

HYALINEA MARMARICA, A NEW SPECIES OF BENTHIC FORAMINIFERA FROM THE SEA OF MARMARA (TURKEY)

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ABSTRACT

Traditionally, the benthic foraminifera *Hyalinea balthica* (Schröter) has been considered a species with high intraspecific variability, possibly related to climatic changes, and, therefore, a potential indicator of paleoclimate in the Mediterranean Sea. However, a stable and characteristic morphology very different from the syntype of the species can be observed in specimens from the Sea of Marmara.

By identification and documentation of this morphology and a subsequent comparison to specimens similar to the type species, clear differences between the two groups have been established. *Hyalinea marmarica* n. sp. is proposed as an example of possible environment-related speciation in benthic foraminifera. It differs from *H. balthica* in having less numerous chambers in the last whorl (maximum of eight), depressed sutures at least in the last four chambers, a moderate increase in chamber size as added, a subacute profile and accessory apertures on the peripheral margin.

Speciation could have occurred between 14 and 12 ka. At this time, increasingly efficient connections were progressively established between the Sea of Marmara and the Eastern Mediterranean Sea, allowing *Hyalinea balthica* to migrate into the Sea of Marmara. Here this species might have modified its morphology in response to the extreme environmental conditions.

INTRODUCTION

The Mediterranean Sea is a complex system subdivided into several basins, which are interconnected by straits and sills. It is presently considered a natural laboratory for studies of climate changes.

The Sea of Marmara is a gateway that connects the Aegean Sea to the west and the Black Sea to the northeast. Two relatively shallow straits, the Dardanelles (average water depth 75 m) and the Bosphorus (average water depth 45 m), connect the Sea of Marmara to the Aegean and Black Seas, respectively.

Today, a two-way flow occurs between the Mediterranean and Black Seas through the Sea of Marmara. Brackish surface water flows from the Black Sea through the Sea of Marmara into the Mediterranean Sea, and saline deeper water flows from the Mediterranean Sea into the Sea of Marmara. Because of the existence of brackish outflow water from the Black Sea, a strong halocline is present in the Sea of Marmara, leading to low-oxygen conditions below the thin, well-mixed surface layer (Kaminski and others, 2002).

Benthic and planktonic foraminifera have been extensively used to study the impact of climate and environmental changes on these semi-enclosed basins (e.g., Blanc-Vernet 1969; Cita and others, 1977; Vergnaud-Grazzini and others, 1977; de Rijk and others, 1999; Robertson and others, 1998; Comas and others, 1999; Ariztegui and others, 2000; Emeis and others, 2000). A species widely used in the Mediterranean Sea to reconstruct paleoclimatic changes is the benthic foraminifera *Hyalinea balthica* (Schröter), which is presently typical of cold, cool and cool-temperate environments (Bock, 1970; Murray, 1971; Hermelin, 1991) and which still lives in the Mediterranean Sea (Cita and others, 1977).

The ingress of this species into the Mediterranean Sea was used to mark the Plio-Pleistocene boundary (e.g., Gignoux, 1910; Emiliani and others, 1961; Flint, 1965; Selli, 1967) until it was demonstrated that the first appearance of *Hyalinea balthica* in this region is diachronous (e.g., Bremer and others, 1980; Lourens and others, 1998). Presently, the ingress of this species into the Mediterranean Sea is placed in proximity to the Santernian-Emilian substage boundary at 1.58 Ma (Vaiani and Venezia, 1999; Vaiani, 2000).

The Pleistocene sedimentary sequence drilled at the Ocean Drilling Program (ODP) Hole 160-963A (Strait of Sicily, Eastern Mediterranean Sea) contains several intervals enriched with *Hyalinea balthica*, thus providing the opportunity to compare the different morphologies of this species. The European Union-funded project AVICENNE "Benthic foraminifera as indicators of heavy metal pollution—a new kind of biological monitoring for the Mediterranean Sea" provided the authors with living specimens of *H. balthica* (cruise AVI-I, Israeli coast). Additionally, several oceanographic campaigns in the Sea of Marmara provided the second author with cores and sediments for the study of this species. This article describes and compares different morphotypes of *H. balthica*, and the species *Hyalinea marmarica* n. sp. is proposed as an example of possible environment-related speciation in benthic foraminifera.

