Paläontologische Zeitschrift
2007, Vol. **81/3**, p. 304–315, 30-09-2007

Melanopsis from Al-Qarn, Jordan Valley (Gastropoda: Cerithioidea)

KLAUS BANDEL, Hamburg; NAOMI SIVAN, Jerusalem & JOSEPH HELLER, Jerusalem

with 8 figures

BANDEL, K.; SIVAN, N. & HELLER, J. 2007. *Melanopsis* from Al-Qarn, Jordan Valley (Gastropoda: Cerithioidea). – Paläontologische Zeitschrift **81** (3): 304–315, 8 figs., Stuttgart, 30. 9. 2007.

Abstract: Fossil species of *Melanopsis* from a freshwater formation in the Jordan Valley (near Al-Qarn) were investigated and the deposits containing these species are formally described as Al-Qarn Formation. Four species were found: *Melanopsis buccinoidea* OLIVIER, *M. tchernovi* HELLER & SIVAN, *M. costata* OLIVIER and *M. aaronsohni* BLANCKENHORN. *Melanopsis costata* was represented by two groups, "stepped" and "non-stepped", the latter differing in its lower figurativity index. Intermediates were found between *M. buccinoidea* and *M. tchernovi*; they may be hybrids. The *Melanopsis* assemblage bridges the faunal gap, in the Jordan Valley, between the 2 Ma lake of 'Erq el Ahmar on the one hand and the 0.8–1.7 Ma lake of 'Ubeidiya on the other. This suggests an early Pleistocene age of about 1.8 million years for the Al-Qarn Formation.

Keywords: gastropods • *Melanopsis* • systematics • fresh water • Jordan Valley • Al-Qarn • Al-Qarn Formation

Kurzfassung: Fossile Arten von *Melanopsis* einer Süßwasserformation im Jordantal (in der Nähe von Al-Qarn) wurden untersucht und die Ablagerungen, die diese Arten enthalten, werden formal als Al-Qarn-Formation beschrieben. Vier Arten wurden gefunden: *Melanopsis buccinoidea* OLIVIER, *M. tchernovi* HELLER & SIVAN, *M. costata* OLIVIER und *M. aaronsohni* BLANCKENHORN. *Melanopsis costata* ist durch zwei Morphotypen vertreten, einen „geschulterten" und „ungeschulterten"; der zweite unterscheidet sich durch seinen niedrigeren „figurativity index" vom ersten. Übergänge wurden zwischen *M. buccinoidea* und *M. tchernovi* gefunden, es könnte sich dabei um Hybride handeln. Die *Melanopsis*-Vergesellschaftung überbrückt die Lücke im Jordantal zwischen dem 2 Ma alten See von 'Erq el Ahmar und dem 0.8–1.7 Ma alten See von 'Ubeidiya. Dies lässt auf ein frühpleistozänes Alter von etwa 1.8 Ma für die Al-Qarn-Formation schließen.

Schlüsselwörter: Gastropoden • *Melanopsis* • Systematik • Süßwasser • Jordantal • Al-Qarn • Al-Qarn-Formation

Introduction

The Jordan Valley, formed during the last 2 million years, as part of the great Afro-Syrian Rift, is today a long (350 km) narrow depression that reaches down from 70 m to –400 m and is flanked by highlands that rise to almost 1000 m (with nearby Mt. Hermon reaching 2,800 m). It is drained by the Jordan River, which passes through two intermediate lakes (the recently dried Lake Hula and Lake Kinneret) until eventually it pours into the Dead Sea, the terminal lake of the entire Jordan Valley. Climate grades from Mediterranean in the north to extremely arid in the south, the flora grades correspondingly, from Mediterranean, via steppe to barren desert. There is a wealth of water in the valley in form of rivers, streams, springs, marshes and lakes. In these water bodies the fauna originates from Africa, from the Orient and from the overall palaearctic province. The freshwater snail *Melanopsis* (Melanopsidae) is today abundant throughout this environment of the Jordan Valley, and its taxonomy has recently been revised by HELLER et al. (1999), BANDEL (2000) and HELLER et al. (2005).

During the late Pliocene and early Quaternary, however, the environment was different. As described by HOROWITZ (2001), the Jordan Valley was then a rather flat country dotted with lagoons and lakes, and fed by wide, meandering rivers. The entire Jordan Valley then drained to the Mediterranean via two separate draining systems: the Hula Valley drained northwards (through

Addresses of the authors: Klaus Bandel, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Bundesstraße 55, 20146 Hamburg, Germany; e-mail <klausbandel@yahoo.com>. – Naomi Sivan and Joseph Heller, Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel; e-mail <heller@vms.huji.ac.il>.

0031–0220/07/0081–304 $ 5.40

the Beqa'a and Tripoli graben) while the central Jordan Valley drained westward (through the Yizre'el Valley). The Pliocene climate of the Jordan Valley was of a wet, temperate, northern Mediterranean (Pontian) type, cooler and more humid to the north, becoming warmer and drier southward. The valley was covered by oak (*Quercetalia* sp.) and conifer (probably *Picea orientalis*) that formed dense forests in the north, grading into open parks further southward. In this relatively flat landscape roamed such African mammals as elephant, giraffe, rhinoceros and hippopotamus, together with such palaearctic mammals as *Leptobos*, *Hipparion* and *Bos* (HOROWITZ 2001 and references therein). Fossil *Melanopsis* of Pliocene and early Quaternary age have been described by HELLER & SIVAN (2001, 2002a, b) and by BANDEL (2000). This present paper concerns fossil *Melanopsis* from a hitherto undescribed formation in the Jordan Valley near Al-Qarn (Fig. 1) some 36 km south of Lake Kinneret. We describe the *Melanopsis* species of Al-Qarn and compare them with Recent and fossil *Melanopsis* of the Jordan Valley.

The Al-Qarn Formation

The name Al-Qarn Formation is introduced for lake deposits located on the banks of the Ghor Canal south of Jebel al-Qarn, near Wadi al-Qarn, and west of the village of Abu Habil (Fig. 1). The sequence containing the Al-Qarn Lake overlies the Oligocene-Miocene deposits of the Tayba Formation (BANDEL & SHINAQ 2003) and is overlain by a pisolitic conglomerate that is exposed on the side of the road that passes below the bridge of the canal.

The lake deposits of the Al-Qarn Formation are composed of fine sand with calcareous intercalations of about 25 m exposed along the eastern slope of the Ghor Canal. The whole sequence consists of strata dipping with about 50° towards the center of the Jordan Valley. The base of this sequence is formed by a fault and below it are beds of gravel with a similar dip towards about NW. The top of the lacustrine Al-Qarn Formation is not exposed due to the road and the slope of Wadi Al-Qarn. But the beds above are again fluviatile conglomerates, also in inclined position, but with less dip of about 30°. Most pebbles of the gravel are flint and limestone coming from Cretaceous and Paleogene deposits exposed at the slopes to the East of the Jordan Rift. Some of these gravel layers are almost completely composed of pisolite gravels with concentric composition. Such pisolites have been growing and have their origin in the soils on the hill sides and mountains nearby to the east. Here during past periods when climatic conditions were more humid than today they formed in the soil. In an outcrop next to the canal and the road passing under it through the bridge they occur on secondary deposition and were washed from these slopes and carried there by a river. Calcareous pisolite pebbles have been deformed by pressure and acquired angular shape.

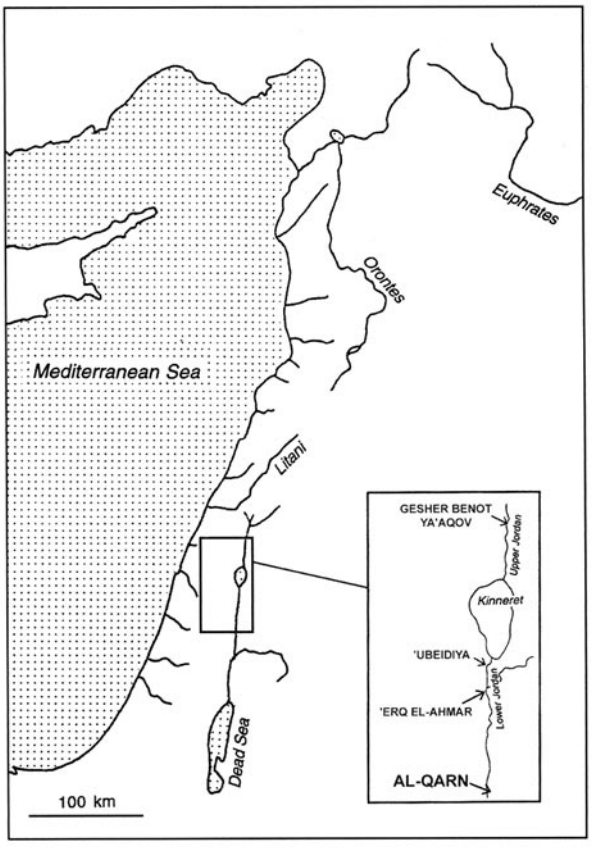

Fig. 1. The Levant, with Al-Qarn and additional fossil-bearing sites of the Jordan Valley.

