FAUNAL EVIDENCE OF A HOLOCENE PLUVIAL PHASE IN SOUTHERN ARABIA WITH REMARKS ON THE MORPHOLOGICAL VARIABILITY OF *HELENINA ANDERSENI*

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ABSTRACT

Although foraminifera have been found living in inland saline lakes isolated from the sea, this phenomenon has rarely been recognized in the fossil record. This study documents the occurrence of benthic foraminifera in Holocene lake sediments located nearly 500 km inland from the Red Sea, in the Al-Mundafan region of southern Saudi Arabia. The lake formed during a regional pluvial period, 10,500–6000 yr BP. The presence of foraminifera and brackish charophytes in the studied section represent an interval when the lake was slightly brackish due to high evaporation. The studied sediments yielded a bispecific benthic foraminiferal fauna comprised of *Helenina anderseni* and *Trichohyalus aguayoi*, as well as the brackish charophyte genus *Lamprothamnium*. The benthic foraminifera are species characteristic of mangrove swamps, salt marshes, and lagoons, which are environments currently widespread along the Red Sea coasts. Because the Al Mundafan area was never connected to the sea during the Quaternary, wading birds must have been the vector that transported the foraminifera to the paleolake.

INTRODUCTION

There have been numerous reports of benthic foraminifera occurring in both Recent and ancient sediments of inland lakes, ponds, springs, and rivers (see summaries in Patterson and others, 1990; Lévy and others, 1995; Patterson and others, 1997; and Wennrich and others, 2007). Nevertheless, these are enigmatic occurrences, each of which presents an enticing challenge to research. In the present study, we document the presence of foraminifera in inland paleolake deposits of southern Arabia, and seek an explanation for this local phenomenon.

The climate of southern Arabia is strongly affected by the African-Asian monsoon. Periods of intensified monsoonal circulation during the late Pleistocene and Holocene caused significantly higher precipitation over the southern Arabian Peninsula (e.g., Fleitmann and others, 2003a). Since lacustrine sediments can provide a detailed record of paleoclimate variability, a multiproxy study of Pleistocene–Holocene lake deposits in the Empty Quarter of Saudi Arabia (Rub' al Khali) was undertaken as part of a Swiss National Science Foundation project seeking to better understand this pluvial period in what is still a largely unexplored region.

During fieldwork in the Al Mundafan region in March 2008, ten outcrops were sampled (Fig. 1). A total of 68 samples were taken for micropaleontological analysis and radiocarbon and OSL dating. One of these outcrops yielded two samples with foraminifera and charophytes (Fig. 2). The primary aim of our study is to reinvestigate this benthic foraminiferal fauna, first reported in the Al Mundafan area by McClure and Swain (1980), and to place it into a paleoenvironmental context.

GEOLOGICAL SETTING

The study area is located 700 km southeast of Mecca at the southern end of the Tuwayq sedimentary escarpment, where Holocene lakebeds are exposed within a single depression of approximately 15 square kilometers. The depression is bordered by the escarpment to the north and by dunes to the south. A modern sabkha occupies the western part of the depression.

MATERIAL AND METHODS

Sediment samples were prepared for micropaleontological quantitative analysis first by drying at room temperature. Aliquots of ~40 and 30 g for samples A4 and A5, respectively, were then washed through a 32-µm satilon net. The two residues were left at room temperature and once dry each was sieved into 250, 125, 63, and 32 µm-size fractions. Each fraction was split three times and the foraminiferal content of one of those splits was quantitatively studied. Approximately 200 adult specimens were picked from the 125–250 µm size-fraction and mounted on slides. Each specimen was analyzed for morphometric parameters using a KEYENCE VHX-600 digital microscope at a magnification of 200×. Measurements were taken of spiral diameters (D and B) and height (H), as well as intersutural length (ISL) of the first and penultimate chambers of the last whorl (Fig. 3) following Pearson and others, 2001. Multivariate (Principal Component Analysis) statistical treatment on morphometric data was performed with the software PRIMER 6 after data normalization (Clarke and Warwick, 2001; Clarke and Gorley, 2006). Scanning electron microscope (SEM) images were obtained at the Department of Geosciences, University of Fribourg.

The chronology of Section 8321.1 is based on radiocarbon dating, measured by accelerator mass spectrometry (AMS) at the ETH/PSI facility in Zurich (Table 1). In order to avoid age offsets due to the so-called ''hard water effect'', the carbonate fraction was dissolved using 5M HCl and only phytoclasts were used for dating. The Holocene radiocarbon age was calibrated to calendar years using

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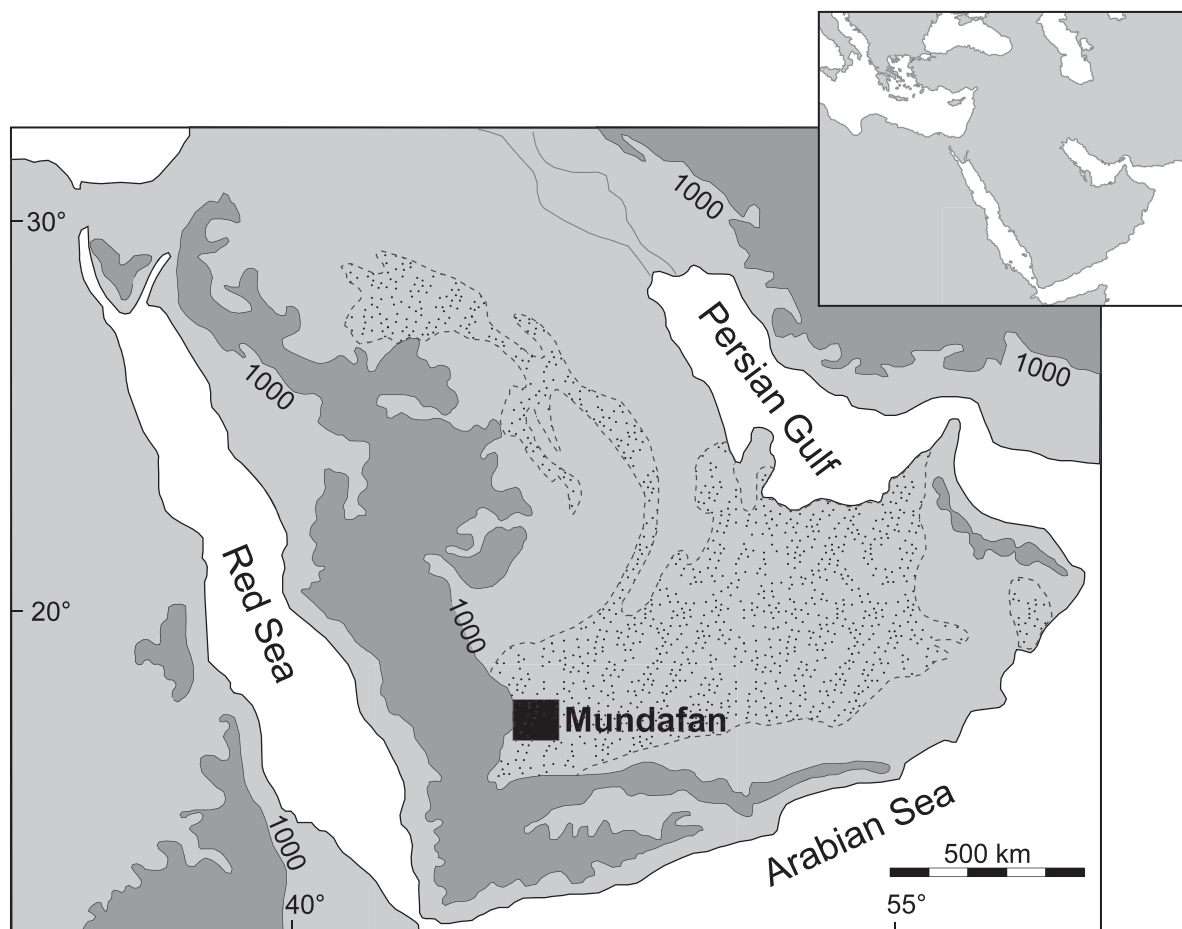[6] Corresponding author. E-mail: giordana.gennari@unifr.ch

