TAXONOMY OF PLIOCENE AND QUATERNARY THIARIDAE (GASTROPODA) OF ISRAEL

NAOMI SIVAN[1], FRIDA BEN AMI[2] & JOSEPH HELLER[1]

[1] Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel.
[2] Evolutionary Biology Group, Zoological Institute, University of Basel, Vesalgasse 1, CH-4051 Basel, Switzerland.

Abstract *This conchometric study explores the taxonomy of both Modern and Plio-Pleistocene Thiaridae of Israel. Modern species include* Melanoides tuberculata*, today widespread in Africa and Asia and Tarebia granifera, recently introduced via aquarist trade. Fossil species include* M. tuberculata, M. dadiana *and* M. jordanica. M. dadiana *differs from* M. tuberculata *in that it has fewer ribs and in the absence or near absence of tubercles.* M. jordanica *differs from* M. tuberculata *in that it has fewer ribs, more conic whorls and a larger aperture. It differs from* M. dadiana *in its more conic whorls, smaller aperture, shorter body whorl and more ribs.*

Key words *Fossil, Levant, Thiaridae, taxonomy*

INTRODUCTION

Thiarids are widespread and abundant aquatic gastropods. Today they are found mainly in the tropics and subtropics. From the Levant five Recent *Melanoides* species have been described, the ubiquitous *Melanoides tuberculata* (Müller) with the endemic variety *M. tuberculata* var. *elongata* Locard and four endemics, namely *M. pyramis* Busch, *M. judaica* Roth, *M. rothiana* Mousson and *M. rubropunctata* Tristram. Tristram (1865) suggested that *elongata, pyramis, judaica* and *rothiana* belong to *tuberculata* and Schütt (1982) included also *rubropunctata* in *M. tuberculata*. In Israel *M. tuberculata* is the most abundant thiarid species and it is found today in springs and streams east of Lake Kinneret, in the Bet Shean Valley (part of the Jordan Valley), in the Coastal Plain (Fig. 1) and sporadically also in Southern Israel (Ben-Ami & Heller, 2005).

In the fossil record of the Levant *M. tuberculata* is mentioned from the Pliocene of the Orontes and Pliocene-Pleistocene of the Jordan Valley ('Erq el-Ahmar and 'Ubeidiya). Two additional fossil species were also described from the Terminal Pleistocene of the Jordan, *M. jordanica* Tchernov ('Erq el-Ahmar); and *M. dadiana* Oppenheim ('Erq el-Ahmar and 'Ubeidiya, Blanckenhorn, 1897; Tchernov, 1973, 1975b). Willman (1981: 170) did not accept Tchernov's assignment of the Jordan Valley specimens to *dadiana*, but he did not explain why.

Whereas some populations of *M. tuberculata* in the Levant are exclusively parthenogenetic, in others high frequencies of males are observed. As expected, genetic homogeneity is high in parthenogenetic populations compared to bisexual populations (Livshits & Fishelson, 1983; Livshits, Fishelson & Wise, 1984). Heller & Farstay (1990) found that male frequency, which varies from 0% to 66%, is not related to trematode infection or to habitat diversity, a conclusion recently confirmed by Ben-Ami & Heller (2005). In all populations males tend to be narrower than females but the difference is too small to identify the sex of an individual specimen (Heller & Farstay, 1989). Brande, Turner, Heller & Ben-Yehuda (1996) developed a statistical differentiation method to optimally predict sex in a population of *M. tuberculata*. Theoretically, this method could be used to identify sex in samples of fossil shells. Unfortunately, the variable that contributes most to the morphological distinction between both sexes, also expresses high geographic variation (Brande et al., 1996). As variation in geographic space suggests the possibility also of variation in time, the method of Brande et al. is applicable only to fossil assemblages with a large number of shells from well-defined layers.

This present study reexamines the taxonomy of the thiarids of Israel. It differs from the previous revisions of Tchernov (1973, 1975a,b) in that it includes additional, quantitative measurements of characters of the shell. The measurements elaborated in this present paper differ from those of Samadi, David & Jarne (2000) in that they include, in addition to shell shape, also elements of shell sculpture. They differ from those of Eldblom and Kristensen (2003) in that they can be used for both Modern and Fossil shells of different size, and even fragments; and in that some characters, such as roundness of whorl and structure of whorl, are given continuous values (rather than only four categories).

Among Modern thiarids of Lake Malawi, Genner

Contact author : heller@vms.huji.ac.il

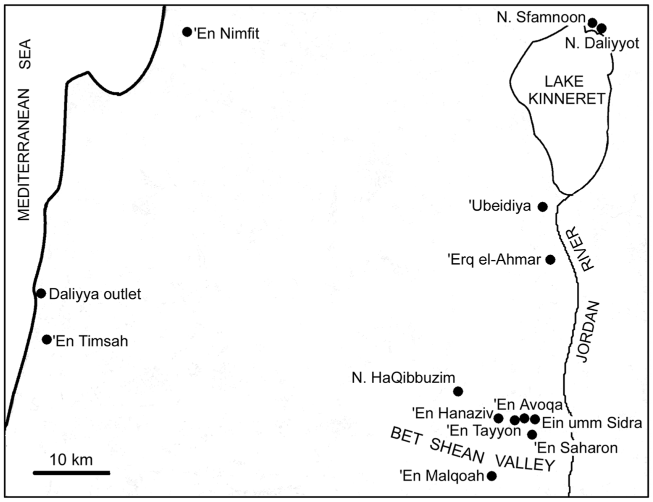

Fig. 1 Map of Northern Israel with sites mentioned in text.

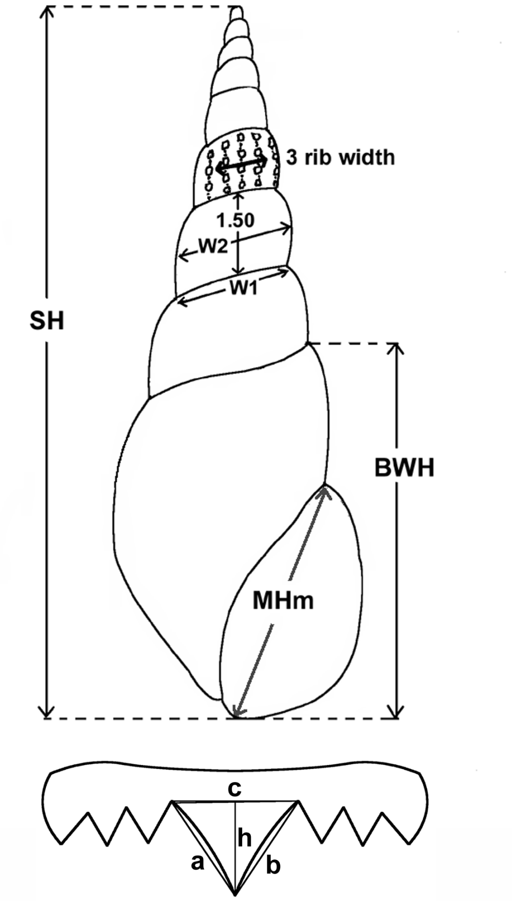

Fig. 2 Measurements used in this study. Top: Shell: SH - shell height, MHm - maximal aperture height, BWM - Body whorl height, W1, W2 - width of whorl with whorl-height 1.5 mm at lower suture and middle of whorl. Bottom: Rhachidian tooth of radula with measurements of central cusp.

et al. (2007) found that shell phenotype corresponded well with molecular genotype; and that correspondence was higher when body whorl shape was complemented by shell colour, ornamentation and sculpture. They commented that, for interpreting the fossil record of thiarids, whorl shape and aperture shape alone may be insufficient for delimiting fine-scaled sympatric units. In the fossils at our disposal shell colour and pattern were not preserved. To compensate for the lack of these two traits we utilized, as far as possible, variation in shell sculpture.