MATERIALS AND METHODS

Three sets of samples for this study were collected and prepared as follows. (1) ODP Hole 160-963A was drilled in the Strait of Sicily at a water depth of 470.5 m (Fig. 1). Samples from Hole 963A were soaked and washed in distilled water and dried at room temperature—no flotation techniques were employed. Dead assemblages were qualitatively studied in the >63- μ m size fraction. (2) Three short cores were retrieved from the Sea of Marmara: Core BX2, BX3 and BX5 (Fig. 1, Table 1). The samples from the Sea of Marmara were recovered in 1988 by box corer during a cruise of the R/V *Knorr*. Cores were cut into 3-cm slabs,

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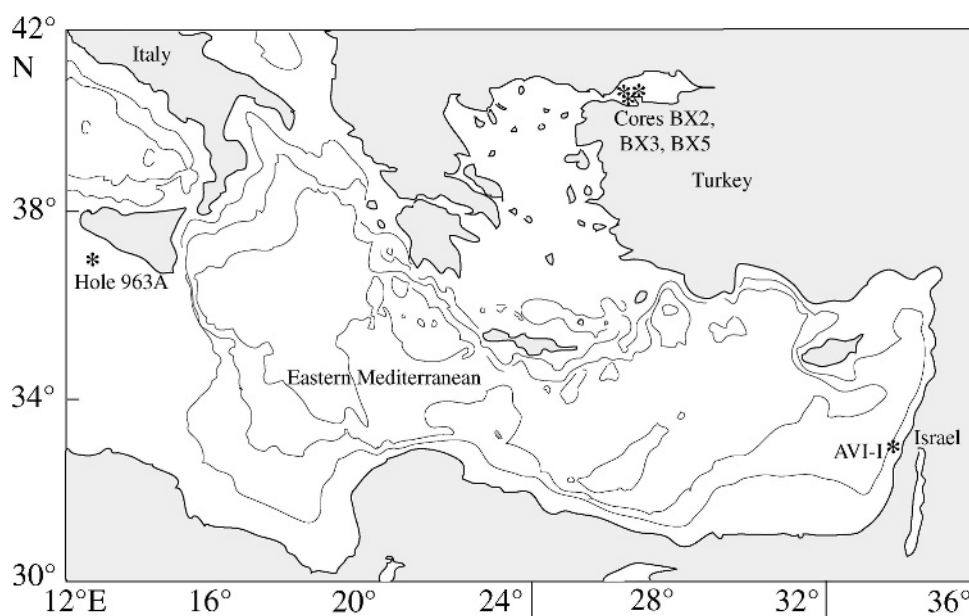


FIGURE 1. Map of the Eastern Mediterranean Sea showing the location of ODP Hole 160-963A (Southern Sicily); AVI-I (Israeli coast); and Cores BX2, BX3 and BX5 (Sea of Marmara) where *Hyalinea balthica* and *H. marmarica* were found. Figure modified after Spezzaferri and others (1998).

each slab was soaked and washed in distilled water, and dried at room temperature—no floatation techniques were employed. Dried samples were then split, and about 300 foraminifera were picked and counted, whenever possible, for population statistics as described in Yanko-Hombach and others (2006). (3) Four stations were sampled along the Israeli coast (Fig. 1, Table 1) as part of the AVIECENNE Project (AVIECENNE Annual Report, 1993; 1995; 1996). The samples from the Israeli shelf were recovered by box corer (BX 700 AI Compact Box Corer) in May 1993 by the R/V *Shikmona*. Samples for foraminiferal analysis were collected onboard from the uppermost 2 cm of the sediment column with the aid of a wooden spatula, and treated in a 4% formalin solution made with seawater buffered by 20 g of Na₂B₄O₇ per liter. The number of living (rose Bengal stained) foraminifera was calculated in wet sediment samples equal to 5 g of dry sediment. When the abundance of benthic foraminifera was low, whole samples were counted. If the number of live specimens was small at a given station (50–100 specimens per 5 g sediment), foraminiferal analysis was repeated on five different aliquots of sediment for each sample, and the mean of the five replicates was used (Yanko and others, 1998).

Radiocarbon ages in conventional ¹⁴C years, without a reservoir correction or further calibration, were obtained for the samples from the Sea of Marmara (Table 2).

TABLE 1. Coordinates, water depth and core length of cores from the Sea of Marmara.

Box core	Latitude (N)	Longitude (E)	Water depth (m)	Core length (cm)
BX-2	40°54.48'	28°56.03'	64	48.0
BX-3	40°49.48'	27°57.35'	1226	50.0
BX-5	40°32.02'	27°09.37'	65	45.5

Measurements were made at the Quaternary Dating Research Unit, CSIRO, Pretoria, South Africa using the conventional beta particle counting technique. The bulk carbonate (consistently 30% of the sediment) from the 2-cm slices of the cores was dried, microscopically analyzed, and treated with hydrochloric acid to release carbon dioxide, which was used for radiometric analysis in a gas proportional counter as described in Yanko-Hombach and others (2006).

Electron scanning microscope (SEM) images were obtained with a FEI XL30 Sirion FEG microscope. Specimens were mounted on an SEM sample holder, coated with 40 nanometers of gold and observed and imaged using a standard beam voltage of 20 kV at a probe current of 15 nA.