FIGURE 1. Simplified relief map of the Arabian Peninsula and surroundings showing the location of Al Mundafan. Dark grey areas are >1000 m in elevation; dotted areas are large areas of sand dunes.

OxCal 3.10 with atmospheric data from Bronk Ramsey (2005).

An additional age for the sand layers underlying Section 8321.1 is based on Optically Stimulated Luminescence (OSL) dating (Table 1). Details on preparation and measurement techniques are described in Wintle and Murray (2006) and Preusser and others (2008). The OSL measurements were performed at the University of Bern using an automated Risoe TL/OSL-DA-20 reader with an attachment for measuring single grains.

MICROPALEONTOLOGY

Although several samples from Section 8321.1 were investigated, only samples A4 and A5 (Fig. 2) contain well-preserved and relatively abundant benthic foraminifera (Table 2; Figs. 4 and 5). These two samples, as well as several others from the same and adjacent sections contain rare to abundant gyrogonites of charophytes ascribed to the genera *Chara* and *Lamprothamnium* (Fig. 6).

FORAMINIFERAL ASSEMBLAGES

Two foraminiferal species were identified in the lowermost lacustrine deposits (samples A4 and A5): *Helenina anderseni* (Warren), which was dominant, and *Trichohyalus aguayoi* (Bermudéz) (Table 2). Both adult and juvenile growth stages were present, with adult forms strongly dominating and representing at least 84% of the species populations. Those juvenile specimens picked from the 32-μm size-fraction that could not be identified at generic level accounted for ~6% of the total assemblage in each sample (Table 2). In each of the adult populations of both *H. anderseni* and *T. aguayoi*, microspheric forms always outnumbered the megalospheric ones. Test abnormalities, mainly deformed chambers and aberrant chamber arrangements, were restricted to *H. anderseni* and accounted for 2–6% of its populations.

MORPHOLOGICAL VARIABILITY AND MORPHOMETRY OF *HELENINA ANDERSENI*

In the studied material, *Helenina anderseni* showed a high degree of morphological variability (Fig. 4). The test outline and shape of the sutures were the most variable features, so we used them to distinguish two extreme morphotypes. Morphotype A has a subcircular profile and the sutures on its spiral side are tangential and deeply incised; sutures on the umbilical side are curved to tangential (Fig. 4.1). Morphotype A closely resembles the holotype. In contrast, morphotype B has an ovate profile and the sutures on both its spiral and umbilical sides are
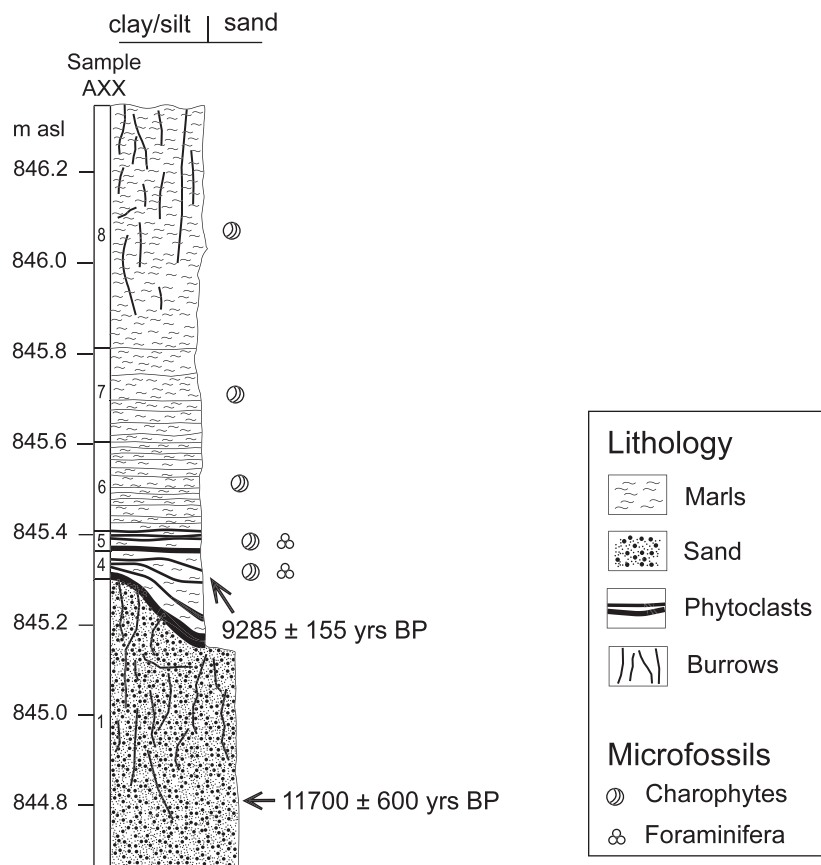
FIGURE 2. Sedimentological profile of outcrop 8321.1 (18°32′43.0″N, 45°21′27.1″E).

straight to slightly curved and deeply incised; its supplementary sutural apertures are generally wider than those of morphotype A (Fig. 4.4–4.6).

