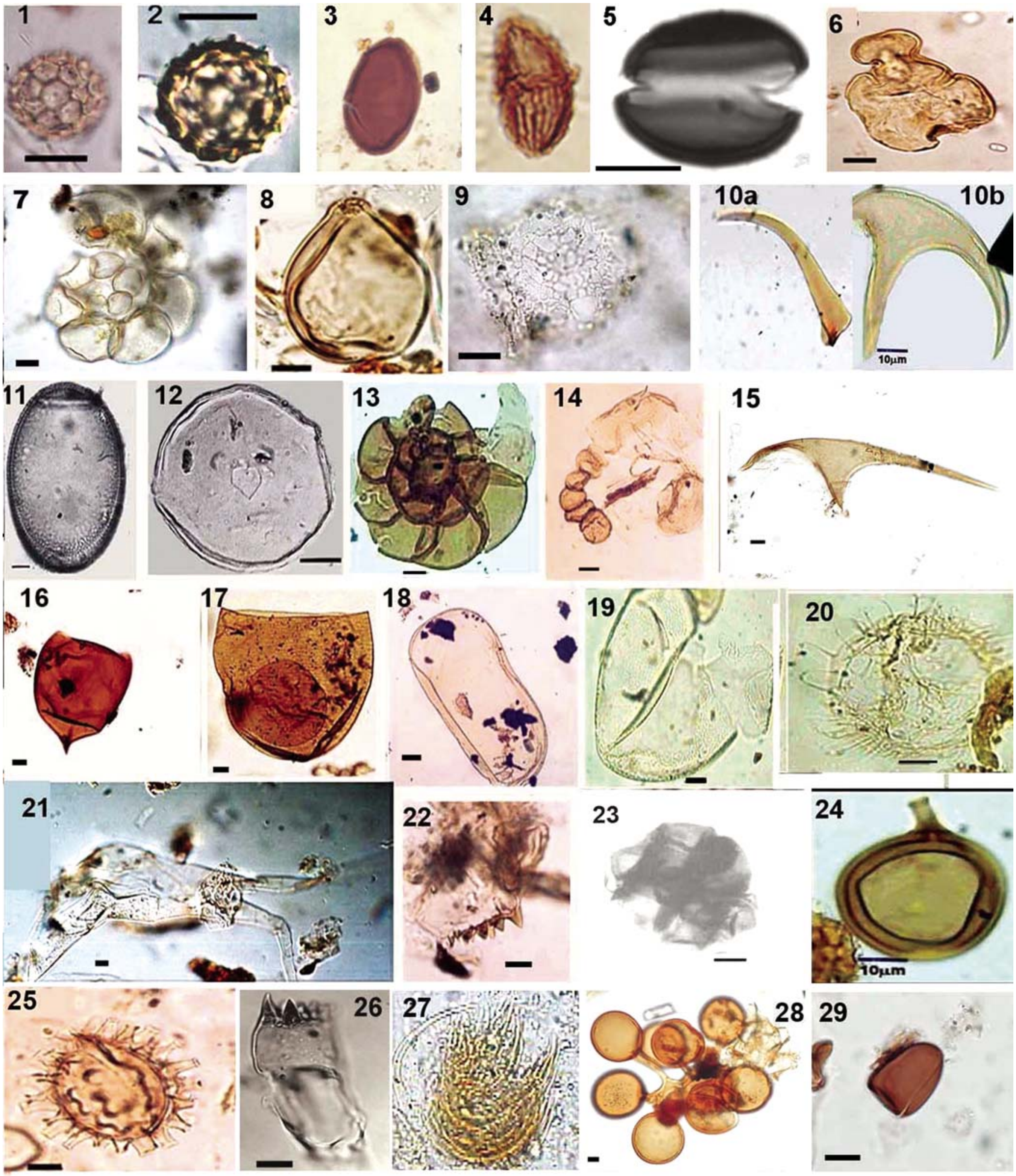
Fossil Cyanobacteria (blue-green algae) are rare in the Black Sea corridor sediments, although the marine unicellular *Synechococcus* cynobacteria occurs in both eutrophic and oligotrophic waters of the Black Sea corridor (Uysal, 2006). *Gloeotrichia* is rare to common in the modern sediments of Lake Sapanca (Table 1; Plate 2, fig. 24), but in the Black Sea, *Gloeotrichia*-type sheaths were found only in the early Holocene sediments (Plate 2, fig. 23). Van Geel (2001) noted that *Gloeotrichia* marks nutrient-poor conditions in late glacial lakes because it is a nitrogen-fixing alga that subsequently makes conditions suitable for other aquatic plants. The planktonic filamentous heterocyst and akinete-producing alga *Anabaena* is present in both Issyk-Kul and the Caspian Sea (Plate 2, fig. 16).