SYSTEMATIC PALEONTOLOGY

Only six specimens of *Hyalinea balthica* were found in the four AVI-I sites. In contrast, both *H. balthica* and *H. marmarica* were relatively abundant in the three cores from the Sea of Marmara from the surface to 37 cm, 50 cm and 45 cm in Cores BX2, BX3 and BX5, respectively (Table 3). *H. balthica* was abundant in the sedimentary sequence from ODP Hole 160-963A, from 200–120 meters below sea floor (mbsf) and from 30–10 mbsf. These sediments were de-

TABLE 2. Uncalibrated radiocarbon age of sediment samples from cores of the Sea of Marmara.

Core	Sampling depth	¹⁴ C age (in conventional years, without reservoir correction or further calibration)	ID number
BX2	3–6.5 cm	6160±120 δ13C = -1.3%	Pta-6880
BX-2	43–48 cm	7030±100 δ13C = -0.9%	Pta-6870
BX-3	48–50 cm	5550±120 δ13C = -2.4%	Pta-6868

TABLE 3. Number of specimens of *Hyalinea balthica* and *H. marmarica* in Cores BX2, BX3 and BX5 (Sea of Marmara) and total abundance of benthic foraminifera in each sample.

Core BX2				Core BX3			Core BX5			
Depth (cm)	Specimens of <i>H. balthica</i>	Specimens of <i>H. marmarica</i>	Total benthic foraminifera	Depth (cm)	Specimens of <i>H. balthica</i>	Total benthic foraminifera	Depth (cm)	Specimens of <i>H. balthica</i>	Specimens of <i>H. marmarica</i>	Total benthic foraminifera
0.0–3.0	0	1	126	0.0–3.0	0	79	0.0–2.0	5	9	421
3.0–6.5	4	1	264	3.0–11.0	0	115	2.0–10.0	5	2	194
6.5–10.0	0	8	279	11.0–14.0	0	34	10.0–12.0	0	17	244
10.0–13.0	0	5	255	14.0–20.0	0	110	12.0–20.0	1	6	224
13.0–16.0	1	13	294	20.0–24.0	0	180	20.0–22.0	3	20	296
16.0–19.0	2	14	316	24.0–27.0	1	234	22.0–26.0	6	12	228
19.0–22.0	1	6	316	27.0–30.0	1	118	26.0–30.0	8	0	162
22.0–25.0	1	4	320	30.0–34.0	0	92	30.0–33.0	3	11	180
25.0–28.0	2	4	263	34.0–37.0	0	139	33.0–37.0	3	12	178
28.0–31.0	2	0	270	37.0–42.0	0	165	37.0–40.0	5	10	185
31.0–34.0	1	0	271	42.0–50.0	1	64	40.0–42.0	3	16	168
34.0–37.0	1	4	256	no samples	-	-	42.0–45.0	4	15	174

posited from 1.5 Ma to ~0.7 Ma and from 0.26 Ma to the uppermost Pleistocene, respectively (Robertson and others, 1996). A morphological study of the different specimens of *H. balthica* and their spatial and temporal distribution has enabled the identification of two stable morphologies described and distinguished below.

Hyalinea balthica (Schröter)

Pl. 1, figs. 1, 3a–b; Pl. 2, figs. 2a–c, 4a–b, 5a–c

1783 *Nautilus balthicus* Schröter in Schröter; p. 20, pl. 1, fig. 2.

1791 *Nautilus balthicus* Schröter in Gmelin in Linnaeus 1791, p. 3370.

1971 *Hyalinea balthica* (Schröter) in Murray, p. 173, Pl. 72, figs. 5–7.

1986 *Hyalinea balthica* (Schröter) in van Mookhaven and others, Pl. 3, figs. 1–3.

2003 *Hyalinea balthica* (Schröter) in Murray, Pl. 8, figs. 8–10.

2004 *Hyalinea balthica* (Schröter) in Meriç and others, Pl. 27, fig. 3.

Repository. Not given.

Diagnosis. This species includes forms resembling the syntype from the Baltic Sea (Pl. 1, fig. 1). Test size is variable, ranging from 125–250 µm. Chamber arrangement is planispiral or slightly trochospiral, with chambers slowly increasing in size as added. Nine to twelve chambers are present in the last whorl and are generally ovate to subtriangular, the peripheral margin is rounded to slightly subacute and the test outline is circular. A keel is always present and strongly marked. The aperture is an extraumbilical, interiomarginal low arch, bordered by a distinct but thin lip. Sutures are straight to arched, strongly limbate and merging with the peripheral keel. The characteristic secondary apertures beneath the umbilical flap are present on both sides of the test.

Remarks. In ODP Hole 160-963A, two forms co-occur: a form that closely resembles the syntype (Pl. 1, figs. 3a–b) and morphotypes that display more inflated chambers and less marked and slightly depressed sutures (Pl. 2, figs. 3a–b). The latter forms resemble the Pliocene specimens from the Arabian Sea that were described by Hermelin (1991) as possessing less limbate sutures and less pronounced keels with respect to upper Pliocene and Pleistocene specimens and which he considered a subspecific group of *Hyalinea balthica*.