A morphometric study was performed to verify the characters that distinguish morphotypes A and B. The morphometric parameters considered were 1) the spiral diameters ratio (D/B), which measures the degree of roundness of the test outline, 2) the Chamber Expansion Index (CEI), which indicates the increase in chamber size in the last whorl, and 3) the Dorsal Chamber View Index (DCVI), which is a measure of the degree of elongation of the penultimate chamber (see Pearson and others, 2001 for equations).

The results of the univariate and multivariate analysis (PCA) are shown in Figures 7 and 8, where they are plotted separately according to whether they have six or seven chambers in the outer whorl (Figs. 7A–C and 8A vs. Figs. 7D–F and 8B). For each group, an equal number of microspheric and megalospheric forms were measured (50 specimens each). Frequency histograms (univariate analysis) for both subsamples have a clear unimodal distribution, showing a continuous transition of the considered morphometric parameters. Results of the PCA are plotted in a PC1-PC2 graph, since the first two components account for
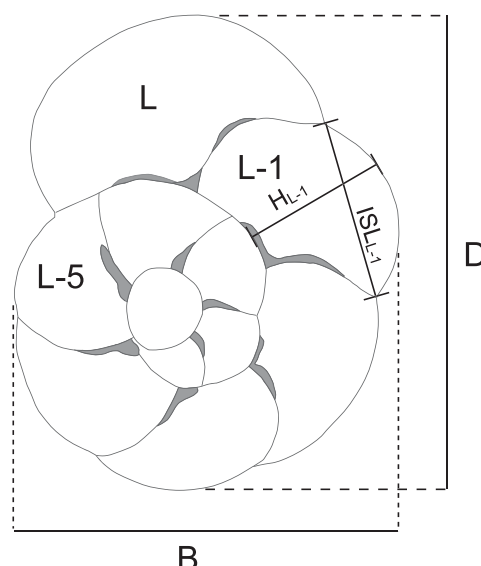

FIGURE 3. Morphometric parameters measured on the dorsal side of *Helenina anderseni*. Last whorl's chambers were numbered from the last one (L) backward to the first one (L-5 in this case). D = greatest spiral diameter; B = spiral diameter perpendicular to D; H = chamber's height; ISL = inter-sutural length.

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TABLE 1. Results of AMS ^{14}C and OSL dating.

Lab code	Outcrop	Sample	Material	Method	n	OD	Age (yr BP)	Calibrated age (yr BP)
ETH-37792	8321.1	A4	Phytoclasts	[14]C	-	-	8300 ± 45	9285 ± 155
ROT-77/160	8321.1	A1	Qtz grains	OSL	24	9.7%	11700 ± 600	

>80% of the variation (Table 3). The PCA plot shows a great morphometric correspondence between specimens attributed to the two identified morphotypes.

SYSTEMATICS AND ECOLOGY OF FORAMINIFERAL SPECIES

Family Heleninidae Loeblich and Tappan, 1987
Genus *Helenina* Saunders, 1961
Helenina anderseni (Warren)
Figures 4.1–4.6, 5.1–5.4

1957 *Pseudoeponides anderseni* Warren, pl. 4, figs. 12–15.
1957 *Helenia anderseni* (Warren), Saunders, p. 374.
1961 *Helenina anderseni* (Warren), Saunders, p. 136, pl. 3, fig. 3.
1996 *Helenina anderseni* (Warren), Culver and others, p. 480, figs. 9.10, 9.11.
1999 *Helenina* sp., Lipps and Langer, pl. 2, figs. 2, 5.
2003 *Helenina anderseni* (Warren), Javaux and Scott, p. 24, figs. 6.3, 6.4.
2005a *Helenina* cf. *H. anderseni* (Warren), Kawagata and others, pl. 2, figs. 8–12.
2005b *Helenina* cf. *H. anderseni* (Warren), Kawagata and others, p. 224, pl. 1, figs. 5–13.

Ecology. This species has been described from estuarine environments, marshes, lagoons, and low-salinity mangrove swamps including those in North America (Culver and Horton, 2005), South America (Steinker and Butcher, 1981; Culver, 1990), the western Pacific (Lipps and Langer, 1999; Kawagata and others, 2005a, 2005b), New Zealand (Gregory, 1973; Hayward and Hollis, 1994; Hayward and others, 1999), New Caledonia and Australia (Debenay and Guillou, 2002), the Red Sea (Halicz and others, 1984), and the Venice lagoon (Serandrei Barbero and others, 2004). Very rarely has it been found in hypersaline lagoons

TABLE 2. Relative abundance (%) of *Helenina anderseni* and *Trichohyalus aguayoi* in total assemblage. For each species, the relative abundance of adults (microspheric and megalospheric forms), juveniles, and abnormal specimens are also indicated. *Juveniles (in 32-μm fraction) not identified at generic level.

Sample	A4	A5
Weight dry sediment (g)	40	30
Total number of counted specimens	3227	2354
Species	Relative abundance (%)	
***Helenina anderseni* in total assemblage**	**93.5**	**87.9**
adults	95.0	94.0
microspheric forms	*62.0*	*59.2*
megalospheric forms	*38.0*	*40.8*
juveniles	5.0	6.0
abnormal specimens	1.9	6.1
***Trichohyalus aguayoi* in total assemblage**	**0.7**	**5.9**
adults	95.5	84.2
microspheric forms	*52.4*	*60.7*
megalospheric forms	*47.6*	*39.3*
juveniles	4.5	15.8
abnormal specimens	-	-
Indet. juveniles* in total assemblage	5.8	6.2

(Debenay and others, 2001). It is purportedly an infaunal species (Culver and Horton, 2005).

Family Trichohyalidae Saidova, 1981
Genus *Trichohyalus* Loeblich and Tappan, 1953
Trichohyalus aguayoi (Bermúdez)
Figures 5.5–5.7

1935 *Discorbis aguayoi* Bermúdez, pl. 15, figs. 10–14.
1950 *Discorbina lacunae* Silvestri, pl. 3, figs. 9, 10.
1991 *Trichohyalus lacunae* (Silvestri), Albani and others, pl. 1, figs. 9, 10.
2004 *Discorinopsis aguayoi* (Bermúdez), Foresi and others, pl. 2, figs. 1–11, pl. 3, figs. 1–12, pl. 4, figs. 1–13.