Fungi and Animal Remains

Other important nonpollen palynomorphs in the Black Sea are derived from fungi and various types of planktonic or benthic zooplankton. Plate 3 illustrates various fungal spores, conidia (Plate 3, figs. 1–5), ascoma (Plate 3, fig. 6), or germlings from Black Sea core 45. There are very few marine fungi, and most of the spores and other fungal remains must have been transported to the inland seas by air or soil erosion. Some dung fungi, such as *Sporormiella* (Plate 3, fig. 29), mark nutrient enrichment from domestic animals and are a reliable proxy for faunal biomass (van Geel and Aptroot, 2006). Several spore types (e.g., *Tilletia*, *Ustilago*) are produced by parasites of specific native plants and domestic crops. In archaeological middens, *Glomus*-type fungal spores (Plate 3, figs. 24 and 28) are extremely resistant to fire and biological degradation; hence, they persist in shell middens and soils after almost all the pollen has disappeared from degradation (Bryant and Holloway, 1983; Leroy et al., 2009), and they may survive very long-distance transport by river water. *Glomus*-type spores are present on the Nile cone and the Red Sea, in addition to the Black Sea and almost all lakes, unless the catchment is very small and the sample is far from the shore.

Various zooplankton remains have been reported for the Black Sea corridor, including the chitinous skeletal remains of a juvenile cladoceran (Plate 3, fig. 21), copepod egg capsules (Plate 3, fig. 19) and their eggs (Plate 3, fig. 20), the organic linings of benthic microforaminifera (Plate 3, figs. 7, 13, 14), polychaete worm jaws and pincers (known to geologists as scolecodonts; Plate 3, fig. 10), and various morphologically similar palynomorphs that include arthropod sclerites (Plate 3, fig. 15). The jaws of unknown ostracods were identified in Lakes Anzaleh and Sapanca (Plate 3, fig. 26) and in early Holocene sediments of the Black Sea (Plate 3, fig. 22). The lining of a very small ostracod (Plate 3, fig. 18; probably *Leptocythere* according to David Horne, 2007, personal commun.) is found in the Black Sea, and ostracod linings were also present in Lake Saki and on the Egyptian shelf. Eggs of the rotiferan *Filinia longiseta* were found only in the freshwater Lake Sapanca. Several types of tintinnid loricas are reported for the Aral Sea (Sorrel et al., 2006) and the Black Sea (Plate 3, fig. 8), and a *Tintinnopsis* is present in Lake Sapanca (Plate 3, fig. 9). The marine palynomorph *Palaeostomocystis* (Plate 3, fig. 11) also resembles tintinnid loricas found in arctic regions (Matthiessen et al, 2000); it is rare in the Marmara Sea. Other relatively large (~60–80 µm), brown, vase-shaped palynomorphs (Plate 3, figs. 16 and 17) occur in the Marmara Sea and on the Egyptian shelf. These nonpollen palynomorphs resemble the resting eggs (oocytes) or egg capsules/cocoons of microturbellarian flatworms (Platyhelminthes, Order Neorhabdocoela), which are mostly freshwater organisms (Haas, 1996); however, other turbellarians are common in coastal marine environments, and predatory marine flatworms parasitize mussels in the Black Sea (Murina and Grintsov, 1998). According to Ole Bennicke (2008, personal commun.), the egg walls of the marine flatworms tend to be thicker than those of the freshwater taxa. Morphologically similar nonpollen palynomorphs that occur in deep-sea sediments of the Banda Sea have been referred to the chitinous loricas of marine tintinnids (van Waveren, 1994). Clearly, more research on this group of palynomorphs is required before these nonpollen palynomorphs can be used reliably as environmental indicators when recovered from brackish-water or marine sediments. There is also further need to confirm the biological link between the brackish-water nonpollen palynomorphs referred to the tintinnids: several illustrations of vase- or urn-shaped testate amoebae living in peatland moss (Swindles and Roe, 2007) are very similar in size and morphology to some of the tintinnid nonpollen palynomorphs found in the Black Sea corridor.

The organic-walled palynomorph *Halodinium* (Plate 3, fig. 12) was first recorded and described as an acritarch of unknown affinity occurring in subarctic marine sediments of the Bering Sea, and it is widely distributed in the Arctic (Matthiessen et al., 2000), including ponds of the Mackenzie Delta. The shape of *Halodinium* is similar to that of the testate amoebas *Cyclopyxis* and *Arcella* (illustrated by Beyens and Meisterfeld, 2001), and it is possible that this palynomorph is the organic lining of a testate amoeba (thecamoebian). The testate amoebas are a polyphyletic group of protozoans, the largest group (75%) being the Arcellinida. The empty tests remain intact after death of the amoeba and can be recovered fully from anaerobic sediments by dispersion in water and gentle sieving, but they decompose within a few weeks under aerobic conditions (Beyens and Meisterfeld, 2001). Extraction by palynological processing with acids and/or alkalis, however, gives variable recovery and does not produce a reliable picture of the thanatocoenoses (Swindles and Roe, 2007).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Halodinium is rare in the Black Sea and present in the Nile Delta and Red Sea. Unspecified thecamoebians have been reported for the calcareous mire near Nowshahr in northern Iran and are present in some freshwater lakes of the region.

