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Conchometrics, systematics and distribution of *Melanopsis* (Mollusca: Gastropoda) in the Levant

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In this conchometric study, the systematics and distribution of the freshwater gastropod *Melanopsis* in the Levant are described. Of the ten species found, three are widespread, two have narrow distributions and five are known only from their type locality. Five smooth-shelled species are recognized (*buccinoidea, ammonis, dircaena, khabourensis* and *meiostoma*). Within *M. buccinoidea*, Jordan Valley populations may belong to a separate subspecies. *M. ammonis* is clearly differentiated from *buccinoidea* of the nearby Jordan Valley, but less so from *buccinoidea* of more distant sites; differences between *ammonis* and *meiostoma* are significant but not diagnostic. Five species have ribbed shells. Within *costata*, four subspecies are recognized (in the northern Orontes, upper Jordan, Sea of Galilee, and in southernmost parts of the Levant). Throughout the Levant, *M. buccinoidea* frequently hybridizes with *M. costata* and fossil evidence suggests that these species have been hybridizing for the last 1.5 Myr. *M. saulcyi* differs from *M. costata* in its narrower shell and shorter, bumpier ribs and frequently hybridizes with *M. buccinoidea* throughout the Levant. Specimens from Homs differ from those of the Jordan Valley in their higher figurativity index, fewer ribs and lower rib density. *M. germaini* differs from *M. costata* in its more numerous ribs, *M. pachya* in its shorter ribs, and *M. infracincta* in its bumpy shell in which each rib has huge tubercles, with a pronounced ridge flanking the columella. Our conclusion that there are ten species in the Levant differs from previous studies that suggested only two subspecies of one species (or superspecies). This difference could stem from (1) our use of nonstandard as well as standard conchometrics, (2) a reappraisal of the importance of the shell vs. the radula in intrageneric systematics, and (3) differences of opinion on the subspecies concept.

ADDITIONAL KEYWORDS: freshwater snails – gastropods – taxonomy.

INTRODUCTION

The Levant occupies the eastern shore of the Mediterranean, a stretch of land about 800 km long and approximately 150 km wide, ranging from the mouth of the River Orontes in the north to the Isthmus of Suez in the south; in the east it merges gradually into the Arabo-Syrian Desert (Heller, 2001: fig. 1). Throughout the Levant the most abundant and most disputed freshwater snail is *Melanopsis* Férussac, 1807 (Melanopsidae). No other genus comes near it in terms of taxonomic controversy.

The first reference to *Melanopsis* in the Levant is in Olivier (1801, 1804), who illustrated two species, *M. buccinoidea* and *M. costata*. In the 80 years that followed Olivier, there were major contributions from Roth (1839; who described *M. costata* var. *jordanica*), Bourguignat (1853; who described *M. saulcyi*), Tristram (1865; *M. ammonis, M. eremita*) and Locard (1883; *M. chantrei, M. lortetiana*). Bourguignat (1884) produced a massive monograph on *Melanopsis* in which he described 43 species from the Levant. Germain (1921) reduced this list to six (*M. praemorsa*, *M. jordanicensis*, *M. bullio*, *M. saulcyi, M. bovieri* and *M. costata*). Some years later, the number increased again, as Pallary (1939) described 26 species; he increased the area by marking the Tigris as the eastern border of the Levantine fauna.

Tchernov (1975) suggested that in *Melanopsis* all shell variation reflects ecotypes belonging to a single circum-Mediterranean species (*M. praemorsum*), but Bilgin (1983) concluded that (smooth) *M. praemorsa*

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and (ribbed) *M. costata* are different species. Mienis (1983) suggested that in the southern Levant (Israel) three species are found, *M. praemorsa*, *M. costata* and *M. cerithiopsis*. Later Mienis & Ortal (1994) presented a different classification of Israeli *Melanopsis* that included *M. praemorsa buccinoidea*, *M. p. eremita*, *M. p. jordanica*, *M. saulcyi* and *M. cerithiopsis*.

Schütt (1983, 1987, 1988; Schütt & Sesen, 1989) assigned all *Melanopsis* of the Levant to *M. praemorsa*. He described *M. p. ferussaci*, *M. p. costata*, *M. p. olivieri*, *M. p. obsoleta* and *M. p. nodosa* from Syria, and *M. p. bandeli* from the Kingdom of Jordan. Burch (1985) and Burch *et al.* (1989) assigned the *Melanopsis* of the Kingdom of Jordan to two subspecies, *M. praemorsa buccinoidea* and *M. p. costata*. Raanan (1986) suggested that in Lake Kinneret (Tiberias) the black and banded morphs of *M. costata* belong to separate species with incomplete reproductive isolation, but this was not supported by the later studies of Altman & Ritte (1996).

Glaubrecht (1996, 1999) suggested one, highly polymorphic circum-Mediterranean superspecies, *Melanopsis praemorsa*, the 'subspecies' of which display minor anatomical variation in the radula but dramatic variation in shell sculpture. In the Levant he recognized two subspecies (*M. p. buccinoidea* and *M. p. costata*) that hybridize widely, to such an extent that they are conspecific. He further suggested that sculptured forms of *Melanopsis* (including *M. p. costata*) appeared only during the Miocene, when the Mediterranean dried up.

From the Jordan Valley and nearby Golan Heights, conchometric analyses (Heller *et al.* 1999; Heller & Sivan, 2000), complemented by comparative studies of the sperm, the radula and allozymes (Hodgson & Heller, 1997; Falniowski *et al.*, 2002a, b; Mazan-Mamczarz, Heller & Szwarowska, 2002) suggested four species (*M. buccinoidea*, *M. costata*, *M. saulcyi* and *M. meiostoma*). From the Kingdom of Jordan Bandel (2000) described seven Recent species (*M. buccinoidea*, *M. doriae*, *M. sharhabili, M. costata*, *M. saulcyi, M. bandeli* and *M. ammonis*) and four fossil ones (*M. noetlingi, M. blanckenhorni*, *M. jordanica* and *M. dufouri*).

Thus, despite 200 years of study since the first descriptions by Olivier, the taxonomy of Levantine *Melanopsis* remains vague. This paper describes, through shell morphometry, the systematics and distribution of Recent *Melanopsis* in the Levant.

METHODS

Our study region includes the area covered by the political borders of Syria, Lebanon, Jordan, Israel and the Palestine Authority. As such, it also includes a stretch of the Euphrates, which is arguably beyond the Levant. Following Glaubrecht (1999: fig. 3) we include this stretch of the Euphrates in our analysis because of its biogeographical interest; some tributaries that today flow to the Euphrates may, in the past, have flowed westward towards the Mediterranean, and this may, perhaps, be reflected in the fauna.

Our study is based mainly upon shell morphometry of museum specimens, as areas of the Levant beyond Israel and its administered areas are presently inaccessible to some of us. We have inspected material in the Natural History Museum, London (BMNH); Geologisch-Paläontologisches Institut und Museum der Universität Hamburg (GPIuMH); the National Mollusc Collection of the Hebrew University, Jerusalem (HUJ); the Muséum d'Histoire Naturelle, Geneva (MHNG; the Bourguignat collection is marked BGT); Muséum National d'Histoire Naturelle, Paris (MNHN); Naturhistorisches Museum, Vienna (NHMW); the National Museum of Wales (NMW); Forschungsinstitut und Naturmuseum Senckenberg (SMF); Zoologisches Institut und Zoologisches Museum, Hamburg (ZMH) and Zoologisches Sammlung, München (ZSM). Overall, the southern Levant is better represented in these collections than is the north.

Glaubrecht (1993), who emphasized the need for quantitative assessments of the various forms of *Melanopsis*, measured shell height and width, mouth height and width, and further classified each shell as either ribbed or smooth. In line with Glaubrecht's general approach, we have expanded conchometrics to include also several details of the ribs, of the whorls and of the siphonal notch.

General conchometrics (Fig. 1) include shell-height, shell-diameter (maximal), mouth-height, mouth-diameter, notch-width and notch-depth; all were measured with a calliper or under the binocular microscope using an eye-piece micrometer to an accuracy of 0.1 mm. From these measurements six ratios were calculated: shell-diameter/shell-height, mouth-height/shell-height, mouth-diameter/mouth-height, mouth-height/shell-diameter, notch-width/notch-depth and notch-width/mouth-diameter.

In addition, the diameter of the shell was measured at four different points under the binocular microscope, using an eye-piece micrometer (a, b, c and d, see Fig. 1; c is two-thirds of the height above the point of insertion of the lip to the last suture, d is one third). From these measurements, we quantitatively express the index of shell shouldering as the ratio b/c (shouldered shells, as in Heller *et al.*, 1999; fig. 4A, C, have low shouldering index). We express the index of shell figurativity ('waist') as the ratio c/d (shells with a waist, as in Heller & Sivan, 2001: fig. 3F, have high figurativity index). We express the index of conicality as the ratio a/b (conic shells, as in Heller *et al.*, 1999; fig. 4A, C, have low conicality index).

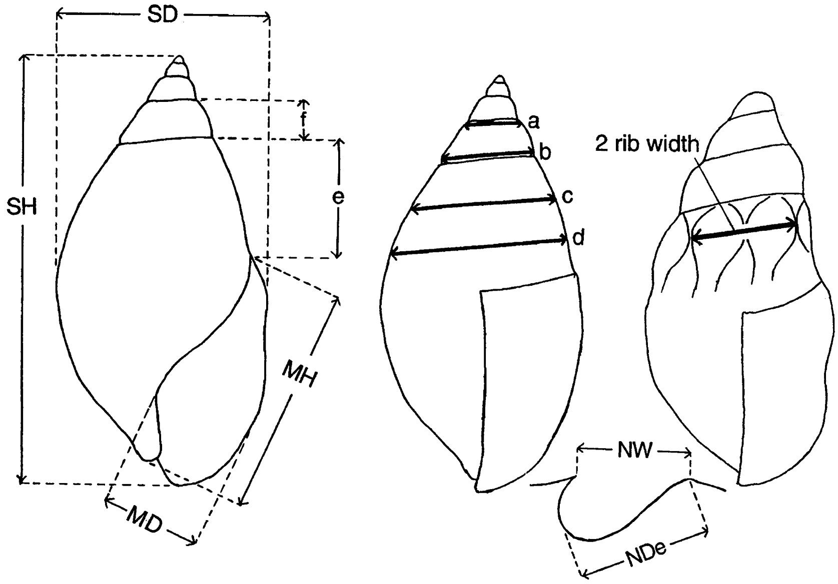

Figure 1. Shell conchometrics. Upper: shell viewed from front (left) and side (middle, right). Lower: notch viewed from below. *Abbreviations:* MH, mouth-height; MD, mouth-diameter; NW, notch-width, Nde, notch-depth; SH, shell-height; SD, shell-diameter.