Remarks. We retain the assignment of this genus to *Trichohyalus* because of its truly calcareous wall texture as opposed to *Discorinopsis*, which is agglutinated with calcareous particles. Foresi and others (2004) placed *T. lacunae* in synonymy with *T. aguayoi* because they concluded that chamber shape is highly variable in this species. Features that they considered as invariant characteristics determined by genetic characters include the numerous chambers in the last whorl, primary and secondary apertures, coarse pores, limbation of the sutures, depressed sutures in the last whorl, and test contortion. Although taxonomy is beyond the scope of this paper, we note that *T. aguayoi* was present in our material as two quite distinct forms that differ in chamber shape in umbilical view. One is *T. aguayoi* sensu stricto (Fig. 5.5) with slightly curved sutures, while the other has the *T. lacunae* morphology (Figs. 5.6, 5.7) with sigmoid sutures resulting from the overlapping of chambers in the last whorl.

Ecology. This species can tolerate a wide range of salinities. Most often, it has been reported in fresh to brackish waters (Wantland, 1975; Javaux and Scott, 2003) and mangrove swamps (Steinker and Butcher, 1981; Javaux and Scott, 2003). It has also been recorded in the Montecatini thermal pool and Orbetello lagoon (Zampi and others, 1996; Foresi and others, 2004). Occurrences in hypersaline lagoons are rare (Debenay and others, 2001).