Ross (1984) provided a good record from the Strait of Sicily of different morphotypes that he considered related to climatic factors. He attributed massive and thick morphologies with strongly limbate sutures and a distinct keel to glacial stages. Accordingly, he attributed more delicate morphotypes with more inflated chambers, a lobate profile, and less thickened (limbate) sutures to the Marine Isotope Stage (MIS) 5e. The rare delicate forms morphologically grading into the thicker ones were described as ecophenotypes. These gradational morphotypes and the delicate forms, similar to those described by Ross (1984) in the Strait of Sicily, were not observed at ODP Hole 160-963A.

However, the levels containing these specimens could have been missed during sampling.

Hyalinea marmarica n. sp.

Pl. 1, figs. 2a–e, 4a–d; Pl. 2, figs. 1a–c

1984 *Hyalinea balthica* (Schröter) sensu Ross (non Schröter, 1783) in Ross, Pl. 1, figs. 14–16.

2002 *Hyalinea balthica* (Schröter) sensu Kaminski and others (non Schröter, 1783) in Kaminski and others, Pl. 3, fig. 13.

2004 *Hyalinea balthica* (Schröter) sensu Chendler and others (non Schröter, 1783) in Chendler and others, Pl. 3, fig. 1a–b.

Holotype specimens. Illustrated in Pl. 1, fig. 2a–e.

Derivation of the name. From the Sea of Marmara.

Type level. Sample BX2, 13–16 cm.

Type section. Core BX2 retrieved in the Sea of Marmara, at 64 m water depth, Lat. 40°54.48'N; Long. 28°56.03'E.

Age available. Between 6160 yr BP (measured at 3 cm depth in core) and 7030 yr BP (measured at 48 cm depth in core). The total stratigraphic range of this species is presently not known.

Sediment lithology. Homogeneous gray mud.

Repository. Natural History Museum of Basel, Switzerland. Ref. C39018. The paratypes (Pl. 1, figs. 4a–d; Pl. 2, figs. 1a–c) are deposited in the AVICENNE collection stored in the Avalon Institute of Applied Science, Winnipeg, Canada.

Diagnosis. Test size is variable and averages from 200–250 µm in maximum diameter. Chamber arrangement is planispiral or slightly trochospiral, with chambers moderately increasing in size as added. A maximum of eight chambers is present in the last whorl. They are, generally, strongly subtriangular, the test outline is lobate and the peripheral margin is always subacute. A keel is sometimes present, especially in the inner chambers of the last whorl, but very weakly developed. The aperture is an extraumbilical, interiomarginal low arch, bordered by a distinct but thin lip. Sutures are strongly sigmoidal, depressed in the last four chambers of the last whorl and slightly limbate in the remaining four chambers. The characteristic secondary apertures beneath the umbilical flap are present on both sides of the test. The flaps are generally well developed. The wall texture displays slightly smaller and denser pores than in *Hyalinea balthica* (Pl. 2, figs. 1d, 5c). Supplementary apertures are often present along the peripheral margin in sutural position (Pl. 1, figs. 2d–e, 4d; Pl. 2, fig. 1c).

Remarks. *Hyalinea marmarica* is relatively abundant in Cores BX2 and BX5. Table 3 shows its abundance with respect to the total abundance of benthic foraminifera.

This species differs from *Hyalinea balthica* in having a maximum of eight chambers in the last whorl, depressed sutures at least in the four last chambers, a moderate increase in chamber size as added, a subacute profile and accessory apertures on the peripheral margin.

It differs from the early Pliocene forms described by Hermelin (1991) in having eight chambers in the last whorl instead of nine to ten,