Above the inclined units all beds are still in horizontal position. Of these Lisan marls are exposed next to the outcrop. They formed during the last cold stage of the Quaternary in the brackish to salty Lisan lake. In the Hemma valley of Mashara to the north the original coast line of that lake and transition of marls into the *Melanopsis* bearing spring deposits are exposed. Below the Lisan marls, further towards the Jordan and thus to the west of the exposure of the Al-Qarn Formation, follow fluviatile sands which may also contain a fauna with *Melanopsis* and *Theodoxus*, for example at the border police station south of Pella creek near the Jordan and in the cliff above it. The layers below may consist of thick conglomeratic river beds, and from here also sandy intercalations with *Unio* are found even deeper below the Lisan marls. This sand is exposed along the road on the Jordan just to the south west of the exposure of the Al-Qarn Formation. The great increase in thickness of the Quaternary sediment column and the intercalation of fluviatile beds without displacement below the Lisan marls indicate that vertical movements in the Jordan rift have been continuous.

According to BENDER (1968) the deposits of rivers and lakes in the northern Jordan Rift are found in the Ghor el Katar Formation, which was typified as exposed 2 km SSE of Kureiyima, a town to the north of Deir Alla and just south of Abu Habil. The extent of this Ghor el

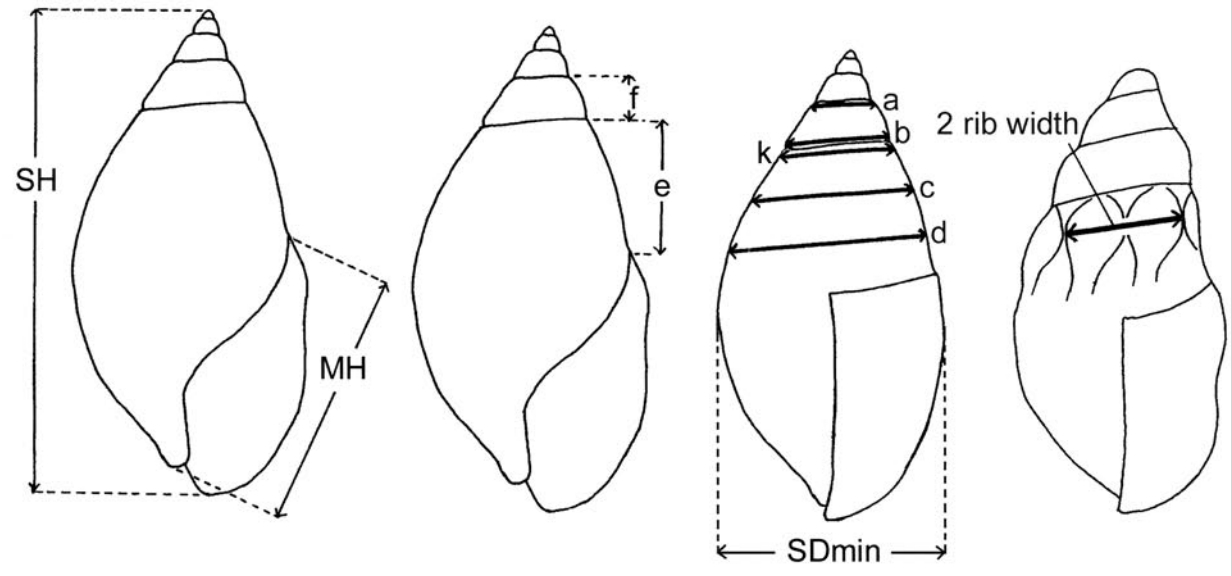

Fig. 2. Measurements used in this study. SH, shell-height; SDmin, minimal shell-diameter; MH, mouth-height. a, b, c, d, e are explained in the text.

Katar Series is not quite clear since large gravel channels come from the east and are exposed to the south of the town of Abu Habil. HUCKRIEDE (1966) noted pebble tools of middle Pleistocene Oldowan age in a part of these deposits.

The sediments of the Al-Qarn Formation consist of fine marly sand, some of it consolidated by calcareous cement. In the beds with well preserved fauna this sand is still unconsolidated. The molluscan fauna consists of some small bivalves of the *Pisidium* type, several gastropods such as *Theodoxus*, *Melanoides*, *Bithynia*, *Ancylus*, *Gyraulus*, a lymnaeid, *Valvata*, species of small hydrobioids (cf. *Orientalina*, cf. *Hydrobia*, and cf. *Pseudamnicola*) and *Melanopsis*. From the land, a variety of pulmonate species have been washed into the lake. Fragments of larger bones are also present, but none of them have been preserved well enough to be determined. Ostracods and remains of crab claws are present as well. Clearly absent from the lake were *Viviparus*, *Unio* and *Dreissena*.

The sequence containing the Al-Qarn lake sediments overlies the Oligocene-Miocene deposits of the Tayba Formation (BANDEL & SHINAQ 2003). This series is considerably older and was in part formed under normal marine conditions. The gravel containing the characteristic pisolites on the eastern side of the Ghor canal overlies the Al-Qarn Formation, on the western side; exposed in the slope of Wadi Al-Qarn it appears to overlie the Tertiary beds of the Tayba Formation. This is evidence for considerable displacement of these rocks near the bridge of the canal crossing Wadi Al-Qarn. The road that crosses the wadi passes it under the bridge of the canal. The lake deposits of the Al-Qarn Formation have thus been tilted and displaced by the Jordan transform fault.

Materials and methods

Melanopsis remains of 646 specimens were collected at Al-Qarn, by one of us (KB). All these specimens were inspected.

Measurements were taken only of adults (of specimens with a shell height of at least 10 mm, see HELLER & SIVAN 2002b). These measurements are similar to those of earlier studies on fossil *Melanopsis* of the Jordan Valley (HELLER & SIVAN 2001, 2002a, b).

General conchometrics (Fig. 2) include shell-height (SH), shell-diameter (minimal) (SD min) and mouth-height (MH); all measured with a caliper to an accuracy of 0.1 mm. From these measurements three ratios were calculated: shell-diameter (min) / shell-height; mouth-height / shell-height; and mouth-height / shell-diameter (min).

In addition, the diameter of the shell was measured at four different points under the stereo microscope, using an eye-piece micrometer (a, b, c and d, see Fig. 2; c is two thirds above the point of insertion of the lip, d is one third). From these measurements, we quantitatively express the index of shell shouldering as the ratio b/c (shouldered shells, e.g. *Melanopsis dufouri*, see BANDEL 2000: figs. 139–142; *M. obediensis*, see HELLER & SIVAN 2001: fig. 3D, have low shouldering index). We express the index of shell figurativity as the ratio c/d (shells with a conic ultimate whorl have low figurativity index, cylindrical shells have high one and shells with a "waist" have the highest index). We express the index of conicality as the ratio a/b (shells with a conic penultimate whorl, as in HELLER et al. 1999: figs. 4A, C, have low conicality index). In the smooth shells we also measured the diameter of the shell just below the suture between the ultimate and penultimate whorl (k), and calculated the ratio b/k, as an additional expression of shouldering.

Whorl height was measured at two points: e - height of penultimate whorl, from the aperture to nearest point on the suture above; and f - height of the previous whorl (Fig. 2). From these measurements we calculated two relative whorl heights, the ratios e/mouth-height and f/mouth-height.