The distribution of these nonpollen palynomorphs in the surface samples of the Black Sea corridor (Table 1) shows that the fungi are most abundant in the low-salinity waters of the inland lakes, and the Black and Marmara Seas, they disappear in the Aegean, and then they return off the Nile Delta, being clearly linked to the proximity of terrestrial environments where they originate. In contrast, microforaminiferal linings continue to be present in the marine and high-salinity waters of the northern Aegean Sea (Aksu et al., 1999; Kotthof et al., 2008) and the Egyptian shelf (Kholeif, 2010), but they are absent from both the anoxic deep basins of the southern Black Sea and from late Holocene marine sediment of the Nile cone in the hyperoligotrophic water of the Levantine basin. Microforaminiferal linings might be expected to be good markers of sustained marine connection with the Mediterranean, but they also occur in the Kara-Bogaz Gol, which, during most of the late Holocene, was only connected to the global oceans by a canal linking the Volga River and the Azov Sea. They are also present in the hypersaline water of Lake Dzharylgach, which has been isolated from the Black Sea during historical time. Kotthoff et al. (2008) reported that microforaminiferal linings are among the most oxidation-sensitive palynomorphs. These palynomorphs are abundant and well-preserved at ~1000 m water depth in the Mt. Athos Basin of the northwest Aegean; therefore, their absence in the anoxic ~2-km-deep basins of the southeastern Black Sea strongly suggests that few benthic foraminifera live under conditions of low surface salinity (<22‰) and anoxia below 200–400 m water depth. Planktonic foraminifera are present in the Mediterranean and Marmara Sea but absent from the Black Sea and the isolated inland seas.

Plate 3. Light microscope photographs of fungi and animal remains from Black Sea cores M02-45T, 30 cm, Marmara Sea core M98-12, Caspian Sea core 31, Lake Sapanca samples (SAK), Lake Dzharylgach, Egypt (NC), and the Red Sea. Scale bar 10 µm. Letters in parentheses are the initials of contributing authors other than P.J. Mudie. Figures 1–5. Fungal spores from SW Black Sea. (1, 2) *Tilletia*-type teliospores, M45T; (3) *Chaetomium* ascospore, M45T; (4) *Valsaria* sp. Ascospore; (5) *Coniochaeta ligniaria* ascospore (MM-F). Figure 6. Fungal germling similar to hyphopodium of *Gaeumannomyces* sp., B7, 70 cm. Figure 7. Caspian microforaminiferal lining CS31-3/2 (S.A.G.L.). Figure 8. *Pacillina*-type tintinnid lorica. Figure 9. Tintinnid lorica, with embedded charcoal fragments, SA0361 (S.A.G.L). Figure 10A. Simple scolecodont, core NC-1, Egyptian shelf (S.E.A.K.). Figure 10B. Bifurcated scolecodont; Red Sea (S.E.A.K.). Figure 11. *Paleostomocytis* sp.; Figure 12. Thecamoeban cf. *Halodinium minor*. Figures 13, 14, Microforaminiferal linings; (13) trochospiral form, NC-1, Egyptian shelf (S.E.A.K.); (14) Black Sea Mar02-45 planispiral, open lining. Figure 15. Arthropod sclerite, Lake Ulubat, AK104_24.5_1 (S.A.G.L.). Figures 16, 17. Cf. tintinnid loricae/turbellarian egg capsules from core M98-12, 30 cm; (16) lorica type 1, with short apiculate base; (17) lorica type 2, with rounded base. Figure 18. Organic lining of brackish water ostracod, cf. *Leptocythere*, M02-45, 790 cm. Figures 19, 20. Copepod eggs; (19) copepod eggs; (12) ?copepod egg capsule with fibrous outer wall; M45. Figure 20. Spiny copepod egg. Figure 21. Exoskeletal parts (probably the first thoracic antenna, 150 µm long) of a juvenile cladoceran, M45P, 440 cm. Figure 22. Mouth part of a small ostracod. Figure 23. *Sorosporium*-type spore mass; Red Sea (S.E.A.K.). Figure 24. *Glomus*-type fungal spore, NC core 2 (S.E.A.K.). Figure 25. M45T Desmid or Tardigrade egg. Figure 26. Ostracod jaw CP14, 45 cm (S.A.G.L.). Figure 27. Unknown amphipod from Lake Dzharylgach, Dz70, 160–155 cm (T.S.). Figure 28. *Glomus* group SA03K71-13 (S.A.G.L.). Figure 29. *Sporormiella* spore SAK71-1 (S.A.G.L.).

DISCUSSION

At this stage of our study, it is not possible to define many clear patterns in nonpollen palynomorphs distributions within the Black Sea corridor, in part because of the different processing methods used, and also because many phytoplankton taxa will grow under a very wide range of temperature and salinity conditions, although they only bloom under optimal conditions. Presence or absence data are therefore not very diagnostic except for taxa with very restricted distributions, such as the brackish-water (2‰–13‰) dinocyst species *Impagidinium caspienense*, *Caspidinium rugosum*, and *Spiniferites cruciformis*. Recently, small amounts of *I. caspienense*, *S. cruciformis*, and *Brigantedinium* spp. were found in the modern (0–55 yr) sediments of freshwater Lake Sapanca between the Marmara Sea and Sakarya River, but it is presently unknown if they are in place or a recent introduction that may not survive in the freshwater environment (Leroy et al., 2009). Other well-known Mediterranean dinocysts are notably absent from the semimarine water of the Marmara Sea, the low-salinity marine waters of the Black Sea, and inland seas or lakes; these taxa include *Impagidinium aculeatum, I. patulum*, *I. sphaericum* and *I. strialatum*, *Nematosphaeropsis labyrinthus*, *Operculodinium israelianum*, and *Polysphaeridium zoharyi*. So far, no dinocysts have been found in either the hypersaline liman-lagoon sediments of the Crimean Peninsula that were treated with hot HCl, or the saline sediments of the Egyptian Fayoum basin (Kholeif et al., 2007), where the normal HCl-HF method of processing was used for palynomorph processing.