Material and Methods

Material

Modern Material (Fig. 1)
Melanoides tuberculata: Bet Shean Valley ('En Avoqa, 'En Hanaziv, 'En Malqoah, 'En Saharon, 'En Tayyon, Ein umm Sidra, N. HaQibbuzim); Coastal Plain (Dalyya outlet, 'En Nimfit, 'En Timsah), Golan heights (east of Lake Kinneret: N. Dalyyot, N. Sfamnoon).
Tarebia granifera: Bet Shean Valley ('En Avoqa, 'En Saharon, 'En Tayyon, Ein umm Sidra).
Whenever possible, 20 shells from each population were used for measures. The material was collected by J. Heller and F. Ben-Ami during 2003-2004 and deposited in the Mollusk Collection of the Hebrew University.
Melanoides anomala: SE Zaire, Kibidwila River, E of Likasi (BMNH 20041346); SE Zaire, Lac de Retenue de la Lufira (BMNH 20041348).
Melanoides victoriae: Zambesi River, Victoria Falls (BMNH 1905.2.24.51-59,1905.10.19.2-4); E Transvaal (BMNH 20041347)

Fossil material (Fig. 1)
All *Melanoides* material from 'Erq el-Ahmar and 'Ubeidiya in the Paleontological Collection of the Hebrew University was inspected. Additional material was collected by J. Heller and F. Ben-Ami at 'Erq el-Ahmar in 2001, and deposited in the collection. Since the exact sedimentary unit from which the material was derived was usually not known, all the material from 'Erq el-Ahmar was pooled. The material from 'Ubeidiya was also pooled since, although the stratigraphic position of the respective samples was known, the number of shells in each layer was too small for conchometric analysis. Whenever the (pooled) fossil material contained more than 20

Table 1 *Melanoides tuberculata*, conchometrics (mean ± SD and observed range): Modern shells from Bet She'an Valley, Coastal Plain of Israel and Golan heights (N=201, pooled from 11 sites) and Fossils from 'Erq el-Ahmar (N=25) and 'Ubeidiya (N=20, including fragments).

	Modern	Fossil	
	Israel	'Erq el-Ahmar	'Ubeidiya
Max. shell-height (mm)	21.75	28.4	20.0
SDs/SH	0.32 ± 0.022 0.27 – 0.40	0.33 ± 0.028 0.27 – 0.37	0.37 ± 0.022 0.36 – 0.40
MHm/SH	0.32 ± 0.024 0.26 – 0.41	0.34 ± 0.027 0.29 – 0.40	0.39 ± 0.032 0.36 – 0.43
MHm/SDs	0.99 ± 0.042 0.87 – 1.09	1.04 ± 0.056 0.95 – 1.15	1.06± 0.042 1.00 – 1.10
BWH/SH	0.49 ± 0.030 0.42 – 0.67	0.51 ± 0.031 0.45 – 0.57	0.58 ± 0.053 0.54 – 0.66
MHm/BWH	0.65 ± 0.022 0.60 – 0.74	0.66 ± 0.032 0.59 – 0.72	0.65 ± 0.027 0.63 – 0.68
W1/W2	0.93 ± 0.024 0.87 – 0.98	0.99 ± 0.026 0.93 – 1.02	0.97 ± 0.018 0.94 – 1.00
Number of ribs	17.95 ± 3.58 12 – 32	14.8 ± 1.494 13 - 19	15.0 ± 1.795 13 - 19
Number of ridges	5.39 ± 1.047 3 – 9	4.0 ± 0.844 3 - 5	5.7 ± 0.065 5 - 7
W1 (mm)	2.39 ± 0.159 1.9 – 2.9	2.68 ± 0.176 2.35 – 3.15	2.64 ± 0.148 2.40 – 2.85
3 ribs width	1.22 ± 0.225 0.65 – 1.9	1.51 ± 0.0.21 1.05 – 2.0	1.54 ± 0.121 1.35 – 1.75

measurable specimens, all were measured.
Melanoides tuberculata: 'Erq el-Ahmar, 'Ubeidiya (layers I-6, II-36, II-37, III-6, III-12, III-63, III-66, IV- 4).
M. dadiana: 'Erq el-Ahmar, 'Ubeidiya (layer III-22).
M. jordanica: 'Erq el-Ahmar

METHODS

Conchometrics Only grown shells (of at least 7 mm shell-height) were measured. General conchometrics include shell height (SH), minimal shell-diameter (SDs), maximal aperture-height (MHm) and height of body-whorl (BWH) (Fig. 2). From these measurements five ratios were calculated: minimal shell-diameter/shell-height, maximal aperture-height/shell-height, maximal aperture-height/minimal shell-diameter, body whorl-height/shell-height and maximal aperture-height/body whorl-height. The use of minimal shell-diameter and maximal aperture-height enables comparisons with fossil shells, where the outer lip is often broken.

Additional measurements and shell-characteristics were performed at a whorl-height of 1.5 mm, which corresponds approximately to the seventh or eighth whorl. This part of the shell is usually preserved even in shells which are damaged or broken in their upper part, as often encountered in fossils. At this point the width of the whorl was measured, both at its center (W2) and at the suture between this whorl and the whorl below (W1). The ratio W1/W2 gives an index of roundness of the specific whorl. In addition, at this same point, the number of ridges between the two sutures was counted. Also counted was the number of ribs or tubercle-rows, from this same point leftwards to a parallel point on the whorl below (namely, one whorl). In addition we measured the width of three ribs at this same point.

In live *M. tuberculata* the gonad of the male is red, while that of the female is cream or yellow. By looking at the shell under a strong light-source, it is possible to distinguish between the sexes (Heller & Farstey, 1989). This method was used for all Modern material, but could of course not be applied to fossil shells. The method of Brande et al. (1996) was not applicable to the Fossil material of the Levant, because of the small number of shells from each site, and especially from each layer within the sites.

Radula The radula of Modern *M. tuberculata* (two populations) and of *Tarebia granifera* (one population) was examined by scanning electron microscopy. We initially dissected the anterior region (head, brood pouch, and part of the foot) along the sagittal plane through the mantle and brood wall. Radular ribbons were cleaned by soaking in a bleaching solution containing sodium hypochlorite at room temperature for 24 h, followed by gentle cleaning with fine needles and thorough rinsing in distilled water. Each radula was mounted damp on a thin layer of polyvinyl acetate glue on a glass cover slip, and viewed in a JEOL 840 SEM. Subsequent measurements of 20-25 teeth from each population were performed using an Image analyzer. On the central cusp of each rhachidian tooth we recorded four measurements labeled a, b, c and h, from which we calculate the total area of the cusp (Fig. 2).

Comparative statistics Statistical comparisons between characters of individual taxa were conducted by t-test. The significant level was set at 0.05. The term "diagnostic" (rather than significant) describes lack of overlap between two different taxa, in a given character. Multivariate comparisons between the different taxa were conducted by Principal Coordinate Analysis (PCO), based on Standardized Euclidian, using the multivariate statistical package of Kovach Computing Services: MVSP. Specimens with missing data were excluded from the multivariate analysis.

Family Thiaridae

Genus ***Melanoides*** Olivier, 1804

Type species *Melanoides tuberculata* (Müller, 1774).

Diagnosis *Melanoides* differs from the type genus (*Thiara*) in that its shell lacks spines; and in that in its genitalia the connecting duct between the posterior end of the seminal receptacle and the diverticle is relatively longer, corresponding to its origin further from the posterior end of the seminal receptacle (Pace, 1973).

Description The shell is solid, mostly turreted, elongate and slender with regularly increasing whorls. The spire is high, usually twice (or more) the height of the aperture. Transverse and spiral sculpture is generally present, commonly producing a tuberculate surface. The aperture is sub-circular, the inner lip somewhat callous; the outer lip is simple.

The operculum is corneous with a basal nucleus and a few rapidly expanding whorls. The mantle border is fringed with papillae. The female has a brood pouch separated from the oviduct. Most (if not all) species are capable of parthenogenesis (Brown, 1994).

About 30 species of *Melanoides* are found in Africa, of which only *M. tuberculata* is today widespread (Brown, 1994). This number of African species is based on morphological differences that do not necessarily reflect important genetic ones (see Genner et al. 2007).

Melanoides tuberculata (Müller, 1774)
Fig. 3A, B, C, Table 1

Type Nerita tuberculata Müller 1774; vol. 2, p. 191.

Type locality Coromandel, India.

Melanoides fasciolata Olivier 1804, pl. 555 fig.7. Type locality: "du canal d'Alexandrie".
Melania rubropunctata Tristram 1865: 541. Type locality: "In fountains near the Dead Sea".
Melania tuberculata Brot 1874: 247-248, pl. 26, figs 11a-h from many sites in Africa and Asia. In the Levant: Syria, Mesopotamia and Arabia.
Melanoides tuberculata, Tchernov 1975a: 157, figs 10-11 from Sea of Galilee, Ginnosar area.
Thiara tuberculata, Pointier 1989, pl. 2 figs 5-7 from Martinique, Dominican Republic and Venezuela.

Syntypes and type locality Coromandel, India (Pointier, 1989, pl. 1 fig. 1).

