



A humid early Holocene in Yemen interpreted from palaeoecology and taxonomy of freshwater ostracods

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Abstract. Lake or marsh sediments in the Qa'a Jahran–Dhamār area indicate a period of higher moisture availability in the early Holocene of the highlands of Yemen. Forty-two marl–peat sediment samples from eight stratigraphic sections of that area have been collected and are examined for the first time for their ostracod associations. Eight species belonging to seven genera and four families are reported. Their ecological tolerances and preferences are used to investigate the climatic and environmental changes in the early to mid-Holocene. Our data are compared and correlated with previous archaeological results, particularly from the region of Qa'a Jahran (Dhamār) in the vicinity of the village of Beyt Nahmi. We conclude that the wettest period of the Holocene was from about 7900 to 7400 cal yr BP, when northwards incursion of the Indian Ocean Monsoon caused intensified monsoon precipitation over southern Arabia.

1 Introduction

Multidisciplinary research including geology, geomorphology, ecology, archaeology and anthropology in different parts of the world has addressed Holocene climatic changes and the development of linked geomorphologic features such as lakes (e.g. Pachur and Hoelzmann, 1991; de Menocal et al., 2000; Mischke, 2001; Fleitmann and Matter, 2009; Broxton et al., 2011; Mischke et al., 2012). Some of these studies reported the distribution and development of Holocene palaeolakes in the Arabian Peninsula, where water availability is a challenge for the future (e.g. Acres, 1982; Wilkinson, 1997; Lézine et al., 1998; Fleitmann et al., 2003; Davies, 2006; Parker et al., 2006; Rosenberg et al., 2011; Engel et al., 2012; Enzel et al., 2015). Understanding changes in the moisture availability of the past is a prerequisite for a sustainable management of water resources. The few previous surveys which have been done in Yemen, to review the relationship between the early human settlements and Holocene climatic changes, recognized lacustrine deposits and extensive scatters of shells of freshwater molluscs in the plain of Qa'a Jahran at very high elevations (2400 m above sea

level) and some deserted districts in Ramlat as-Sab'atayn and Wadi Juba in Marib (Acres, 1982; Wilkinson, 1997; Lézine et al., 1998; Davies, 2006). These studies illustrate that the Yemeni inland desert and highlands experienced strong climatic changes leading to the development and disappearance of freshwater lakes. The presence of dried palaeolakes in the Dhamār highlands is one of the striking geomorphological features in Yemen; however, little is known of their history and distribution. The deposits that are exposed in the quarries and shallow dry wells dug by local people can be considered excellent evidence for the formation of such lakes in tectonic depressions. The fluctuations of both moisture and aridity during the Holocene are the major factors affecting the development of lakes in the Arabian Peninsula (Mayewski et al., 2004).

Ostracoda are small crustaceans characterized by having a bivalve shell hinged along the dorsal margin. Most species are of microscopic size. Their shell is composed of low-magnesium calcite, may be smooth or ornamented, and fossilizes well. The rich ostracod fossil record is not only due to the fossils' ease of preservation but also due to their

high adaptability to different environmental conditions. Ostracods are sensitive to fluctuations of ecological parameters mainly at the water–sediment interface; these parameters can be temperature, salinity, pH, oxygen, turbulence or trophic level amongst other factors. The record of these variations can be observed at several levels: abundance, diversity, species composition and morphological variability (Carbonel et al., 1988). Furthermore, shell chemistry, i.e. stable isotope and trace element signatures, provides additional information about past environmental conditions.

Only a few papers have been published on freshwater ostracods of Yemen. Malz (1976) discussed the changes in carapace morphology and the taxonomic problems of the Holocene genera *Heterocypris* Sars and *Cyprinotus* Brady and their fossil relative *Cheikella* Sohn and Morris, 1963 described from Cenozoic freshwater deposits in Saudi Arabia. His study also includes some specimens from Yemen. The work by Dumont et al. (1986) focused on the taxonomy and distribution of Cladocera, Copepoda and Ostracoda from freshwaters of South Yemen. Three valves of *Cyprinotus rostrata* Lowndes have been discovered by Munef Mohammed (unpublished data) from Anthropocene dry mud of the city of Aden. Mazzini and Sardella (2004) found some freshwater ostracods during their study of the Quaternary of Socotra Island. Mohammed et al. (2013) studied the taxonomy and distribution of Holocene freshwater ostracods from the northern part of Socotra Island. Taking into consideration this poor knowledge of Quaternary Ostracoda from Yemen, our study contributes to the record of Ostracoda biodiversity.

The present study aims to investigate the taxonomy and palaeoecology of freshwater ostracods extracted from marl–peat sediments of the Holocene palaeolake deposits of the Qa'a Jahran–Dhamār highlands. It will provide a contribution to the knowledge of climate change during the Holocene.

2 Study area

Yemen is situated at the south-western corner of the Arabian Peninsula framed by the Gulf of Aden and the Red Sea. Four main physiographic provinces can be recognized: the coastal plain province, the high volcanic mountains province, the Hadhramaut–Mahara Plateau province and the desert terrain province (Rub Al-Khali). The study area is an inland intermountain plain within the high volcanic mountains province (Al-Rawi, 2008). This province is characterized by the occurrence of Cenozoic (Yemen trap series) and Quaternary (Yemen volcanic series) volcanoes. The main volcanic activity in the study area is related to the Dhamār–Rada volcanic field, an extensively faulted and fractured graben and half graben area, probably related to the Red Sea rifting. The late Cenozoic and Quaternary volcanic activities (about 5 Ma ago) were confined to the area around Dhamār (Geukens, 1966; Mattash et al., 2013) and are represented in the study area by the volcanic mountains of Isbil and Al-Lisi. Archae-