DISCUSSION

PALEOENVIRONMENTAL INTERPRETATION

Regional climate records (McClure, 1976; Lezine and others, 1998; Burns and others, 2001; Preusser and others, 2002; Radies and others, 2005; Fleitmann and others, 2007) indicate an early Holocene wet phase in southern Arabia. In particular, speleothems from Oman provide a record of pluvial intervals beween 10,500–6,000 yr BP (Fleitmann and others, 2003a, 2003b, 2007). The radiocarbon age of 9285±155 cal. yr BP we obtained from sample A4 phytoclasts falls within this interval (Table 1). As a result of increased monsoon precipitation at that time, the Al
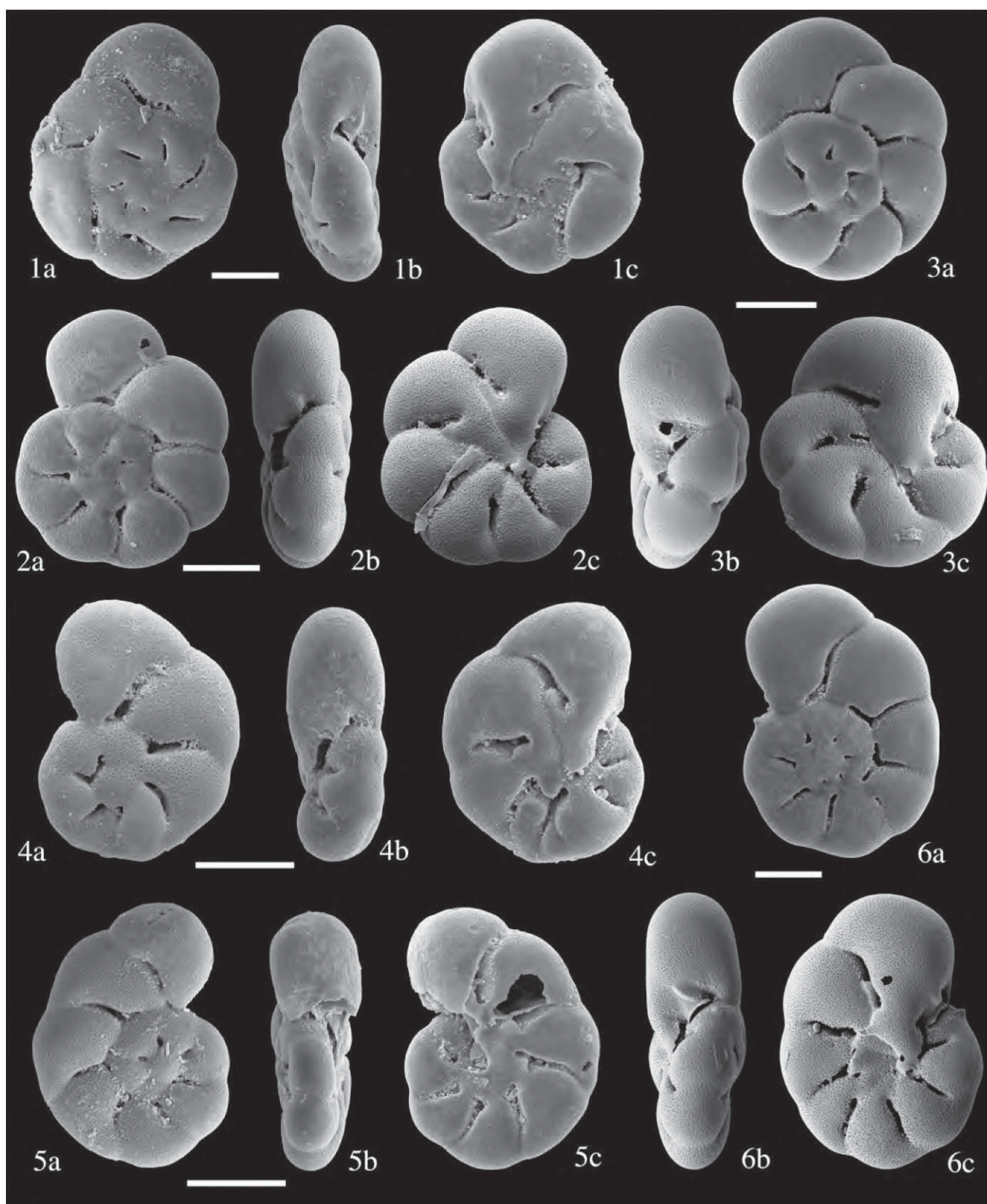
FIGURE 4. **1** *Helenina anderseni*, specimen strongly resembling the holotype, morphotype A: a, spiral view; b, side view; c, umbilical view. **2, 3** *H. anderseni*, intermediate morphotype: a, spiral view; b, side view; c, umbilical view. **4–6** *H. anderseni*, morphotype B: a, spiral view; b, side view; c, umbilical view. Scale bars = 100 μm.
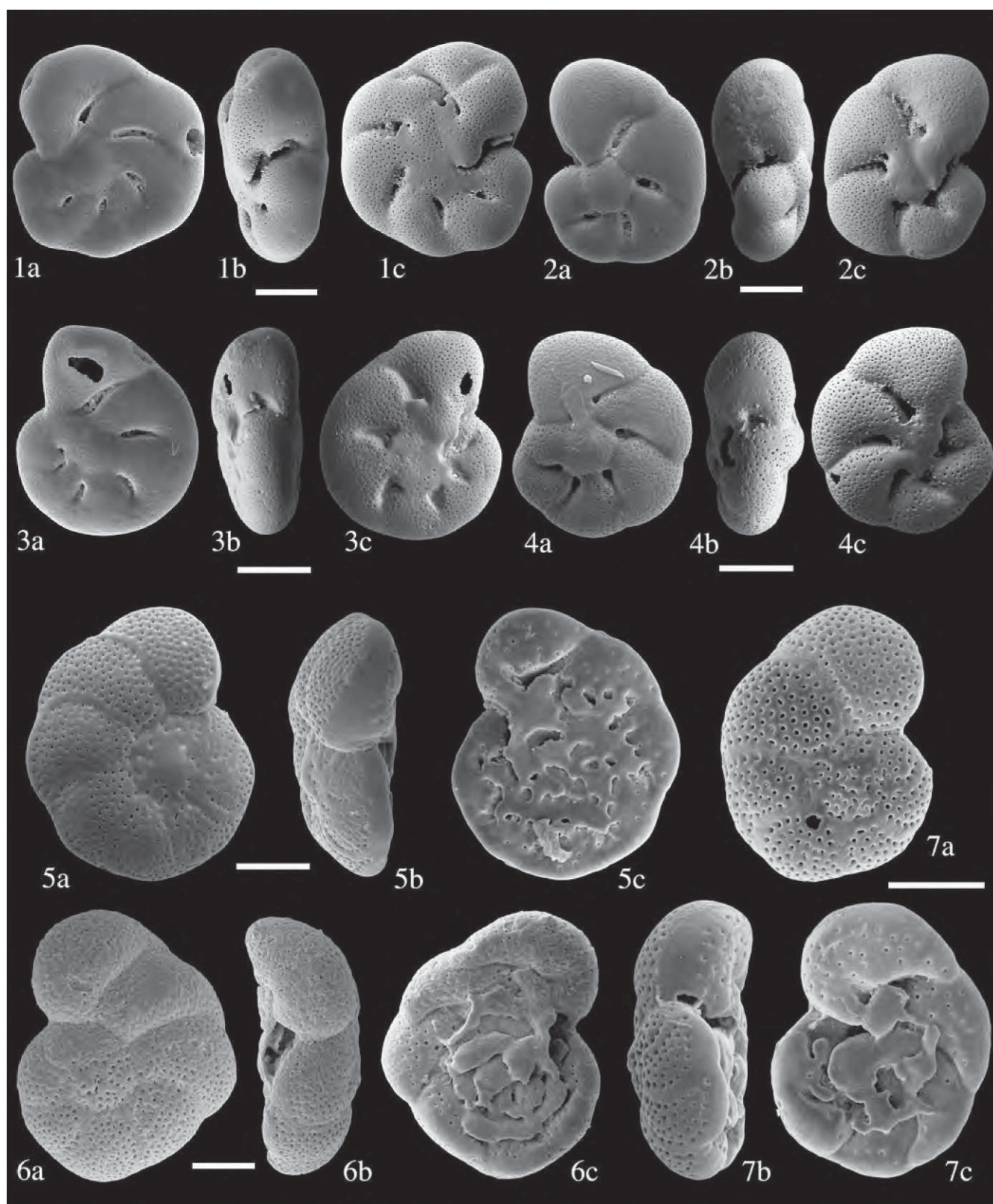
FIGURE 5. **1–4** *Helenina anderseni*, juvenile specimens: a, spiral view; b, side view; c, umbilical view. **5** *Trichohyalus aguayoi* (sensu stricto): a, spiral view; b, side view; c, umbilical view. **6, 7** *T. aguayoi* (*T. lacunae*-type): a, spiral view; b, side view; c, umbilical view. Scale bars 1–4 = 50 μm, 5–7 = 100 μm.
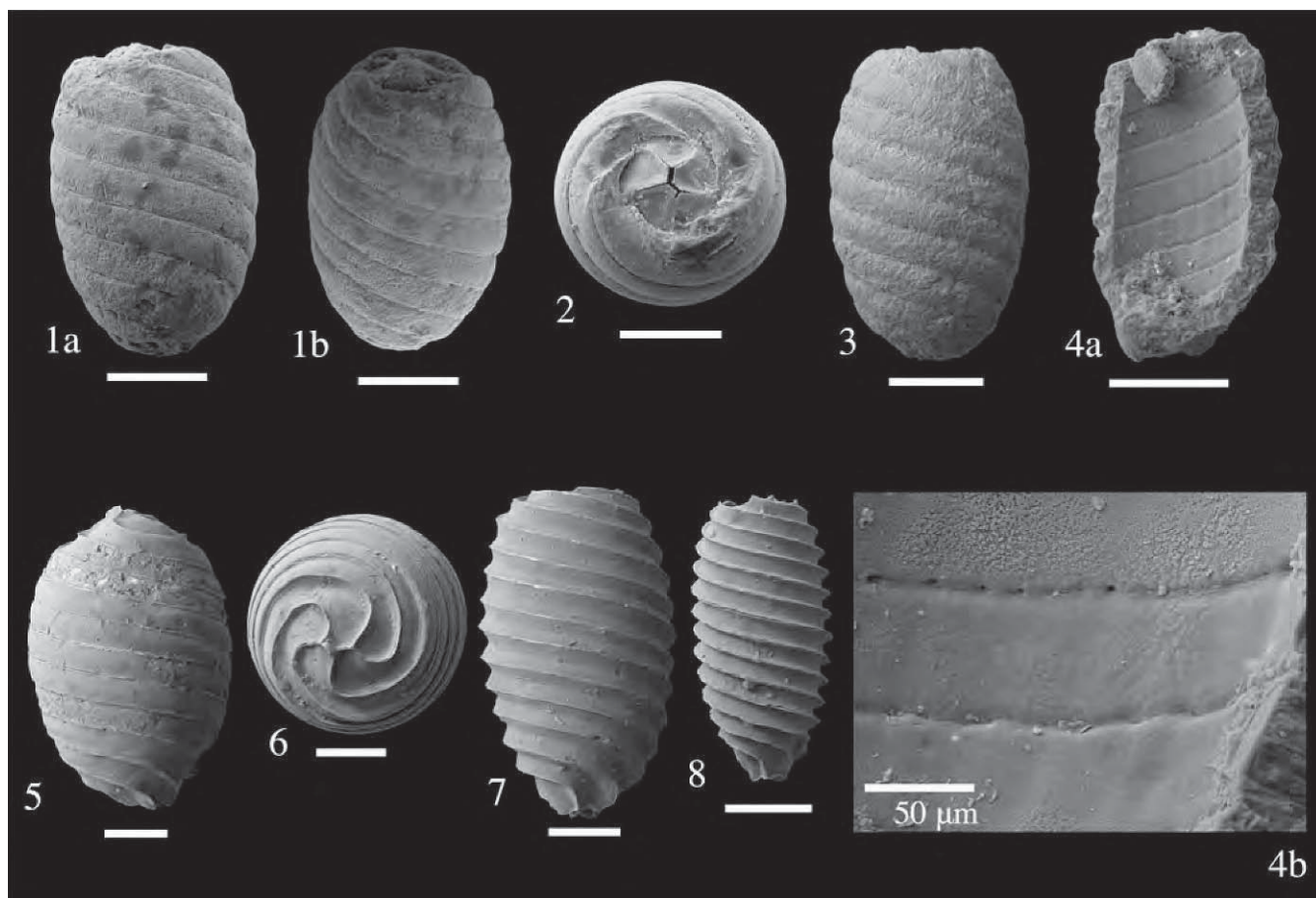
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FIGURE 6. **1** *Lamprothamnium* sp.: a, lateral view; b, oblique lateral view. **2** apical view; **3** *Lamprothamnium* sp., lateral view. **4** *Lamprothamnium* sp.: a, internal view; b, internal view: undulated intercellar sutures. **5–8** *Chara* sp. (?*Ch. globularis* var. *aspera*): 5, regular morphotype, lateral view; 6, regular morphotype, apical view; 7, large elongate morphotype, lateral view; 8, small elongate morphotype, lateral view. Scale bars = 200 μm, unless otherwise specified.