Material examined Modern: Bet Shean Valley ('En Tayyon, 'En Saharon, 'En Malqoah, 'En Hanaziv, Ein umm Sidra, N. HaQibbuzim), Coastal Plain of Israel (Dalyya outlet, 'En Timsah, 'En Nimfit), Golan heights (N. Dalyyot, N. Sfamnoon). Fossil: 'Erq el-Ahmar and 'Ubeidiya, from the Paleontological

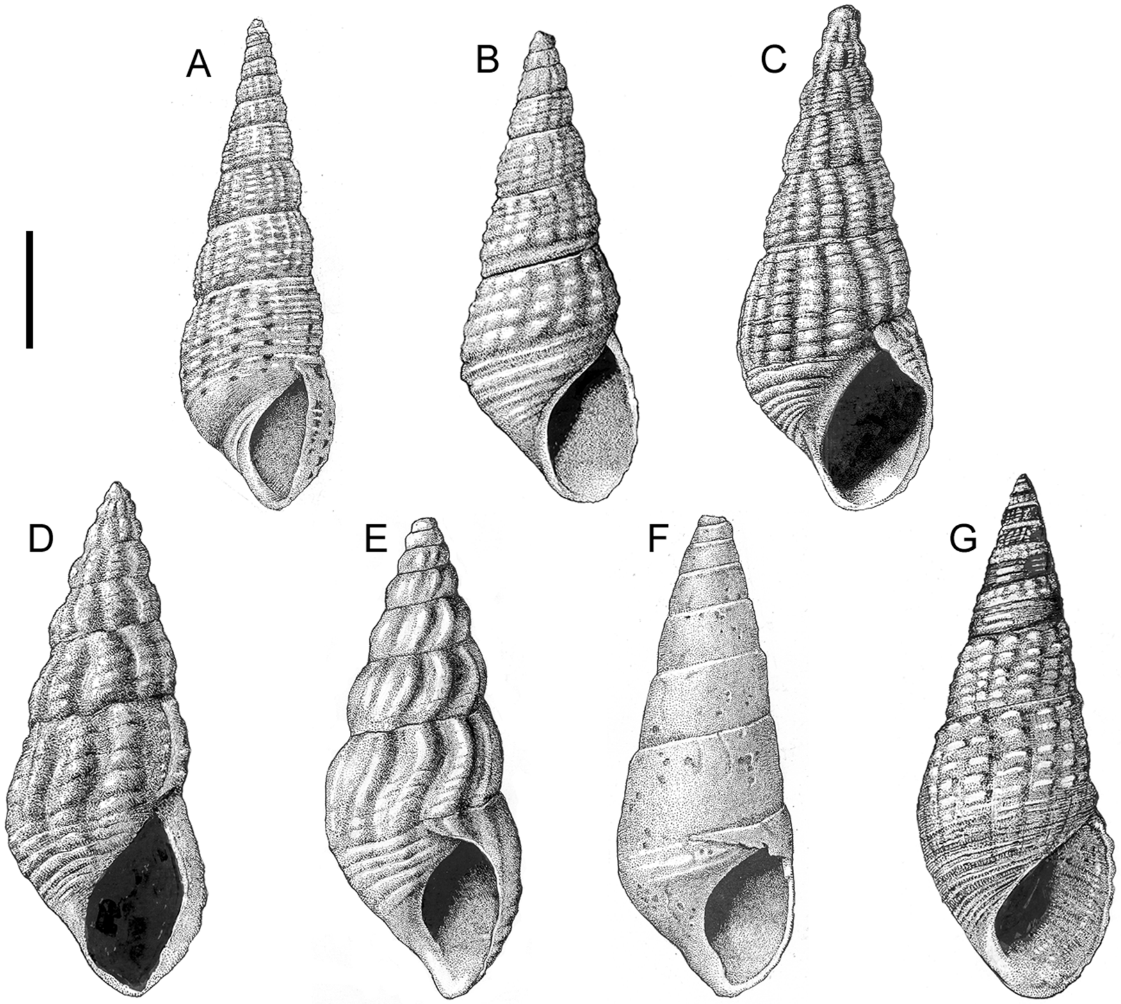

Fig. 3 Modern and Fossil *Melanoides* and *Tarebia* species of Israel: A - Modern *M. tuberculata* ('En Tayyon), B - Fossil *M. tuberculata*, 'Erq el-Ahmar, C - Fossil *M. tuberculata*, 'Ubeidiya, D - Fossil *M. dadiana*, 'Erq el-Ahmar, E - Fossil *M. dadiana*, 'Ubeidiya, F - Fossil *M. jordanica,* 'Erq el-Ahmar, G - Modern *Tarebia granifera* ('En Tayyon).

collection of the Hebrew University, Jerusalem.

Measurements Measurements and ratios of Modern and Fossil material are given in Table 1. In the Modern material we found males only in the sample from Nahal Dalyyot, where they represented 20 % of the population (similar to the result of Heller & Farstey, 1990, table 1).

Description The shell is dextral, turriform, usually with up to 14 regularly increasing, moderately rounded whorls separated by moderately impressed sutures. The typical tuberculate shell sculpture is formed by a combination of closely spaced axial ribs and spiral ridges; the ribs are usually more accentuated than the spiral ridges. At the base of the last whorl, usually only spiral sculpture is present and there are no ribs. The aperture is ovate, about one-third the shell height and two thirds of the body whorl. Shell colour is cream to gray, with reddish brown flame-like patches.

The operculum is corneous, opaque, with coarse, irregular growth lines and with the nucleus in the far bottom left corner.

In the radula the central tooth is rectangular, has one large central cusp with 4-5 lateral cusps on each side, and a pair of lateral cusps (Fig. 4A). The marginal teeth have 7-9 cusps and their shaft is shorter relative to the head (as compared to *Thiara scabra*; Pace, 1973). The first and second marginal teeth are spoon-shaped, and their anterior apical margins have about 7-9 denticles (Starmühlner & Edlauer 1957).

Geographic range Modern: *M. tuberculata* is found indigenously in much of Africa, the eastern Mediterranean, Arabia, the islands of the Indian Ocean, India, South East Asia, Malaysia, China, Japan, northern Australia and the New Hebrides. It has been introduced into USA, throughout the Neo-tropics (Pointier, Facon, Jarne & David, 2003) and New Zealand (Duggan, 2002). On the Arabian Peninsula it is the most common freshwater snail (Neubert, 1998). In the Sahara it is the only thiarid to occur (Van Damme, 1984).

Fossil: In Africa the oldest occurrence of *M. tuberculata* dates from the Middle Miocene (Van Damme & Pickford, 2003), and it was widespread throughout the Sahara during the Pleistocene-Holocene (Van Damme, 1984). From Greece, Willmann (1981: 169, tables 1-2, pl. 11 fig. 1) described and illustrated fossil *M. tuberculata* from Pliocene formations in Rhodes and Kos. From Rhodes he further described and illustrated three fossil subspecies, *M. t. destefani* (Magrograssi), *M. t. monolithica* (Bukowski) and *M. t. curvicosta* (Deshayes; see Willmann, 1981: pl. 10, figs 1-11). From Kos he described a fossil subspecies, *M. t. dadiana*, which will be discussed below under *M. dadiana*.

Pointer (1999) suggests that *M. tuberculata* originated in the Middle East and East Africa, while Van Damme & Pickford (2003) assume that it is an Asian species that invaded Africa during the Late Cenozoic.

Distribution in the Levant Modern: In Sinai *M. tuberculata* is found in isolated populations (Ein Musa, Wadi Isla, Ein Araba and Ein Hudra) that show only negligible differences in shell and radula with those from Israel (Tchernov, 1971). The occurrence of *M. tuberculata* in isolated springs of Sinai was considered by Tchernov (1975a) as evidence for the long presence of the species in the Levant, but according to Van Damme (1984) the species is spread by birds and hence can easily reach isolated waters. In Israel it has been recorded from the marshes of Kurdani, Nahal Tanninim and many other sites (Ben Ami & Heller, 2005; Heller & Farstey, 1990; Mienis, 1970; Mienis & Ortal, 1996). In Jordan it was found in various sites (Azraq Druz, Yarmouk, Nahr el Hammam, Zerqa Main near Dead Sea, el Quneiya-El Masarra, Sukhna, Deir Alla; see Burch, 1985; Schütt, 1983); in Syria it was found near Damascus, in Palmyra, and in Ceylanpinar on the Syrian-Turkish border (Germain, 1921; Pallary, 1939; Schütt, 1987; Schütt & Sesen, 1989).