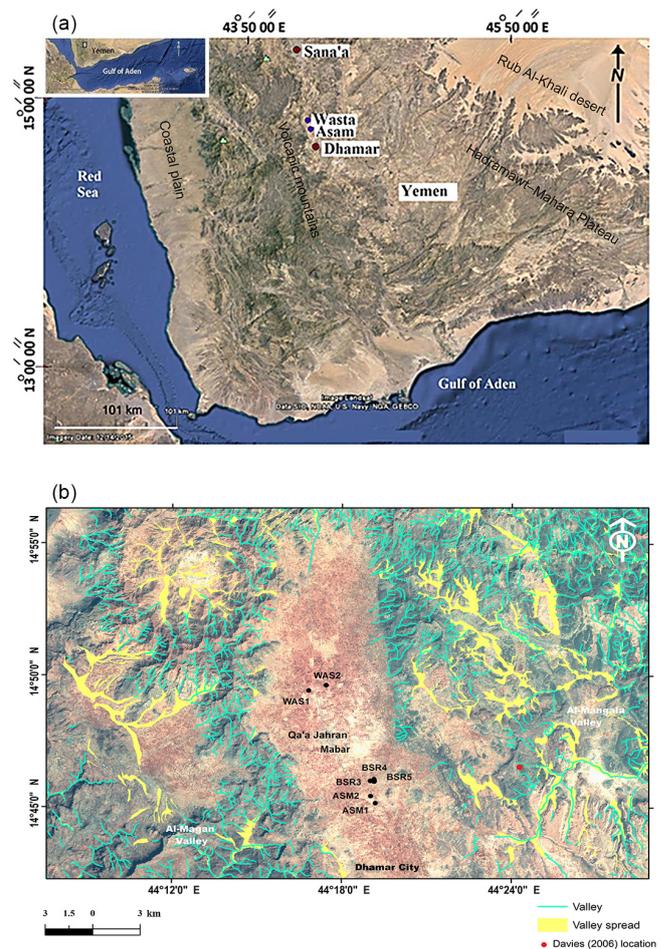


Figure 1. Study area in Yemen (a) and studied sections on a Landsat ATM + image of Qa'a Jahran (b).

ological and historical studies support the record of continuous Quaternary volcanic activity almost to the present day. These studies provide information on the volcanic history of the region and its effects on human populations, e.g. through the exploitation of obsidian sources in the past (Khalidi et al., 2010).

The NW–SE-oriented Qa'a Jahran plain (Fig. 1) is a semi flat area surrounded by high plateaus rising approximately 500+ m (Davies, 2006). It is situated in a graben trough related to the tectonic regime of the opening Red Sea. Quaternary alluvium and lake deposits varying in thickness were deposited on the top of this plain (Davies, 2006). Runoff channels from upslope and intermittent valleys which run along the tectonic zones are mostly dry stream beds and only flood during the high rainy seasons. The region is a semi-arid steppe with annual rainfall less than 300 mm. It receives limited moisture twice yearly in the form of winter north-westerly circulation and summer monsoonal rains (Parker et al., 2006; Davies, 2006).

Table 1. Sampled sections with geographical and sediment data.

Stratigraphic columns	Location	Latitude	Longitude	Sediments
ASM1	Asam	14°45'10.00" N	44°19'12.00" E	Peat–marl, gastropods, ostracods, shell debris and rock fragments
ASM2	Asam	14°45'26.00" N	44°19'2.00" E	Peat–marl, gastropods, debris of ostracod shells and rocks
WAS1	Wasta	14°49'26.00" N	44°16'50.00" E	Peat–marl, few gastropods, debris of ostracod shells and rocks.
WAS2	Wasta	14°49'38.00" N	44°17'27.00" E	Peat–marl, gastropods, ostracods, shell and rock debris
WAS2a	Wasta	14°49'38.00" N	44°17'27.00" E	Peat–marl, gastropods, ostracods, shell and rock debris
BSR3	Beyt Rashed	14°46'0.48" N	44°19'0.84" E	Peat–marl, debris of ostracod shells and rocks
BSR4	Beyt Rashed	14°46'4.32" N	44°19'9.18" E	Peat–marl, ostracods, shell and rock debris
BSR5	Beyt Rashed	14°46'0.004" N	44°19'9.18" E	Peat–marl, fragments of ostracod shells and rocks

Wilkinson (1997) and Davies (2006), in their investigations of the Holocene lacustrine deposits of the Dhamār highlands, reported that these semi-arid valleys responded to past changes in atmospheric circulation by the rapid development of lakes and marshes during wet times and the expansion of soils during drier phases. They deduced that the alternating development of highland lakes and soils resulted from the shifts in Holocene palaeoclimate due to fluctuations in the Indian Ocean Monsoon between moist and dry phases.

3 Material and methods

Two field trips were made to the Qa'a Jahran–Dhamār area during November 2013 and March 2014 to collect the material used in the current study. Grey to dark grey marl layers were traced laterally through eight exposed sections in the northern part of the basin of Qa'a Jahran. The layers under investigation show similarity in lithology but differ in thickness. They are overlain by a modern agricultural horizon of fine sandy silt loam and underlain by light grey marl deposits.

Forty-three marl samples of variable thickness were collected from those eight sections from eight shallow wells dug by villagers (Figs. S1 and S2 in the Supplement). They were mostly taken at intervals of 10–20 cm focusing on the darker layers. The sampling locations along with geographical coordinates and the deposit descriptions are given in Table 1. All the samples were subject to standard micropalaeontological techniques (Moore, 1961). A unit weight of 250 g (ca. 5 cm thick) of fresh unweathered sediment sample was always taken. Samples were covered in a pan with 29% hydrogen peroxide to separate the mud and clay from the shells. After allowing a sample to soak for about 12 h, water was added and boiled. The samples were washed with running tap water over a 200 mesh sieve (opening of 0.074 mm) to remove mud-size sediment. About 10 to 20 g of washed residue of sandy sediment, shells and rock fragments were extracted from each sample. The ostracods were collected by using a 00 brush under a stereomicroscope, placed into micro-slides and identified. No ostracods with complete soft parts were found. Representatives of the recorded ostracods

were sent to Hamburg, Jena and Rome. Scanning electron microscope (SEM) photos were taken at the Zoological Institute and Museum at Hamburg University, the Institute of Zoology at Jena University and the Istituto di Geologia Ambientale e Geoingegneria Roma. Specimens of all ostracod species were deposited in the Department of Earth and Environmental Sciences, Faculty of Science, Sanaa University. All measurements are given in millimetres. Statistical analysis using the program package PAST (Hammer et al., 2001) was done to support the interpretation of the palaeoenvironments. The ostracods collected in this study are in the collections of the first author except for the depicted material that is deposited in Hamburg, Jena and Rome.

4 Systematic palaeontology

The systematics are based on Moore (1961), Hartmann and Puri (1974), Meisch (2000), and Karanovic (2012). References within the synonymy lists are selected based on taxonomic, biogeographic and ecological significance. The abbreviations used are as follows: RV – right valve; LV – left valve; C – carapace; V – valve; L – length; H – height; ASM – Asam sections; WAS – Wasta sections; BSR – Beyt Rashed sections.

Family **Cyprididae** Baird, 1845

Subfamily **Cyprinotinae** Bronstein, 1947

Genus *Heterocypris* Claus, 1892

Heterocypris salina (Brady, 1868)

(Plate 1, figs. 1–3)

*1868 *Cypris salina* Brady: 368, pl. 28, figs. 8–13.