Mundafan depression, presently occupied by a sabkha, was a large paleolake of ~15 km². Enhanced wadi flow into the depression and possibly groundwater infiltration, produced a lake with temporarily brackish conditions in which foraminifera could thrive.

This investigation found adults and juveniles in association for both *H. anderseni* and *T. aguayoi*. The presence of both growth stages indicates that a population is reproducing and is a good indication that the environment is favorable to the species (Wennrich and others, 2007). In our study, the adults were always strongly dominant (Table 2), which suggests that the lake conditions were sufficiently stable to allow juveniles to reach maturity (Almogi-Labin and others, 1992).

The adult populations of *H. anderseni* and *T. aguayoi* were characterized by a preponderance of microspheric tests (i.e., the main form of reproduction was sexual). This is peculiar because most natural populations of benthic foraminifera are predominantly asexually produced megalospheric tests (see Alve and Goldstein, 2003 and references therein). Alve and Goldstein (2003) proposed that an unusual abundance of microspheric forms may be due to the different dispersal potentials of microspheric versus megalospheric proloculi. Such a dimorphic ratio has also

been linked to unfavorable or highly variable environmental conditions (Boltovskoy and Wright, 1976; Hallock, 1985) and to seasonality (Alve and Goldstein, 2003). In particular, the presence of abundant microspheric individuals in unstable environments may result in higher genetic variability and different ecological preferences (Alve and Goldstein, 2003). Morphology, which for some benthic foraminifera is also related to environmental preference, may also be affected. The presence of morphotypes in *H. anderseni* and possibly in *T. aguayoi* (see Figs. 5.5–5.7) suggests that the hypothesis of unstable environmental conditions or seasonality cannot be ruled out. Further studies on the ecology and biology of *H. anderseni* are needed, including its poorly understood reproductive cycle.

Alve (1991) noted that some degree of environmental stress is suggested by populations with >1% abnormal tests. In our study, deformed *H. anderseni* ranged 2–6%, below the 10–20% values reported from highly stressed paralic environments (see review in Geslin and others, 2002).

Charophytes present throughout the studied section provide additional paleoenvironmental information. The family Characeae is represented by six living genera (*Chara*, *Lamprothamnium*, *Lychnothamnus*, *Nitellopsis*, *Nitella*, and
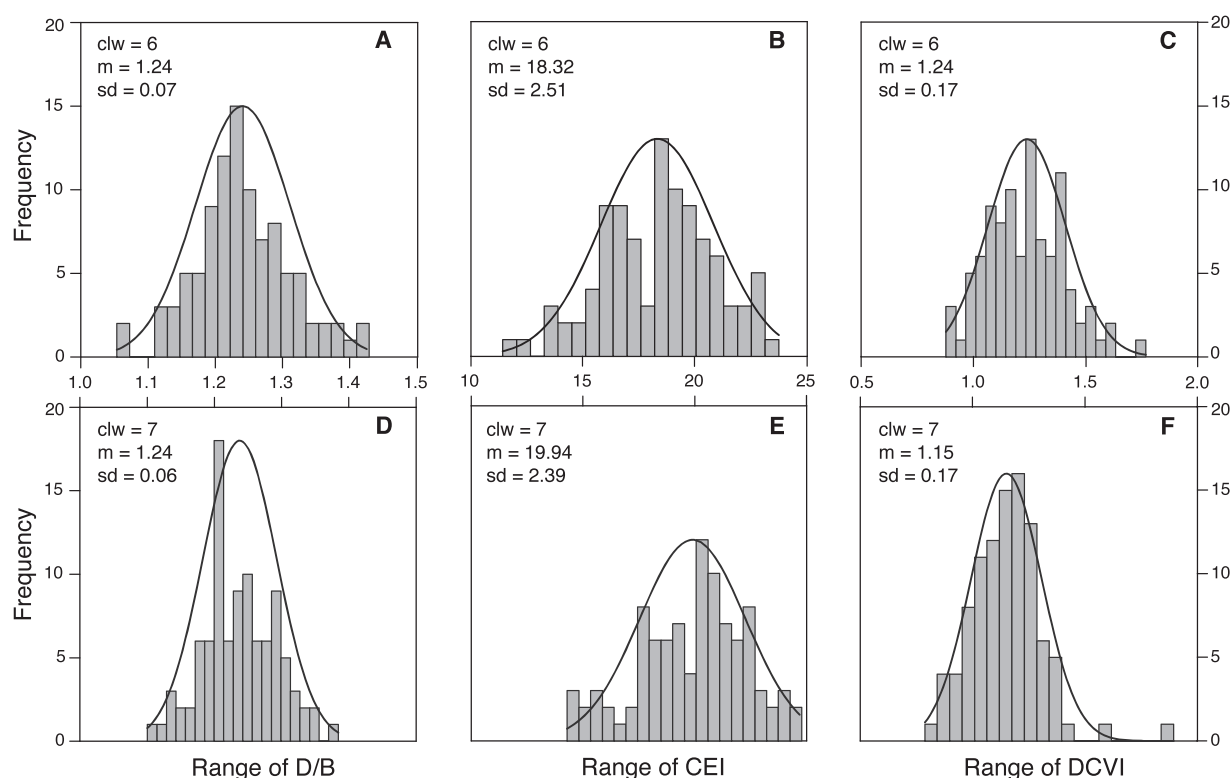
FIGURE 7. Morphometric data measured on *Helenina anderseni* plotted as standard histograms (frequency). Normal Curve Shape is shown as a solid line. D/B = spiral diameters ratio; CEI = Chamber Expansion Index; DCVI = Dorsal Chamber View Index; clw = number of chambers in last whorl; m = mean; sd = standard deviation (Pearson and others, 2001).