To measure rib characteristics, each shell was scored for presence or absence of ribs. When ribs were present, at first three rib characteristics were scored: a) Rib number, from uppermost point of insertion of the aperture on the last whorl dextrally, to the corresponding point on the previous whorl. b) Rib density, as the number of ribs from uppermost point of insertion of aperture 5 mm leftwards (from the point of insertion of the outer lip on the whorl), counted under the micrometer of the binocular. c) Rib length, examined on the last whorl. This characteristic is continuous. To describe increasing rib length four categories were selected: ribs very short, not reaching the shell aperture (1); ribs reach from the suture down to the aperture (2); ribs reach beyond the aperture, but do not extend the entire height of the body whorl (3); ribs reach the entire height of the last whorl (4).

To measure (when relevant) the extent to which ribs are wavy (rather than straight) curvature was measured on the fifth rib of the last whorl (to the left of the aperture) using the eye-piece micrometer of the binocular. Curvature is the distance (mm) to which a wavy rib deviates from an imaginary straight line that connects the upper and lower part of the rib. On the shells from Al-Qarn only left curvature was measured.

To express (when relevant) the width of the ribs at the tubercle (or at similar level in ribs without tubercle), the width of two ribs (on the last whorl, above the aperture) was measured (Fig. 2). From this measurement we calculated relative rib width as the ratio 2-rib width/shell-diameter.

These measurements differ from those used by GEARY et al. (2002) in that they were taken directly on the shells themselves, not from digitalized video images. Certain indirect measurements that suit flat images are rather difficult on real three-dimensional shells (e.g. their shouldering). Also, we measured shell-width as minimal shell-width (not maximal, as did GEARY et al. 2002) so as to gain information even from shells in which the aperture was not complete.

Statistical comparisons between different taxonomic groups were conducted by t-test. Significance level was set at $P = 0.05$. In our systematic descriptions the term "diagnostic" (rather than significant) describes lack of overlap between two different taxa, in a given character. For multivariate comparisons between the different *Melanopsis* taxa we applied Principal Coordinate Analysis (PCO) (by UPGMA based on Standardized Euclidian, using the multivariate statistical package of Kovach Computing Services: MVSP).

The *Melanopsis* of Al-Qarn are deposited, partly in the Paleontology Collection of the University of Hamburg and partly in the Paleontology Collection of the Hebrew University of Jerusalem.

Systematic paleontology

Family Melanopsidae H. & A. ADAMS, 1854

Type genus: *Melanopsis* FÉRUSSAC, 1823.

Diagnosis: The shell has a cyrtoconoid outline with the last whorl more or less inflated and whorls of the spire hardly rounded and smooth, or ornamented by axial ribs. The aperture is depressed and egg-shaped with a regularly rounded outer lip, an anterior (= lower) notch and a smooth inner lip, which is usually thickened by a posterior (= upper) callus pad. There is no umbilicus. The protoconch is simple and is not clearly demarcated from the teleoconch.

Genus *Melanopsis* FÉRUSSAC, 1823

Type species: *Buccinum praemorsum* LINNAEUS, 1758, from southern Spain.

Diagnosis: The shell is thick and imperforate, and may be smooth or heavily ribbed. A notch is present at the base of the mouth, where the outer and inner lips meet. The upper part of the mouth is narrowly constricted. On the inner lip, the upper part usually contains a callus; in the lower half, the columella is truncate (HELLER et al. 1999, 2005).

Melanopsis buccinoidea (OLIVIER, 1801)

Fig. 3A, Tab. 1

*1801	Melanie buccinoide OLIVIER: pl. 17 fig. 8.
1999	*Melanopsis buccinoidea* (OLIVIER, 1801). – HELLER et al.: 56–59, fig. 4A.
2000	*Melanopsis buccinoidea* FÉRUSSAC, 1823. – BANDEL: 151–152, figs. 20–24, 71, 124–126, 133.
2002a	*Melanopsis buccinoidea* (OLIVIER, 1801). – HELLER & SIVAN: 42–43, fig. 3A.
2002b	*Melanopsis buccinoidea* (OLIVIER, 1801). – HELLER & SIVAN: 611–613, fig. 3A.

Material: 183 shell remains.
Holotype and **type locality**: "Melanie buccinoide, *M. buccinoidea* de Scio" (OLIVIER 1801: pl. 17 fig. 8).
Occurrence: Today *Melanopsis buccinoidea* is widely distributed in the Levant, in a wide range of habitats; it is absent from the Jordan River and Lake Kinneret. Fossils in the Levant are known from the mid Pleistocene and Lower Pleistocene of the Jordan Valley (HELLER et al. 2005).

Diagnosis: *Melanopsis buccinoidea* differs from *M. praemorsa* LINNAEUS, the type species of *Melanopsis*, in that it is larger and more cylindrical.

Description: The shell has up to seven whorls that are smooth. It has a pointed spire and flattened whorls that increase regularly in diameter and which are separated by very shallow sutures. In the protoconch the first three quarter of a whorl is without growth lines; from there

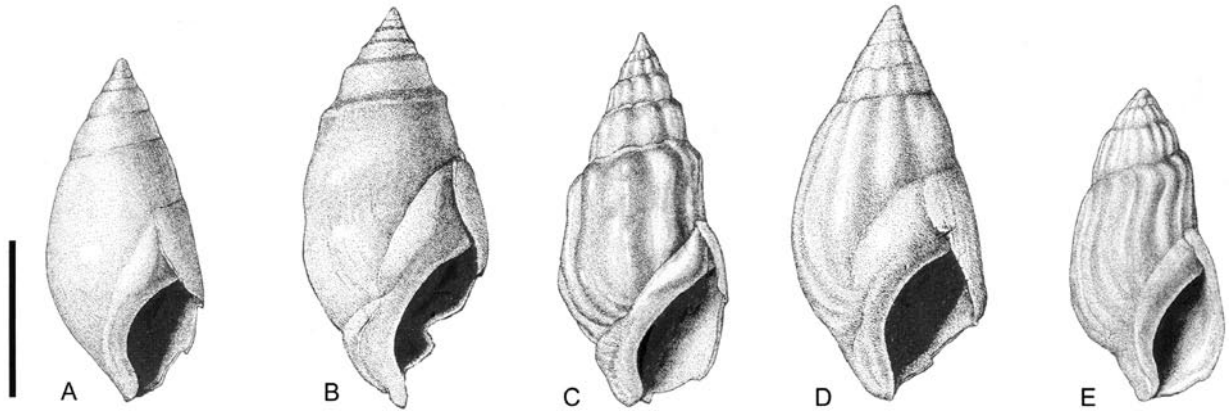

Fig. 3. *Melanopsis* species of Al-Qarn. – **A**: *M. buccinoidea*; **B**: *M. tchernovi*; **C**: *M. costata* "stepped"; **D**: *M. costata* "non-stepped"; **E**: *M. aaronsohni*. – Scale bar = 10 mm.

onward there are growth lines up to the hatching point, at about one and a half whorls (RIEDEL 1993; BANDEL 2000). The height of the mouth is over half the height of the shell. The posterior (= upper) part of the mouth forms a narrow slit.

Measurements: Measurements and ratios of *Melanopsis buccinoidea* from Al-Qarn (n = 20) are given in Tab. 1.

Comparisons: Differences between the *M. buccinoidea* of Al-Qarn and *M. buccinoidea* of other sites in the Jordan Valley are significant, but not diagnostic. The Al-Qarn *M. buccinoidea* differ from Recent *M. buccinoidea* of the Jordan Valley in that they have lower values of the ratio b/k. They differ from fossil *M. buccinoidea* of Gesher Benot Ya'aqov in their larger mouth (higher values of the ratios mouth height/shell height and mouth height/shell diameter), higher conicality index, higher figurativity index and lower whorls (smaller e/mouth-height and f/mouth-height). They differ from fossil *M. buccinoidea* of 'Ubeidiya, in being slimmer (lower ratio shell diameter/shell height), having a larger mouth (mouth height/shell height and mouth height/shell diameter), higher conicality index, lower shouldering index and lower whorls (smaller e/mouth-height and f/mouth-height). They differ from fossil *M. buccinoidea* of 'Erq el-Ahmar in their higher conicality index, lower shouldering index and higher figurativity index (compare with HELLER et al. 1999: 57 and App. 1A; HELLER & SIVAN 2001, 2002a, b). Some of these comparisons are shown in Fig. 4.

Tab. 1. Measurements and ratios of *Melanopsis buccinoidea* from Al-Qarn (n = 20).