1980 *Hemicypris posterotruncata* Bate; McClure & Swain: pl. 2, fig. 6.

1996 *Heterocypris salina* (Brady); Schöning: 41–42, figs. 1–4, 7–9.

2000 *Heterocypris salina* (Brady); Meisch: 354, fig. 148A–G.

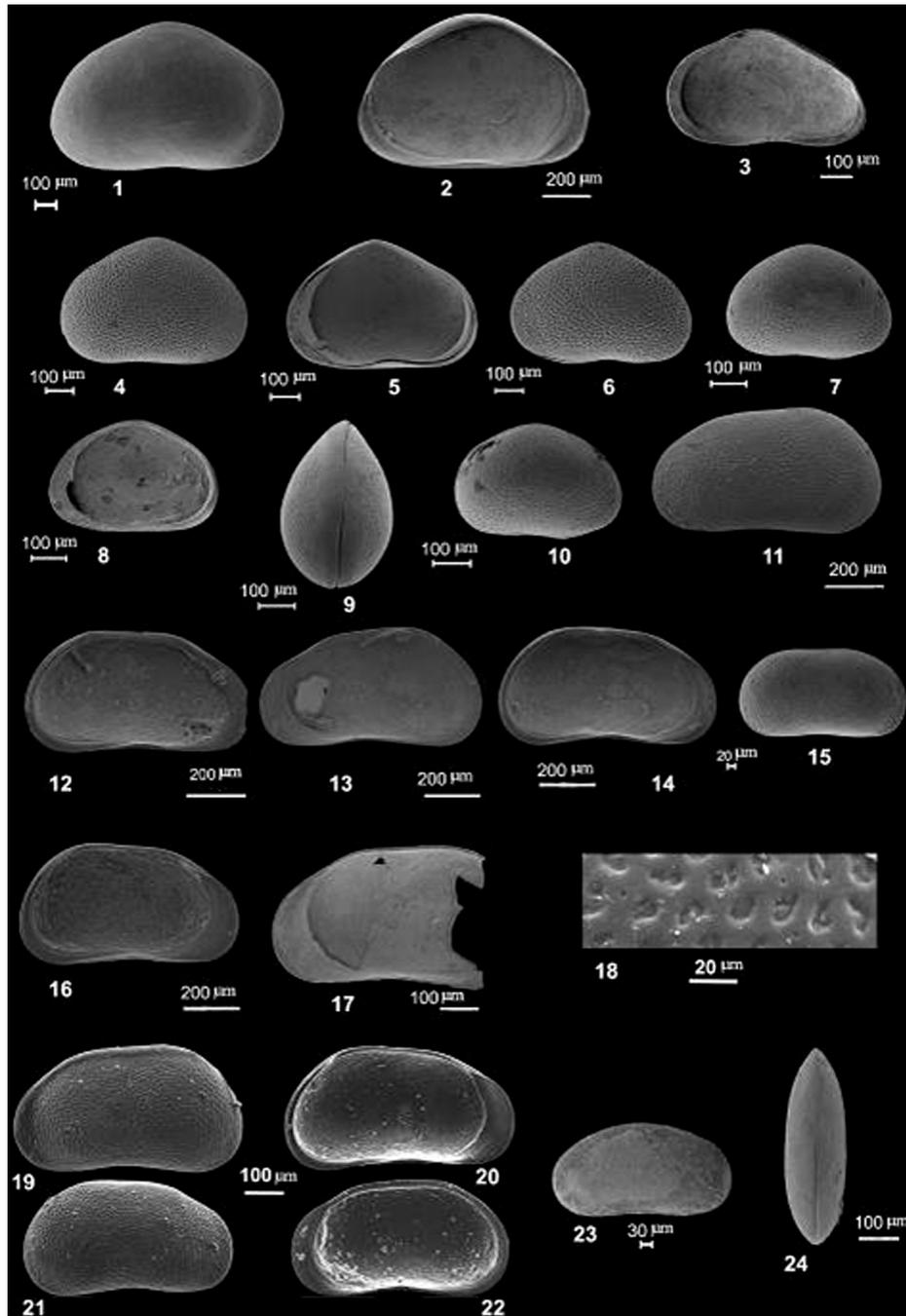


Plate 1. (1–3) *Heterocypris salina* (Brady, 1868): (1) RV, external lateral view, section ASM1, sample 1; (2) LV, internal lateral view, section WAS2a, sample 2; (3) Juv., RV, internal lateral view, section ASM1, sample 1. (4–6) *Sarscypridopsis aculeata* (Costa, 1847): (4) LV, external, lateral view, section ASM1, sample 1; (5) RV, internal, lateral view, section ASM1, sample 1; (6) LV, external, lateral view, section ASM1, sample 2. (7–10) *Cypridopsis concolor* Daday, 1900: (7) RV, external, lateral view, section ASM1, sample 2; (8) RV, internal, lateral view, section ASM1, sample 1; (9) Carapace, dorsal view, section ASM1, sample 1; (10) RV, external, lateral view, section ASM1, sample 1. (11–22) *Pseudocandona* cf. *albicans* (Brady, 1864): (11) LV, external, lateral view, section WAS2, sample 2; (12) LV, internal, lateral view, section WAS2, sample 2; (13) RV, internal, lateral view, section WAS2a, sample 2; (14) LV, internal, lateral view, section WAS2, sample 2; (15) RV, juv., external, lateral view, section ASM1, sample 1; (16) LV, internal, lateral view, section WAS2, sample 2; (17) RV, internal, lateral view, section WAS2, sample 2; (18) Detail of surface ornamentation, RV, section WAS2, sample 2; (19) LV, external, lateral view, WAS2, sample 2; (20) LV, internal, lateral view, section WAS2, sample 1; (21) Juv., RV, external, lateral view, section WAS2, sample 2; (22) Juv., RV, internal, lateral view, section WAS2, sample 2. (23–24) *Fabaeformiscandona* cf. *breuili* (Paris, 1920): (23) Carapace, RV, external lateral view, section WAS2a, sample 2; (24) Carapace, dorsal view, section WAS2a, sample 3.

2001 *Heterocypris salina* (Brady); Griffiths et al.: 763.

2004 *Heterocypris salina* (Brady); Rosenfeld et al.: 173, pl. 1, fig. 15.

2008 *Heterocypris salina* (Brady); Beker et al.: 18, 19, pl. 3, figs. 6–8.