Tolypella), determined at the specific level on the basis of the morphology of both vegetative parts and reproductive organs (gyrogonites). Since only gyrogonites have been preserved, their taxonomic attributions, and consequently their ecological value, are restricted. There are ~400 charophyte species in modern flora, six strictly brackish, ten species brackish to freshwater, and the rest freshwater (Corillion, 1972). Thus, fossil charophytes are typically assumed to be freshwater indicators. The charophyte assemblage of Al Mundafan is represented mostly by forms very similar to *Chara globularis* var. *aspera* (Figs. 6.6–6.8) with very elongated morphotypes characteristic of slightly brackish environments (salinity ~2‰; Soulie-Märsche, 1989). Levels A7, A8, and possibly A6 yielded rare specimens ascribed to *Lamprothamnium* (Figs. 6.1–6.5), which is one of the most typical brackish genera (Corillion, 1972). Large amounts of fragile gyrogonites are strong indication that these fossil floras are in situ. This implies that deposition occurred in water depths shallower than six meters, which is the limit for charophytes to fructify (Becker and others, 2002; Picot, 2003).

TRANSPORTATION MECHANISM AND PROVENANCE OF BENTHIC FORAMINIFERA

The presence of benthic foraminifera in inland saline or brackish waters is rare, but cannot be considered unusual (Resig, 1974). Most of their fossil record has probably been erased primarily because they have thin shells that are susceptible to dissolution (e.g., Jonasson and Patterson, 1992; Culver and Horton, 2005).

As reported by Resig (1974), three hypotheses have been proposed to explain the occurrence of these forms in inland waters that were never connected to the sea: endemism (Daday, 1884), marine reliction (Brodsky, 1928; Gauthier-Lièvre, 1935), and transport via avian or human means (Arnal, 1954; Almogi-Labin and others, 1992; Patterson and others, 1997).

Species diversity in comparable environments varies considerably. In the Hawaiian Salt Lake, Resig (1974) recorded 41 species, including calcareous and agglutinated forms. In stark contrast, Almogi-Labin and others (1992) reported monospecific assemblages of *Ammonia tepida* in the Dead Sea, and Wennrich and others (2007) found only two species in two inland brackish lakes (Salziger See and Suesser See) in central Germany. Moderate numbers of species were documented by Abu-Zied and others (2007), with 15 calcareous species from Lake Qarun (Egypt). In the meromictic Mecherchar Jellyfish Lake in Palau, Lipps and Langer (1999) identified 15 species (agglutinated and calcareous) in surface sediments, while Kawagata and others (2005b) observed ten calcareous species in a sediment core retrieved from the same lake, with only two species (*Helenina* cf. *H. anderseni* and *Bolivina striatula*) common to the two studies. All of these studies discussed the provenance of their benthic foraminiferal assemblages from nearby or relatively far marine coastal environments when there were temporary connections with the sea or dry
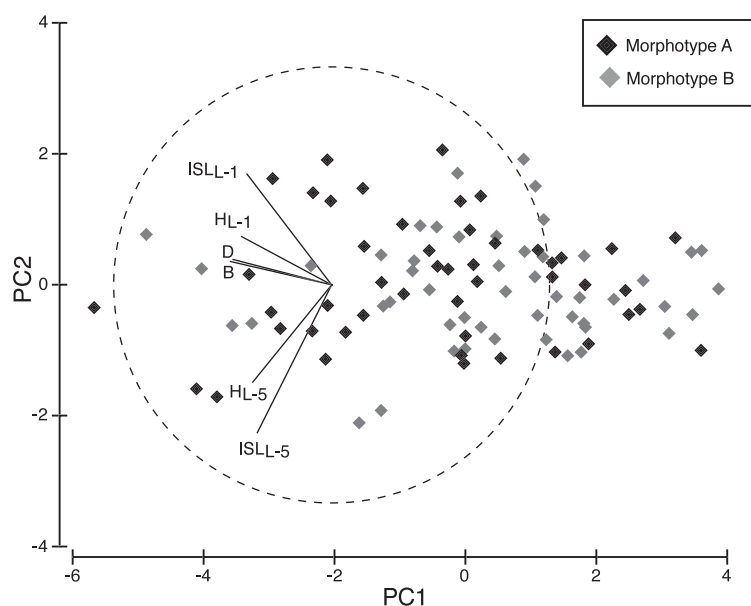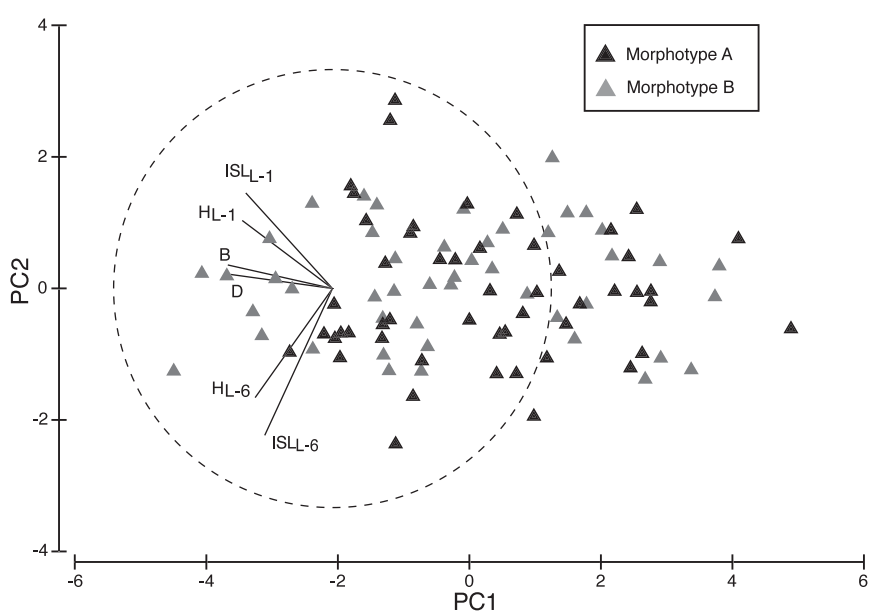
FIGURE 8.   Principal component analysis applied to morphometric measurements of *Helenina anderseni*. A = specimens with six chambers in the last whorl; B = specimens with seven chambers in the last whorl. D = greatest spiral diameter; B = spiral diameter perpendicular to D; H = chamber's height; ISL = inter-sutural length.