Whorl height was measured at two points: e – height of ultimate whorl, from the mouth to nearest point on the suture above, and f – height of the penultimate whorl (Fig. 1). 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, three characteristics were scored: (a) rib number, from uppermost point of insertion of the shell mouth on the body whorl dextrally, to the corresponding point on the penultimate whorl; (b) rib density, as the number of ribs from uppermost point of insertion of the mouth 5 mm sinistrally, measured and counted using the binocular micrometer; (c) rib length, examined on the body whorl.

Four categories were defined to describe increasing rib length: (1) ribs very short, not reaching the shell mouth; (2) ribs reaching from the suture down to the mouth; (3) ribs reaching beyond the mouth, but not extending the entire height of the body whorl; (4) ribs reaching the entire height of the body whorl.

To express, when relevant, the width of the ribs at the tubercle (or at a similar level in ribs without a tubercle) the width of two ribs (on the ultimate whorl, above the mouth) was measured (Fig. 1). From this measurement we calculated relative rib width as the ratio 2-rib width/shell-diameter.

Statistical comparisons between characters of individual taxa were conducted by *t*-test. If not otherwise indicated, the significance level was set at $P < 0.01$. 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 Cluster Analysis or Principal Coordinate Analysis (PCO) (both by UPGMA based on Standardized Euclidean, using the multivariate statistical package of Kovach Computing Services: MVSP); all characters measured in the relevant taxa were used.

Not all examined material was included in the tables and statistical analysis, as some of the shells were broken or juveniles. On the maps, each symbol represents one or more specimens of the relevant taxa.

SYSTEMATIC DESCRIPTION

FAMILY MELANOPSIDAE

GENUS *MELANOPSIS* FÉRUSSAC, 1824

Description

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).

The present study reveals ten *Melanopsis* species in the Levant: three are widespread (*M. buccinoidea*, *M. costata*, *M. saulcyi*), two have narrow distributions (*M. dircaena*, *M. ammonis*), and five are known only from their type localities (*M. khabourensis, M. meiostoma, M. pachya*, *M. germaini* and *M. infracincta*).

The ten *Melanopsis* species of the Levant are described below. For convenience of description, all the smooth-shelled species are presented first, then all the ribbed ones. Within each of these groups, the order of the species follows their year of original description.

MELANOPSIS BUCCINOIDEA (OLIVIER, 1801) (FIG. 2A, B; TABLE 1)

Melanie buccinoide Olivier, 1801: pl. 17, fig. 8.
Melanopsis ferussaci Roth, 1839: 24, pl. 2, fig. 10.
Melanopsis sesteri Bourguignat, 1884: 119, from Hula Valley ('Ain al Bass') and environs of Aleppo (Sadjour-Sou 70 km NE Aleppo, near 'Ain Taib'); not *sesteri* var. *diadema* Bourguignat from Sadjour-Sou.
Melanopsis praemorsa, Germain, 1921: pl. 19; Bandel & Salameh, 1981; fig. 23; Heller & Abotbol, 1997.
Melanopsis buccinoidea, Pallary, 1939: 84–85, pl. 6, figs 1–4, 64, 65; Heller *et al*., 1999: 56–59, fig. 4A; Bandel, 2000, figs 1, 20–24, 71.
Melanopsis denegabilis, Pallary, 1939: 85–86, pls. 6, figs 9–12.
Melanopsis prophetarum, Pallary, 1939: 83–84, pl. 6, figs 16, 17, 23–26, 36, 57.

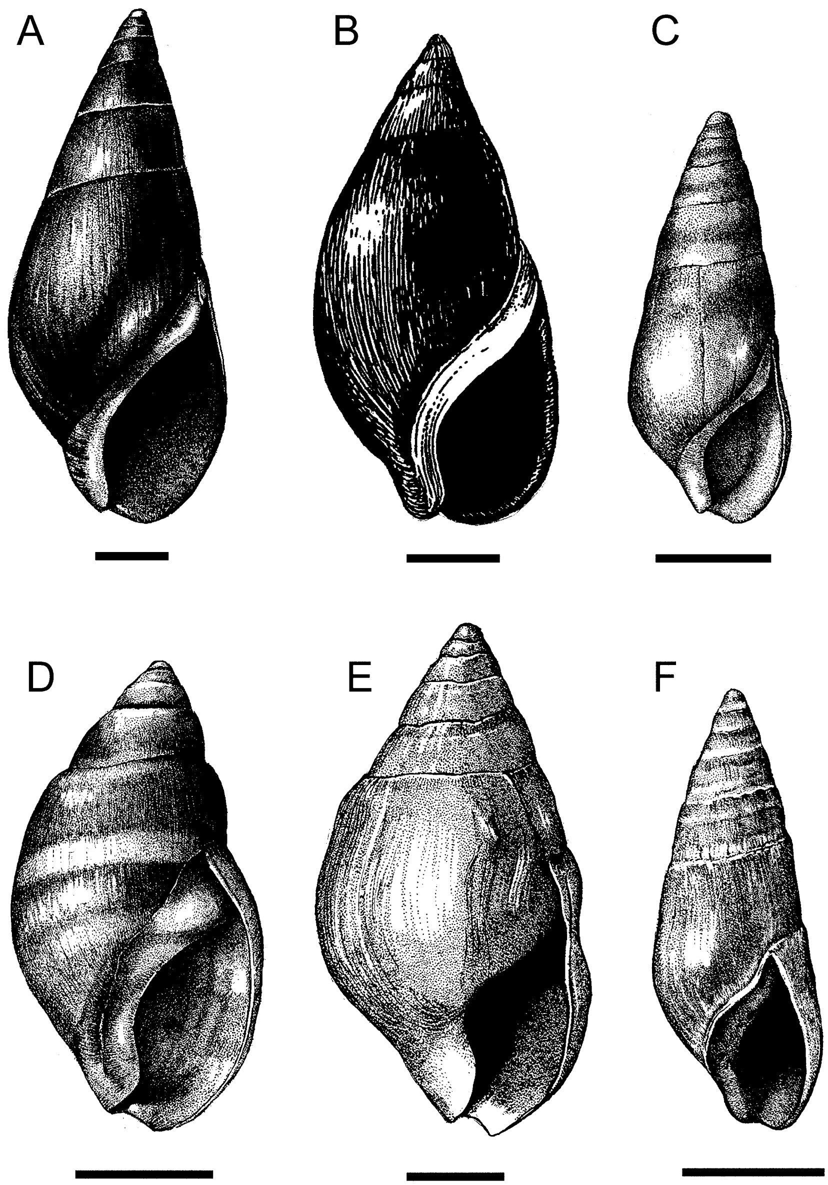

Figure 2. Smooth-shelled *Melanopsis* of the Levant. A & B, *M. buccinoidea* (elongate and Jordan Valley forms). C, *M. ammonis*. D, *M. dircaena*. E, *M. khabourensis*. F, *M. meiostoma*.

Table 1. *Melanopsis buccinoidea,* conchometrics (mean ± SD and observed range): pooled data, synonyms and intraspecific variation. MbL: *M. buccinoidea* Levant excluding Jordan catchment area $N = 110$ (pooled); MbJ: *M. buccinoidea* Jordan catchment area $N = 157$ (pooled); MsS: *M. sesteri* Sadjour-Sou $N = 7$; MpA: *M. prophetarum* Akbes $N = 8$; Mpf: *M. praemorsa ferussaci* Ghab-form $N = 14$ (pooled); Mpo *M. praemorsa olivieri* Northern Syria $N = 2$; MbB: *M. brevis* Ba'albek $N = 10$

	MbL	MbJ	MsS	MpA	Mpf	Mpo	MbB
Max. shell-height	35.1 mm	29.3 mm	24.7 mm	21.4 mm	32.6 mm	24.2, 28.1 mm	15.8 mm
Max. shell-diameter	15.4 mm	14.9 mm	10.7 mm	10.7 mm	15.4 mm	11.9, 13.2 mm	8.7 mm
Max. mouth-height	17.8 mm	19.0 mm	12.7 mm	12.5 mm	17.8 mm	13.4, 17.0 mm	7.7 mm
Shell-diameter/ shell-height	0.46 ± 0.03/0.39–0.54	0.50 ± 0.02/0.44–0.56	0.45 ± 0.02/0.42–0.48	0.50 ± 0.02/0.48–0.53	0.47 ± 0.03/0.43–0.51	0.48, 0.49	0.54 ± 0.03/0.52–0.59
Mouth-height/ shell-height	0.55 ± 0.04/0.44–0.64	0.62 ± 0.04/0.51–0.70	0.54 ± 0.03/0.51–0.58	0.60 ± 0.03/0.56–0.64	0.54 ± 0.04/0.49–0.61	0.54, 0.60	0.56 ± 0.03/0.51–0.62
Mouth-diameter/ mouth-height	0.42 ± 0.03/0.36–0.52	0.39 ± 0.04/0.33–0.58	0.42 ± 0.03/0.39–0.47	0.42 ± 0.03/0.38–0.46	0.43 ± 0.03/0.39–0.49	0.46, 0.40	0.49 ± 0.04/0.44–0.57
Mouth-height/ shell-diameter	1.19 ± 0.07/1.00–1.35	1.24 ± 0.06/1.08–1.41	1.19 ± 0.08/1.05–1.27	1.20 ± 0.06/1.14–1.31	1.16 ± 0.06/1.02–1.24	1.13, 1.29	1.02 ± 0.04/0.93–1.09
Notch-width/ notch-depth	0.87 ± 0.08/0.60–1.10	0.85 ± 0.07/0.68–1.09	0.82 ± 0.05/0.76–0.91	0.91 ± 0.03/0.86–0.93	0.92 ± 0.05/0.86–1.00	–, 0.78	1.10 ± 0.08/1.00–1.25
Notch-width/ mouth-diameter	0.54 ± 0.07/0.39–0.69	0.48 ± 0.07/0.30–0.66	0.49 ± 0.06/0.43–0.61	0.53 ± 0.06/0.46–0.62	0.59 ± 0.04/0.51–0.66	–, 0.46	0.57 ± 0.09/0.48–0.75
e/mouth-height	0.34 ± 0.05/0.23–0.47	0.28 ± 0.04/0.19–0.38	0.35 ± 0.06/0.29–0.46	0.27 ± 0.03/0.24–0.33	0.36 ± 0.04/0.30–0.42	0.37, 0.31	0.39 ± 0.04/0.34–0.44
f/mouth-height	0.21 ± 0.03/0.12–0.31	0.16 ± 0.02/0.12–0.23	0.22 ± 0.02/0.19–0.25	0.17 ± 0.02/0.15–0.18	0.22 ± 0.03/0.16–0.27	0.22, 0.19	0.20 ± 0.03/0.17–0.22
Conicality (a/b)	0.73 ± 0.05/0.65–0.88	0.74 ± 0.05/0.65–0.84	0.76 ± 0.06/0.69–0.88	0.72 ± 0.02/0.69–0.74	0.74 ± 0.04/0.63–0.80	0.78, 0.82	0.73 ± 0.08/0.65–0.79
Figurativity (c/d)	0.89 ± 0.03/0.73–0.96	0.87 ± 0.03/0.76–0.92	0.91 ± 0.03/0.86–0.96	0.88 ± 0.01/0.86–0.89	0.90 ± 0.02/0.86–0.93	0.92, 0.95	0.89 ± 0.02/0.87–0.92
Shouldering (b/c)	0.82 ± 0.03/0.75–0.90	0.80 ± 0.03/0.74–0.92	0.79 ± 0.02/0.76–0.82	0.79 ± 0.02/0.77–0.82	0.81 ± 0.03/0.72–0.85	0.80, 0.78	0.85 ± 0.03/0.82–0.89

Melanopsis olivieri, Pallary, 1939: pl. 4, fig. 11.
Melanopsis praemorsa ferussaci, Schütt, 1983: 40–41, pl. 2, figs 42, 44, not fig. 43.
Melanopsis praemorsa ferussaci, Ghab form, Schütt, 1983: 41–42, pl. 2, fig. 47.
Melanopsis praemorsa olivieri, Schütt, 1983: 44.