The usual methods used for palynological processing and the examination of residues mounted on microscope slides are not the best techniques for study of the animal remains of Ostracoda, Cladocera, and Chironomidae because only small parts of the whole fossil are recovered. Other techniques exist that are specific to each arthropod group and can provide a wealth of new data on paleotemperature, paleosalinity, and paleonutrients. Likewise, thecate amoebians are fully studied using different extraction and observation methods than those used in palynology. The recovery of just a few organic linings and sclerotized or chitinized body parts, however, may provide valuable clues to the need for further specialized studies of sedimentary intervals where the skeletons of animals are rare because of unsuitable preservation, including dissolution of carbonate and silicate shells. For example, in the early Holocene sediments of the Black

Sea, foraminiferal and ostracod linings were recovered in older sediments below those in which the animals were first visible in sieved samples examined by binocular microscope.

In the Black Sea corridor, the most restricted distributions are shown by an unnamed desmid/tardigrade egg (Plate 3, fig. 25) and acanthomorphic acritarch (Plate 2, fig. 13) so far reported only for the Black Sea. *Halodinium* (Plate 3, fig. 12) and *Paleostomocystis* may also be confined to the Black Sea. Possibly, these nonpollen palynomorphs can help us distinguish the paleoenvironments of inland seas with quasi-permanent interglacial marine connections from the inland lakes that have been isolated throughout the Holocene. Rotifer eggs (including those of *Filinia*) were found only in Lakes Anzaleh and Sapanca, and the tintinnid genus *Tintinnopsis* was found only in Lake Sapanca. Nonpollen palynomorphs identified as the mouthpart or jaws of polychaetes so far have been reported only for the Marmara and Red Seas, suggesting that they indicate a neritic marine influence, as noted by Head (1992). In contrast, the mandibles of ostracods have been found only in the low-salinity or freshwater lakes, and an unnamed nonpollen palynomorph that may be an amphipod mouthpart (Plate 3, fig. 27) so far has been found only in the hypersaline liman-lagoon of Lake Dzharylgach. Other large (>200 μm) arthropod parts from lake sediments include a sclerite from an aquatic Hemipteran (Plate 3, fig. 15), and it is possible that the smaller (<100 μm) rod- or Y-shaped scolecodonts resembling simple polychaete worm jaws may actually include sclerotinized rostral spines of freshwater or marine copepods (van Waveren, 1994) or the claws of chironomid larvae (Plate 3, fig. 10B; according to Dirk Verschuren, 2008, personal commun.).Throughout the Black Sea corridor, there is a conspicuous absence of the gelatinous filaments of the periphytic Rivulariaceae (sometimes classified with the Cyanobacteriales), which includes marine littoral and freshwater species, most commonly in clear, unpolluted, streams, but also found in stagnant waters (Graham and Wilcox, 2000).

The hypersaline Lake Saki (~45°2 N, 33.5°E, water depth <1 m) is of considerable interest because it is a possible analogue for an early Holocene Black Sea arid environment (Gerasimenko and Subetto, 2007). At present, Lake Saki is a salt lake (predominantly NaCl) separated from the Black Sea by a large sand bar up to 5 m high. The liman-lagoon occupies the estuary of a former drainage basin that was cut off by the construction of two dams in 1895 (Solomina et al., 2005), and its freshwater inflow is now limited to precipitation and Black Sea water. This liman-lagoon has a salinity range of 40‰–80‰ in its outer "natural" part and 15‰0–200‰ in the inner dammed section. The liman-lagoon contains black to gray clay annually varved sediments: eolian sediments accumulate mainly in summer, and total varve thickness is a proxy for intensity of river erosion, which corresponds to the precipitation regime. Time-series analysis of the varves and local pine tree rings shows that both record regional moisture regimes that are correlated with shifts of the North Atlantic Oscillation and its East Atlantic–Western Russia teleconnection (Solomina et al., 2005). It is of major interest to find that both sectors of the alkaline Lake Saki sediments have high concentrations of well-preserved pollen, because, in some circumstances, these alkaline environments are problematic for pollen preservation (Bryant and Holloway, 1983). In other situations, such as laminated sediments of the Dead Sea, however, the preservation is excellent (Heim et al., 1997), and it is possible that the poor preservation is more linked to oxidation than pH. In Lake Saki, nonpollen palynomorphs are extremely sparse in the inner liman-lagoon, but low-diversity assemblages are common in the outer section. The nonpollen palynomorph assemblages are dominated by *Micrhystridium* and colonial algae. Well-known cyanobacterial palynomorphs are unexpectedly absent, given that the filamentous algae *Cladophora* and *Gloeotrichia* grow in the lake (Mukhanov et al., 2004). *Cladophora* is not known to produce fossilizable resting spores, but elsewhere in the Black Sea corridor, heterocysts of *Gloeotrichia* are found (Plate 2, fig. 16). In Lake Saki, it is possible that very common unicellular brownish spores (Plate 2, figs. 15a and 15b) are akinetes of *Gloeotrichia*. Fungal spores are also common in Lake Saki, including *Glomus*-type spores that are derived from mycorrhizal root-fungi and thus indicators of severe soil erosion. *Pseudoschizaea* cf. *S. circula* is rare. Overall, the Lake Saki nonpollen palynomorph assemblage bears no resemblance whatsoever to the early Holocene nonpollen palynomorph assemblages in the Marmara and Black Seas, and contradicts the idea that the outer Black Sea shelf was aerially exposed and dissected by estuaries with sand barriers and liman-lagoons at that time.