In the Levant *M. tuberculata* is common in water bodies with muddy bottoms. It occurs also in waters with a salinity of up to 4000 mg Cl/l (Tchernov, 1975a) and even in streams with high concentrations of hydrogen sulphide, which is poisonous to aerobic organisms, as it inactivates the cytochrome oxidase enzyme. *M. tuberculata* may perhaps survive in these high sulphide concentrations by breathing air at the water surface (Heller & Ehrlich, 1995).

Fossil: *M. tuberculata* was described from the 2 My old Terminal Pliocene site of 'Erq el-Ahmar, in the Jordan Valley south of Lake Kinneret (Tchernov, 1975b). The 'Erq el-Ahmar fossiliferous deposits were formed in a shallow lake that persisted during a period of ca. 20,000-30,000 years (Heller & Sivan, 2002).

The Pleistocene site of `Ubeidiya, also in the Jordan Valley south of Lake Kinneret, consists of sediments of a large lake that existed 1.4 Myr ago. *M. tuberculata* was found sporadically in the lower layers of 'Ubeidiya, and in large quantities only in layer III-63, one of the younger layers (Tchernov, 1973).

M. tuberculata was also found in Pliocene deposits of the Orontes (Blanckenhorn, 1897). It is odd that *M. tuberculata* is absent in the Syrian Pleistocene as well in the Neogene and Pleistocene of Asia Minor. Tchernov (1975b), who noted this, suggested that *M. tuberculata* extended northwards into the Orontes from the Jordan Valley.

Intra-specific variation No diagnostic difference was found between the 11 populations of *M. tuberculata*. In some specific ratios significant differences were found among specific samples, but even in these cases there was an overlap. All these populations are pooled in Table 1.

As expected, the males of Nahal Dalyyot are slightly slimmer than the females from the same site, but only two of the specimens fall outside the range of the females (Fig. 5). The males are included in the Modern material of Table 1, and in the statistical comparisons between the groups.

We measured the area of the rhachidian tooth of two populations of *M. tuberculata* ('En Tayyon and 'En Saharon), and found no significant difference between them.

Between Modern *M. tuberculata* and Fossil ones from 'Erq el-Ahmar and from 'Ubeidiya, and also between the two Fossil samples, some differences are significant but none are diagnostic (Table 1).

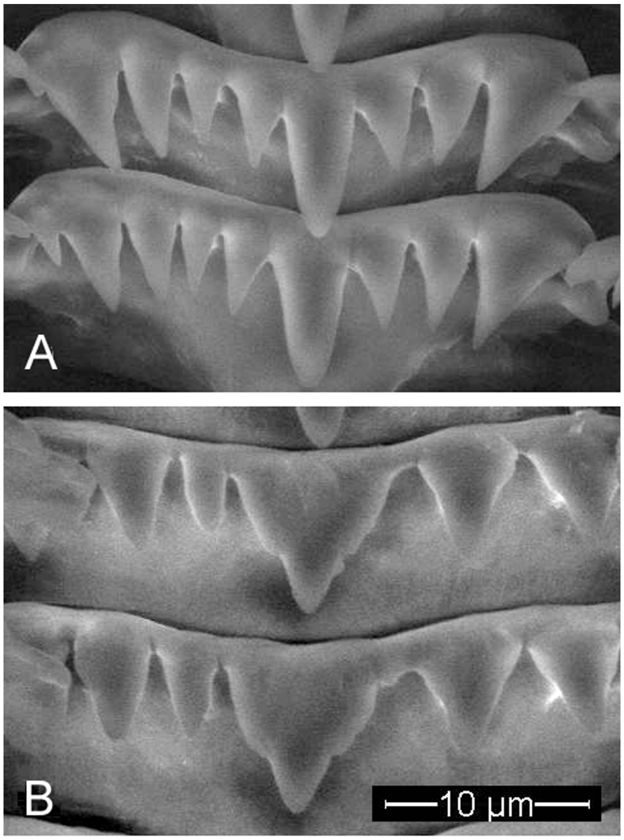

Fig. 4 SEM photographs of central tooth of radula of thiarids from Bet Shean Valley. A. *Melanoides tuberculata* from 'En Tayyon. B. *Tarebia granifera* from 'En Saharon.

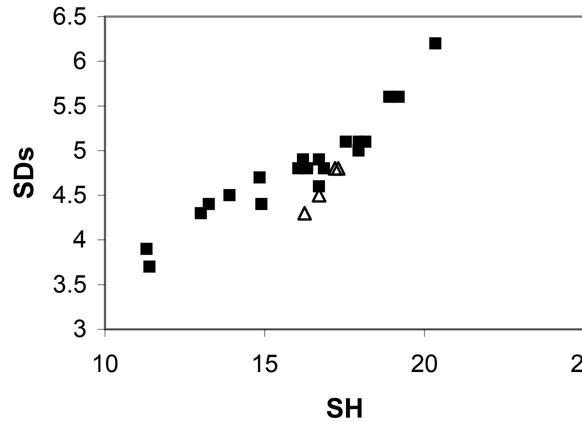

Fig. 5. Conchometric differences between male (triangles) and female (squares) *Melanoides tuberculata* of N. Dalyyot): small shell diameter versus shell height.

M. tuberculata from 'Erq el-Ahmar differs from Modern specimens in having a bigger aperture (higher ratios MHm/SH and MHm/SDs), a higher body-whorl as compared to shell-height, more conic whorls (higher value of W1 and higher ratioW1/W2), fewer ribs and higher 3 rib width, and fewer spiral ridges. The tubercles on the shells of 'Erq el-Ahmar are much more distinct than in Modern shells.

M. tuberculata from 'Ubeidiya differs from Modern specimens in being stouter (higher SDs/SH), having a bigger aperture (higher MHm/SH and MHm/SDs), higher body-whorl as compared to shell-height, more conic whorls (higher value of W1 and higher ratioW1/W2), fewer ribs and higher 3 rib width. The tubercles of the 'Ubeidiya material appear similar to those of Modern shells.

In comparison to 'Erq el-Ahmar, *M. tuberculata* of 'Ubeidiya has significantly more spiral ridges, is slightly stouter (higher SDs/SH, p=0.015) and has a slightly higher ratio MHm/SH (p=0.035).

Synonyms From `fountains near the Dead Sea', Tristram (1865: 541) described *Melania rubropunctata,* that he considered distinctive, differing from *M. tuberculata* by its smaller aperture and the absence of longitudinal sculpture on the lower whorls. The type specimen of *M. rubropunctata* is a heavily eroded shell with the apex missing. It has a small shell-diameter of 5.6 mm and a maximal aperture-height of 5.3 mm, giving a ratio MHm/SDs of 0.94. In populations of *M. tuberculata* available to us the ratio MHm/SDs ranges from 0.87 to 1.09 (mean 0.99) thereby including the ratio of *M. rubropunctata*; and longitudinal sculpture frequently is absent on the lower whorls. We therefore join Schütt (1982) in considering *M. rubropunctata* to be a synonym of *M. tuberculata.*

Remarks Tchernov (1975a) noted that in Israel *M. tuberculata* is common in all water bodies with muddy bottoms, and that saline and hot waters produce large individuals (e.g. in springs near the Dead Sea). In Malaysia *M. tuberculata* reaches a shell height of 8mm in 100 days and 15mm in 500 days (Berry & Kadri,1974); in the West Indies a shell height of 15mm is reached within less than a year, and it takes three years to reach 25mm (Pointier, Perera, Yong & Ferrer, 1991). In the laboratory mean generation time is about 12 months (Pointier, Toffart & Lefèvre, 1991). To study adaptive shell morphology, Dussart & Pointier (1999) investigated the hydrodynamic performance of various sized shells over a range of flow rates; their findings were inconclusive.

Table 2 *Melanoides dadiana*, conchometrics (mean ± SD and observed range): Fossils from 'Erq el-Ahmar (N=13) and 'Ubeidiya (N=27).