Types and type locality

'Melanie buccinoide*, M. buccinoidea de Scio*' (Olivier, 1801; pl. 17, fig. 8)*.* In the Muséum National d'Histoire Naturelle (Paris) Tillier & Mordan (1983: pl. 5, fig. 11) found ten possible syntypes of *M. buccinoidea*, labelled '*M. praemorsa* L., Tripoli, M. Olivier, 1803'. *M. buccionoidea* was synonymized with *M. praemorsa* by Germain (1921: 477).

Material examined

SYRIA: Kara Sou (BMNH 20030348), Nahr Afrin (SMF 282748), Sadjour-Sou (BGT 11341), Antiochia (SMF 290751), Haleb (NHMW 84539), Orontes (SMF 282770, 282771, 282772), Akbes (BMNH 1901.11.26.88–92), Barda River (BMNH 20030350). LEBANON: Jeble (SMF 282739, 282740), Beirut (SMF 115083, 115084, 290783, 290741, NHMW, 1894, 57575), Nahr el Kabir (SMF 282729, 282745), Nahr el Kelb (ZMH), Hermel (BMNH 20030351), Baalbek (BMNH 1931.12.30.10345–7, 1933.8.11.72–82, 20030353). JORDAN: Near Irbid, Azraq North, Azraq South, Al Shuna, North Shuna, Wadi Karkara, Hisbon Quelle, Hamam Salomon (all in GPIuMH). ISRAEL: JORDAN VALLEY: Nahal Dan, Nahal Snir, Nahal Gilbon, Nahal Meshoshim, Yehudiya, Enot Huga, En Hanaziv, En Parta, En Sultan (all in HUJ); Ain el Bas (BGT 11340). COSTAL PLAIN AND ELSEWHERE: Nahal Bezet (HUJ), En Tamid (HUJ), Nahal Kishon (BMNH 20030349), Nahal Taninim (HUJ), Nahal Yarqon (HUJ, ZMH), Yafo (ZMH), Nazareth (ZMH),

Diagnosis

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

Description

The shell has up to seven whorls. It has a pointed spire, flattened whorls separated by very shallow sutures, and is smooth. In the sperm, the midpiece is exceptionally long (Hodgson & Heller, 2000); the radula is highly variable (Mazan-Mamczarz *et al*., 2002). The variability range of allozymes is exceptionally wide, with populations scattered among clusters of other species, suggesting a broad extent of hybridization with other species (Falniowski *et al*., 2002a, b) that has been going on in the Levant since the Lower Pleistocene and is still widespread today (Heller *et al*., 1999; Heller & Sivan, 2002a: table 1).

Synonyms

Bourguignat (1884) described *M. sesteri* from the Hula Valley ('Ain al Bass') and Sadjour-Sou. As the type specimens of *M. sesteri* (MHNG 11340, 11341) fall within the conchometric (as opposed to geographical) range of *M. buccinoidea* from the coastal plain (Table 1) we consider *M. sesteri* a synonym of *M. buccinoidea*.

Pallary (1939: 82–83, fig. 9) described *M. laevigata* Lamarck from the Levant. His assigning of Levantine *Melanopsis* to *laevigata* is difficult to investigate, because he illustrated the type shell of *laevigata*, which is not from the Levant, but his *laevigata* from the Levant are not illustrated. We assume that *laevigata* from the Levant are synonyms of *buccinoidea,* whereas the North African *M. episema* Bourguignat and *M. callichroa* Bourguignat, which Pallary considered varieties of *laevigata*, are not. *M. prophetarum* described by Pallary (1939) (BMNH 1901.11.26.88–92) does not differ from typical *M. buccinoidea* from the Jordan Valley (Table 1) and thus we consider *M. prophetarum* a synonym of *M. buccinoidea*. Pallary (1939) described *M. denegabilis* de Férussac as a smooth *Melanopsis* of intermediate dimensions, and illustrated specimens from Lakbe and from Tripoli. His figures of *M. denegabilis* are all within the range of *M. buccinoidea*, hence we consider *denegabilis* a synonym of *buccinoidea*.

Schütt (1983) considered all *Melanopsis* of the Levant as subspecies of *M. praemorsa* (the type species of *Melanopsis*, from Spain). He assigned the smooth-shelled *Melanopsis* of the coast and south-eastern parts of the Levant to *M. p. ferussaci* Roth, which differs from the large, narrow, red-brown *M. p. buccinoidea* Olivier of Greece and the Aegean in being small and dark-coloured. Whether these smooth *Melanopsis* of the Levant are separate from *M. buccinoidea* of Greece (as suggested by Schütt, 1983), synonymous with *M. buccinoidea* (as suggested by Glaubrecht, 1993) or synonymous with *M. praemorsa* (as suggested by Tchernov, 1975), is beyond the scope of this present study.

Within his *M. p. ferussaci*, Schütt (1983) placed some Orontes populations as a separate '*praemorsa ferussaci* Ghab form', which differs from the coastal *M. p. ferussaci* in its large size, and in always being completely smooth. The measurements and ratios of his *M. p. ferussaci* Ghab form (Table 1) do not differ from *M. buccinoidea* from the Syrian coast. We therefore consider the *M. p. ferussaci* Ghab form a synonym of *M. buccinoidea*.

M. olivieri was described by Bourguignat (1884) from several sites throughout the Levant (the environs of Aleppo, Sajour-Sou, Beirut, Damascus and Jericho); Schütt (1983) placed it as a separate subspecies of north-eastern parts of the Levant, characterized by a shell even larger and wider than the *M. p. ferussaci* Ghab form. Measurements of two specimens from northern Syria defined by Schütt as *M. praemorsa olivieri* (NHMW 84539 from Aleppo and SMF 282828 from the Quaik River, near Tell Arsof) are presented in Table 1. The shells fall within the range of *M. buccinoidea* in all characters. We therefore consider *M. praemorsa olivieri* a synonym of *M. buccinoidea*.

Distribution and habitat

M. buccinoidea is widely distributed in the Levant (Fig. 3). In the southern Levant it occurs in a wide variety of aquatic habitats that range from small trickles to springs and streams, where it lives on stones, sometimes also in silty mud; it is absent from the Jordan River and from Lake Kinneret (Heller *et al.*, 1999, 2002). A generalist feeder, it frequently feeds on dry willow leaves and is an important litter shredder in certain desert oasis ecosystems (Heller & Abotbol, 1997). Parasites include the eye fluke *Philopthalamus lucipetus* (Rudolphi, 1819) (Radev *et al.*, 1999). In the Levant, fossils of *M. buccinoidea* are known from the mid-Pleistocene, Lower Pleistocene and Pliocene of the Jordan Valley (Heller & Sivan, 2001, 2002a, b). Both Glaubrecht (1993) and Falniowski *et al.* (2002b) considered *M. buccinoidea* a stem species, from which ribbed species of the Levant eventually evolved.

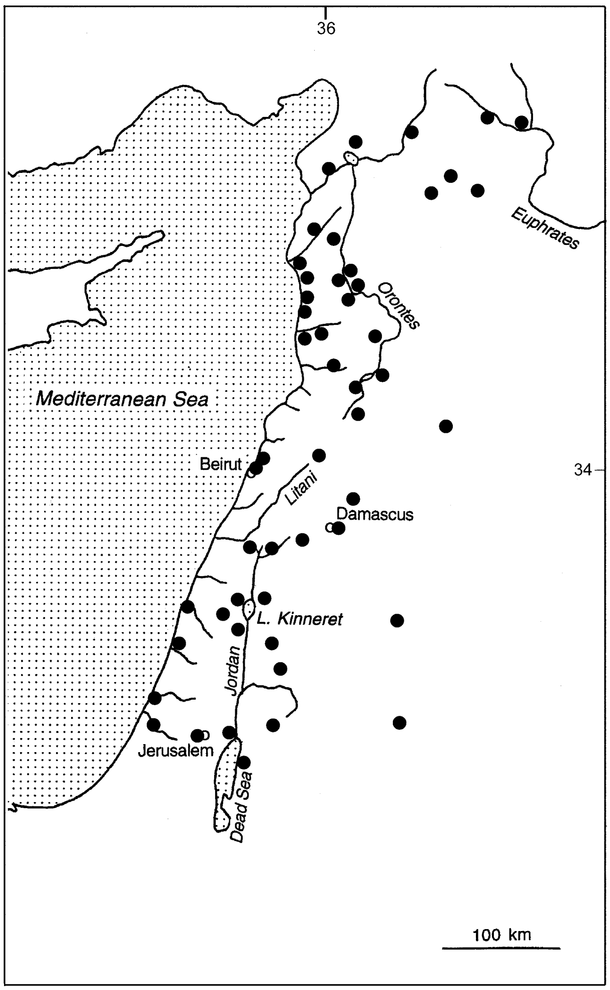

Figure 3. Distribution of *Melanopsis buccinoidea* in the Levant (inspected records).

Intraspecific variation

There is considerable variation among *M. buccinoidea* populations of the Levant. Compared to shells from elsewhere in the Levant, shells from the Jordan catchment area tend to be stouter (shell-diameter/shell-height is 0.50 ± 0.02 vs. 0.46 ± 0.03 elsewhere; the Nahal Taninim population on the coast of Israel is an exception in that it too has stout shells), they have significantly larger mouth-height/shell-height ratio (0.62 ± 0.04, vs. 0.55 ± 0.04 elsewhere) and a lower f/mouth-height ratio (0.16 ± 0.02, vs. 0.21 ± 0.03 elsewhere) (Table 1, Fig. 4).

The Jordan catchment area *M. buccinoidea* may perhaps be a separate subspecies. We have previously referred to this (Heller, Sivan & Ben-Ami, 2002), noting that on the coast of the Levant, *M. buccinoidea* tends to be more elongate than in the Jordan Valley. We return to this point below, when discussing *M. ammonis*. It is noteworthy in the dendrogram of Figure 7 that, within the Jordan Valley, samples of *M. buccinoidea* from the northern region of the valley (e.g. Azraq, Al Shuna II) cluster separately from those of the southern region (e.g. N. Gilbon, Yehudiya).