2010 *Heterocypris* cf. *salina* (Brady); Mischke & Almogi-Labin: fig. 9.

2011 *Heterocypris salina* (Brady); Rosenberg et al.: Supplementary data 33–34 [partim non *Heterocypris salina*].

2012 *Heterocypris salina* (Brady); Mischke et al.: pl. 2, figs. 7–10, 18.

2012 *Heterocypris salina* (Brady); Fuhrmann: 228, pl. 108, figs. 1a–d, 2a–d.

2014 *Heterocypris salina* (Brady); Kalbe et al.: fig. 3j.

2015 *Heterocypris salina* (Brady); Mischke et al.: 157.

2016 *Heterocypris salina* (Brady); Kalbe et al.: fig. 6g–h.

Material: Adults: 8 RV, 9 LV; juveniles: 25 RV, 20 LV.

Size: RV: $L - 1.13$ mm; $H - 0.70$ mm. LV: $L - 1.2$ mm; $H - 0.77$ mm.

Occurrence: ASM1, WAS2a.

Geographical distribution: Holarctic with introductions into the Southern Hemisphere (Meisch, 2000); Anthropocene sediments from Sudan (Schöning, 1996); Holocene from Jordan (Mischke et al., 2012) and Israel (Flako-Zaritsky et al., 2011; Mischke et al., 2014).

Remarks: A large number of the specimens recorded in the present study are juvenile carapaces and valves.

Subfamily **Cypridopsinae** Kaufmann, 1900

Tribe **Cypridopsini** Bronstein, 1947

Genus *Sarscypridopsis* McKenzie, 1977

Sarscypridopsis aculeata (Costa, 1847)

(Plate 1, figs. 4–6)

*1847 *Cypris aculeata* Costa: 11–12, pl. 3, fig. 5.

2000 *Sarscypridopsis aculeata* (Costa); Meisch: 392, fig. 163A–D.

2001 *Sarscypridopsis aculeata* (Costa); Griffiths et al.: 763.

2012 *Sarscypridopsis aculeata* (Costa); Karanovic: 422, fig. 4d, fig. 135e–f, fig. 137d.

2012 *Sarscypridopsis aculeata* (Costa); Fuhrmann: 248, pl. 118, fig. 1a–d.

Material: Adults: 13 C, 23 RV, 22 LV; juveniles: 16 RV, 12 LV.

Size: RV: $L - 0.70$ mm; $H - 0.43$ mm. LV: $L - 0.66 - 0.69$ mm; $H - 0.44 - 0.45$ mm.

Occurrence: ASM1, WAS2a.

Geographical distribution: A cosmopolitan species (Meisch, 2000).

Genus *Cypridopsis* Brady 1867

Cypridopsis concolor Daday, 1900

(Plate 1, figs. 7–10)

*1900 *Cypridopsis vidua* var. *concolor* Daday: 190, pl. 30a–c.

2000 *Cypridopsis vidua concolor* Daday; Meisch: 372.

2012 *Cypridopsis concolor* Daday; Fuhrmann: 238, pl. 113, fig. 2a–d.

Material: 4 C, 4 RV, 2 LV.

Size: RV: $L - 0.48$ mm; $H - 0.31$ mm. LV: $L - 0.45$ mm; $H - 0.30$ mm, $W - 0.32$ mm.

Occurrence: ASM1, WAS2a.

Geographical distribution: Budapest in Hungary; Negorci wetland in Macedonia; fossil from Pleistocene deposits in central Germany.

Remarks: The present study follows Fuhrmann (2012) in separating *C. concolor* from *C. vidua* because of the differences in size, the outline of the carapace and the design of the postero-internal border zone of the left valve.

Family **Candonidae** Kaufmann, 1900

Subfamily **Candoninae** Kaufmann, 1900

Tribe **Candonini** Kaufmann, 1900.

Group **Compressa**

Genus *Pseudocandona* Kaufmann, 1900

Pseudocandona cf. *albicans* (Brady, 1864)

(Plate 1, figs. 11–22)

*1864 *Candona albicans* Brady: 61, pl. 4, figs. 6–10.

1968 *Candona albicans* Brady; Bhatia: 471, pl. 2, fig. 4a–c.

1973 *Pseudocandona albicans* (Brady); Danielopol: 235.

1999 *Pseudocandona albicans* (Brady); Mazzini et al.: pl. 2, fig. 6.

?2001 *Pseudocandona albicans* (Brady); Griffiths et al.: 762.

2011 *Pseudocandona albicans* (Brady); Özulug: 95, fig. 2.

?2012 *Pseudocandona parallela* (Müller 1900); Fuhrmann: 86, pl. 37, figs. 1a–e, 2a–e.

Material: Adults: 18 RV, 17 LV; juveniles: 6 C, 11 RV, 12 LV.

Size: LV: $L - 0.7$ mm; $H - 0.5$ mm.

Occurrence: ASM1, WAS2, WAS2a.

Geographical distribution: Probably Holarctic (Meisch, 2000).

Remarks: There is some confusion about the identification of the current species because its morphology closely resembles a number of taxa belonging to the Candonini group. Our adult specimens are ornamented with dense pits corresponding to the original description of *Candona albicans* by Brady (1864); however, later literature reported smooth carapaces from different regions of the world and regarded Brady's specimens as juveniles. The pitted adult valves of *P. albicans* documented in the present study may indicate a response of the animals to some specific environmental factor(s).

Genus *Fabaeformiscandona* Krstic, 1972

Fabaeformiscandona cf. *breuili* (Paris, 1920)

(Plate 1, figs. 23, 24; Plate 2, figs. 25, 26)

1920 *Candona breuili* Paris: 477, pl. 18 figs. 1–3.

2000 *Fabaeformiscandona breuili* (Paris); Meisch: 135, figs. 56A–C.

2012 *Fabaeformiscandona breuili* (Paris); Fuhrmann: 46, pl. 17, figs. 1a–f, 2a–b, 3a–b.

Material: 5 C.

Size: LV: $L - 0.46$ mm; $H - 0.23$ mm.

Occurrence: ASM1, WAS2, WAS2a.

Geographical distribution: Germany, France and the Czech Republic.

Remarks: The present species resembles *Fabaeformiscandona breuili* (Paris, 1920) in lateral outline and the overlapping of valves, but it is smaller in size.

?*Fabaeformiscandona* sp.

(Plate 2, fig. 27)

Material: 1 juvenile LV.

Size: LV: $L - 0.26$ mm; $H - 0.12$ mm.

Occurrence: ASM1.