Lake Dzharylgach (~45°34.7 N, ~32°51.7 E) is similar in size and water depth to Lake Saki, but it was progressively disconnected from the Black Sea from ca. 4.7 to 2.57 ka, and has been an isolated salt lake for more than 2000 yr, with a present-day salinity of ~100‰. Like the inner part of Lake Saki, pollen and spores are common and nonpollen palynomorphs are sparse in Lake Dzharylgach, and include only *Micrhystridium*, Charophycean remains, rare fungal spores (not the *Glomus*-type), linings of ostracods, and planispiral open microforaminifera. *Pediastrum* is rare, being present only in the interval just before 2000 yr B.P.

The deep time (>14,000 yr) distribution of some nonpollen palynomorphs in the Marmara Sea core 98-12 (Mudie et al., 2002) shows that that there are no very clear patterns of nonpollen palynomorph increase/decrease except in the pollen and total organic carbon (TOC) signals after 10 ka, and in the peak of multicellular fungal spores that coincides with the high sediment influx ca. 14–10 ka. The *Pediastrum*, prasinophyte (mostly *Pterosperma*), and acritarch records (mostly *Sigmopollis*) show variable oscillations that are not clearly linked with lithofacies or cyclicity.

In the southwestern Black Sea core MAR02-45 (Marret et al., 2009; Hiscott et al., 2007), where sample processing without acetolysis yielded a full complement of both oxidation-resistant and oxidation-sensitive peridinioid dinocyst heterotrophs (Fig. 6), we find a succession from assemblages dominated by the brackish-water species *Spiniferites cruciformis* and