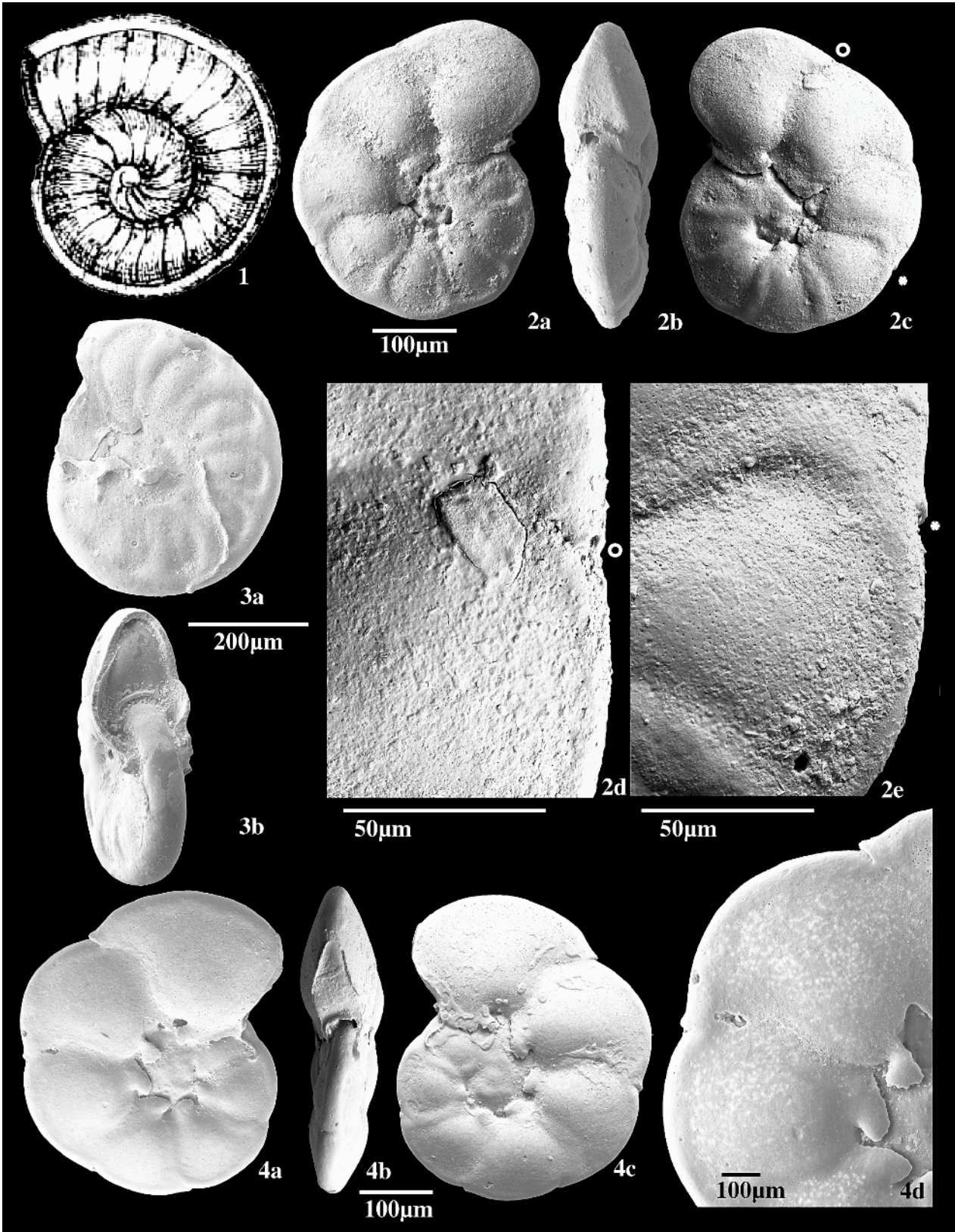


PLATE 1

Comparison between *Hyalinea marmorica* Spezzaferri and Yanko-Hombach and *H. balthica* (Schröter). 1 Syntype of *H. balthica* (Schröter), *Nautilus balthicus* as described by Schröter in 1783 and successively illustrated by Gmelin in Linnaeus (1791). 2a-e *Hyalinea marmorica* Spezzaferri and Yanko-Hombach, holotype: 2a lateral view; 2b side view; 2c lateral view; 2d detail of the supplementary aperture at the intersection between the last and the previous chamber of the last whorl located along the peripheral margin; 2e detail of the supplementary aperture at the intersection

a subacute profile and less inflated chambers. It differs from the interglacial related morphotypes of *Hyalinea balthica* described by Ross (1984) in having less numerous chambers in the last whorl (eight instead of nine to ten), less limbate sutures and less inflated chambers.

It differs from *Hyalinea inflata*, described by Ujiie and Kusukava (1969), in having a subacute and slightly keeled peripheral margin, eight chambers in the last whorl, sigmoidal sutures and supplementary apertures along the peripheral margin, instead of a rounded, non-keeled peripheral margin, six chambers in the last whorl, curved sutures and lacking a supplementary aperture along the peripheral margin.

DISCUSSION

In biology, the presence of specimens displaying a certain morphology grading into another morphology within the same assemblage is generally interpreted as species variability within a taxon (e.g., Simpson, 1961, p. 150–153). Additionally, the presence of specimens displaying a certain morphology grading into another morphology across an ecological gradient is generally interpreted as ecophenotypic variation. Accordingly, Ross (1984) interpreted the delicate forms of *Hyalinea balthica*, which are present in interglacial MIS 5e, as ecophenotypes of the typical *H. balthica* that is present in glacial stages, because he observed rare morphological gradation between the two forms. Following Ross's (1984) observations, *H. balthica* has always been considered a species with high intraspecific variability. Transitional specimens were not observed in the samples investigated from the Sea of Marmara. On the contrary, within the same assemblages, very rare specimens of *H. balthica* similar to the syntype (Pl. 2, figs. 2a–c) coexist with *H. marmarica*, without gradational morphologies between the two forms.