Remarks: The single left valve of a juvenile of this species was not enough to identify it precisely.

Family **Ilyocyprididae** Kaufmann, 1900

Genus *Ilyocypris* Brady & Norman, 1889

Ilyocypris bradyi Sars, 1890

(Plate 2, figs. 29–37)

*1890 *Ilyocypris bradyi* Sars: 59.

2000 *Ilyocypris bradyi* Sars; Meisch: 253, figs. 107A–C.

2001 *Ilyocypris bradyi* Sars; Griffiths et al.: 762.

2012 *Ilyocypris bradyi* Sars; Mischke et al.: pl. 2, fig. 23–25.

2012 *Ilyocypris bradyi* Sars; Fuhrmann: 150, pl. 69, figs. 1a–f, 2a–d.

2014 *Ilyocypris bradyi* Sars; Kalbe et al.: fig. 3e–f.

2015 *Ilyocypris* cf. *bradyi* Sars; Mischke et al.: figs 7–15.

2015 *Ilyocypris bradyi* Sars; Kalbe et al.: fig. 7m–n.

Material: Adults: 30 RV, 27 LV, juveniles: 21 RV, 23 LV.

Size: RV: $L - 0.80$ mm; $H - 0.42$ mm. LV: $L - 0.84$ mm; $H - 0.45$ mm.

Occurrence: ASM1, WAS2, WAS2a, BSR4.

Geographical distribution: Holarctic (Meisch, 2000).

Remarks: There are several problems in the identification of *I. bradyi* because of the intraspecific variability of its characters and the very close morphological features with other representatives of the genus. Based on descriptions of modern animals with soft parts and analysing the morphology of the valves, van Harten (1979), Janz (1994) and Mazzini et al. (2014) provided important clues about the morphological structures of the carapaces of some abundant

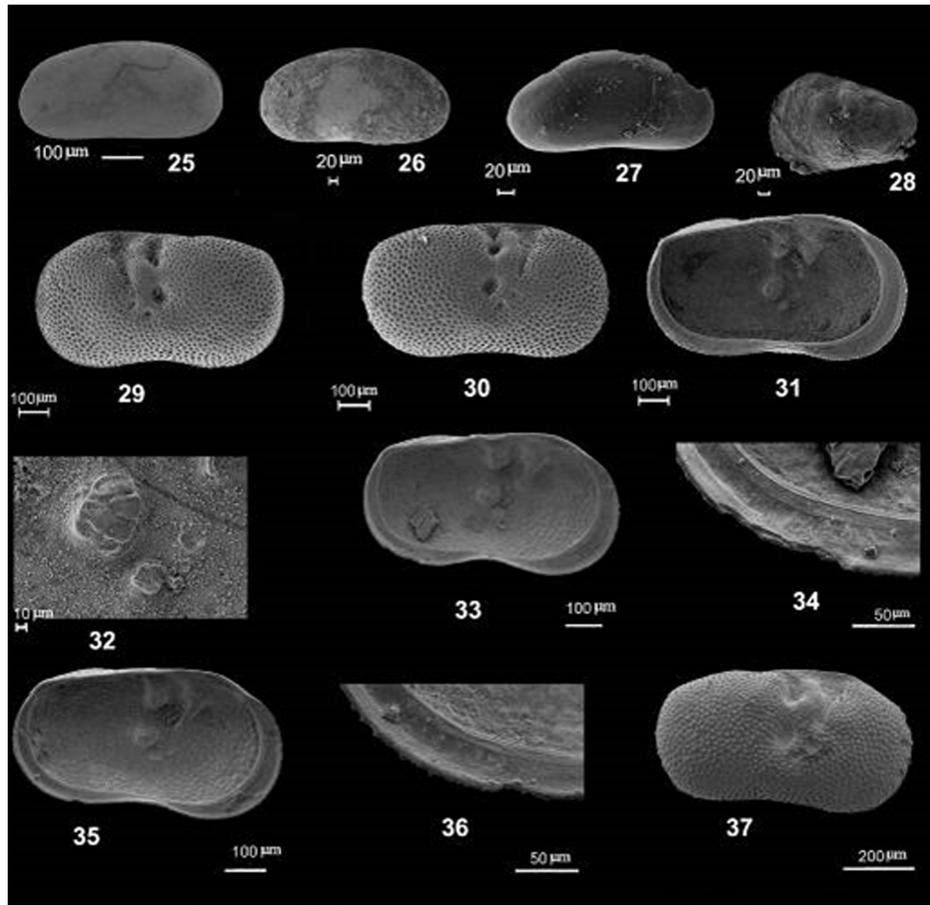


Plate 2. (25–26) *Fabaeformiscandona* cf. *breuili* (Paris, 1920): (25) Carapace, LV, external lateral view, section ASM1, sample 1; (26) Carapace, LV, external lateral view, section ASM1, sample 1. (27) ?*Fabaeformiscandona* sp., juv., RV, external lateral view, ASM1, sample 2. (28) *Leucocythere* sp., juv., LV, external, lateral view, section ASM1, sample 2. (29–37) *Ilyocypris bradyi* (Ramdohr, 1808): (29) LV, external, lateral view, section ASM1, sample 1; (30) RV, external, lateral view, section ASM1, sample 1; (31) LV, internal, lateral view, section ASM1, sample 1; (32) Muscle scars, LV, ASM1, sample 1; (33) LV, internal, lateral view, section WAS2a, sample 2; (34) Postero-ventral marginal area of LV, internal, lateral view, WAS2a, sample 2; (35) LV, internal, lateral view, WAS2a, sample 2; (36) Postero-ventral marginal area of LV, internal, lateral view, WAS2a, sample 2; (37) RV, external, lateral view, WAS2a, sample 2.

Holocene species and discussed the assumption that the marginal ripple structure on the inner lamella of *Ilyocypris* left valves is of primary taxonomic value. The position of the marginal ripples on the inner lamella in conjunction with the inner or outer list is used here to differentiate between *I. bradyi* and the non-tuberculate *I. gibba*.

Family **Limnocytheridae** Klie, 1938
Genus *Leucocythere* Kaufmann, 1892

Leucocythere sp.
(Plate 2, fig. 28)

Material: 1 juvenile LV.

Size: LV: $L - 0.27$ mm; $H - 0.18$ mm.

Occurrence: ASM1.

Remarks: This single juvenile left valve was not sufficient to be identified to the species level.