We are undecided as to the taxonomic status of three samples of short, eroded, smooth shells from Ba'alBek (BMNH 1931.12.30.10345–47, 1933.8.11.72–82 and 20030353, labelled *M. brevis*). With a shell-diameter/shell-height of 0.54 ± 0.03 these shells are significantly stouter, not only than those of Lebanon, but even than those from the Jordan Valley. Further, mouth-height relative to shell-diameter in these specimens is only 1.02 ± 0.04, smaller than that of all other populations of *M. buccinoidea*, and the mouth is more rounded (mouth-diameter/mouth-height 0.49 ± 0.04). The type locality of *Melanopsis brevis* Mousson 1854, to which these shells are referred, is the Litani (Germain, 1921: 463). Pallary (1939) discussed the taxonomy of *brevis* and concluded that it is a synonym of *laevigata*.

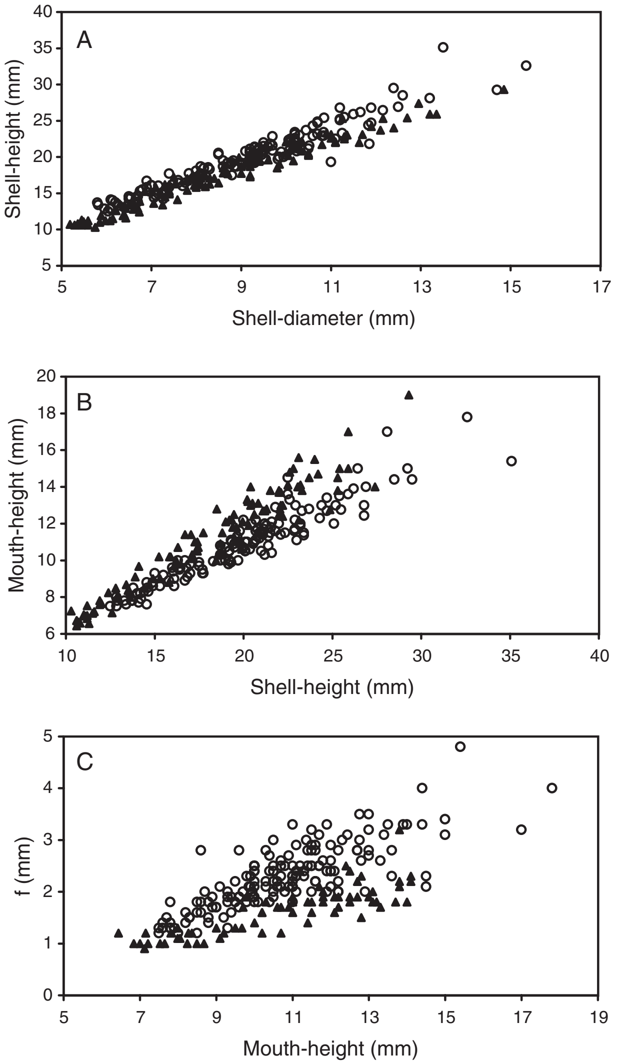

Figure 4. *Melanopsis buccinoidea* from the Jordan Valley (excluding Dan and 'En Bass') (▲) compared with *M. buccinoidea* from elsewhere in the Levant (○). A, shell-height vs. shell-diameter; B, mouth-height vs. shell-height; C, whorl-height vs. mouth-height.

Melanopsis sharhabili was recently described by Bandel (2000: 156, figs 119–123, type no. 4267 in GPI-uMH) from a 'spring and creek next to Wadi Raiyan Plantation in the Jordan Valley near the town of Wadi Raiyan and close to the mosque of Sharhabil Ibn Haddanna'. The typical *M. sharhabili* differs from *M. buccinoidea* of the Jordan Valley in that its four last whorls are more expanded, as compared to the previous whorls. The shell consists of nine whorls. The first five to six increase regularly in diameter; the next increases rapidly, both in diameter and in height, so that it is two-thirds of total shell height. Bandel (2000) noted that *M. sharhabili* grades in shape (not in size) into local *M. buccinoidea,* and suggested that it is probably a hybrid of *M. buccinoidea* and one of the ribbed species, *M. saulcyi* or *M. bandeli*, that live in the same creek and spring. As *M. sharhabili* grades into *M. buccinoidea* in the only locality from which it is known, we are undecided as to its subspecific position.

MELANOPSIS AMMONIS (TRISTRAM, 1865)
(FIG. 2C, TABLE 2)

Melanopsis ammonis Tristram, 1865: 542, no. 102.
Melanopsis eremita Tristram, 1865: 542–3, no. 107.
Melanopsis ammanensis, Pallary, 1939: 88–89, pl. 4, fig. 3.
Melanopsis praemorsa eremita, Mienis & Ortal, 1994: II.
Melanopsis doriae, Bandel, 2000: 152, figs 25–29. Not *Melanopsis doriae* Issel, 1886.
Melanopsis ammonis, Bandel, 2000: 177, figs 117, 118.

Material examined

Types: four syntypes (BMNH 1968665) from 'streams at Heshbon and Ammon, east of Jordan'.
Additional material: JORDAN: Rabat Ammon (BMNH 1936.3.10.7–11), W. Walla, Hamam Yarmouk, Rumeimin, opposite Enot Qane (all in GPIuMH). ISRAEL: En Boqeq (BMNH 1968666, 1936.3.10.12–18), En Amatziahu, En Tamar, En Namer (all in HUJ). Gaza (BMNH 1937.12.30.10402–16).

Diagnosis

Melanopsis ammonis differs from *M. buccinoidea* of the Jordan Valley in its higher penultimate whorl, as expressed in its higher values of the ratio f/mouth-height.

Description

The shell is smooth, narrow, tall and elongate with a pointed spire. It consists of up to nine whorls, which are high, very flattened and separated by very shallow sutures. Shell colour is almost always uniform black, or reddish brown; sometimes it is greyish yellow. The callus is white. Conchometrics of three of the four syntypes, BMNH 1968665, together with BMNH 1936.3.0.7–11, are in Table 2.

Synonyms

Tristram (1865: 542–3) described *M. eremita* from 'the little stream of the Wady Um Baghek, between Sebbeh and Jebel Usdum, at the south-west corner of the Dead Sea' (today this stream is named En Boqeq). He described it as spindle-shaped, semitransparent,

Table 2. *Melanopsis ammonis*, conchometrics (mean ± SD and observed range): pooled data, type, synonyms and the Gaza population. MaSL: *M. ammonis* Southern Levant $N = 89$ (pooled); MaJ: *M. ammonis* type Jordan $N = 8$; MeE: *M. eremita* En Boqeq $N = 15$; MaG: *M. ammonis* Gaza $N = 9$

	MaSL	MaJ	MeE	MaG
Max. shell-height	27.1 mm	27.1 mm	17.9 mm	20.7 mm
Max. shell-diameter	10.8 mm	10.8 mm	8.1 mm	10.0 mm
Max. mouth-height	12.3 mm	12.3 mm	8.8 mm	8.9 mm
Shell-diameter/shell-height	0.44 ± 0.02/0.39–0.49	0.43 ± 0.03/0.39–0.48	0.46 ± 0.02/0.40–0.49	0.45 ± 0.02/0.42–0.48
Mouth-height/shell-height	0.50 ± 0.03/0.43–0.56	0.48 ± 0.03/0.45–0.53	0.52 ± 0.02/0.48–0.56	0.50 ± 0.03/0.47–0.55
Mouth-diameter/mouth-height	0.43 ± 0.02/0.38–0.49	0.43 ± 0.02/0.41–0.45	0.44 ± 0.03/0.38–0.49	0.45 ± 0.02/0.40–0.47
Mouth-height/shell-diameter	1.14 ± 0.05/1.03–1.26	1.12 ± 0.05/1.03–1.20	1.13 ± 0.05/1.05–1.21	1.13 ± 0.03/1.08–1.17
Notch-width/notch-depth	0.83 ± 0.05/0.71–0.96	0.81 ± 0.06/0.74–0.88	0.83 ± 0.05/0.71–0.88	0.93 ± 0.07/0.83–1.00
Notch-width/mouth-diameter	0.50 ± 0.06/0.35–0.63	0.46 ± 0.09/0.35–0.55	0.46 ± 0.07/0.38–0.55	0.58 ± 0.06/0.52–0.66
e/mouth-height	0.38 ± 0.05/0.28–0.49	0.40 ± 0.06/0.31–0.46	0.36 ± 0.04/0.28–0.42	0.41 ± 0.03/0.36–0.46
f/mouth-height	0.25 ± 0.03/0.20–0.34	0.28 ± 0.05/0.21–0.34	0.23 ± 0.02/0.20–0.27	0.25 ± 0.03/0.19–0.30
Conicality (a/b)	0.77 ± 0.05/0.65–0.88	0.77 ± 0.02/0.65–0.83	0.75 ± 0.04/0.65–0.83	0.74 ± 0.02/0.72–0.79
Figurativity (c/d)	0.92 ± 0.02/0.87–0.95	0.91 ± 0.02/0.87–0.94	0.91 ± 0.02/0.87–0.94	0.90 ± 0.01/0.88–0.93
Shouldering (b/c)	0.83 ± 0.03/0.76–0.91	0.83 ± 0.02/0.79–0.86	0.83 ± 0.02/0.79–0.86	0.86 ± 0.02/0.83–0.90

smooth, glossy, with very faint nonregular bands, and eight whorls that grow regularly. He commented that in this region 'which supplies the smallest of its group, the common *Melanopsis praeorsa* [*buccinoidea* of this study] attains its greatest magnitude'. Measurements and ratios of eight of the 12 types (BMNH 1968666) and seven additional specimens (BMNH 1936.3.10.12–18) of *M. eremita* (Table 2) illustrate that *M. eremita* is broadly similar to *M. ammonis,* differing only in its slightly higher ratios of shell-diameter/shell-height and mouth-height/shell-height. These differences are not diagnostic, whereby we consider *M. eremita* a synonym of *M. ammonis*. In a recent visit to En Boqeq, the type locality of *M. eremita*, no *M. eremita* but only *M. buccinoidea* were found.

Bandel (2000: figs 25–29) described *Melanopsis doriae* Issel from northern regions in the Kingdom of Jordan (a thermal spring at Hamma, in the Yarmouk Valley). From his figures we could not determine any differences between his *M. doriae* on the one hand and our *M. ammonis* from nearby sites of the Yarmouk and Jordan valleys on the other. We therefore consider Bandel's *M. doriae* a synonym of *M. ammonis*.