	Range	Mean ± SD
Max. shell-height	18.5 mm	
Shell-diameter (min) / shell-height	0.41–0.51	0.45 ± 0.028
Mouth-height / shell-height	0.54–0.64	0.60 ± 0.026
Mouth-height / shell-diameter (min)	1.19–1.44	1.32 ± 0.070
e / mouth-height	0.24–0.35	0.30 ± 0.035
f / mouth-height	0.13–0.23	0.16 ± 0.021
Conicality index (a/b)	0.72–0.83	0.77 ± 0.033
Figurativity index (c/d)	0.87–0.94	0.91 ± 0.021
Shouldering index (b/c)	0.71–0.84	0.77 ± 0.030
b/k	0.81–0.91	0.86 ± 0.032

Intermediates were found at Al-Qarn, between *M. buccinoidea* and *M. tchernovi*; these are described below.

Melanopsis tchernovi HELLER & SIVAN, 2002

Fig. 3B, Tab. 2

2000 *Melanopsis dufouri* FÉRUSSAC, 1823. – BANDEL: 147–148, figs. 139–142.

* 2002b *Melanopsis tchernovi* HELLER & SIVAN: 619–622, fig. 3F.

Material: 190 shell remains.

Holotype and **type locality**: The holotype of *Melanopsis tchernovi*, from 'Erq el-Ahmar, is in the Paleontology collection of the Hebrew University of Jerusalem (HUJ 9016) (HELLER & SIVAN 2002b).

Occurrence: *Melanopsis tchernovi* is known only from the type locality ('Erq el-Ahmar, HELLER & SIVAN 2002b) and from Al-Qarn (this study).

Diagnosis: *Melanopsis tchernovi*, a fossil species of *Melanopsis*, differs from *M. buccinoidea* in that its last whorls possess a distinct keel that protrudes from the shell (HELLER & SIVAN 2002b).

Description: The shell is smooth, cylindrical, stepped and usually has a protruding keel at the upper part of the last whorl. Beneath this keel there is a moderate, rounded ridge in form of a slight swelling; it is located at the level of the suture formed by the mouth. The contour of the last whorl thus consists (from the suture downwards)

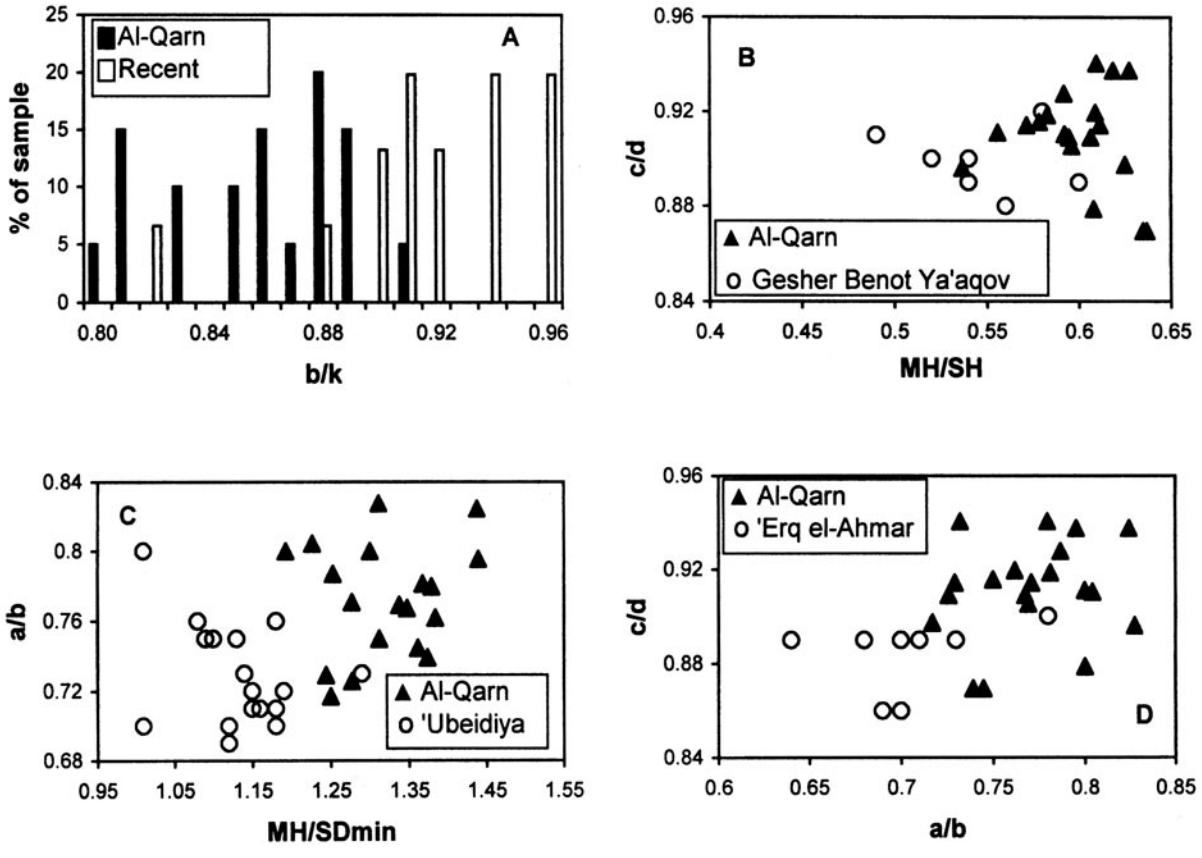

Fig. 4. *Melanopsis buccinoidea,* from Al-Qarn and from other sites in the Jordan Valley. – **A**: Al-Qarn versus Recent: Frequency of the ratio b/k. – **B**: Al-Qarn versus Gesher Benot Ya'aqov: Figurativity (c/d) versus the ratio mouth-height/shell-height. – **C**: Al-Qarn versus 'Ubeidiya: Conicality (a/b) versus the ratio mouth-height/shell-diameter (min). – **D**: Al-Qarn versus 'Erq el-Ahmar: Figurativity (c/d) versus conicality (a/b).

of a shoulder or keel, a slightly concave area, a slight swelling, another concave area and finally a rounded transition to the base of the shell. The shell consists of between 8 and 9 whorls of which the first five are conic with flattened sides; the sixth has a shoulder; and in later whorls, this shoulder may develop into a pronounced keel. The aperture has a thick callus.

Measurements: Measurements and ratios of *M. tchernovi* from Al-Qarn (n = 20) are given in Tab. 2.

Comparisons: *Melanopsis tchernovi* was described from 'Erq el-Ahmar by HELLER & SIVAN (2002b), based on the type specimen only. We compared the stepped, smooth shells from Al-Qarn with this shell and some additional fragments of *M. tchernovi* from 'Erq el-Ahmar. The material was too scarce for statistical comparison, but the few shells from 'Erq el-Ahmar fall within the range of those from Al-Qarn.

Melanopsis tchernovi differs diagnostically from *M. buccinoidea* of Al-Qarn in that it is more stepped (lower b/k, Fig. 5). It further differs significantly in that it has a bigger mouth (higher values of mouth-height/shell-height and mouth-height/shell-diameter (min), lower whorls (f/mouth-height) and is more cylindrical (higher figurativity index and conicality index).

Two more cylindrical, smooth species have been described from the Rift Valley: *Melanopsis vincta* BLANCKENHORN, 1897 from the mid-Pleistocene of

Tab. 2. Measurements and ratios of *Melanopsis tchernovi* from Al-Qarn (n = 20).

	Range	Mean ± SD
Max. shell-height	25.2 mm	
Shell-diameter (min) / shell-height	0.39–0.50	0.45 ± 0.029
Mouth-height / shell-height	0.59–0.71	0.64 ± 0.033
Mouth-height / shell-diameter (min)	1.33–1.64	1.44 ± 0.082
e / mouth-height	0.18–0.40	0.326 ± 0.061
f / mouth-height	0.11–0.17	0.13 ± 0.018
Conicality index (a/b)	0.78–0.99	0.94 ± 0.021
Figurativity index (c/d)	0.89–0.99	0.94 ± 0.021
Shouldering index (b/c	0.64–0.78	0.73 ± 0.040
b/k	0.70–0.80	0.75 ± 0.032

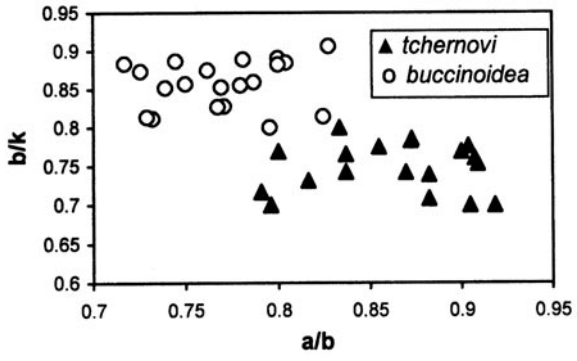

Fig. 5. Differences between *Melanopsis tchernovi* and *M. buccinoidea*, both from Al-Qarn: Shouldering (as expressed by b/k) versus conicality (a/b).