AUTECOLOGY OF *HYALINEA BALTHICA* AND *H. MARMARICA*

In the following sections, the ecological preferences of *Hyalinea balthica* in terms of salinity, dissolved oxygen and temperature are compared with those of *H. marmarica*. Table 4 shows the average values of these parameters at the sea floor and at 400–500 m water depth in the Sea of Marmara, the Eastern Mediterranean Sea and the North Atlantic Ocean, respectively.

According to the existing literature, *Hyalinea balthica* is an epifaunal species living within the first 0.5 cm of sediments (Murray, 2003) between 50–4000 m water depth (e.g., Cita and others, 1977). In the Atlantic Ocean and Mediterranean Sea, the greatest abundance of this species is found between 400–500 m depth (Blanc-Vernet, 1969; Colom, 1974; Cita and others, 1977; de Rijk and others, 1999; Meriç and others, 2004).

In the North Atlantic Ocean (e.g., in the northwest European shelf seas), *Hyalinea balthica* lives in environments where bottom temperature is $\sim 4^{\circ}\text{C}$ in winter and $\sim 7.5^{\circ}\text{C}$ in summer (Elliott and others, 1991; Murray, 2003;

Norman, 2001; Husum and Hald, 2004), and mean bottom salinities are $\sim 34.0\text{--}35.0$ psu (Murray, 2003). At the preferred depth of this species (400–500 m), bottom temperature reaches 7.5°C , salinity is constantly $\sim 34.0\text{--}35.0$ psu and oxygen content is variable depending on local factors (Table 4).

In the Mediterranean Sea, at the preferred depth of this species (300–500 m), bottom temperature reaches $14.5\text{--}15^{\circ}\text{C}$ and salinity is $\sim 38\text{--}39$ psu (POEM Group, 1992). Dissolved oxygen content does not vary from 400–500 down to the sea floor and displays values of $\sim 4.2\text{--}4.4$ ml/l (Table 4; Roether and Well, 2001).

In the Sea of Marmara, rare specimens of *Hyalinea balthica* have been found at water depth of 64 and 65 m (Core BX2 and BX5, respectively), and at 111 m (Kaminski and others, 2002). Core BX3, retrieved at a water depth of 1226 m, contains only very rare specimens (Table 3). In this basin, bottom salinity is presently ~ 38 psu (e.g., Chendes and others, 2004). Direct measurement of water temperature from 50–500 m gives values consistently near 18°C (Chendes and others, 2004). No direct measurements are available for bottom temperature. Oxygen content decreases from 2 ml/l at about 65 m to 1.1 ml/l at the sea floor (Chendes and others, 2004).

The biogeography and the habitat of foraminiferal taxa can be satisfactorily determined only from direct observation of living individuals (Murray, 2003). However, because living specimens of *Hyalinea marmarica* have not been observed in the studied material, the comparison between the ecological preferences of the two species must be complemented by the examination of the ecological preferences of *H. balthica* in the past.

Rich *Hyalinea balthica* assemblages, dated from 7600–5700 yr BP, have been found in northern Norway. These paleoenvironments are characterized by a water depth of about 450 m and bottom temperatures derived from oxygen isotopes of $\sim 6\text{--}11^{\circ}\text{C}$ (Husum and Hald, 2004), indicating ecological preferences similar to those of living specimens from the northwest European shelf seas and not far from those of living specimens in the Mediterranean Sea. Moreover, the paleoceanographic reconstruction made by Aksu and others (2002) for the Sea of Marmara in the interval between 6000–7000 yr BP reveals that salinity and temperature in the area did not sensibly differ from those of the present.

In summary, the interpretation of the ecological preference of *Hyalinea marmarica* is based on the ecological preferences of living and fossils *H. balthica*, and on the ecological parameters summarized in Table 4. In particular, *H. marmarica* is interpreted to be tolerant of a wider range of temperatures with respect to *H. balthica* and perhaps has a higher optimal temperature ($\sim 18^{\circ}\text{C}$). It is less tolerant

←
between the fifth and the sixth chamber of the last whorl located along the peripheral margin. In the holotype, these supplementary apertures are not strongly developed. Sample BX2, 13–16 cm. **3a,b** *Hyalinea balthica* (Schröter): **3a** lateral view; **3b** side view, this specimens resemble the holotype of figure 1, with numerous chambers in the last whorl and strongly marked sutures; ODP Sample 160-963A-22H-CC. **4a–d** *Hyalinea marmarica* Spezzaferri and Yanko-Hombach: **4a** lateral view; **4b** side view; **4c** lateral view; **4d** details of the supplementary apertures along the peripheral margin; Sample BX5, 0–2 cm.