	'Erq el-Ahmar	'Ubeidiya
Max. shell-height (mm)	20.1	15.1
SDs/SH	0.39 ± 0.038 0.34 – 0.47	0.41 ± 0.025 0.38 – 0.48
MHm/SH	0.40 ± 0.019 0.37 – 0.44	0.41 ± 0.022 0.38– 0.48
MHm/SDs	1.04 ± 0.091 0.94– 1.25	1.00 ± 0.028 0.96– 1.06
BWH/SH	0.59 ± 0.025 0.56 – 0.63	0.60 ± 0.023 0.56 – 0.63
MHm/BWH	0.68 ± 0.011 0.67 – 0.70	0.67 ± 0.025 0.63 – 0.74
W1/W2	0.96 ± 0.020 0.92 – 1.00	0.96 ± 0.018 0.93 – 1.00
Number of ribs	9.9 ± 1.46 8 – 12	10.3 ± 1.38 8 - 13
Number of ridges	0 - 7	0 - 3
W1 (mm)	2.98 ± 0.163 2.60 – 3.20	2.96 ± 0.200 2.55 – 3.25
3 ribs width (mm)	2.42 ± 0.283 2.10 – 2.85	2.27 ± 0.284 1.75 – 2.85

M. tuberculata exhibits extensive variation in shell color and sculpture, some of which is heritable and allows the definition of discrete entities (`morphs', Pointier 1989), each corresponding to a single genetic clone and separate from other morphs by substantial genetic differences (Samadi, Mavarez, Pointier, Delay & Jarne, 1999). Shell shape, on the other hand, is not associated with genetic units and is therefore not sufficient to infer genetic changes from the fossil record (Samadi et al., 2000; these authors define shape as the ratio between shell height and shell diameter).

Melanoides dadiana Oppenheim, 1918
Fig. 3D, E, Table 2

Type *Melanoides dadiana* Oppenheim, 1918; pl. 2 fig. 6.

Type locality Neogene of Dadia, Asia Minor.
Melanoides dadiana, Tchernov 1973, pl. 5, figs 1-4 from 'Ubeidiya.
Melanoides dadianus, Tchernov 1975b, pl. 2, fig. 7 from 'Erq el-Ahmar.

Material examined Fossil material from `Erq el-Ahmar and `Ubeidiya in the Paleontological collection of the Hebrew University, Jerusalem.

Measurements Measurements and ratios of *M. dadiana* from `Erq el-Ahmar and `Ubeidiya are given in Table 2.

Diagnosis *M. dadiana* differs from *M. tuberculata* in that it has only 8-12 ribs (at whorl height 1.5mm).

Description The shell is robust. The whorls are rounded with distinct, sparsely spaced ribs, which are not tuberculate or only weakly so. The number of ribs per whorl does not increase with growth of the shell. The ribs flatten towards the upper suture. The aperture is large.
Geographic range In Israel *M. dadiana* is found in `Erq el-Ahmar and in `Ubeidiya; it has also been recorded from Neogene deposits of Rhodes and from Asia Minor (Tchernov, 1973, 1975b).

Comparisons There is no significant difference between the *dadiana* assemblage of 'Erq el-Ahmar and that of 'Ubeidiya.

In the 'Erq el-Ahmar deposits *M. dadiana* differs diagnostically from *M. tuberculata* in having fewer ribs and a higher 3-rib width. In addition it is significantly more robust, has bigger aperture as compared to shell-height and body-whorl height, has a larger body whorl height as compared to shell height, has more rounded whorls (lower W1/W2) and higher W1.

In the 'Ubeidiya deposits M *dadiana* differs from M *tuberculata* by the significantly fewer ribs, higher W1 and lower 3 rib width.

When all the material is taken into consideration (Fossil *dadiana* as compared to Modern and Fossil *tuberculata*), *M. dadiana* differs from *M. tuberculata* in that it is significantly more robust (lower SDs/SH); has a larger aperture (higher MHm/SH and MHm/BWH); has lower BWH/SH; has more rounded whorls (lower W1/W2), higher W1, and higher 3 tubercle width. It further differs in the absence, or near absence of tubercles. Our conchometrics are broadly close to those of Tchernov 1975b (table 4), with the exception that for the ratio body-whorl height/ shell length, Tchernov obtained a mean value of 0.52, whereas we obtained 0.60.

Tchernov (1973) noted that the principal difference between *M. tuberculata* and *M. dadiana* is that *M. tuberculata* has a larger number of whorls (twelve), which slowly and regularly increase in diameter. Its conspicuous transversal keels and longitudinal ribs give the impression of tuberculation.

Tchernov (1973, 1975b), who discussed in length the synonymy of *M. dadiana*, commented that while in Asia Minor and the Orontes system *M. dadiana* had already become extinct during the Pliocene, along the Jordan it appeared only at the beginning of the Pleistocene, where it persisted until the early Middle Pleistocene to vanish shortly after. It never reached the Upper Jordan Valley. In `Ubeidiya it significantly outnumbers *M. tuberculata* in the lower members of the formation; towards the later cycles, *M. dadiana* gradually rarifies.

Melanoides dadiana has been described and illustrated by Willmann (1981: 170, tables 2, pl. 11 figs. 2-8) as *Melanoides tuberculata dadiana* from the Vakasia, Irakli and Elia formations in Kos and from the Neogene of Datca (Turkey). Willmann states that *dadiana* is not a synonym of *Melania dadiana* Tchernov 1973 (`Ubeidiya) nor of *Melanoides dadiana* Tchernov 1975b ('Ubeidiya and 'Erq el-Ahmar) yet he gives no evidence to support his statement.

Melanoides dadiana somewhat resembles Modern *M. anomala* Dautzenberg & Germain 1914 from Zaire as described and illustrated by Brown (1994: 105, fig. 51 e, not fig. 51 i). However, specimens of *M. anomala* differ from *M. dadiana* in having a smaller aperture relative to shell-height (SDs/SH = 0.36) and to body-whorl height (MHm/BWH=0.66); in having a smaller body-whorl height relative to shell-height (BWH/SH=0.54); and in having a different rib sculpture.

Melanoides jordanica Tchernov 1975
Fig. 3F, Table 3

Type *Melanoides jordanicus* Tchernov, 1975b, p. 24, pl. III: 3.

Syntypes and type locality The Holotype (HUJ-19-21/30/162; Tchernov 1975b, pl. III, fig. 3) and Paratypes (HUJ-22-25/3/162; 19-32/194) are from the Terminal Pleistocene of `Erq el-Ahmar, Jordan Valley, Israel.

Material examined Material in the Paleontological collection of the Hebrew University, Jerusalem; and specimens collected by us at the type locality.

Measurements Measurements and ratios of *M. jordanica* from `Erq el-Ahmar are given in Table 3.

Diagnosis *M. jordanica* differs from *M. tuberculata* in that it nearly always possesses less than 13 ribs (as counted at 1.5mm whorl height). *M. jordanica* differs from *M. dadiana* in that it possesses conic whorls ($W1/W2 \geq 1$) with shallow sutures, while the whorls of *dadiana* are rounded ($W1/W1 \leq 1$) and separated by deep sutures.

Description The shell is broadly conical, usually with regularly increasing flat, conic whorls, separated by very shallow sutures. Ornamentation, when present, consists of a few, sparsely spaced, weak ribs (at 1.5mm whorl height, usually 8- 11 ribs; in some shells, however, rib number may reach 16). The ribs are not tuberculate, or only weakly so.

Geographic range *M. jordanica* is known only from the type locality, `Erq el- Ahmar (Israel).

Comparisons In addition to the above cited difference in the number of ribs, *M. jordanica* differs from *M. tuberculata* also in the weaker ribs and the more conic whorls (higher W1/W2). Although these differences are not diagnostic, they are significant. In the `Erq el-Ahmar deposits *M. jordanica* is nearly smooth, whereas *M. tuberculata* is heavily tuberculate.

In addition to the distinctive conic shape, *M. jordanica* differs significantly from *M. dadiana* also in having smaller SDs/SH, MHm/SH, MH/SDs, BWH/SH, W1 and 3 rib width. Further, *M. jordanica* is nearly smooth, while *M. dadiana* has distinct ribs.

Tchernov (1975b) states that *M. jordanica* specimens are characterized by a conspicuous

Table 3 Conchometrics of Fossil *Melanoides jordanica* from 'Erq el-Ahmar (N=27), and Modern *M. victoriae* from Transvaal and Victoria Falls (N= 10; mean ± SD and observed range):

	M. jordanica	*M. victoriae*
Max. shell-height (mm)	25.0	27.5
SDs/SH	0.34 ± 0.031 0.27 – 0.39	0.35 ± 0.016 0.32 – 0.36
MHm/SH	0.37 ± 0.029 0.27 – 0.42	0.35 ± 0.018 0.32 – 0.37
MHm/SDs	1.08 ± 0.083 0.89– 1.35	0.98 ± 0.046 0.92 – 1.08
BWH/SH	0.55 ± 0.026 0.46 – 0.59	0.54 ± 0.026 0.51 – 0.58
MHm/BWH	0.66 ± 0.033 0.59 – 0.72	0.64 ± 0.018 0.62 – 0.67
W1/W2	1.03 ± 0.018 1.00 – 1.05	1.06 ± 0.026 1.04 – 1.10
Number of ribs	10.8 ± 1.44* 8 – 13	
Number of ridges	4.1 ± 0.29* 4 – 5	
W1 (mm)	2.85 ± 0.114 2.65 – 3.05	2.94 ± 0.205 2.62 – 3.18
3 ribs width	2.1 ± 0.198 1.65 – 2.50	

* Only shells which were not completely smooth

Table 4 *Tarebia granifera*, conchometrics (mean ± SD and observed range): Modern shells from Bet She'an Valley (N=46, pooled from four sites).