Distribution

All records are from the southern Levant (Fig. 5), mostly from the Jordan Valley: (Heshbon, Wadi Mujib near its outlet to the Dead Sea, Wadi Walla and Yarmouk in the Kingdom of Jordan; En Boqeq and En Amatziahu in Israel). A sample from Gaza (coastal plain of the Palestinian Authority, conchometrics in Table 1; originally labelled *Melanopsis ferussaci* Roth) is the single record beyond the Jordan Valley.

Comparisons

M. ammonis differs almost diagnostically from *M. buccinoidea* of the Jordan Valley in its higher ratio of f/mouth-height (0.25 ± 0.03 vs. 0.16 ± 0.02) (Table 2, Fig. 6A). In addition it differs significantly in its ratios shell-diameter/shell-height (0.44 ± 0.02 vs. 0.50 ± 0.02), mouth-height/shell-height (0.50 ± 0.03 vs. 0.62 ± 0.04), mouth-height/shell-diameter (1.14 ± 0.05 vs. 1.24 ± 0.06), e/mouth-height (0.38 ± 0.05 vs. 0.28 ± 0.04), mouth-diameter/mouth-height and shouldering. Figure 7 presents relationships among the samples of smooth shells from the Jordan Valley catchment area. In this dendrogram the samples from the Yarmuk, Wadi Walla, En Boqeq, En Amatziahu and Heshbon, fall into one group (*M. ammonis*), whereas those of Nahal Gilabon, Yehudiya, Nahal Snir, En Hanatziv, En Sultan and En Huga fall into another (*M. buccinoidea*).

M. ammonis of the Jordan Valley catchment area is clearly distinguished from *buccinoidea* of the same area. However, it is less well-separated from

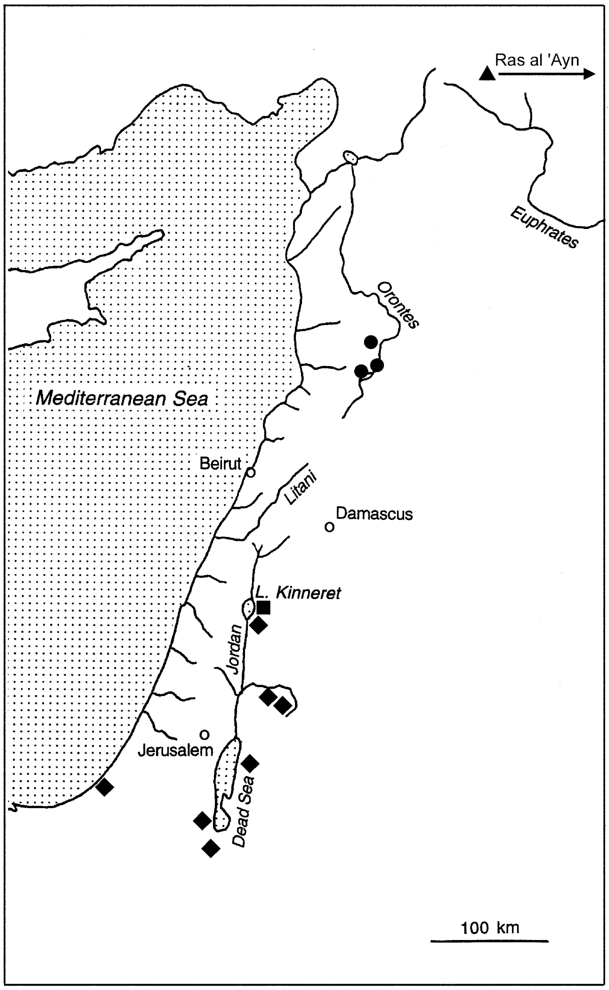

Figure 5. Distribution of *Melanopsis ammonis* (◆), *M. dircaena* (●), *M. khabourensis* (▲) and *M. meiostoma* (■) in the Levant (inspected records).

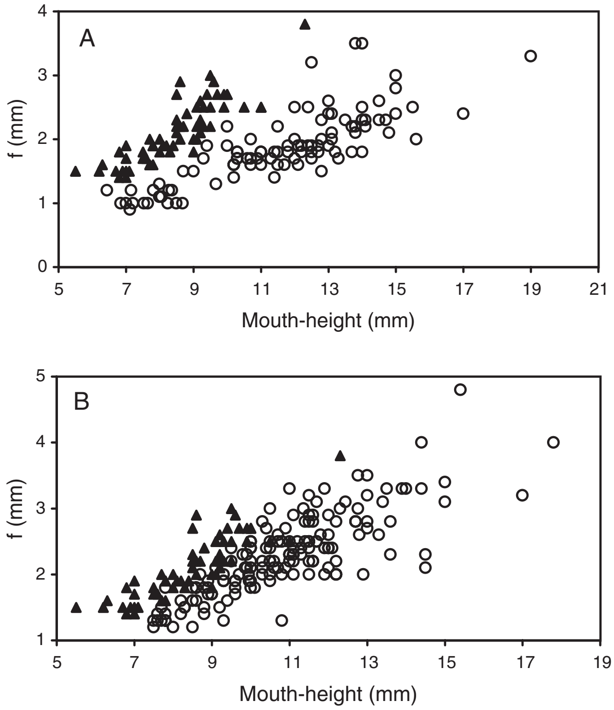

Figure 6. Whorl-height vs. mouth-height. A, *Melanopsis ammonis* of the Jordan Valley (▲) compared with *M. buccinoidea* of the Jordan Valley (○); B, *M. ammonis* of the Jordan Valley (▲) compared with *M. buccinoidea* of elsewhere in the Levant (○).

M. buccinoidea of elsewhere in the Levant (Fig. 6B). In separating *M. ammonis* as a distinct species we place more weight upon comparisons between close populations (in geographical terms) than between distant ones. To conclude, in the Jordan Valley region, *M. ammonis* can be clearly separated from *M. buccinoidea*; elsewhere in the Levant this separation is more difficult.

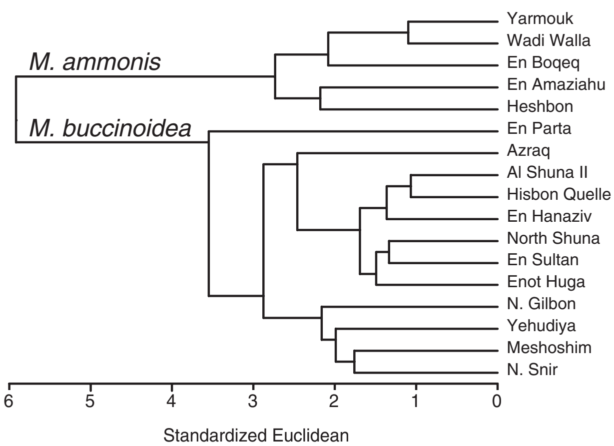

Figure 7. *Melanopsis ammonis* and *M. buccinoidea* of the Jordan Valley catchment area, UPGMA dendrogram.

MELANOPSIS DIRCAENA PALLARY, 1939
(FIG. 2D, TABLE 3)

Melanopsis dircaena Pallary, 1939: 87–88, pl. 6, figs 31–35.
Not *Melanopsis dircaena* var. ex-colore *luctuosa* Pallary, 1939: 88, pl. 4, fig. 19.

Material examined
Types: six syntypes in BMNH (1937.12.30.10.383–88); all from 'lac de Homs' (Pallary, 1939: 140).
Additional material: SYRIA: vicinity of Homs (SMF 282785, 283565, 290938, 290954).

Table 3. *Melanopsis dircaena*, conchometrics (mean ± SD and observed range).

Homs $N = 6$ (pooled)	*M.dircaena*
Max. shell-height	16.8 mm
Max. shell-diameter	9.2 mm
Max. mouth-height	10.0 mm
Shell-diameter/shell-height	0.59 ± 0.05/0.56–0.66
Mouth-height/shell-height	0.60 ± 0.04/0.54–0.66
Mouth-diameter/mouth-height	0.44 ± 0.02/0.42–0.46
Mouth-height/shell-diameter	1.04 ± 0.04/1.00–1.09
Notch-width/notch-depth	0.85 ± 0.08/0.75–0.91
Notch-width/mouth-diameter	0.51 ± 0.10/0.39–0.63
e/mouth-height	0.36 ± 0.09/0.28–0.51
f/mouth-height	0.18 ± 0.03/0.14–0.21
Conicality (a/b)	0.81 ± 0.02/0.78–0.84
Figurativity (c/d)	0.90 ± 0.01/0.89–0.92
Shouldering (b/c)	0.73 ± 0.03/0.69–0.76

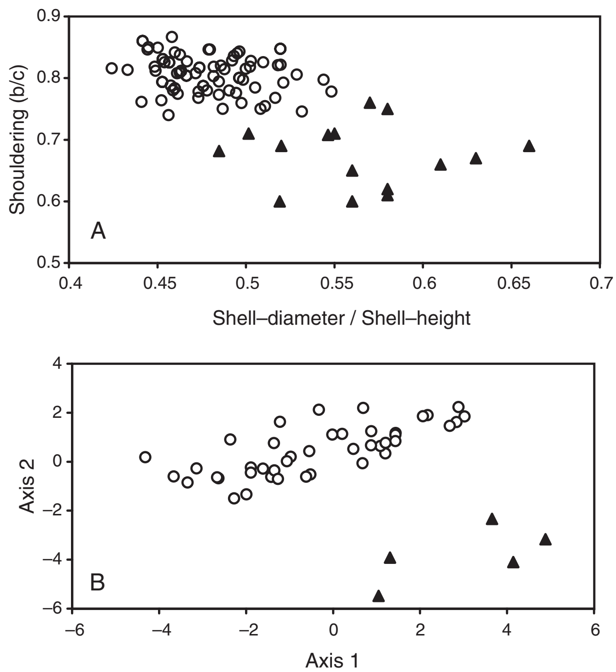

Figure 8. *Melanopsis dircaena* (▲) and *M. buccinoidea* (○). A, shouldering vs. the ratio shell-diameter/shell-height, B, PCO scores.

Diagnosis

Melanopsis dircaena differs from *M. buccinoidea* in that it is almost always more stepped.

Description

The shell is stout, smooth and has up to seven whorls. It has a short spire, and heavily shouldered whorls separated by deep sutures. The mouth-height is large (relative to shell-height). Shell colour is either uniform black or pale brown with three dark bands. The ground colour of the columella and (well-developed) callus is whitish; the callus is tinted brown. Conchometrics ($N = 6$) are presented in Table 3.

Comments

The Senckenberg Museum has four samples from the vicinity of Homs (290938, labelled *M. costata bullio*; 290954, labelled *M. costata jordanica*; 282785 and 283565, both labelled *M. praemorsa costata*). Samples 290938 and 282785 contain only smooth shells; 290954 and 283565 contain a mixture of smooth and ribbed shells, and perhaps also hybrids. We assign all of these samples to *M. dircaena*.

Distribution

Localities available to us include, in addition to that of the type samples, also samples from Lake Homs, from south-west of Rastane (above the Stan Lake) and from Sheizar (Fig. 5).