Gesher Benot Ya'aqov (HELLER & SIVAN 2001) and Recent *M. dircaena* PALLARY, 1939 from the Orontes (HELLER et al. 2005). These two species lack the keel that is characteristic of *M. tchernovi*. *M. tchernovi* further differs from *M. vincta* in that it has bigger mouth-height as compared to shell-height, lower whorls as compared to mouth-height, lower conicality index and lower figurativity index. It differs from *M. dircaena* in that it is slimmer, has smaller mouth-height as compared to shell-height and shell-diameter, and lower whorls as compared to mouth-height.

Melanopsis tchernovi, a keeled species, is similar to Recent *M. dufouri* FÉRUSSAC, 1823 of Morocco (see HELLER & SIVAN 2002b: 621–622) and to *M. delessei* TOURNOUER, 1875 from the Pliocene of Kos (WILLMANN 1981: pl. 8 figs. 19–21). This could perhaps suggest that an ancient keeled group of species once ranged around the Mediterranean, eventually becoming extinct in the eastern and northern parts of its palaeo-range, and surviving in the Maghreb.

Intermediates between *Melanopsis buccinoidea* and *M. tchernovi*, in which the keel is less conspicuous or even absent, were also found at Al-Qarn (Tab. 3). The shell data suggest that these intermediates are closer to *M. buccinoidea* than to *M. tchernovi*. Of all 437 smooth shells present in our Al-Qarn collection, we classify 42 % as *M. buccinoidea*, 43 % as *M. tchernovi* and 15 % as *M. buccinoidea–M. tchernovi* intermediates.

Transitions between *Melanopsis buccinoidea* and *M. tchernovi* were first noted by BANDEL (2000: figs. 137–138). These intermediates may be hybrids. Hybrids are common in Recent and fossil *Melanopsis*. *Melanopsis costata–M. buccinoidea* hybrids are found among Recent *Melanopsis* of the Jordan Valley, in zones of contact between *M. costata* and *M. buccinoidea*, at low frequencies of 2–6 % per sample (HELLER et al. 1999). Among fossil *Melanopsis*, *M. costata–M. buccinoidea* hybrids were found in Gesher Benot Ya'aqov (HELLER & SIVAN 2001). Also in 'Ubeidiya shells were found that are intermediate between *M. costata* and *M. buccinoidea*. Such intermediates were found in many layers, in average frequencies of 6.2 % (HELLER & SIVAN 2002a).

Tab. 3. Measurements and ratios of intermediates between *Melanopsis buccinoidea* and *M. tchernovi* from Al-Qarn (n = 12).

	Range	Mean ± SD
Max. shell-height	27.4 mm	
Shell-diameter (min) / shell-height	0.43–0.50	0.46 ± 0.021
Mouth-height / shell-height	0.60–0.68	0.64 ± 0.027
Mouth-height / shell-diameter (min)	1.25–1.51	1.39 ± 0.073
e / mouth-height	0.24–0.34	0.28 ± 0.035
f / mouth-height	0.11–0.17	0.14 ± 0.018
Conicality index (a/b)	0.70–0.85	0.76 ± 0.049
Figurativity index (c/d)	0.89–0.95	0.91 ± 0.018
Shouldering index (b/c)	0.75–0.86	0.78 ± 0.031
b/k	0.78–0.91	0.83 ± 0.033

In fossil assemblages, intermediates may represent either gradual evolution from one species into another, or hybridization. As evidence for gradual evolution, one would expect a sequence consisting of an ancestral taxon in deep layers, intermediate forms in transitional layers and a derived taxon in high layers. On the other hand, a sequence in which intermediates occur repeatedly would suggest repeated hybridization. This question has been addressed by GEARY (1990) in *Melanopsis* intermediates of the Miocene in which, in one case (*M. impressa–M. fossilis*) she found evidence of gradual evolutionary transition from one species to another, in another (*M. fossilis–M. vindobonensis*), of hybridizaton (GEARY 1990).

In 'Ubeidiya, the low frequency of the *M. buccinoidea–M. costata* intermediates and also their scattered chrono-distribution throughout the layers suggest that they are hybrids (HELLER & SIVAN 2002a). Also at Gesher Benot Ya'aqov *M. buccinoidea–M. costata* hybrids were found (HELLER & SIVAN 2001).

Among Recents of the Jordan Valley, *M. buccinoidea* and *M. costata* generally remain distinct, but in zones of contact intermediate hybrids may be found, at low frequencies and over distances of no more than a few hundred meters. These contact zones are connected to major ecotones: from gently running stream outlets, inhabited by *M. buccinoidea*, into the choppy and wavy Lake Kinneret, inhabited by *M. costata* (HELLER et al. 1999).

This 'Ubeidiya–Gesher Benot Ya'aqov–Recent chain of hybrids indicates that *M. costata* and *M. buccinoidea* of the Jordan Valley may have been (continuously?) hybridizing since the early – mid-Pleistocene

(HELLER & SIVAN 2002a). We similarly suggest that the Al Qarn *M. tchernovi–M. buccinoidea* intermediates are hybrids.

Melanopsis costata (OLIVIER, 1804)

Figs. 3C, D, Tabs. 4–5

*1804 *Melania costata* OLIVIER, 1804: pl. 31 fig. 3.
1999 *Melanopsis costata* (OLIVIER, 1804). – HELLER et al.: 59–61, fig. 3B.
2000 *Melanopsis costata* OLIVIER, 1804. – BANDEL: 166–167, figs. 72–75.
2000 *Melanopsis blanckenhorni* SCHÜTT, 1988. – BANDEL: 172–173, figs. 97–103.
2000 *Melanopsis orientalis* BUKOWSKI, 1895. – BANDEL: 180–182, figs. 104, 107–110.
2002a *Melanopsis costata* (OLIVIER, 1804). – HELLER & SIVAN: 43–44, fig. 3B.

Holotype and **type locality**: "Melanie a cotes, *Melania costata*; de Orontes" (OLIVIER 1804: pl. 31 fig. 3).
Synonyms: *Melanopsis orientalis* BUKOWSKI, 1895 originally described from Al-Qarn (see BANDEL 2000: figs. 104, 110) should be assigned to *M. costata*, as it falls well within the range of *M. costata* in every parameter of the shell.
Occurrence: Today *Melanopsis costata* is found throughout the Levant, from Kara Sou in the north down to the environs of the Dead Sea in the south. Fossils of this species are known from the lower and middle Pleistocene of the Jordan Valley (HELLER et al. 2005).

Tab. 4. Measurements and ratios of *Melanopsis costata* "stepped" from Al-Qarn (n = 20).

	Range	Mean ± SD
Max. shell-height	25.3 mm	
Shell-diameter (min) / shell-height	0.42–0.50	0.46 ± 0.021
Mouth-height / shell-height	0.47– 0.56	0.52 ± 0.025
Mouth-height / shell-diameter (min)	1.04–1.25	1.13 ± 0.072
e / mouth-height	0.39–0.53	0.45 ± 0.034
f / mouth-height	0.18–0.27	0.22 ± 0.025
Conicality index (a/b)	0.85–0.98	0.91 ± 0.036
Figurativity index (c/d)	0.96–1.03	0.99 ± 0.018
Shouldering index (b/c)	0.65–0.77	0.72 ± 0.032
Rib number	10–14	11.9 ± 1.41
Rib density	2–4	2.97 ± 0.523
Rib length	All 4	
2 rib width / shell-diameter (min)	0.31–0.50	0.38 ± 0.045
Rib curvature	all 0 mm	

Diagnosis: *Melanopsis costata* differs from *M. buccinoidea* and from *M. tchernovi* in that it is ribbed.