	T. granifera
Max. shell-height (mm)	24.45
SDs/SH	0.37 ± 0.018 0.32 – 0.40
MHm/SH	0.41 ± 0.019 0.38 – 0.45
MHm/SDs	1.13 ± 0.007 1.08 – 1.24
BWH/SH	0.60 ± 0.039 0.54 – 0.74
MHm/BWH	0.69 ± 0.039 0.53 – 0.73
W1/W2	1.03 ± 0.022 1.00 – 1.08
Number of ribs	13.6 ± 1.38 11 - 17
Number of ridges	4.8 ± 0.64 4 – 6
W1 (mm)	3.16 ± 0.25 2.60 – 3.75
3 ribs width (mm)	1.86 ± 0.317 1.30 – 2.65

transversal ridge near the shoulder of each whorl, immediately below the suture; and that a few transversal keels are present at the base of the body whorl. However, we do find these characters also in *M. tuberculata*. He also points out that *M. tuberculata* is slender and tall whereas *M. jordanica* is low and broad, but his inclusion of his "short form" of *M. tuberculata* in this species (Tchernov, 1975b, pl. 3, fig. 1) renders this character useless for classification.

We have difficulties in comparing our conchometrics with those presented by Tchernov (1975b) in his table 4. Tchernov found that in the ratio greater diameter/length, *jordanica* reaches a mean value of 0.40 (versus 0.29 for *M. tuberculata*). We, in using a closely similar ratio (minimum shell diameter/shell height) obtained a mean of 0.34 for *M. jordanica* versus 0.33 for *tuberculata* (not a significant difference). Tchernov found that in the ratio aperture length/length, *jordanica* reaches a mean value of 0.43 (versus 0.29 in *tuberculata*); we, in using this same ratio (here named aperture-height/shell height) reached a mean value of 0.37 for *jordanica*, versus 0.34 in *tuberculata* - a significant, but much smaller difference. Tchernov found that in the ratio body whorl length/length, *jordanica* reaches a mean value of 0.60 (versus 0.43 in *tuberculata*); we, in using this same ratio (here named body-whorl height/shell height) obtained a mean value of 0.54 in *jordanica*, versus 0.51 in *tuberculata* - a significant, but much smaller difference.

M. jordanica is closely similar to *M. victoriae* Dohrn 1865 as described and illustrated by Brown (1994: 110-11, fig. 51 f-h) from Transvaal and the Victoria Falls, and which occurs also in South Africa (de Kock & Wolmarans, 2005). These two species differ significantly, but not diagnostically, in the ratios MHm/SDs and MHm/BWH (Table 3). The PCO of these two species shows an overlap (Fig. 6). *M. jordanica* may be a synonym of *M. victoriae* but we postpone this decision until further knowledge is gained as to the morpho-

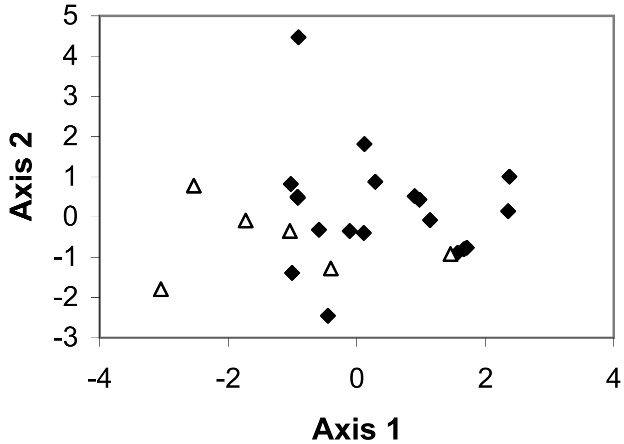

Fig. 6. Principal coordinate analysis (Axis 1 = 34.6%, Axis 2 = 30.2%) of *Melanoides jordanica* of ‘Erq el-Ahmar (full rhombs) versus *M. victoriae* of Africa (open triangles).

logical range of *M. victoriae* and the distribution of *Melanoides* species in Africa during the Plio-Pleistocene.

Comments Tchernov (1975b), in describing *M. jordanica,* commented that this species shows closer affinities with the Asia Minor - Rhodes group than with *M. tuberculata*; and that it is probably of Sarmatic origin, while *M. tuberculata* is essentially a widespread Palaeotropical element. He suggested that *M. jordanica* could have undergone speciation within the Jordan Valley, or during its course of migration from the north.

In fossil *Melanoides*, where two or three species coexisted, it is important to have diagnostic characters which can be used to identify the species from each site or period. Fig. 7A presents a combination of two characters, 3 rib width and W1/W2, which can be measured also on shell fragments, and can be used to classify shells from ‘Erq el-Ahmar as belonging to one of the three species at this site. Fig. 7B presents a combination of 3rib width and rib number, which can be used to classify shells from ‘Ubeidiya as belonging to one of the two species at this site.

Genus ***?Tarebia*** H. and A. Adams, 1854

Genotype *Tarebia semigranosa* (von dem Busch 1842) by subsequent designation (Morrison 1952, 1954).

Diagnosis “Shell ovato-fusiform, whorls granulose or tessellated with nodules; outer lip sinuated towards the hind part; interior of aperture often furnished with spiral grooves” (H. Adams and A. Adams, 1853: 303-304).

Comments The vague generic position of *Tarebia* may be due to the absence of a clear diagnosis in the original description of “sub-gen. *Tarebia*”. This vagueness is reflected in the current literature, in which there is considerable inconsistency as to the taxonomic position to which *granifera*, the most widely described species within *Tarebia,* is assigned. Thus Pointier (1989), Pointier, Samadi, Jarne & Delay (1998) and Samadi *et al.* (2000) assign *granifera* to *Thiara* sensu stricto, Abbott (1952) and Pace (1973) to *Thiara* (subgenus *Tarebia*), Pointier (2001) to *Tarebia* and Supian & Ikhwanuddin (2002) to *Melanoides*. Similarities in the structure of the protoconch suggest to Bandel & Kowalke (1997) a close relation between *Melanoides* and *Tarebia*. Only a comprehensive study of the Thiaridae would serve to solve the precise generic/sub-generic status of *Tarebia*. Since such a study is beyond the scope of this present research, and since only two genera are involved in this study; we provisionally accept the current use of *Tarebia* as a genus.

Tarebia granifera (Lamarck, 1822)
Fig. 3G, Table 4

Type *Melania granifera* Lamarck, 1822: 167.
Type Locality The island of Timor (Lamarck, 1822).
Thiara granifera, Pointier, 1989: 207, pl. 1, fig. 2 from Timor.
Material examined Bet Shean Valley (‘En Avoqa, ‘En Saharon, ‘En Tayyon and Ein umm Sidra).

Measurements Measurements and ratios of *T. granifera* from Israel are given in Table 4.

Diagnosis *Tarebia granifera* differs from *M. tuberculata* in that each whorl is flat, rather than rounded; this difference is expressed in higher values of the ratio W1/W2.