Comparisons

M. dircaena differs from *M. buccinoidea* (to which it is closer than to other smooth species of the Levant) in that it is diagnostically more stepped (shouldering 0.73 ± 0.03 vs. 0.82 ± 0.03) and stout (shell-diameter/shell-height 0.59 ± 0.05 vs. 0.46 ± 0.03) (Tables 1, 2 and Fig. 8A). It further differs in that the mouth is wider as compared to mouth-height, mouth-height is lower relative to shell-diameter, and the shell is less conic (as expressed by higher values of conicality and figurativity). These differences contribute to the separate clustering of the *M. dircaena* samples in Figure 8B.

Pallary (1939) suggested that *M. dircaena* was the stem species, from which all ribbed species of the Orontes eventually evolved. Pérès (1946) however, suggested that it is a degenerate species.

MELANOPSIS KHABOURENSIS PALLARY, 1939
(FIG. 2E, TABLE 4)

Melanopsis (Mesopotamia) khabourensis Pallary, 1939: 102–104, pl. 5, figs 13–15, 21.

?*Melanopsis (Mesopotamia) khabourensis* var. *elongata* Pallary, 1939: 103, pl. 5, fig. 16.

Not *Melanopsis (Mesopotamia) khabourensis* var. *dolichosoma* Pallary, 1939: 103, pl. 5, fig. 18.

Not *Melanopsis (Mesopotamia) khabourensis* var. *plicata* Pallary, 1939: 103, pl. 5, fig. 19.

Not *Melanopsis (Mesopotamia) khabourensis* var. *gradata* Pallary, 1939: 103, pl. 5, fig. 120.

Table 4. *Melanopsis khabourensis*, conchometrics (mean ± SD and observed range).

Ras al 'Ayn' $N = 6$	*M. khabourensis*
Max. shell-height	29.1 mm
Max. shell-diameter	15.3
Max. mouth-height	16.0
Shell-diameter/shell-height	0.53 ± 0.02/0.51–0.56
Mouth-height/shell-height	0.54 ± 0.03/0.42–0.58
Mouth-diameter/mouth-height	0.43 ± 0.02/0.40–0.45
Mouth-height/shell-diameter	1.01 ± 0.04/0.97–1.07
Notch-width/notch-depth	0.70 ± 0.03/0.64–0.74
Notch-width/mouth-diameter	0.38 ± 0.04/0.32–0.42
e/mouth-height	0.39 ± 0.05/0.32–0.42
f/mouth-height	0.21 ± 0.02/0.19–0.24
Conicality (a/b)	0.79 ± 0.04/0.75–0.83
Figurativity (c/d)	0.91 ± 0.01/0.88–0.93
Shouldering (b/c)	0.79 ± 0.02/0.76–0.81

Material examined

Types: six syntypes (BMNH 1937.12.30.293–302); all from 'Sources du Khabour, dites Ras el "Ain", northern Syria' (Pallary, 1939: 102).

In the type series, together with *M. khabourensis* we also found another species, which we assign to *M. infracincta* (see below); shells intermediate between these two species suggest some degree of hybridization.

Diagnosis

Melanopsis khabourensis differs from *M. buccinoidea* in that mouth-height is small relative to shell-diameter.

Description

The shell is smooth, stout and consists of seven whorls separated by shallow sutures. The spire is short, the callus weak and the columella broad. The notch is deep and from it a hollow ridge extends upwards, winding around and above the columella and ending in the mouth. This ridge separates the columella from the parietal lip with its callus. Shell colour is greyish-brown, usually with two dark bands; the columella is white. Conchometrics ($N = 6$) are in Table 4.

Distribution

Ras al 'Ayn' (Fig. 5), a series of Karst springs in northern Syria which together form the main spring of the river Khabur, a tributary of the Euphrates, is on the boundary between two different landscapes, the mountains of Turkey in the north and the semidesert flats of Syria in the south (Schütt & Sesen, 1989).

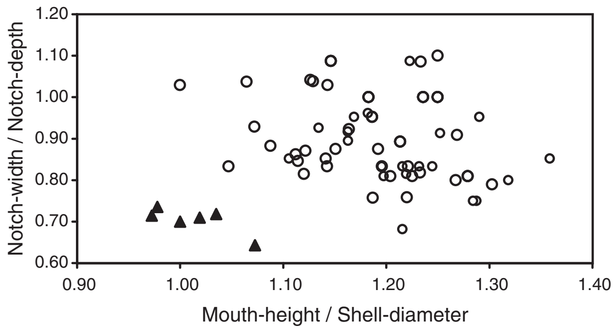

Figure 9. *Melanopsis khabourensis* (▲) and *M. buccinoidea* (○). The notch-width/notch-depth vs. mouth-height/shell-diameter ratio.

Comparisons

A major difference between *M. khabourensis* and other smooth-shelled species is that the hollow ridge that extends from the notch upwards is very pronounced, and the columella is very wide. We could not conveniently measure and express this character in quantitative terms. In the conchometrics used in this study, *M. khabourensis* further differs from *buccinoidea* in that it has almost diagnostically lower ratios mouth-height/shell-diameter (1.01 ± 0.04 vs. 1.19 ± 0.07) and notch-width/notch-depth (0.70 ± 0.03 vs. 0.87 ± 0.08) (Fig. 9). *M. khabourensis* differs from *M.* d*ircaena* in its diagnostically lower ratio notch-width/mouth-diameter (0.38 ± 0.04 vs. 0.51 ± 0.10) and notch-width/notch-depth (0.70 ± 0.03 vs. 0.85 ± 0.08), and almost diagnostically higher ratio b/c (0.79 ± 0.02 vs. 0.73 ± 0.03) (Tables 3, 4). It further differs from *dircaena* in its lower mouth-height relative to shell-height.

Within *Melanopsis*, Pallary (1939) placed *M. khabourensis* in *Mesopotamia*, a separate subgenus that he characterized by a shell with two distinct cords at the base of the lower whorl. Whether or not *Mesopotamia* should be a separate group is beyond the scope of this study. We note however, that *M. khabourensis* has only one ridge. Within *Mesopotamia*, Pallary (1939) described *M. khabourensis* as differing from other species in that it has only two dark bands on the shell, whereas other species have three; the limited material available to us supports this difference.

MELANOPSIS MEIOSTOMA HELLER & SIVAN, 2000 (FIG. 2F)

Melanopsis meiostoma Heller & Sivan, 2000.

Material examined

Types: Holotype HUJ 7966 and 39 paratypes (HUJ 7967, all from 'En Haruv', a small spring in the southern parts of the Golan Heights.

Diagnosis
Melanopsis meiostoma differs from *M. buccinoidea* in that it almost always has a smaller mouth-height relative to shell-height.

Description
The shell is small, narrow, and has up to eight whorls. It has a pointed spire, flattened whorls separated by very shallow sutures, and is smooth. The mouth is small (relative to shell-height) and rather round, due to an outward flaring of the outer lip. Shell colour is uniform, dark-brown to black; also the columella and the (weakly developed) callus are blackish. Conchometrics of *M. meiostoma* are in Heller & Sivan (2000).

Distribution and habitat
M. meiostoma is recorded only from its type locality 'En Haruv' (Fig. 5) a small brackish spring that pours into a cement pool, on the walls of which the snails were found.

Comparisons
M. meiostoma differs from *M. buccinoidea* in having a more narrow shell and smaller, more rounded mouth (lower ratios of shell-diameter/shell-height, mouth-height/shell-height and mouth-height/shell-diameter, higher ratio of mouth-diameter/mouth-height; Heller & Sivan, 2000: fig. 2). It also has a larger notch relative to mouth size (higher ratios notch-width/mouth-diameter and notch-depth/mouth-diameter; Heller & Sivan, 2000: fig. 3).

The sperm of *M. meiostoma* differs from that of *M. buccinoidea* in its larger nucleus, larger acrosome, and shorter midpiece (Hodgson & Heller, 2000). The radula of *M. meiostoma* differs from that of *M. buccinoidea* in the long central cusp of its rachidian tooth (Mazan-Mamczarz *et al*., 2002). In allozyme studies however, *M. meiostoma* invariably adjoins the cluster of *M. saulcyi* (Falniowski *et al*., 2002a, b).

Conchometric differences between *M. meiostoma* and *M. ammonis* are slight. *M. meiostoma* has a smaller mouth-height, relative to shell-height and shell-diameter (0.47 ± 0.02 vs. 0.50 ± 0.03, 1.05 ± 0.05 vs. 1.14 ± 0.05), a larger mouth-diameter relative to mouth-height, a less conic shape, a wider notch (in relation to both notch-depth and to shell-diameter) and higher whorls.

Evidence concerning the separate identity of *M. meiostoma* is thus conflicting. It is placed as a species separate from *M. buccinoidea* on grounds of the shell, sperm and radula, but not so on grounds of electrophoresis; and as separate from *M. ammonis* on grounds of conchometric differences that are significant but not diagnostic.

MELANOPSIS COSTATA (OLIVIER, 1804) (FIG. 10, TABLE 5)

Melania costata Olivier, 1804: pl. 31, fig. 3.
Melanopsis costata, Pallary, 1939: 90–91; Heller *et al*., 1999: 59–61, fig. 4C; Bandel, 2000: 166, figs 72–75.
Melanopsis praemorsa jordanica, Mienis & Ortal, 1994: II.

Type and type locality
'Melanie a cotes, *Melania costata;* de Orontes' (Olivier, 1804; pl. 31, fig. 3). Olivier's type material is not found in the Muséum National d'Histoire Naturelle (Paris) and has probably been lost (Tillier & Mordan, 1983).

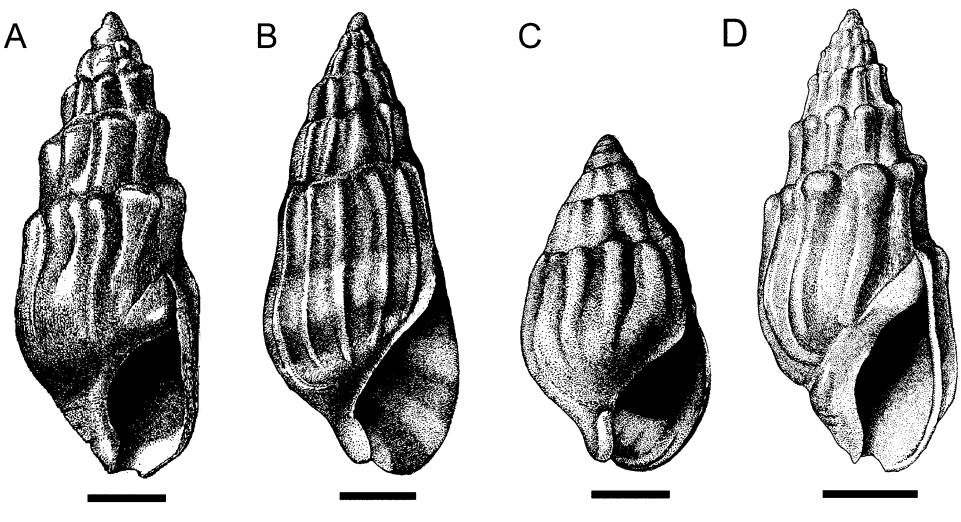

Figure 10. *Melanopsis costata* of the Levant. A, *M. c. costata.* B, *M. c. lampra.* C, *M. c. jordani.* D, *M. c. obliqua*.