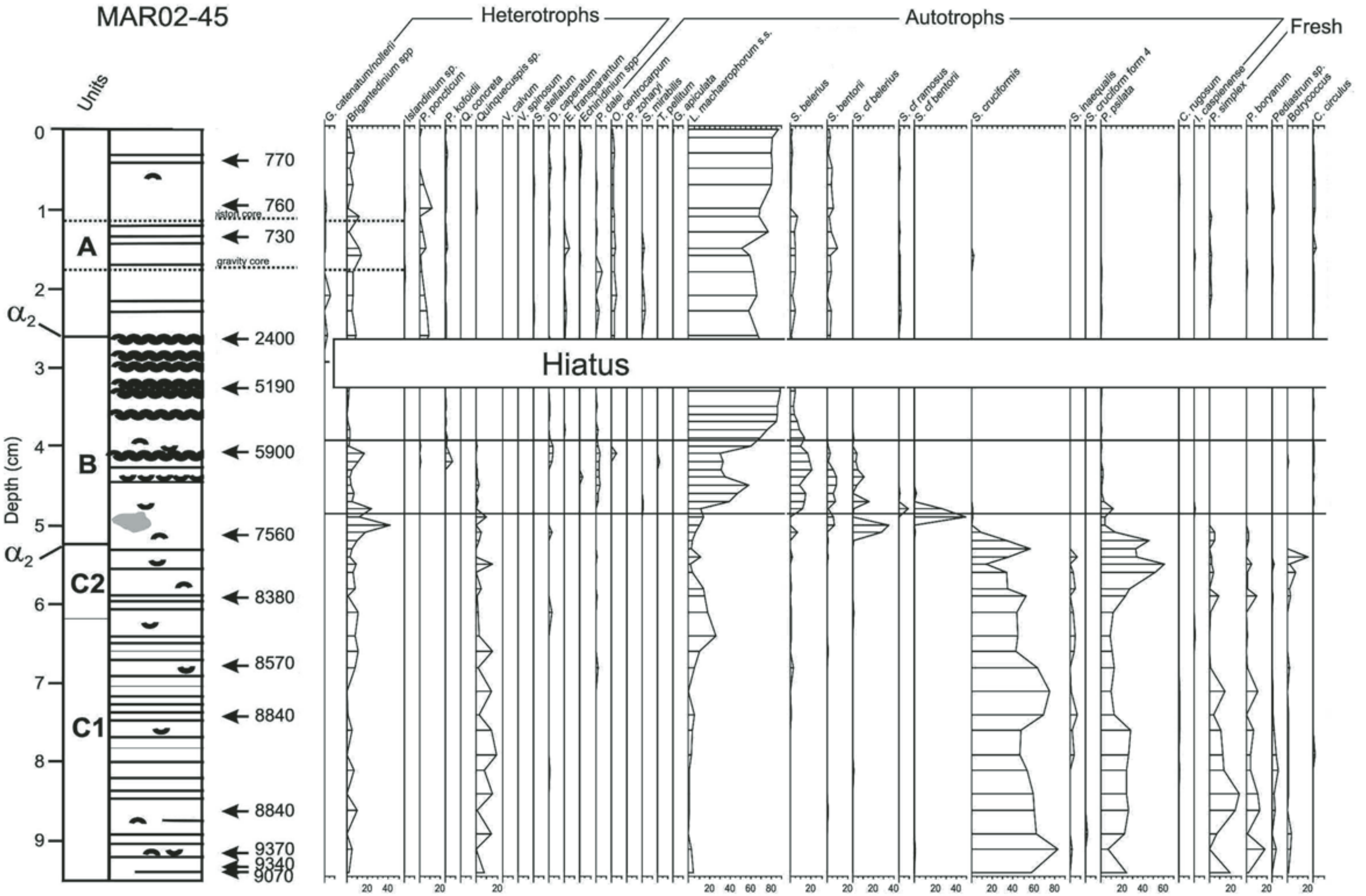

Figure 6. Distribution of nonpollen palynomorphs in Black Sea core M02-45 (from Marret et al., 2009). Alpha-2 marks a regionwide sedimentary hiatus.

Pyxidinopsis psilata that live in the Caspian today, to a gradual replacement by the red tide–producing, euryhaline, eutrophic species *Lingulodinium machaerophorum* and protoperidinioid heterotrophs that thrive in highly eutrophic waters. The colonial alga *Pediastrum* only dominates from ca. 9.3 to 8.6 ka, during the gradual sea-level rise and salinity increase from ~5‰–13‰ to 16‰, and then it becomes sparse in the upper Holocene, where salinity is 16‰–20‰, like today. Zygnematacean spores of *Spirogyra* and *Zygnema* (Plate 2, figs. 11, 12, and 20) are confined to this interval. A few semicells of *Cosmarium* were also found in the overlying sapropelic silty mud unit, together with occasional *Mougeotia* spores. Few *Cosmarium* zygotes were observed, suggesting that the desmids were not growing and reproducing in the sea but were transported as empty hemicells from onshore habitats. As noted for the St. Erth nonpollen palynomorph assemblages (Head, 1992), it is likely that most of the sporadically occurring Zygnematacean spores in the Black Sea are transported by rivers. There is one small peak of *Botryococcus* at the end of the initial period of Mediterranean inflow of sulfur-rich water (ca. 8.6–8 ka), which also marks the onset of strongly stratified conditions that would favor *Lingulodinium.* Linings of the brackish-water ostracods overlap with the peak of the combined colonial algae coenobia, and then the microforaminiferal linings become more prevalent. There is a notable absence of the acritarch *Radiosperma corbiferum* or *Radiosperma* cf. *corbiferum*, which, together with *Operculodinium centrocarpum*, characterizes the slightly brackish Yoldia Sea phase of the Baltic Sea (Brenner, 2005, 2006).

For future studies, it would be helpful to describe and illustrate the microforaminiferal linings found in the Caspian/Aral Seas because distinctive grouping of benthic foraminifera, e.g., elongate uni- or biserial miliolids versus spherical trochamminids (Fig. 7), can be distinguished by the similar shape of their chitinous linings: uni-/biserial, planispiral proximate/open, trochospiral, etc. (Mathison and Chmura, 1995; Stancliffe, 1996). It is possible that some of these nonpollen palynomorphs are the key markers for the inland seas that have been essentially isolated from the world's oceans for the past 15,000 yr, compared to the more persistently connected Black and Marmara Seas. It may also be useful to record the species of *Pseudoschizaea* (Fig. 7) because *P. rubina* seems to have a more limited distribution in the coastal Eastern Mediterranean region, whereas *P. circula* has a very widespread distribution, occurring from mountain to coastal regions. More information is also needed about ostracod versus polychaete jaw characteristics. Saniawski (1996) illustrated the chitinous mandibles and jaw supports of two extant polychaete worm families, but there is little information on Holocene taxa, and at present, it is not clear how to distinguish small simple polychaete worm jaws from the sclerotized mouthparts of either Cladocerans (Korhola and Rautio, 2002) or Chaetognaths (arrow worms). The toothed jaws of scolecodonts from the Marmara Sea are similar to Scolecodont Form 4 of Head (1993, fig. 6-4), whereas those found in the mangrove swamp sediment of the Red Sea and Egyptian shelf are simple (rod-shaped) or bifurcated and more similar in shape to sclerites from body parts of small arthropods. Similar bifurcated jaws are found in beach and shallow-marine deposits of southwestern India (Limaye et al., 2007). Relatively large (>100 μm) sclerites of arthropods are frequently found in freshwater lakes and lagoons, e.g., Lakes Ulubat and Sapanca, and in the inland brackish Caspian Sea. The size and shape of these nonpollen palynomorphs differ considerably from the sclerotic mouthparts of copepods and polychaetes found in continental shelf sediments off California (Mudie, 2009, personal observation).

Ostracoda, Cladocera, and Chironomidae are arthropod groups that have received a lot of attention recently in Holocene studies owing to their potential to reconstruct past water temperatures and salinities (Smol et al., 2001). Ostracod mandibles (Fig. 5) and shells (Plate 3, fig. 18) and Cladoceran (Plate 3, fig. 21) remains are complex structures, and their identification is outside of the normal specialization of a palynologist. The jaws of ostracods (Plate 3, figs. 22 and 26) can be distinguished from the similar but more complicated mouthparts of chironomid midge larvae (Fig. 5; Walker, 2001; Eggermont et al., 2008). Chironomids have a joined symmetrical left and right part with identical rows of teeth, and the palynomorphs are usually found with cojoined central and ventral jaw parts. In contrast, the left and right teeth of ostracods are not joined, and the palynomorphs are found as single jaws with toothed ends.