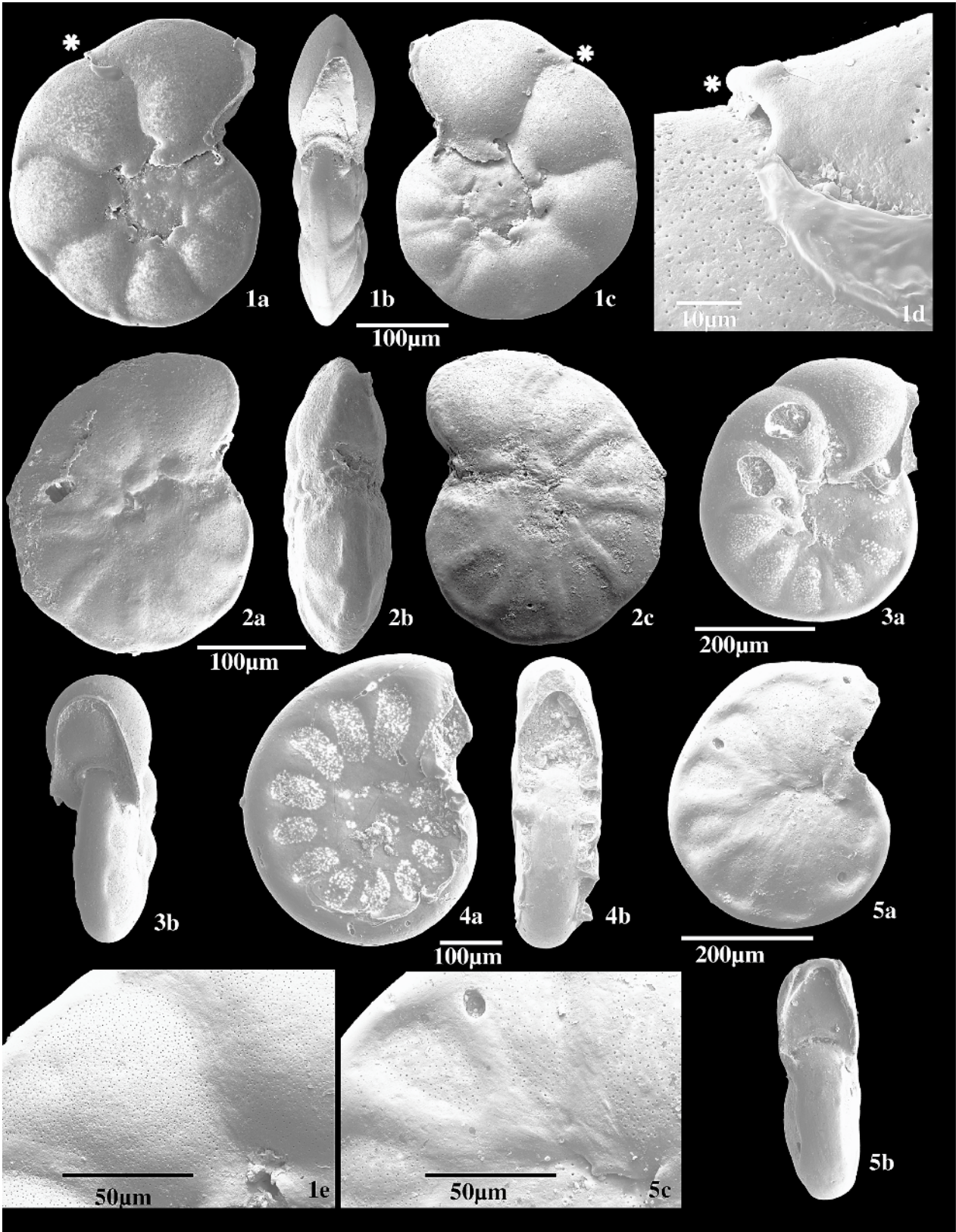


PLATE 2

Hyalinea marmarica Spezzaferri and Yanko-Hombach and *H. balthica* (Schröter). **1a–e** *Hyalinea marmarica* Spezzaferri and Yanko-Hombach: **1a** lateral view; **1b** side view; **c** lateral view; **1d** details of a supplementary aperture (marked by a star) along the peripheral margin; **1e** detail of the wall texture showing denser and smaller pores than in *H. balthica*; Sample BX5, 0–2 cm. **2a–c** *Hyalinea balthica* (Schröter): **2a** lateral view; **2b** side view; **2c** lateral view. This specimen displays the features typical of the species, which co-exists with *H. marmarica* in absence of intermediate morphotypes.

TABLE 4. Ecological parameters (salinity, dissolved oxygen and temperature) in the Sea of Marmara, Eastern Mediterranean Sea and North Atlantic Ocean at the sea floor and at 400–500 m. Data compiled from the POEM Group (1992); Roether and Well (2001); Normann (2001); Özsoy and others (1995); Husum and Had (2003); Murray (2003); Falkner and others (2005); Chandes and others (2004); Mudie and others (2004). NA = not available.