5 Distribution of Ostracoda in the stratigraphic sections

Ostracod shells were found in 15 samples belonging to four sections (ASM1, WAS2, WAS2a and BSR4) associated with molluscs and small numbers of charophyte oospores. However, a large amount of ostracod shell debris was recorded in almost all the studied samples. Levels with increased coarse grains and/or mollusc shell fragments were considered as representing an erosional unconformity. The different thicknesses of the studied sections is related to the varying mor-

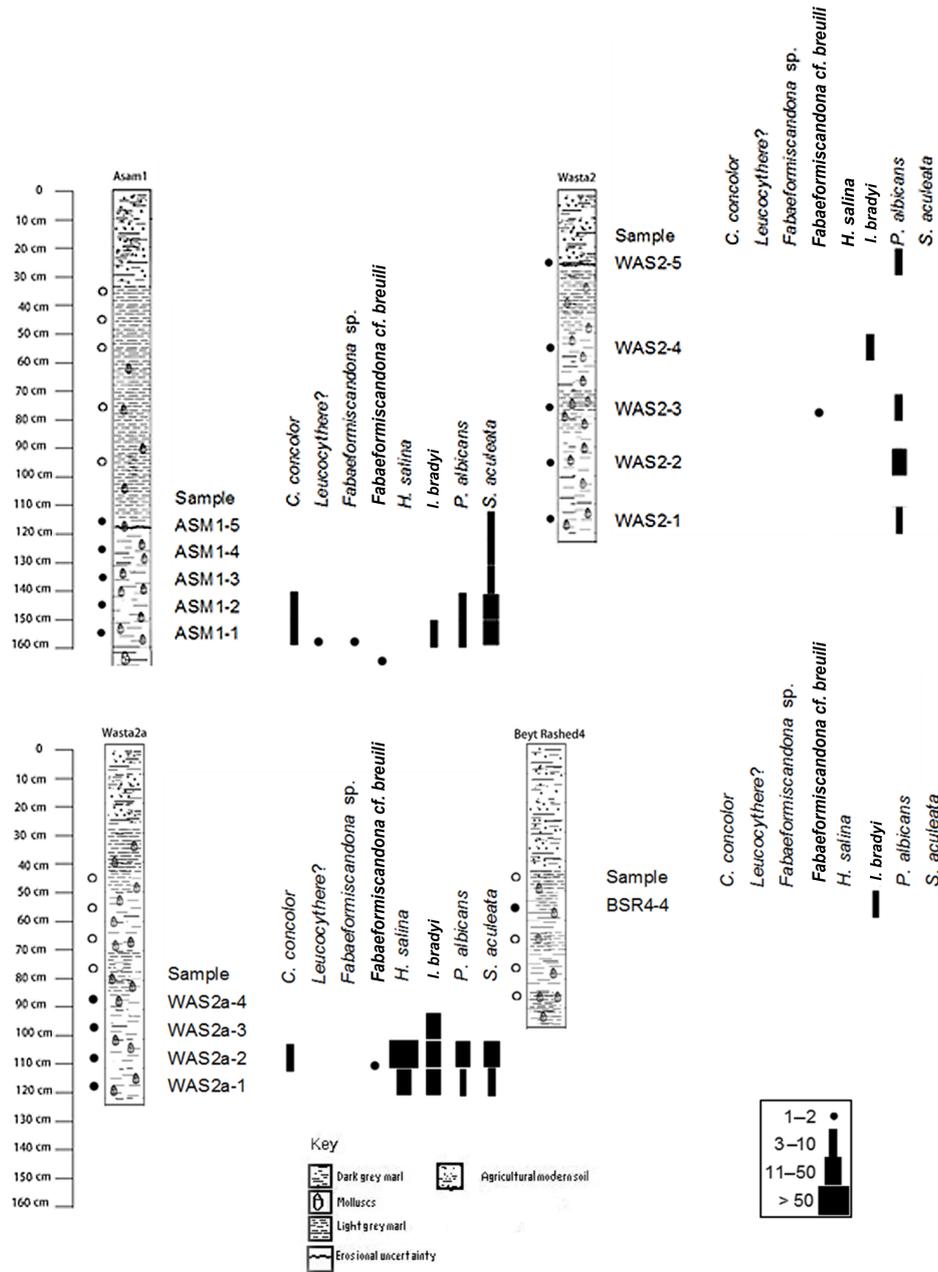


Figure 2. Distribution of ostracods within the studied sections.

phology of the basin. The distribution of ostracods along the studied sections is illustrated in Fig. 2.

6 Ecology of modern ostracods

Many ecological observations on living Ostracoda can be readily applied to fossil ostracods especially when dealing with the same or closely related taxa (Martens, 1994). Information on the ecology of the species encountered in the current study has been gathered from several previous contributions (Hiller, 1972; Hartmann and Hiller, 1977; Meisch,

2000; Frenzel et al., 2010; Fuhrmann, 2012). The freshwater taxa *Leucocythere* sp. and *Fabaeformiscandona* sp. are not included in the following discussion of palaeoecology because of their uncertain species attribution and scarcity.

Fabaeformiscandona breuili (Paris, 1920)

Poorly known: Reported from drainage pipes, springs, caves and the interstitial groundwater.

Heterocypris salina (Brady, 1868)

Salinity: 0.4–8.6‰, oligohaline to low mesohaline. Animals may occur even in pure freshwater habitats.

Temperature: Thermoeuryplastic, 16–22 °C. Ganning (1971) explained that the species prefers habitats that are high in nutrients (eutrophic) and have low temperature and found that no animals survived for longer than 3 days at 30 °C.

Water depth and energy: Frequent occurrence in pools along the coast (Ganning, 1971) and in salinized ponds or streams on the mainland (Klie, 1938), mesorheophilic (frequently found in flowing waters with various velocities).

Habitat and substrate: Permanent and temporary ponds; sediment and phytal, nectobenthic.

O₂: Low oxygen, < 1 mL L⁻¹.

Life history: In ephemeral waterbodies, *Heterocypris salina* needs 40 days to reach the adult stage (Ganning, 1971).

Ilyocypris bradyi Sars, 1890

Salinity: 0–4.5 ‰, freshwater to oligohaline.

Temperature: Polythermophilic, 0.1–25 °C.

Water depth and energy: Very shallow, mesorheophilic; it prefers slowly flowing, cooler waters of springs, streams and ponds fed by springs (Mischke, 2001).

Habitat and substrate: Springs, ponds, swamps and estuaries, and temporary waters. The animals recorded in lakes are usually reported as discharged by nearby springs; endobenthic. Often in running water.

O₂: Probably high oxygen > 2.5 mL L⁻¹.

Life history: The species produces two generations annually.