intervals characterized by increasing salinity. In our materials, benthic foraminifera are represented by two genera (*Helenina* and *Trichohyalus*) characteristic of mangrove swamps, salt marshes, and lagoons (e.g., Tufesco, 1969; Javaux and Scott, 2003; Culver and Horton, 2005). To explain the presence of benthic foraminifera in the Mundafan region, we can exclude endemism and marine reliction, as it was never connected to the sea during the Quaternary. The most likely explanation for their occurrence in the Mundafan paleolake is avian-mediation, which

Patterson and others (1997) suggested being a much more important foraminiferal dispersal mechanism than usually realized. Although there is extensive literature on the mangrove swamps, salt marshes, and lagoons flanking the Red Sea (e.g., Mohamed, 1984; Saleh, 2007), little is known about their foraminifera. Because these transitional environments are suitable habitats for *H. anderseni* and *T. aguayoi*, it is reasonable to assume that those along the Egyptian-Sudanese and Saudi Arabian coasts of the Red Sea most likely are the provenance of the *H. anderseni* and

TABLE 3. Principal components analysis: eigenvalues and eigenvectors (coefficients in the linear combinations of variables making up the principal components) for the six analyzed variables. *Normalized before PCA analysis.

No. ch.	PC	Eigenvalues	% Variation	Cum. % Variation	Variable	PC1	PC2	PC3	PC4	PC5	PC6
6	1	4.17	69.4	69.4	D	−0.455	0.118	0.016	−0.048	0.715	0.515
	2	0.756	12.6	82.0	B	−0.467	0.108	−0.039	−0.105	0.274	−0.826
	3	0.504	8.4	90.4	H_{L-1}	−0.416	0.223	−0.473	−0.541	−0.470	0.199
	4	0.284	4.7	95.2	ISL_{L-1}	−0.390	0.511	0.250	0.627	−0.353	0.079
	5	0.198	3.3	98.4	H_{L-5}	−0.364	−0.448	0.718	−0.294	−0.244	0.070
	6	9.34E-2	1.6	100	ISL_{L-5}	−0.342	−0.680	−0.443	0.462	−0.091	0.036
7	1	3.93	65.5	65.5	D	−0.473	0.065	−0.028	0.013	−0.576	−0.663
	2	0.922	15.4	80.8	B	−0.478	0.108	−0.046	0.022	−0.450	0.745
	3	0.478	8.0	88.8	H_{L-1}	−0.412	0.311	0.255	0.690	0.436	−0.051
	4	0.335	5.6	94.4	ISL_{L-1}	−0.396	0.437	−0.022	−0.691	0.415	−0.047
	5	0.275	4.6	99.0	H_{L-6}	−0.353	−0.498	−0.728	0.092	0.297	−0.023
	6	6.07E-2	1.0	100	ISL_{L-6}	−0.310	−0.670	0.634	−0.194	0.123	0.017

T. aguayoi specimens that pioneered the Mundafan paleolake. The absence of other taxa in the paleolake may relate to the low diversity of the foraminiferal faunas in mangrove swamps (e.g., Culver, 1990). Therefore, we postulate that avian-mediated transport from the margins of the Red Sea introduced the two foraminiferal species that colonized the Mundafan brackish paleolake.

CONCLUSIONS

The presence of two benthic foraminiferal species, *Helenina anderseni* and *Trichohyalus aguayoi* and charophytes in lacustrine sediments of the Al Mundafan section are linked to the continental pluvial periods that occurred in the area 10,500–6,000 yr BP (Fleitmann and others, 2003a, 2003b, 2007). Enhanced precipitation created a freshwater lake with temporarily brackish conditions. This is corroborated by the presence of reproducing populations of foraminifera and in situ brackish charophytes. Because the Al Mundafan paleo-lake was never connected to the sea, the foraminifera were most likely introduced by avian-mediated transport from mangrove swamps along the coasts of the Red Sea.

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APPENDIX 1

Taxonomic notes on *Helenina anderseni* (Warren).

Helenina anderseni, morphotype A. The test of this type is calcareous, finely perforate, and generally small to very small in size. The trochospire is low and consists of about two whorls. Six to eight chambers gradually increasing in size as added are present in the last whorl. On the umbilical side successive chambers extend toward the umbilicus producing umbilical flaps that conceal the umbilicus. The profile is subcircular and the peripheral margin is rounded. The sutures on the spiral side are tangential and deeply incised. On the umbilical side, sutures are curved to tangential. Elongated and slit-like supplementary apertures are present along the sutures on both sides. The primary aperture is a very umbilical-extraumbilical low arch at the base of the last chamber. The two small openings at the base of the apertural face as described in Warren (1957) are probably the opening along the insertion of the lobe like extension of the last chamber on the umbilical side.

Helenina anderseni, morphotype B. The test of this type is calcareous, finely to moderately coarsely perforate, small to very small in size. The trochospire is low and consists of two whorls. Six to eight chambers are present in the last whorl and increase rapidly in size as added. The profile is oval and the peripheral margin is rounded. The sutures on the spiral and umbilical sides are straight to slightly curved and deeply incised. Elongated and wide supplementary apertures are present along the sutures on both sides. The primary aperture is a very umbilical-extraumbilical low arch at the base of the last chamber. A flap-like prolongation of the chambers in the last whorl extends on the umbilical side and conceals the umbilicus.

APPENDIX 2

Morphometric measurements of *Helenina anderseni*.

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