Description The shell is in shape of a moderate cone with regularly increasing nearly flat whorls, separated by moderately impressed, slightly irregular sutures. The body whorl reaches about 60% of the shell height. Shell sculpture consists of five

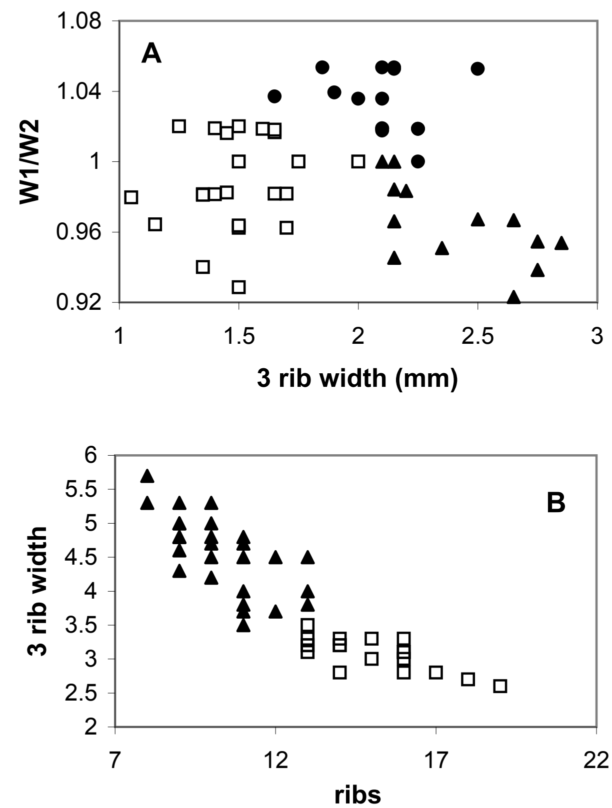

Fig. 7 A. Conchometric differences between *Melanoides tuberculata* (open squares), *M. dadiana* (full triangles) and *M. jordanica* (full circles) of 'Erq el-Ahmar: 3 rib width versus the ratio W1/W2. B. Conchometric differences between *Melanoides tuberculata* (open squares) and *M. dadiana* (full triangles) of 'Ubeidiya: 3 rib width versus rib number.

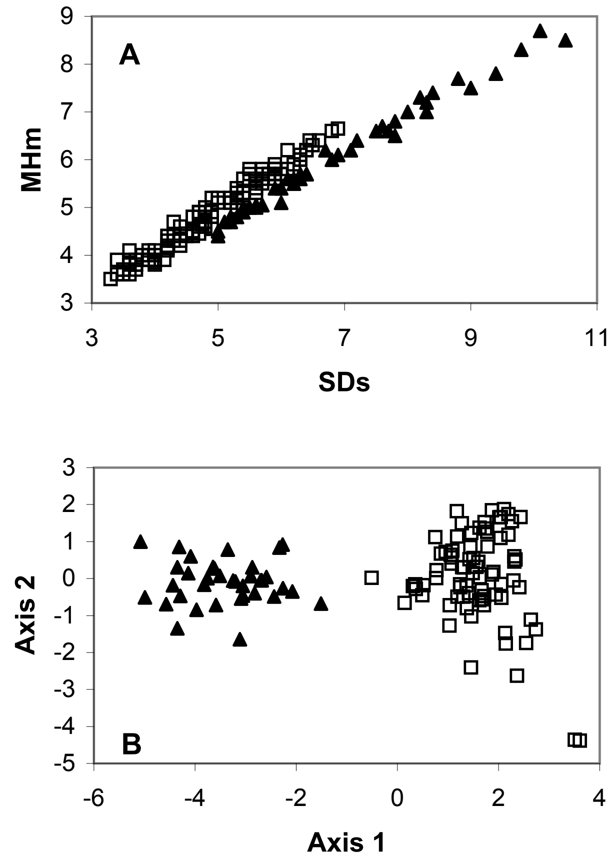

Fig. 8 *Tarebia granifera* (full triangles) versus *Melanoides tuberculata* (open squares) of the Bet Shean Valley: A. Conchometric differences: maximal aperture-height versus small shell-diameter. B. Principal coordinate analysis (Axis 1 = 66.6%, Axis 2 = 12.8%).

spiral ridges, covered with round to rectangular beads that give the shell a nodular appearance. The last whorl, including the base of shell, bears 10 to 14 spiral ridges; of which the upper half bear beads whereas the lower half are simple, raised ridges without beads. In each whorl, the beads of the top row have a tendency to become more pointed than those beneath. Sometimes the beads of successive ridges combine to some extent, thereby forming axial ribs. The aperture is moderately ovate, more than one-third the shell height, and its outer lip is thin. Shell color is yellowish brown, sometimes inlaid with a few small, red-brown blotches.

The operculum is elongate, corneous, opaque, paucispiral, with the nucleus placed in the far bottom left corner.

In the radula the central tooth is rectangular, has one large central cusp with 3-4 lateral cusps on each side, (Fig. 4B). The marginal teeth have 7-9 cusps.

Comparisons We compare *Tarebia granifera* with Modern *Melanoides tuberculata* of the Bet Shean Valley, as this is where these two species co-occur.

In addition to its more conic whorls (expressed in higher values of the ratio W1/W2), *T. granifera* differs almost diagnostically from *M. tuberculata* in the ratio aperture-height/shell-diameter, which is higher (Table 4, Fig. 8A). It is also stouter (SD reaches 39% of shell height, versus 35 % in *M. tuberculata*) its aperture is bigger relative to shell-height (MHm reaches 41 % of SH, versus only 32 % in *M. tuberculata*), rib density is lower and each whorl has fewer ridges. The PCO of Fig. 8B clearly separates *T. granifera* from *M. tuberculata*.

We compared the radula of *T. granifera* (from 'En Saharon) to that of *M. tuberculata*. The area of the rhachidian tooth of *T. granifera* is significantly larger than that of *M. tuberculata* (58.8 μm^2 versus 26.1-33.8 μm^2)

Comments *Tarebia granifera*, was recently introduced into the Bet Shean Valley presumably by aquarist trade; it is found in a handful of springs, together with *Melanoides tuberculata*. Similarly *T. granifera* was accidentally introduced from the Far East into Texas, in 1935. From there it rapidly spread through the southern USA, Porto Rico, Cuba, Venezuela and the French West Indies (Pointier, Facon, Jarne & David, 2003). In the Caribbean it has a powerful restraining influence on populations of *Biomphalaria glabrata*, the major intermediate host of *Schistosoma mansoni* (Pointier & Augustin, 1999; Prentice 1983). In Martinique, where *T. granifera* co-occurs with *M. tuberculata,* it rapidly outnumbers the latter (Pointier et al.1998). *T. granifera* serves as the intermediate host of the trematode *Philopthalmus megalurus,* which infects the nictating membrane of aquatic birds (Jacobson, 1975).

Acknowledgements

This study was supported by grant 665/02 of the Israel Science Foundation.

The specimens for this research were collected under permit no. 6094 from the Authority of Nature Reserves and National Gardens.

References

Abbott RT 1952 A study of an intermediate snail host (*Thiara granifera*) of the oriental lung fluke (*Paragonimus*) *Proceedings of the United States National Museum* 102: 71-116.

Adams H & Adams A 1853 *The Genera of Recent Mollusca* John Van Voorst, London, 3 volumes.

Bandel K & Kowalke T 1997 Eocene *Melanotarebia* n.g. and its relation among modern Thiaridae (Caenogastropoda: Cerithioidea) *Neues Jahrbuch für Geologie und Paläontologie* 11: 683-695.

Ben-Ami F & Heller J 2005 Spatial and temporal patterns of parthenogenesis and parasitism in the freshwater snail *Melanoides tuberculata Journal of Evolutionary Biology* 18: 136-146.

Berry AJ & Kadri AH 1974 Reproduction in the Malayan freshwater cerithicean gastropod *Melanoides tuberculata Journal of Zoology, London* 172: 369-381.

Blanckenhorn M 1897 Zur Kenntnis der Süswasserablagerungen und Mollusken Syriens *Palaeontographica* 44: 1-144.

Brande S, Turner M, Heller J & Ben-Yehuda O 1996 Statistical discrimination of sex in *Melanoides tuberculata* (Gastropoda: Thiaridae) *Biological Journal of the Linnean Society* 59: 87-112.

Brown D 1994 *Freshwater Snails of Africa and their Medical Importance.* Taylor and Francis, London, 608pp.

Brot A 1874 Die Melaniaceen (Melaniidae) in Abbildungen nach der Natur mit Beschreibungen *In* FMH Martini & JH Chemnitz (eds) Systematisches Conchylien-Cabinet 1: 1-488 Bauer & Raspe, Nürnberg.

Burch JB 1985 *Handbook on schistosomiasis and other snail-mediated diseases in Jordan* University of Michigan, Ann Arbor and Ministry of Health, Amman, 224 pp.

De Kock KN & Wolmarans CT 2005 Distribution and habitats of *Bulinus depressus* and possible role as intermediate host of economically important helminth parasites in South Africa *Water SA* 31: 491-496.

Duggan IC 2002 First record of a wild population of the tropical snail *Melanoides tuberculata* in New Zealand natural waters *New Zealand Journal of Marine and Freshwater Research* 36: 825-829.

Dussart GBJ & Pointier J-P 1999 A comparative study of the hydrodynamic performance of shells of *Thiara granifera* (Lamarck, 1922) and *Melanoides tuberculata* (Müller, 1774) *Malacological Review* supplement 8:19-29.