Parameter	Sea of Marmara	Eastern Mediterranean Sea	North Atlantic Ocean
Salinity in psu (bottom)	38.8–38.6	Variable from 38 to hypersaline	34–35
Salinity in psu (400–500 m)	38.8–38.6	38.5–39	34–35
Oxygen in ml/l (bottom)	dysoxic	4.2–4.4	Variable
Oxygen in ml/l (400–500 m)	Lower than 1.1	4.2	Variable
Temperature in °C (bottom)	N.A. but lower than 18	4–10	4
Temperature in °C (400–500 m)	About 18	14–14.5	7–10

with respect to variation in salinity than *H. balthica*, which can live in water with salinity ranging from 34–39 psu in both the Atlantic Ocean and Eastern Mediterranean Sea.

The presence of *Hyalinea marmarica* and *H. balthica* in sediments retrieved from a water depth of 65 m, where dissolved oxygen is ~1.8–2.0 ml/l, and the presence of *H. balthica*, even if rare, in the absence of *H. marmarica* in deeper water (Core BX3), where dissolved oxygen is <1.1 ml/l (Chendes and other, 2004), suggest that *H. balthica* is more tolerant of a low level of dissolved oxygen than is *H. marmarica*. The absence of *H. marmarica* in Core BX3, retrieved at a water depth of 1226 m, and its common occurrence at 64–65 m might suggest that this species prefers shallower waters than *H. balthica*. However, further sampling and studies are needed to confirm the depth and ecological preference of *H. marmarica*.

PALEOCEANOGRAPHIC IMPLICATIONS

In the eastern Mediterranean Sea, the abundance of *Hyalinea balthica* is variable (Ross, 1984), and its presence through the Quaternary is discontinuous (Lourens and others, 1998), reflecting environmental and climatic changes (e.g., Robertson and others, 1996). This species has been present in the Mediterranean Sea for 1.58 m.y. (e.g., Vaianni, 2000), and its appearance in the basin coincides with the ingression of cold-water, North Atlantic species into the Mediterranean Sea.

For the last ~1.4 m.y., the Mediterranean Sea, like the global oceans, has been under the influence of glacial-interglacial climate oscillations. The early to late Pleistocene $\delta^{18}\text{O}$ record of ODP Site 160-963 indicates that major climatic cooling occurred at approximately 0.98 and 0.45 Ma (Howell and others, 1998). These cooling episodes were optimal for the proliferation and life of *Hyalinea balthica*, as suggested by its abundance in samples from ODP Hole 160-963A (Robertson and others, 1996). Interglacial times probably were not conducive to the proliferation of this species.

The latest post-glacial sea level rise started at about 14 ka in the Eastern Mediterranean region (Chappel and Shack-

leton, 1986; Fairbanks, 1989). Probably from 14 to 12 ka, increasingly efficient connections between the Sea of Marmara (bedrock sill depth of the Dardanelles Strait is 70 m) and the Eastern Mediterranean Sea were progressively established (e.g., Kaminski and others, 2002). It can be proposed that the migration of *Hyalinea balthica* into the Sea of Marmara occurred at this time. Some specimens of *H. balthica* possibly entered the Sea of Marmara through the Dardanelle Strait. In the Sea of Marmara, they might have modified their morphology in response to the extreme environmental conditions, giving rise to *H. marmarica* and leaving robust forms of *H. balthica* as a minor component of the assemblages (Fig. 2).

CONCLUSIONS

The benthic foraminifera *Hyalinea balthica* is a species with great morphological variability. The morphological adaptations of *H. balthica* found in the Mediterranean Sea have been related to climatic changes. Since its Pleistocene ingression into the Mediterranean Sea at 1.58 Ma, this species has been subject to periodic, climate-driven modifications. In the Sea of Marmara, these modifications ultimately gave rise to stable morphologies that differ from those of the syntype. The comparison of these specimens to those similar to the holotype has allowed the distinction and codification of the criteria for the identification of the species *H. balthica*. The documentation of these different morphologies leads to the proposal of the species, *Hyalinea marmarica* n. sp., as an example of environment-related speciation.

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Sample BX5, 0–2 cm. **3a,b** *Hyalinea balthica* (Schröter): **3a** lateral view, **3b** side view. This specimen has a more rounded peripheral margin and less developed keel than specimens typical of this species and the two forms are found together in the same assemblage. ODP Sample 160-963A-22H-CC. **4a,b** *Hyalinea balthica* (Schröter), **4a** lateral view, **4b** side view. Typical specimen from ODP Sample 160-963A-22H-CC. **5a–c** *Hyalinea balthica* (Schröter), typical specimen from ODP Sample 160-963A-22H-CC. **5a** lateral view, **5b** side view, **5c** detail of the wall texture showing less dense and slightly larger pores than in *H. marmarica*.

Hyalinea balthica and *H. marmarica* has been obtained with the SEM of the University of Fribourg, and we warmly thank C. Neururer for his assistance. A warm thank goes to Richard Waite for his correction of the English form. The comments of C. Brunner, R. Fleisher and M.-T. Venec-Peyré greatly improved the manuscript.

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