Pseudocandona cf. *albicans* (Brady, 1864)

Salinity: < 6.3 ‰, freshwater to low mesohaline (optimum salinity 5.5 ‰).

Temperature: Mesothermophilic, 2–24 °C.

Water depth and energy: Very shallow; mesorheophilic, frequently found in flowing waters with various velocities; however, it prefers stagnant and slow flowing waters.

Habitat and substrate: Lagoons and estuaries, swamps, ponds and lakes, temporary waters; muddy bottom and phytal.

O₂: Low oxygen, > 0 mL L⁻¹.

Sarscypridopsis aculeata (Costa, 1847)

Salinity: 0.5–17 ‰; oligohaline to mesohaline (optimum salinity 17 ‰). It prefers slightly brackish small waterbodies of both inland and coastal type, where it often produces large populations, the species is rare in freshwater.

Temperature: Thermoeuryplastic, 3–25 (26) °C.

Water depth and energy: Very shallow, mesorheophilic (frequently found in flowing waters with various velocities).

Habitat and substrate: Temporary and permanent ponds, sand and phytal, nectobenthic.

O₂: Low oxygen, < 1 mL L⁻¹.

Life history: Development of juveniles is very rapid; sexual maturity is reached within 30 days (Mischke, 2001).

Cypridopsis concolor Daday, 1900

No details on the ecological requirements of the species have been found in the literature. It was recorded from freshwater of lowland wetlands in Europe. It prefers smaller and probably also temporary warm waters (Melovski et al., 2013; Fuhrmann, 2012).

7 Interpretation and discussion

In her study site located outside the village of Beyt Nahmi, Davies (2006) found a sediment sequence of 2.50 m thickness from a deep trench composed of three discrete marl horizons alternating with three humus-rich horizons or palaeosols. They represent the northern margin of early to mid-Holocene deposits of lacustrine origin and marshes. Based on the location of sites, lithology and stratigraphic position, the thickest section ASM1 of the current study can be correlated to the Beyt Nahmi “section 1” of Davies (2006), which is about 4 km from the present study location (Fig. 1). This enabled us to find the levels extending from about 1.40 to 0.50 m between the grey calcareous silt marl (M3) and the uppermost palaeosol (Ab3), corresponding to levels of the grey to dark grey marl (1.70 to 0.40 m) of the ASM1 section. We could therefore use the ¹⁴C dates of “section 1” to correlate ages of about 7940 to 3900–3690 cal yr BP for the studied stratigraphic units (Fig. 3).

At the ASM1 section, ostracod associations are composed of *Cypridopsis concolor*, *Fabaeformiscandona* cf. *breuili*, ?*Fabaeformiscandona* sp., *Ilyocypris bradyi*, *Heterocypris salina*, *Leucocythere* sp., *Pseudocandona* cf. *albicans* and *Sarscypridopsis aculeata*. The most dominant species in the assemblage is *S. aculeata*, which has been recorded between 1.7 and 1.3 m, suggesting conditions of slightly higher salinity. *I. bradyi* and *C. concolor* are recorded with less abundance between 1.70 and 1.40 m, reflecting fresh to oligoha-

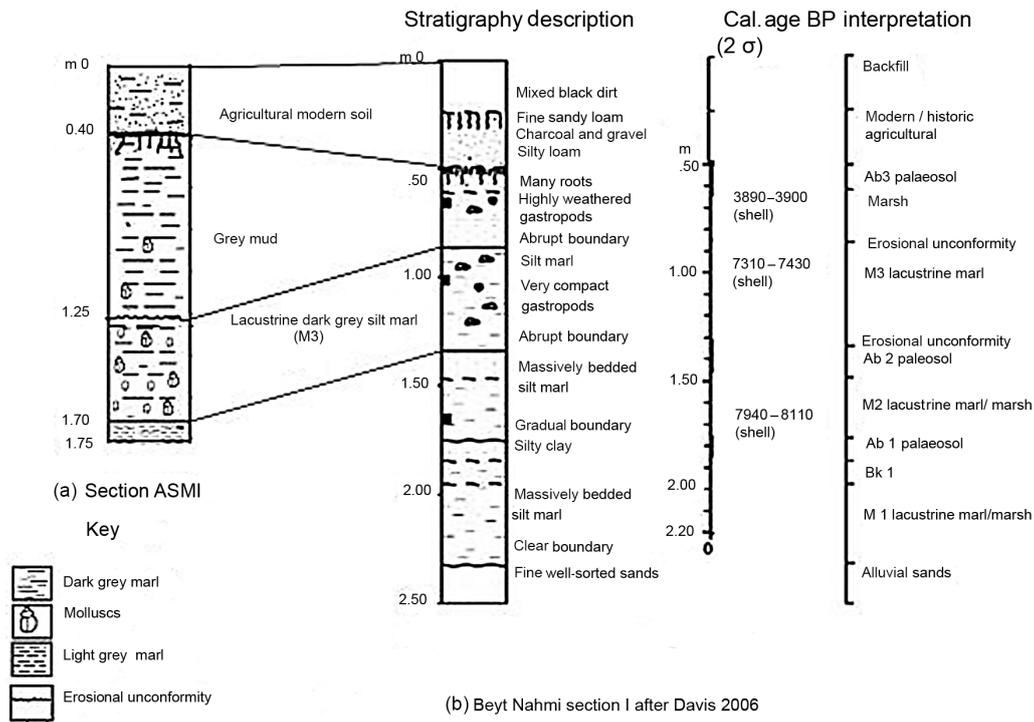


Figure 3. Stratigraphic correlation between (a) present study ASM1 section and (b) Beyt Nahmi “section 1” of Davies (2006).

line conditions. The rare occurrence of *P. cf. albicans* in-stars, *H. salina*, *Leucocythere* sp. and *Fabaeformiscandona* sp. is attributed to post-mortem transport from nearby habitats. *F. cf. breuili* may indicate a groundwater flow through the lake. The darker grey sediments at the lowermost part of the section (1.7 to 1.5 m), which includes *S. aculeata* in higher abundance, is considered to reflect saline water (up to mesohaline) and low-oxygen conditions of a shallow lake. However, the co-occurrence of the mesorheophilic and freshwater species *I. bradyi* and *C. concolor* with the stagnant saline water-loving *S. aculeata* could be due to the mixing of different waterbodies.