Anthropogenic influences in the Black Sea corridor are most clearly marked by changes in forest pollen influxes (Mudie et al., 2007) that correspond to deforestation after ca. 7.5 ka and by the appearance of cereal pollen around 5 ka, followed by various horticultural taxa, e.g., olives and vine grapes. However, nonpollen palynomorphs are unique palynomorphs for tracing the history of livestock production from marine sediment records. For example, the occurrence of herbivore dung fungal spores of *Sporormiella* at coastal sites off Varna clearly shows that livestock agriculture was practiced by the Bronze Age, but there is no evidence of earlier animal farms. In Lake Durankulak, dung-fungus spores of *Chaetomium*, *Coniochaeta*, *Podospora*, and *Sordaria* indicate extensive local stockbreeding and grazing during the Early Bronze Age (Marinova and Atanassova, 2006). Peaks of *Neurospora* spores, a fire indicator, correspond to maxima in charcoal particles and *Glomus*-type spores that indicate soil erosion (Marinova and Atanassova, 2006). The smut fungus *Sorosporium* parasitizes mainly grasses, including important crops like sorghum, maize, and millet, and the presence of *Sorosporium*-type spores in the Red Sea marks long-distance transport from highland regions where the crops are mainly grown (Kholeif, 2004). In Issyk-Kul, increased *Botryococcus* and fungal spore percentages are taken as signs of greater erosion and heavier grazing in the catchment after A.D. 1560 (Giralt et al., 2004).

Dinocyst records are also important for understanding the history of toxic red-tide blooms in the Black Sea corridor. In MAR02-45, it is clear that blooms of the toxic species *L. polyedrum* are endemic to the Black Sea waters. In contrast, the late arrivals of the toxic red-tide species *Gymnodinium catenatum* and *Alexandrium*-cyst species around 2400 and 500 yr B.P., respectively, appear to be related to recent introductions via ship-ballast discharge, which today persists as a serious environmental problem in the Black Sea (e.g., Moncheva and Kamburska, 2002). Recent toxic cyst–forming species include *Alexandrium monolatum* (first seen in 1991), *Gymnodinium uberrimum* (1994), *G. fuscum* (1970–1980), and *Gyrodinium* cf. *aureolatum* or *G. mikkimotoi* (1970–1980). These cysts have not yet been recovered as fossils in the surface sediments, however, so it is not yet clear if they survive and reproduce in the Black Sea.

CONCLUSIONS

There is a large range of nonpollen palynomorphs in the Black Sea corridor that remain to be fully exploited by palynologists. Only a small proportion has been identified and related to living organisms or, failing that, have been given a name or a type number. Nonetheless, the change from use of geological fossil names (e.g., *Cymatiosphaera*) to biological names (e.g., *Pterosperma*) by Quaternary paleoecologists illustrates the great progress made in the study of Holocene micro- and macrofossil groups during the last decades. Within much of the old geological