Table 5. *Melanopsis costata*, conchometrics (mean ± SD and observed range): pooled data, type locality and synonyms. MccL: *Melanopsis c. costata,* Levant $N = 77$ (pooled); MccD: *M. c. costata* Djishr ech Chegour $N = 14$ (pooled); MhA: *M. hoernesi* Aleppo $N = 1$; Mcl: *M. c. lampra* Jordan Valley $N = 140$ (pooled); MbH: *M. bovieri* Hamik $N = 4$; Mcj: *M. c. jordanica* Kinneret $N = 120$ (pooled); Mco: *M. c. obliqua* Lower Jordan Valley $N = 63$ (pooled)

	MccL	MccD	MhA	Mcl	MbH	Mcj	Mco
Max. shell-height	29.7 mm	29.7 mm	21.7 mm	29.2 mm	25.7 mm	20.6 mm	24.6 mm
Max. shell-diameter	13.7 mm	13.7 mm	8.6 mm	13.2 mm	12.9 mm	11.0 mm	11.5 mm
Max. mouth-height	14.0 mm	14.0 mm	10.0 mm	15.3 mm	14.8 mm	11.4 mm	12.5 mm
Shell-diameter/ shell-height	0.44 ± 0.03/0.37–0.52	0.43 ± 0.02/0.39–0.46	0.39	0.48 ± 0.03/0.39–0.56	0.51 ± 0.01/0.49–0.52	0.54 ± 0.03/0.48–0.63	0.47 ± 0.05/0.38–0.59
Mouth-height/ shell-height	0.50 ± 0.05/0.41–0.63	0.45 ± 0.03/0.40–0.51	0.47	0.54 ± 0.03/0.44–0.63	0.57 ± 0.06/0.57–0.58	0.56 ± 0.03/0.48–0.63	0.51 ± 0.03/0.44–0.57
Mouth-diameter/ mouth-height	0.43 ± 0.03/0.37–0.51	0.44 ± 0.02/0.41–0.53	–	0.44 ± 0.02/0.38–0.52	0.41 ± 0.02/0.39–0.42	0.46 ± 0.03/0.38–0.57	0.44 ± 0.03/0.37–0.51
Mouth-height/ shell-diameter	1.12 ± 0.07/0.96–1.34	1.07 ± 0.07/0.88–1.15	1.15	1.14 ± 0.06/1.01–1.30	1.13 ± 0.04/1.08–1.17	1.03 ± 0.05/0.90–1.17	1.08 ± 0.09/0.88–1.27
Notch-width/ notch-depth	0.83 ± 0.07/0.65–0.96	0.82 ± 0.05/0.71–0.89	–	0.91 ± 0.07/0.76–1.11	0.84, 0.92	0.91 ± 0.06/0.73–1.07	0.87 ± 0.08/0.70–1.14
Notch-width/ mouth-diameter	0.53 ± 0.06/0.35–0.72	0.53 ± 0.05/0.45–0.60	–	0.52 ± 0.07/0.39–0.76	0.54, 0.61	0.52 ± 0.07/0.35–0.78	0.58 ± 0.13/0.39–0.83
e/mouth-height	0.40 ± 0.06/0.25–0.53	0.45 ± 0.06/0.36–0.53	0.41	0.36 ± 0.04/0.28–0.44	0.32 ± 0.03/0.28–0.35	0.37 ± 0.06/0.27–0.46	0.40 ± 0.05/0.31–0.55
f/mouth-height	0.25 ± 0.05/0.13–0.40	0.28 ± 0.05/0.22–0.40	0.30	0.22 ± 0.03/0.16–0.34	0.19 ± 0.02/0.16–0.21	0.21 ± 0.03/0.17–0.28	0.25 ± 0.04/0.18–0.33
Conicality (a/b)	0.93 ± 0.05/0.79–1.02	0.94 ± 0.03/0.90–0.99	1.02	0.86 ± 0.05/0.76–1.00	0.83 ± 0.06/0.75–0.89	0.82 ± 0.04/0.73–0.90	0.90 ± 0.05/0.73–1.00
Figurativity (c/d)	1.00 ± 0.04/0.88–1.08	1.00 ± 0.02/0.97–1.05	1.06	0.92 ± 0.05/0.76–1.00	0.95 ± 0.01/0.93–0.96	0.94 ± 0.02/0.91–0.99	0.96 ± 0.03/0.88–1.00
Shouldering (b/c)	0.74 ± 0.04/0.65–0.91	0.77 ± 0.03/0.73–0.82	0.73	0.77 ± 0.05/0.60–0.98	0.79 ± 0.02/0.77–0.81	0.73 ± 0.04/0.65–0.84	0.78 ± 0.04/0.71–0.91
Number of ribs	9.4 ± 1.1/8–13	9.9 ± 1.6/8–12	10	11.0 ± 1.14/9–14	11.8 ± 0.96/11–13	10.8 ± 1.22/8–14	10.4 ± 1.04/8–12.5
Rib length	2.97 ± 0.53/1.5–4	3.29 ± 0.32/2.5–3.5	3	3.55 ± 0.43/3.0–4.0	3.88 ± 0.25/3.5–4	3.72 ± 0.34/3–4	3.97 ± 0.12/3.5–4
Rib density	2.45 ± 0.55/1.5–4	1.93 ± 0.27/1.5–2.5	2	2.85 ± 0.53/2–4	2.13 ± 0.25/2.0–2.5	2.71 ± 0.44/2–3.5	2.71 ± 0.50/2–4
2 rib width/ shell-diameter	0.48 ± 0.07/0.29–0.62	0.42 ± 0.06/0.29–0.48	0.48	0.35 ± 0.05/0.24–0.46	0.33 ± 0.05/0.29–0.40	0.35 ± 0.03/0.29–0.41	0.39 ± 0.05/0.24–0.54

Diagnosis
Melanopsis costata differs from *M. buccinoidea* in its ribbed shell.

Description
The shell is ribbed, except for its uppermost whorls. The ribs almost always extend the entire height of each whorl and most of them descend vertically; sometimes however, the ribs above the mouth may bend leftwards, towards the columella. The ribs are almost always uniform rather than bumpy and the upper section of each rib (near the suture) is almost always rounded. Shell colour, which varies from greyish yellow to reddish brown or black, may be uniform or banded. In the sperm of *M. costata* the nucleus and acrosome are longer and the midpiece shorter than in *M. buccinoidea* (Hodgson & Heller, 2000).

Distribution
Throughout the Levant, from Kara Sou in the north via Orontes River, coastal plain of northern Israel, Jordan River, Lake Kinneret, Yarmouk River and Azraq Oasis, down to the environs of the Dead Sea in the south (Fig. 11). In the Levant, fossils of *M. costata* are known from the Mid- and Lower Pleistocene of the Jordan Valley (Heller & Sivan, 2001, 2002a). Bandel (2000) suggested that *M. costata*, together with *M. saulcyi* and *M. bandeli*, forms a group that originated in the Balkan, during the Late Miocene or Early Pliocene.

M. costata–M. buccinoidea intermediates
Intermediates between *M. costata* and *M. buccinoidea* are frequently reported in the literature. Germain (1921; figs 51–56) described and mentioned such intermediates from Qusayr (on the Orontes south of Homs), Jayrud (north-east of Damascus) and Baalbek; Schütt (1983) noted that intermediates occur at Cebelib (40 km north of Iskenderun), Samandagi (= Suwaidiya) on the Orontes and Qala'at al Mudiq.

Glaubrecht (1993: figs 5–9) described in detail three sites in the Kingdom of Jordan at which both smooth, ribbed and intermediate shells were found. However, as Glaubrecht assigned all ribbed specimens to *M. costata* (not being aware that another ribbed species, *M. saulcyi*, also occurs in this region; see below) his analysis of these populations should be approached with some caution. His fig. 5 suggests that at one of these sites, Ash Shunah, ribbed and smooth shells are well separated (unfortunately Glaubrecht blurred the picture by adding to this figure also his data from a nearby site, that of North Shuna). Further intermediates were found in the Jordan Valley, in three streams that flow into the Kinneret, and also in the lower Hasbani (a tributary of the Jordan; Heller *et al*., 1999); and in the Azraq oasis (Bandel, 2000).

At least some of these intermediates are hybrids. Evidence for hybridization between *M. costata* and *M. buccinoidea,* but without merging of their genetic pools, was found also at the level of allozymes, in a study that suggested to Falniowski *et al*. (2002a, b) that *M. costata* speciated from *M. buccinoidea* by a mild founder effect. Further, *M. costata–M. buccinoidea* hybrids have been found at a Lower Pleistocene site of the Jordan Valley, in the southern Levant (Heller & Sivan, 2002a).

M. costata–M. dircaena intermediates
Five samples from the Orontes (from the environs of Hamma) contain shells that seem intermediate between *M. costata* and *M. dircaena*: the shell is stout and the ribs are poorly developed. They may be hybrids between these two species. Transitions, of possible hybrid origin, between *M. dircaena* and *M. costata* were noted also by Pérès (1946).

Germain (1921; perhaps in the footsteps of Dautzenberg, 1894) described *M. bullio* from the Lake of Homs (without illustrating it) as having ribs that are pronounced near the suture, where they sometimes form tubercles, and gradually become shorter, until they disappear from the basal part of the last whorl. Pérès (1946) considered *M. bullio* a synonym of *M. costata*. He placed it as a separate variety only to mark a step in the scale of variation of *costata*, but noted a completely gradual transition between a typical *M. costata* and a typical *M. bullio*. The specimens determined as *M. bullio* by Germain are illustrated by Pérès (1946; pl. 2, figs 4–9). They may perhaps be *M. costata–M. dircaena* intermediates.

Intraspecific variation
Within *M. costata* we distinguish four groups that differ significantly (not always diagnostically) in their conchometrics and distribution. These groups are hereby described as four subspecies: *M. c. costata*, *M. c. lampra*, *M. c. jordanica* and *M. c. obliqua*.

MELANOPSIS COSTATA COSTATA
(FIG. 10A)

Melania costata Olivier, 1804: pl. 31, fig. 3.
?Melanopsis callista Bourguignat, 1884: 118.
?Melanopsis sesteri Bourguignat, 1884: 119.
?Melanopsis alepi Bourguignat, 1884: 119–120.
Melanopsis hiera Bourguignat, 1884: 121–122.