Description: The shell has up to eight whorls. The first three whorls are smooth whereas the three-five lower whorls are ribbed. The ribs are pronounced and extend vertically, the entire length of each whorl.

Intraspecific variation: Within *Melanopsis costata* from Al-Qarn two shell groups ("stepped" and "non-stepped") are present, and are hereby described.

Melanopsis costata "stepped"

Fig. 3C, Tab. 4

Material examined: 200 shells.

Morphology: The overall appearance of the shell is stepped (= shouldered). The ribs are sometimes broader in their upper part.

Measurements: Measurements and ratios of *M. costata* "stepped" from Al-Qarn (n = 20) are given in Tab. 4.

Comparisons: In terms of geography, chronology and morphology, *Melanopsis costata* of Al-Qarn is close to *M. praecursor* SCHÜTT & ORTAL, 1993 of 'Erq el-Ahmar (see HELLER & SIVAN 2002b). The Al-Qarn *Melan-*

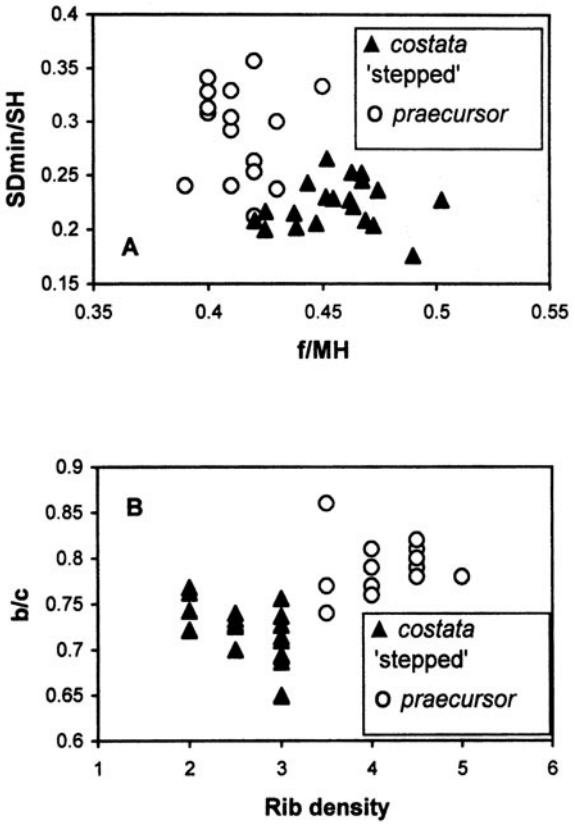

Fig. 6. Differences between *Melanopsis costata* "stepped" from Al-Qarn and *M. praecursor* from 'Erq el-Ahmar. – **A**: The ratio shell-diameter (min)/shell-height versus relative whorl height (f/mouth-height). – **B**: Shouldering (b/c) versus rib density.

opsis costata "stepped" differs diagnostically from *M. praecursor* in that it has less dense ribs. It differs significantly in that it is stouter, has higher whorls (higher ratio f/MH) is more stepped (lower ratio b/c) (Figs. 6A, B), has a larger mouth as compared to shell height, and has higher conicality index and figurativity index.

Melanopsis costata "stepped" of Al-Qarn differs from *M. multiformis* BLANCKENHORN, 1897 of 'Erq el Ahmar (see HELLER & SIVAN 2002b), in that it does not have a thickened, broad tubercle in the upper part of each rib. It further differs in that it has more ribs, and a larger mouth relative to shell diameter (min). These (significant) differences are not diagnostic and the boundary between the two species seems rather hazy.

Melanopsis costata "non-stepped"

Fig. 3D, Tab. 5

Material examined: 23 shells.

Morphology: *Melanopsis costata* "non-stepped" differs from *M. costata* "stepped" of Al-Qarn in its conic shell, as expressed in a lower figurativity index.

Measurements: Measurements and ratios of *Melanopsis costata* "non-stepped" from Al-Qarn (n = 11) are given in Tab. 5.

Comparisons: *Melanopsis costata* "non-stepped" differs diagnostically from *M. costata* "stepped" of Al-Qarn in having a lower figurativity index. It further differs significantly in that it has a higher shell mouth compared to shell height and to shell diameter (min), is more conic, less stepped, has lower whorls and lower values of the ratio 2-rib width/shell diameter (min). Fig. 7A presents conchiometric differences between the two groups, Fig. 7B presents PCO.

Because Recent populations of *Melanopsis costata*, consisting of four different subspecies in the Levant, bridge the gap between the two groups (Figs. 7A, B), we are undecided as to whether the two Al-Qarn groups represent separate species or subspecies. To compare with a well separated fossil species, also *Melanopsis aaronsohni* of Al-Qarn is included in Fig. 7B.

Melanopsis aaronsohni BLANCKENHORN & OPPENHEIM, 1927

Fig. 3E, Tab. 6

*1927 *Melanopsis aaronsohni* BLANCKENHORN & OPPENHEIM: 37, pl. 1 figs. 14–15.

2002b *Melanopsis aaronsohni* BLANCKENHORN & OPPENHEIM, 1927. – HELLER & SIVAN: 616–618, fig. 3F.

Material: Nine shell remains.

Holotype and **type locality**: The holotype of *Melanopsis aaronsohni*, from 'Djisr el-Medjami' (= 'Erq el-Ahmar) is in the Paleontology Collection of the Hebrew University of Jerusalem.

Tab. 5. Measurements and ratios of *Melanopsis costata* "non-stepped" from Al-Qarn (n = 11).

	Range	Mean ± SD
Max. shell-height	25.6 mm	
Shell-diameter (min) / shell-height	0.45–0.51	0.48 ± 0.017
Mouth-height / shell-height	0.56–0.67	0.60 ± 0.033
Mouth-height / shell-diameter (min)	1.19–1.33	1.25 ± 0.044
e / mouth-height	0.23–0.39	0.32 ± 0.042
f / mouth-height	0.14–0.18	0.16 ± 0.011
Conicality index (a/b)	0.73–0.90	0.82 ± 0.045
Figurativity index (c/d)	0.90–0.93	0.92 ± 0.010
Shouldering index (b/c)	0.72–0.81	0.76 ± 0.028
Rib number	11–13	12.1 ± 0.83
Rib density	2–3	2.64 ± 0.45
Rib length	3.5–4	3.86 ± 0.234
2 rib width / shell-diameter (min)	0.28–0.38	0.33 ± 0.038
Rib curvature	all 0 mm	

Tab. 6. Measurements and ratios of *Melanopsis aaronsohni* from Al-Qarn (n = 9).

	Range	Mean ± SD
Max. shell-height	16.3 mm	
Shell-diameter (min) / shell-height	0.46–0.51	0.48 ± 0.021
Mouth-height / shell-height	0.52–0.65	0.57 ± 0.045
Mouth-height / shell-diameter (min)	1.11–1.21	1.19 ± 0.073
e / mouth-height	0.30–0.52	0.43 ± 0.079
f / mouth-height	0.15–0.28	0.20 ± 0.047
Conicality index (a/b)	0.78–0.89	0.83 ± 0.036
Figurativity index (c/d)	0.93–0.95	0.94 ± 0.008
Shouldering index (b/c)	0.67–0.75	0.72 ± 0.031
Rib number	13–19	12.1 ± 0.83
Rib density	3.5–6	4.47 ± 0.93
Rib length	3.5–4	3.83 ± 0.258
2 rib width / shell-diameter (min)	0.21–0.34	0.31 ± 0.041
Rib curvature (left)	0.5–1.1 mm	0.83 ± 0.207