The northern section WAS2a contains *C. concolor*, *F. cf. breuili*, *H. salina*, *I. bradyi*, *P. cf. albicans* and *S. aculeata*. It is dominated by the freshwater to oligohaline species *I. bradyi*, *H. salina*, *S. aculeata* and *P. cf. albicans*. Only a few individuals of *C. concolor* have been recorded in this section. The assemblage points to fresh-oligohaline conditions, probably near the shoreline or inlet of the lake since the discharge of streams frequently lowers salinity. Evidence of transportation is provided by the abundance of *I. bradyi*, which prefers slowly flowing water. The occurrence of *H. salina* and *P. cf. albicans* in this habitat is reasonable because they tolerate a wide range of salinity. Furthermore, evidence of short periods of increased evaporation could be indicated by the mesohaline-preferring *S. aculeata*, which is recorded from the lowermost samples (1.2 to 1.1 m) of the section.

At section WAS2, the ostracod association displays lesser diversity than in the nearby section WAS2a. Shells of *P. cf. albicans* were found more often than the only other species, *I. bradyi*. The characters of this ostracod association indicate oligohaline waters in a small isolated habitat.

The three sections of Beyt Rashed (BSR3, BSR4, BSR5) are generally barren of Ostracoda, except at 0.6 m of BSR4, in which a few valves of *I. bradyi* were encountered. This may indicate the development of a small pond at the eastern shore of the lake with only a discontinuous supply of water.

The statistical analysis of ostracod distribution over all sections (Fig. 4) shows highest relative abundances of *S. aculeata* and *P. cf. albicans* and lowest negative values for *I. bradyi* along the top axis. Because *I. bradyi* is a species of permanent waters and because *S. aculeata* as well as many *Pseudocandona* species often occur in temporary waters (Meisch, 2000), we assume the top axis to mirror ecological instability, i.e. temporary vs. permanent habitats. The left-hand axis reflects salinity as the high loadings of *S. aculeata* and its lonely presence in those samples indicate. This species tolerates salinities of up to 17, which is the highest salinity tolerance of the documented species (Frenzel et al., 2010). Considering the position of samples within the principle component analysis, a low salinity of probably fresh to oligohaline conditions is assumed for the lower and middle levels of the sections (WAS2, WAS2a and BSR4) and an elevated salinity of probably mesohaline to oligohaline conditions at ASM1. Furthermore, a trend to higher salinity and temporary waters

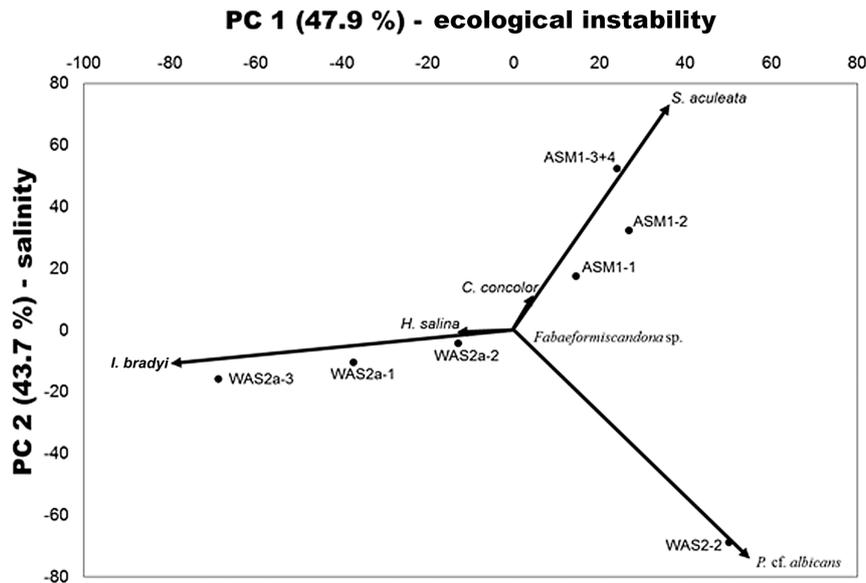


Figure 4. Principal component analysis of relative ostracod abundances in samples of at least 20 counted valves from all studied sections. The percentage values of the axes show how much variance they explain. The top axis represents ecological instability, e.g. temporary vs. permanent waterbodies; the left-hand one mirrors salinity. All loadings of taxa are enlarged 100-fold for better visibility.

is visible in the arrangement of samples of section ASM1 reflecting the shallowing, disintegration and finally drying out of the waterbodies in an arid climate towards the middle Holocene.

In general, the environment was a shallow fragmented lake or ponds, which could only be formed during a period of humid climate. These levels correspond to the grey silt marl (M3), which was interpreted by Davies (2006) to indicate shallow lake conditions developed during the wettest period of the Holocene ranging from 7940 to 7310–7430 cal yr BP. The uppermost part of the sections reflects a period of strong aridity. Enzel et al. (2015) regarded the sediment successions of Davies (2006) as being wetland deposits.

Several studies such as de Menocal et al. (2000), Mischke (2001), Engel et al. (2012) and Enzel et al. (2015) reported the wet period of the Holocene in a wider area including Arabia, Africa and Asia and discussed the solar cycle effects on Indian monsoon climate. Our record fits a moist period documented for the early to mid-Holocene (Fleitmann and Matter, 2009).

8 Conclusion

Eight cosmopolitan ostracod species belonging to seven genera and four families have been recorded from the lower to middle levels of Holocene stratigraphic sections of the Qa'a Jahran basin–Dhamār highlands. The palaeoenvironment was inferred relying on the ecology of their modern representatives, in order to reconstruct the history of a Holocene palaeolake. The ostracod assemblages from the Qa'a Jahran

sections indicate a very shallow lake or several ponds formed during the wettest period during the early Holocene.

Northward incursion of the Indian Ocean Monsoon due to increased solar radiation caused intensified monsoon precipitation over southern Arabia during the early to mid-Holocene. The morphological setting of the studied area led to the formation of wetlands, which provided habitats for many types of plants and animals. Wetlands were distributed unevenly throughout the area because of variations in geomorphology and sources of water. The fragmented lake became more and more unstable and saline over time (from oligohaline to mesohaline) owing to the reduction in precipitation due to the retreat of the Indian Ocean Monsoon. However, the grey marl sediments which extend to the upper levels of the studied sections may indicate less wet conditions persisting for a longer period of time.

Geoarchaeological investigations on the atmospheric processes and human activity during the humid period of the Holocene in southern Arabia and in the Dhamār highlands indicate Neolithic populations.

Data availability. Specimens of all ostracod species were deposited in the department of Earth and Environmental Sciences, Faculty of Science, Sana'a University, under the title "First paper of Qa'a Jahran ostracods", abbreviation "Qaj, Qa'a Jahran", repository of the material.

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