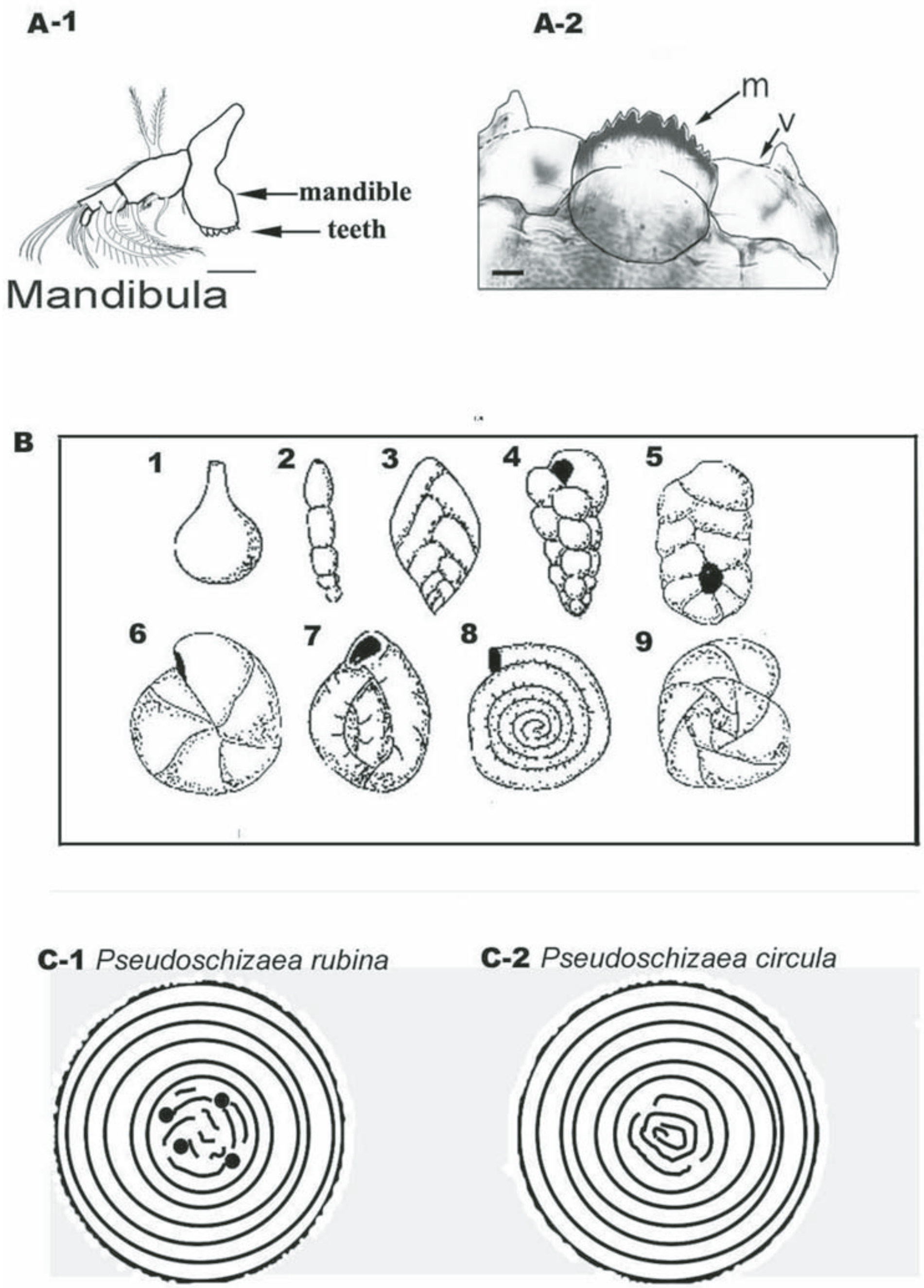

Figure 7. Diagrams of characteristic features of nonpollen palynomorphs with possible environmental importance in the Black Sea–Mediterranean corridor. (A-1) Ostracod mandible, showing last mandible coxa and teeth (from Horne et al., 2002); scale bar = 50 µm. (A-2) Chironomid mouthparts (from Walker, 2001). m—mentum; v—ventromentum plates. (B) Microforaminiferal shapes (after Stancliffe, 1996): 1—single chamber; 2—uniserial;3—biserial type ii; 4—coiled biserial; 5—coiled uniserial; 6—planispiral; 7—spiral uniserial; 8—spiral coiled; 9—trochospiral. (C) *Pseudoschizaea* species (after Christopher, 1976).

information, the new biological identifications have led to new, more in-depth interpretations of environmental change. These powerful new paleoenvironmental tools are likely to spread fairly quickly to the whole of the Pleistocene and further down the Cenozoic.

Depending on the awareness of the various palynologists, and the use of acetolysis versus hydrofluoric acid for sediment processing, only a small portion of the nonpollen palynomorphs in marine/brackish water lakes in the Black Sea corridor has been regularly counted and published. However, our overview of the available, mostly qualitative data clearly shows the value of extracting the full complement of nonpollen palynomorphs, particularly thin-walled peridinioid dinocysts and fungal spores, because of the potential for detailed interpretation of paleoenvironmental conditions and human activity (e.g., livestock husbandry, agriculture, and burning). The most important initial results are summarized as follows.

1. The surface distributions of the nonpollen palynomorphs dinocysts, *Pediastrum* and *Botryococcus*, zygnematacean algae, and zooplankton remains show that during the early Holocene, the Black Sea was a brackish sea like the modern Caspian Sea or the outer Baltic Sea: It was not a freshwater lake. The presence of *Pediastrum* may indicate relatively high phosphorus levels from river inflow, but there are no nonpollen palynomorph indices of fire, soil erosion, or human settlement.

2. Core-top samples from the wide range of salinity in the Black Sea corridor show that the prasinophyte *Pterosperma* (fossil name *Cymatiosphaera*) and other small unicellular acritarchs are usually more abundant in low-salinity environments and they include freshwater species; hence, Traverse's marine influence index cannot be used as a reliable marker of detailed sea-level change.

3. Peaks in the fossil *Cymatiosphaera globosa* (= Prasinophyte *Pterosperma*), colonial algae, and some dinocysts, e.g., *Lingulodinium machaerophorum* (= *L. polyedrum*), mainly reflect nutrient levels and stratification of the water column, and are not reliable markers of sea-level change.

4. Fungal spores appear to be the best index of terrigenous input from soil erosion, and they are important markers of Bronze Age farming practices.

5. Laminated sediments in the hypersaline liman-lagoons of the Crimean Peninsula are characterized by high concentrations of pollen regardless of salinity, by an absence of dinocysts, and variable amounts of low-diversity nonpollen palynomorph assemblages. Ponds with NaCl salt concentrations greater than 100‰ have few nonpollen palynomorphs compared to ponds with a salinity of 40‰–80‰. High concentrations of the acritarch *Micrhystridium* may characterize these environments.

6. In palynological preparations for arthropod and polychaete groups, only partial information is left that does not allow detailed paleoenvironmental reconstruction compared to the algal nonpollen palynomorphs groups, e.g., Chlorophyceae and Cyanobacteria, where identification to generic and species level is possible and leads to significant enhancement of palynological spectra interpretation. More research on the biological links between sclerotized microfaunal remains and morphologically similar nonpollen palynomorphs in brackish and marine environments is required before precise environmental interpretations can be made from this group of Pleistocene–Holocene palynomorphs.

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