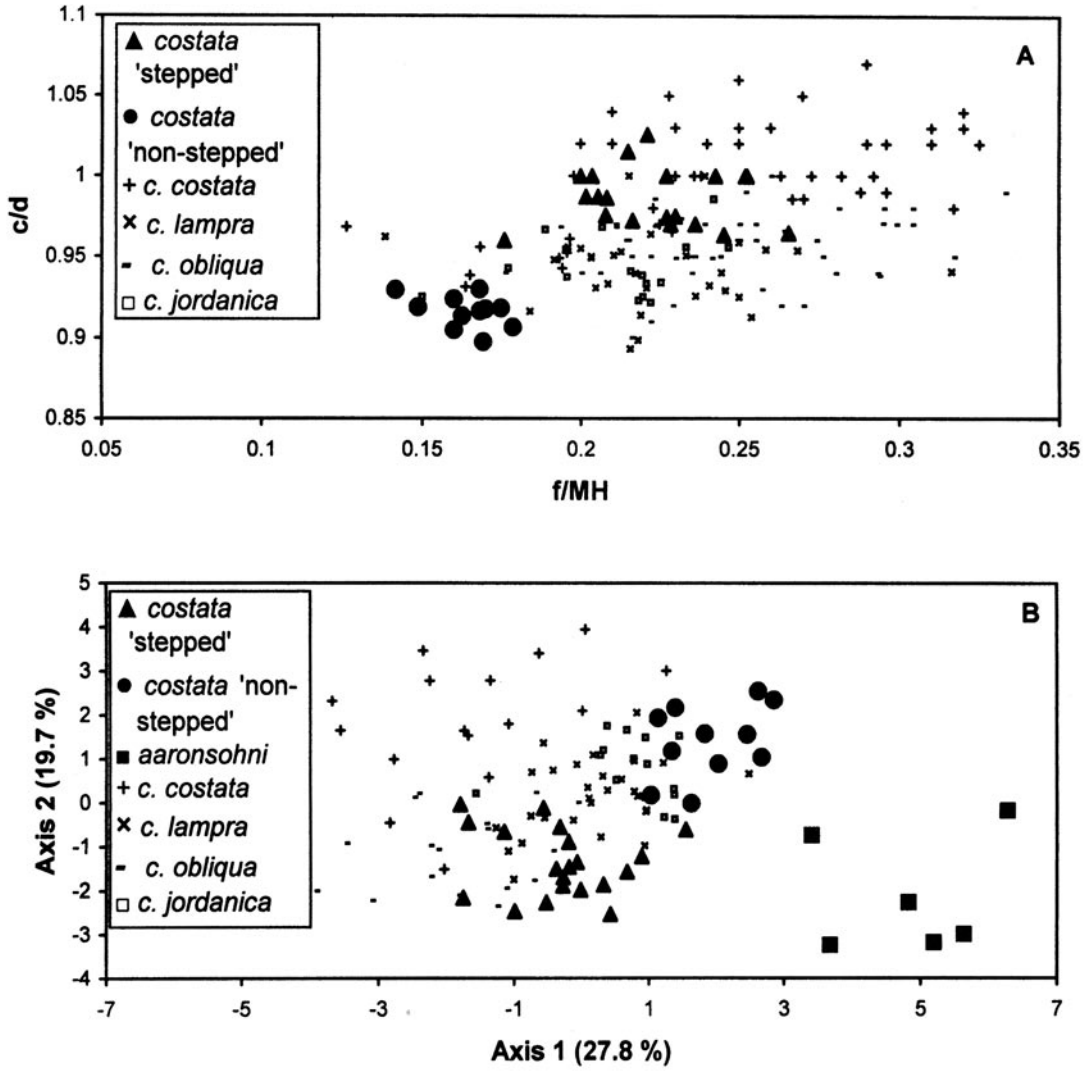

Fig. 7. A: *Melanopsis costata* "stepped" and *M. costata* "non-stepped" from Al-Qarn: Figurativity (c/d) versus relative whorl height (f/mouth-height). Also included are four Recent subspecies of *M. costata* from the Levant (*M. c. costata*, *M. c. lampra*, *M. c. obliqua* and *M. c. jordanica*). – **B**: Principal Coordinate Analysis, including all shell proportions and rib characters, of *Melanopsis costata* "stepped", *M. costata* "non-stepped" and four Recent subspecies of *M. costata* from the Levant (*M. c. costata*, *M. c. lampra*, *M. c. obliqua* and *M. c. jordanica*). Also included is *M. aaronsohni* from Al-Qarn, to illustrate a ribbed species well-separated from *M. costata*.

Occurrence: *Melanopsis aaronsohni* is known only from the Lower Pleistocene site of 'Erq el-Ahmar (BLANCKENHORN & OPPENHEIM 1927; PICARD 1934; TCHERNOV 1975; HELLER & SIVAN 2002b) and from Al-Qarn (present study).

Diagnosis: *Melanopsis aaronsohni* differs from *M. costata* of Al-Qarn in its dense, curved ribs.

Description: The shell is ovoid, with a short spire and stepped whorls. The 2–3 upper whorls are smooth and (when not eroded) form a small cone on top of the shell; the 3–4 lower whorls are ribbed. Many moderately pronounced ribs extend the entire height of each whorl; they are uniform in breadth, and lack tubercles. The lower part of each rib bends leftward. The callus is usually very bulky.

Measurements: Measurements and ratios of *Melanopsis aaronsohni* from Al-Qarn (n=9) are given in Tab. 6.

Comparisons: *Melanopsis aaronsohni* from Al-Qarn differs from *M. aaronsohni* of 'Erq el-Ahmar in that it has more ribs. The difference is significant but not diagnostic. The shell with 19 ribs is much larger than the *M. aaronsohni* of 'Erq el-Ahmar.

Melanopsis aaronsohni of Al-Qarn differs from *M. costata* "stepped" of Al-Qarn in that it is more conic (lower a/b and c/d), has more ribs which are denser, and has lower values of the ratio 2-rib width/shell diameter (min) (Fig. 8A). The ribs on the last whorl usually have a left curve, whereas in *M. costata* they are usually straight.

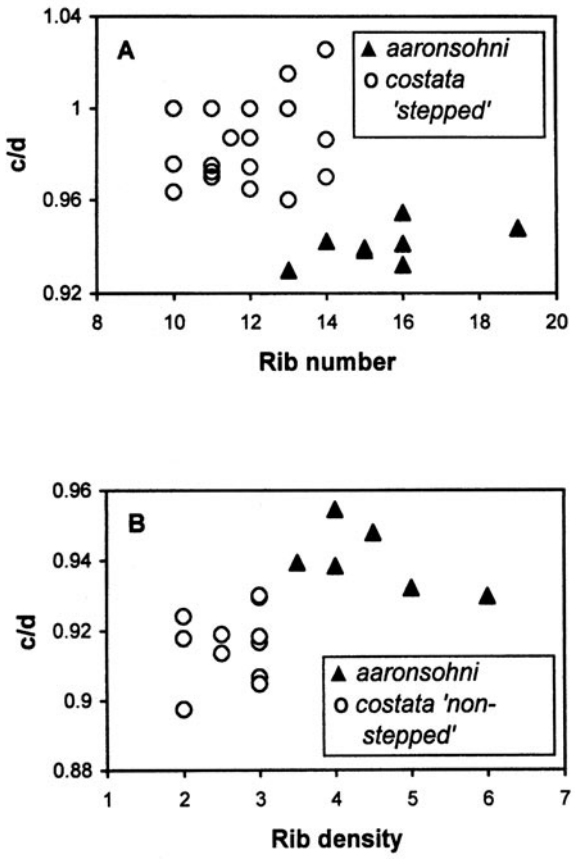

Fig. 8. Differences between *Melanopsis aaronsohni* and *M. costata*, both from Al Qarn. – **A**: *M. aaronsohni* versus *M. costata* "stepped", figurativity (c/d) versus rib number. – **B**: *M. aaronsohni* versus *M. costata* "non-stepped", figurativity (c/d) versus rib density.

Melanopsis aaronsohni of Al-Qarn differs from from *M. costata* "non-stepped" of Al-Qarn in that it has more ribs which are curved and redundant. It further has a more cylindrical shape, which is expressed by a higher figurativity index (Figs. 7B, 8B).

Discussion

Of the four *Melanopsis* species found at Al-Qarn, two are extinct (*M. aaronsohni, M. tchernovi*) whereas two occur in the Levant also today (*M. buccinoidea, M. costata*).

Within the Jordan Valley, in geographic terms, Al-Qarn is close to the upper Pliocene site of 'Erq el-Ahmar (2 Ma) and also to the lower Pleistocene lake of 'Ubeidiya (0.8–1.7 Ma; dates from HOROWITZ 2001). As illustrated in Tab. 7, three of the Al-Qarn *Melanopsis* taxa occur also in 'Erq el-Ahmar (*M. buccinoidea, M. tchernovi, M. aaronsohni*) and one does not (*M. costata*); one of the 'Erq el-Ahmar species is not found at Al-Qarn (*M. praecursor*). Two of the Al-Qarn taxa occur also in 'Ubeidiya (*M. buccinoidea, M. costata*) whereas *M. tchernovi* and *M. aaronsohni* do not; and three of the 'Ubeidiya *Melanopsis* do not occur in Al-Qarn (*M. turriformis, M. obediensis, M. multiformis*; HELLER & SIVAN 2002a). The Al-Qarn Formation thus bridges the gap in the Jordan Valley, between the aquatic fauna of the late Pliocene on the one hand and that of the early Pleistocene on the other (see also HELLER & SIVAN 2002a). We therefore suggest that the Al-Qarn Formation is intermediate, in time, between the 'Erq el Ahmar and 'Ubeidiya formations, at about 1.8 Ma. This coincides with the suggestion of HOROWITZ (2001).