Eldblom C & Kristensen T 2003 A revision of the genus *Melanoides* (Gastropoda: Thiaridae) in Lake Malawi. *African Zoology* 38: 357-369.

Genner MJ, Todd JA, Michel E, Erpenbeck D, Jimoh A, Joyce DA, Piechocki A & Pointier J-P 2007 Amassing diversity in an ancient lake: evolution of a morphologically diverse parthenogenetic gastropod assemblage in Lake Malawi *Molecular Ecology* 16: 517-530.

Germain L 1921 *Mollusques terrestres et fluviatiles de Syrie.* 2 vols, Baillière et Fils, Paris, 523 pp.

Heller J & Ehrlich S 1995 A freshwater prosobranch, M*elanoides tuberculata*, in a hydrogen sulphide stream *Journal of Conchology* 35: 237-241.

Heller J & Farstey V 1989 A field method to separate males and females of the freshwater snail *Melanoides tuberculata Journal of Molluscan Studies* 55: 427-429.

Heller J & Farstey V 1990 Sexual and Parthenogenetic populations of the freshwater snail *Melanoides tuberculata* in Israel *Israel Journal of Zoology* 37: 75-87.

Heller J & Sivan N 2002 *Melanopsis* from the Pliocene site of 'Erq el-Ahmar, Jordan Valley (Gastropoda: Cerithioidea) *Journal of Conchology* 37: 607-626.

Jacobson MK 1975 The freshwater prosobranch, *Tarebia granifera*, in Oriente, Cuba *Nautilus* 89:106.

Lamarck JBPA de M de 1822 *Histoire Naturelle des Animaux sans Vertèbres* Verdière, Paris. (7 vols).

Livshits G & Fishelson L 1983 Biology and reproduction of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia) in Israel *Israel Journal of Zoology* 32: 21-35.

Livshits G, Fishelson L & Wise GS 1984 Genetic similarity and diversity of parthenogenetic and bisexual populations of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia) *Biological Journal of the Linnean Society* 23: 41-54.

Mienis HK 1970 Some notes on freshwater Mollusca from the marshes of Kurdani, Galilee *Argamon* 1: 51-54.

Mienis HK & Ortal R 1996 Freshwater and amphibious molluscs collected during the Nahal Tanninim Campaign - 1986. In R. Einav & Y. Sharon (eds): Nahal Tanninim, 80-89, Jerusalem.

Morrison JPE 1952 World relations of the Melanians *American Malacological Bulletin and Report* 18:6-9.

Morrison JPE 1954 The relationships of Old and New world Melanians. *Proceedings of the United States National Museum* 103: 357-394.

Müller OF 1774 *Vermium terrestrium et fluviatilium* Havniae and Lipsidae, Copenhagen, 349pp.

Neubert E 1998 Annotated checklist of the terrestrial and freshwater mollusks of the Arabian Peninsula with descriptions of new species *Fauna of Arabia* 17: 333-461.

Olivier GA 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. 2., Agasse, Paris, 466 pp. Paris.

Oppenheim P 1918 Das Neogen in Kleinasia *Zeitschrift der Deutchen Geologischen Gesellschaft* 70: 1-210.

Pace GA 1973 The freshwater snails of Taiwan (Formosa) *Malacological Review, Supplement* 1: 1-118.

Pallary P 1939 Deuxième addition à la faune malacologique de la Syrie *Mémoires de l'Institut d'Egypte* 39: 1-43.

Pointier JP 1989 Conchological studies of *Thiara (Melanoides) tuberculata* (Mollusca: Gastropoda: Thiaridae) in the French West Indies *Walkerana* 3: 203-209.

Pointier JP 1999 Invading freshwater gastropods: some conflicting aspects for public health *Malacologia* 41: 403-411.

Pointier JP 2001 Invading freshwater snails and biological control in Martinique Island, French West Indies *Memórias do Instituto Oswaldo Cruz* 96: 67-74.

Pointier JP & Augustin D 1999 Biological control and invading freshwater snails. A case study *Comptes rendus de l'Académie des sciences* 322: 1093-1098.

Pointier JP, Toffart JL & Lefèvre M 1991 Life tables of freshwater snails of the genus *Biomphalaria* (*B. glabrata, B. alexandrina, B. straminea*) and of one of its competitors *Melanoides tuberculata* under laboratory conditions *Malacologia* 33:43-54.

Pointier JP, Facon B, Jarne P & David P 2003 Les thiaridés, des gastéropodes envahisseurs des eaux douces tropicales *Xenophora* 104: 14-20.

Pointier JP, Perera G, Yong M & Ferrer JR 1991 Growth studies of some freshwater prosobranchs from West Indies *Proceedings of the Tenth International Malacological Congress (Tubingen 1989)* pp. 233-237.

Pointier JP, Samadi S, Jarne P & Delay B 1998 Introduction and spread of *Thiara granifera* (Lamarck, 1822) in Martinique, French West Indies *Biodiversity and Conservation* 7: 1277-1290.

Prentice MA 1983 Displacement of *Biomphalaria glabrata* by the snail *Thiara granifera* in field habitats in St. Lucia, West Indies *Annals of Tropical Medicine and Parasitology* 77: 51-59.

Samadi S, David P & Jarne P 2000 Variation of shell shape in the clonal snail *Melanoides tuberculata* and its consequences for interpretation of fossil series *Evolution* 55: 492-502.

Samadi S, Mavarez J, Pointier JP, Delay B & Jarne P 1999 Microsatellite and morphological analysis of population structure in the parthenogenetic freshwater snail *Melanoides tuberculata*: insights onto the creation of variability *Molecular Ecology* 8: 1141-1153.

Schütt H 1982 Die Molluskenfauna der Süsswasser im Einzugsgebiet des Orontes unter Berucksichtung benachbarter Flussystem *Archiv für Molluskenkunde* 113: 17-91.

Schütt H 1983 Die bisher aus Jordanien bekannten susswasser- und landbewohnenden Mollusken anhand der Aufsammlungen von Dr. Bandel 1978 *Natur und Mensch* 49-64.

Schütt H 1987 The mollusks of the Oasis Palmyra *In* F. Krupp, W. Schneider & R. Kinzelbach (eds) *Proceedings of the symposium on the fauna and zoogeography of the Middle East, Mainz 1985. Tübinger Atlas des Vorderen Orients,* Beihefte A 28: 215-219 Reichert, Wiesbaden.

Schütt H & Sesen R 1989 The freshwater mollusks of Ceylanpinar *Zoology in the Middle East* 3: 55-58.

Starmühlner F & Edlauer A 1957 Ergebnisse der Osterreichischen Iran- Expedition 1949/50. Beitrage zur Kenntnis der Molluskenfauna des Iran *Sitzungsberichten der Osterreichische Akademie der Wissenschaften, mathematisch naturwissenschaftlichen Klasse* 166.

Supian Z & Ikhwanuddin AM 2002 Population dynamics of freshwater mollusks (Gastropoda: *Melanoides tuberculata*) in Crocker Range Park, Sabah *Asean* July-Sept.

Tchernov E 1971 Freshwater molluscs of the Sinai Peninsula *Israel Journal of Zoology* 20: 209-221.

Tchernov E 1973 *On the Pleistocene Molluscs of the Jordan Valley* Israel Academy of Sciences and Humanities, Jerusalem, 50pp. 7pl.

Tchernov E 1975a Molluscs of the Sea of Galilee *Malacologia* 15: 147-184.

Tchernov E 1975b *The early Pleistocene Molluscs of Erq el-Ahmar* Israel Academy of Sciences and Humanities, Jerusalem, 36pp. 4pl.

Tristram HB 1865 Report on the terrestrial and fluviatile Mollusca of Palestine. *Proceedings of the Zoological Society of London* 1865: 530-545.

Van Damme D 1984 *The Freshwater Mollusca of Northern Africa* Dr W. Junk Publishers, Dordrecht, 164 pp.

Van Damme D & Pickford M 2003 The late Cenozoic Thiaridae (Mollusca, Gastropoda, Cerithioidea) of the Albertine Rift Valley (Uganda-Congo) and their bearing on the origin and evolution of the Tanganyikan thalassoid malacofauna *Hydrobiologia* 498: 1-83.

Willmann R 1981 Evolution, Systematik und stratigraphische Bedeutung der neogenen Süsswassergastropoden von Rhodes und Kos/ Ägäis *Palaeontographica* 174: 10-235.