Tab. 7. *Melanopsis* species at four fossil-bearing sites, Jordan Valley.

Species	'Erq el-Ahmar (2 Ma)	Al-Qarn	'Ubeidiya (0.8–1.7 Ma)	Gesher Benot Ya'aqov (0.78 Ma)
praecursor	+			
tchernovi	+	+		
aaronsohni	+	+		
buccinoidea	+	+	+	+
multiformis	+		+	
costata		+	+	+
turriformis			+	+
obediensis			+	+
corrugata				+
vincta				+
sigmocorrugata				+

In both space and time, Al-Qarn is more distant from the mid-Pleistocene lake of Gesher Benot Ya'aqov 100 km further north and dating 780,000 years ago. Two species are common to these two sites (*Melanopsis buccinoidea, M. costata*) but another five species of Gesher Benot Ya'aqov were not found at Al-Qarn (*M. obediensis* PICARD, *M. corrugata* SCHÜTT, *M. vincta* BLANCKENHORN, *M. sigmocorrugata* HELLER & SIVAN and *M. turriformis* PICARD; see HELLER & SIVAN 2001). Hydrological connections between the Upper and Central sectors of the Jordan systems thus seem to have been poor during the late Pliocene and early Pleistocene; it was only during the later Middle Pleistocene that firm links were established between both Jordan basins, following the secondary tectonic movements along the Rift Valley (HOROWITZ 2001; HELLER & SIVAN 2002a).

Acknowledgments

This study was partly funded by grant 665/02 of the Israel Science Foundation to J. HELLER. We thank Mathias Harzhauser (Naturhistorisches Museum Wien) and Dana Geary (University of Wisconsin, Madison), reviewers of this paper, for their helpful comments.

References

ADAMS, H. & ADAMS, A. 1853. The Genera of Recent Mollusca, Vol. 1. – 484 p., London (J. van Voorst).

BANDEL, K. 2000. Speciation among the Melanopsidae (Caenogastropoda). Special emphasis to the Melanopsidae of the Pannonian Lake at Pontian time (Late Miocene) and the Pleistocene and Recent of Jordan. – Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg **84**: 131–208.

BANDEL, K. & SHINAQ, R. 2003. The sea in the Jordan Rift (Northern Jordan) during Oligocene/Miocene transition with implications to the reconstruction of the geological history of the region. – Freiberger Forschungshefte **499**: 97–115.

BENDER, F. 1968. Geologie von Jordanien. Beiträge zur Regionalen Geologie der Erde **7**. – 230 p., Berlin (Gebrüder Borntraeger).

BLANCKENHORN, M. 1897. Zur Kenntnis der Süsswasserablagerungen und Mollusken Syriens. – Palaeontographica **44**: 1–144.

BLANCKENHORN, M. & OPPENHEIM, P. 1927. Neue Beiträge zur Kenntnis des Neogens in Syrien und Palästina. – Geologische und Palaeontologische Abhandlungen **15**: 321–356.

BUKOWSKI, G. 1895. Die levantinische Molluskenfauna der Insel Rhodus. Teil II. – Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse **63**: 1–70.

FÉRUSSAC, M. 1823. Monographie des espèces vivantes et fossiles du genre Mélanopside, *Melanopsis*. – Mémoire du Muséum National d'Histoire Naturelle, Paris **1**: 132–164.

GEARY, D.H. 1990. Patterns of evolutionary tempo and mode in the radiation of *Melanopsis* (Gastropoda: Melanopsidae). – Paleobiology **16**: 492–511.

GEARY, D.H. 1992. An unusual pattern of divergence between two fossil gastropods: ecophenotypy, dimorphism, or hybridization? – Paleobiology **18**: 93–109.

GEARY, D.H.; STALEY, A.W. & MÜLLER, P. 2002. Iterative changes in Lake Pannon *Melanopsis* reflect a recurrent theme in gastropod morphological evolution. – Paleobiology **28**: 208–221.

HELLER, J. & SIVAN, N. 2001. *Melanopsis* from the Mid-Pleistocene site of Gesher BenotYa'aqov (Gastropoda: Cerithioidea). – Journal of Conchology **37**: 127–147.

HELLER, J. & SIVAN, N. 2002a. *Melanopsis* from the Pleistocene site of 'Ubeidiya, Jordan Valley: direct evidence of early hybridization (Gastropoda: Cerithioidea). – Biological Journal of the Linnean Society **75**: 39–57.

HELLER, J. & SIVAN, N. 2002b. *Melanopsis* from the Pliocene site of 'Erq el-Ahmar, Jordan Valley (Gastropoda: Cerithioidea). – Journal of Conchology **37**: 607–625.

HELLER, J.; SIVAN, N. & MOTRO, U. 1999. Systematics, distribution and hybridization of *Melanopsis* from the Jordan Valley (Gastropoda: Prosobranchia). – Journal of Conchology **36**: 49–81.

HELLER, J.; MORDAN, P.; BEN-AMI, F. & SIVAN, N. 2005. Conchometrics, systematics and distribution of *Melanopsis* (Mollusca: Gastropoda) in the Levant. – Zoological Journal of the Linnean Society **144**: 229–260.

HOROWITZ, A. 2001. The Jordan Rift Valley. – 730 p., Lisse (A.A. Balkema).

HUCKRIEDE, R. 1966. Das Quartär des Arabischen Jordan-Tales und Beobachtungen über Pebble Culture und Prauringac. – Eiszeitalter und Gegenwart **17**: 211–212.

LINNAEUS, C. 1758. Systema Naturae, 10th edition, Vol. 1. – 824 p., Stockholm [Holmiæ].

OLIVIER, G.A. 1804. Voyage dans l'Empire Othoman, l'Egypte et la Perse, fait par ordre du Gouvernement, pendant les six premières années de la République, Vol. 1. – 432 p., Paris (Agasse).

OLIVIER, G.A. 1801. Voyage dans l'Empire Othoman, l'Egypte et la Perse, fait par ordre du Gouvernement, pendant les six premières années de la République, Vol. 2. – 466 p., Paris (Agasse).

PALLARY, P. 1939. Deuxième addition à la faune malacologique de la Syrie. – Memoires de l'Institut d'Egypte **39**: 1–43.

PICARD, L. 1934. Mollusken der Levantinischen Stufe Nordpalästinas (Jordantal). – Archiv für Molluskenkunde **66**: 105–139.

RIEDEL, F. 1993. Early ontogenetic shell formation in some freshwater gastropods and taxonomic implications of the protoconch. – Limnologica **23**: 349–368.

SCHÜTT, H. 1988. Ergänzungen zur Kenntnis der Molluskenfauna oberpliozäner Süsswasserkonglomerate Syriens. – Archiv für Molluskenkunde **118**: 129–143.

SCHÜTT, H. & ORTAL, R. 1993. A preliminary correlation between the Plio-Pleistocene malacofaunas of the Jordan Valley (Israel) and the Orontes Valley (Syria). – Zoology in the Middle East **8**: 69–111.

TCHERNOV, E. 1975. The Early Pleistocene mollusks of 'Erq el-Ahmar. – 36 p., Jerusalem (Israel Academy of Sciences and Humanities).

TOURNOUER, R. 1875. Diagnoses d'espèces nouvelles de Coquilles d'eau douce, recuellies par M. Gorceix dans les terrains tertiaires supérieurs de l'île de Cos. – Journal de Conchyliologie **15**: 76–78.

WILLMAN, R. 1981. Evolution, Systematik und stratigraphische Bedeutung der neogenen Süsswassergastropoden von Rhodos und Kos/Ägäis. – Palaeontographica **174**: 10–235.

Manuskripteingang / manuscript received 24. 12. 2006;
Manuskriptannahme / manuscript accepted 11. 6. 2007.