?*Melanopsis hiera* Bourguignat, 1884: 121, from Lake Homs; not *Melanopsis hiera* Bourguignat, 1884: 121, from Hula Valley ('Ain Mallaha').
Melanopsis costata var. *hörnesi* Blanckenhorn, 1897: 130, pl. 10, figs 9, 10.
Melanopsis costata Olivier, cotypes: Pallary, 1939: pl. 5, figs 26–28.
Melanopsis costata var. *strigosa* Pallary, 1939: 90, pl. 5, figs 35, 36.
Melanopsis costata var. *subnodata* Pallary, 1939: 90, pl. 5, figs 30–32.
Melanopsis costata var. *obliquata* Pallary, 1939: 91, pl. 5, fig. 34.
Melanopsis orontis var. *elevata* Pallary, 1939: 92, pl. 6, fig. 74.
Not *Melanopsis costata costata* Heller *et al*., 1999: 61–64.

Types and type locality

'Melanie a cotes, Melania costata; de Orontes' (Olivier, 1804: pl. 31, fig. 3).

Material examined

Types: the six syntypes of *Melanopsis costata*, as determined by Pallary (1939) (BMNH 1937.12.30.10361–66) are from the 'R. Orontes'. Another lot, determined by Pallary as 'locality original' (BMNH 1933.8.11.352–59) are from the Orontes at 'Djishr ech Cheghour', between Lattaquie and Aleppo; Pallary noted that this is where Olivier originally collected his *M. costata*.

Additional material: SYRIA: Orontes River and tributaries (BMNH 1933.8.11.14–21, 1933.8.11.33–42, 20030346; NHMW 1838.4.16, 55113; SMF 167427, 282787, 282792, 282805, 282806, 282807, 282812, 282813, 282816, 282824, 283565, 290956, 290984); Aleppo (SMF 271604).

Description

The shell is elongate, with stepped whorls. The uppermost whorl is smooth, the six lower whorls are ribbed. Ribs extend almost the entire height of each whorl and most of them descend vertically, or in a slightly diagonal direction. The upper section of each rib (near the suture) is rounded. Shell colour is greyish yellow to almost black. Conchometrics (of 14 specimens, those labelled cotypes and those labelled as from Djisr ech Cheghour) are given in Table 5.

Synonyms

Blanckenhorn (1897) described *Melanopsis costata* var. *hörnesi* from Aleppo. The type specimen of *M. c. hörnesi* (NHMW 1838.4.16; Table 4) has slightly higher values of conicality and figurativity than in *M. c. costata* (conicality index 1.02 as compared to 0.90–0.99; figurativity index 1.06 as compared to 0.97–1.05); all its other conchometric characters fall within the range of *c. costata*. We therefore consider *M. c. hörnesi* a synonym of *M. c. costata*.

From the type locality of *M. c. costata* (Djishr ech Chegour), Pallary (1939) described six varieties of *M. c. costata*: *inflexa*, *strigosa*, *subnodata*, *obliquata*, *inodata* and *lineata*. These taxa are all so similar that we could not find conchometric gaps between them, whereby we consider them as synonyms of *M. c. costata*. Also listed as synonyms are *M. orontis* var. *elevata* Pallary from Djishr ech Cheghour, and a sample in the Pallary collection (BMNH 1933.8.11.14–21) labelled *M. stephanota* Bourguinat from Kara Sou, 80 km north of Djishr ech Cheghour. These taxa are all so similar that, again, we could not find conchometric gaps between them.

Distribution

Kara Sou, Sadjour Sou, Aleppo and the Orontes River (Fig. 11).

Comments

In addition to the shells of *M. c. costata* that are typically characterized by well-developed ribs, many samples also contain shells with weak ribs, which are frequently not traceable on the last whorl. Such are the type specimens of *M. alepi* from the environs of Aleppo, *M. callista* from Sadjour Sou, and some of the *M. sesteri* from Sadjour Sou. These weak-ribbed shells may perhaps lie within the normal range of variation of *M. c. costata*, or they may perhaps represent an eastern form of *M. c. costata*, or they may even be hybrids between *M. c. costata* and some smooth species.

The *M. costata* of the upper Jordan Valley were previously considered as *M. c. costata* (Heller *et al*., 1999). However, the additional material available in this study reveals a conchometric gap between *M. costata* of the type locality on the one hand, and those of the upper Jordan Valley, some 300 km further south, on the other. We therefore reassign the upper Jordan Valley *M. costata* to a separate subspecies, *M. c. lampra*.

MELANOPSIS COSTATA LAMPRA BOURGUIGNAT (FIG. 10B)

Melanopsis lampra Bourguignat, 1884: 132–133.
Melanopsis phoeneciaca Bourguignat, 1884: 133–134.
Melanopsis belusi Bourguignat, 1884: 134.
Melanopsis tanousi Leternoux, in Bourguignat, 1884: 137–138.

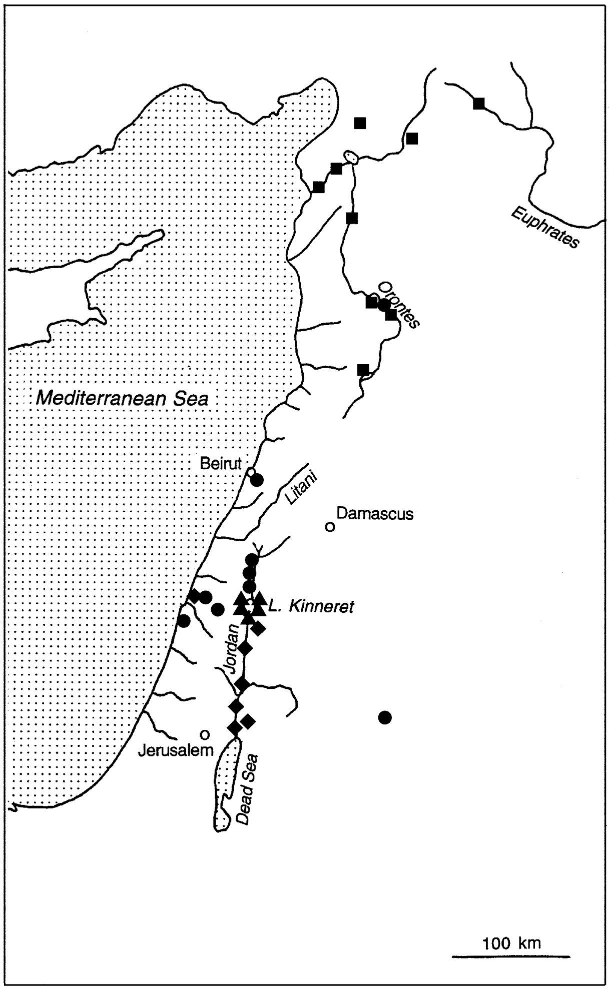

Figure 11. Distribution of *Melanopsis costata costata* in the Levant (inspected records). *M. c. costata* (■), *M. c. lampra* (●), *M. c. jordani* (▲) and *M. c. obliqua* (◆).

Melanopsis jordanica Roth var. *parvula* Bourguignat, 1884: 141–142.
Melanopsis eumorphia Bourguignat, 1884: 146.
Melanopsis praemorsa costata, Schütt, 1983: 42–44, pl. 2, figs 48–56.
Melanopsis costata costata, Heller *et al*.,1999: 61–64, fig. 4B.
Melanopsis bovieri, Germain, 1921: 504–505, pl. 20, figs 7, 8.

Material examined

Types: The syntypes of *M. c. lampra* (MHNG unnumbered; $N = 102$) are from 'Bélus, prés de Saint-Jean-d'Acre' (environs of the Na'aman of today).
Additional material: SYRIA: Orontes (SMF 282816). LEBANON: Hamik (BMNH 1937.12.30.10341–44). JORDAN: Azraq (ZMH). ISRAEL: seven sites along the upper Jordan River, as given by Heller *et al*. (1999).

Diagnosis

M. c. lampra differs from *M. c. costata* in that it is almost always stouter and its whorls are almost always more conic.

Description

The shell is conic, the ribs are mildly pronounced and their shoulders are rounded. *M. c. lampra* further differs from *M. c. costata* in that it has a larger mouth (higher mouth-height/shell-height), higher number of ribs, and these are denser. Conchometrics are in Table 5 (from Heller *et al*., 1999; with additional data). The radula of *M. c. lampra* is described by Mazan-Mamczarz *et al*. (2002) and allozyme variation by Falniowski *et al*. (2002b).

Synonyms

From the swamp of Hamik (in Lebanon, near the Nahr ez Zair bridge on the route to Damascus; 33°43′N, 35°35′E) Pallary (in Germain, 1921: vol. 1: 504–505, vol. 2, pl. 20, figs 7, 8) described *Melanopsis bovieri,* in which the upper whorls are smooth and the lower ones sparsely ribbed, each with a nodosity on its upper part. Germain commented (p. 505) that this species differs from *M. costata* and *M. saulcyi* mainly in its 'trochiform shape with a broad base'. Pallary (1939) illustrated *M. bovieri* (pl. 5, figs 40–43) and mentioned (p. 93) that on visiting the site in 1934, he found that this species had become rare; Pérès (1946) considered it a separate taxon, close to *M. saulcyi*. We examined four specimens of *M. bovieri* in the Pallary collection (BMNH 1937.12.30.10341–44). They fall within the range of *M. c. lampra* (Table 5), whereby we consider *M. bovieri* a synonym of *M. c. lampra*.

Distribution and habitat

M. c. lampra is distributed in the upper Jordan River (Hula Valley), coastal plain of northern Israel and, in the Kingdom of Jordan, the Azraq Oasis (Fig. 11). The northern range of *M. c. lampra* is difficult to assess. We assign to *M. c. lampra* some specimens available to us from the region of Hamma, and to *M. c. costata* some others, from the same sample. We note that Pallary (1939: 91–92, pl. 5, fig. 29) described *M. atramentatria* from Acharne (on the Orontes, between Hamma and Qala'at al Madiq) and commented that this species (or variety) that differs from *M. c. costata* in its more solid, stout shape, lives in the Orontes together with *M. c. costata.* We consider *M. atramentatria* a synonym of *M. c. lampra*; this extends the distribution of *M. c. lampra* to the north of Hamma.

In the Jordan Valley, the dominant habitats of *M. c. lampra* used to be Lake Hula (surface area

14 km^2, depth 1.5–2.5 m), its several tributaries and its outlet (the upper Jordan River). This lake was drained in 1958. Today this subspecies has a narrow, linear distribution along the upper Jordan River and its tributaries, where it is found near overhanging vegetation, especially of *Salix* (Heller *et al.*, 1999). In the coastal plain of the southern Levant it was recently described from 'En Afeq (biblical Na'aman, later named Belus) on muddy substrates, submerged plants and bits of vegetation (Heller *et al.*, 2002).

Comparisons and intraspecific variation

As compared to *M. c. costata,* in *M. c. lampra* the shell is almost always stouter (shell diameter/shell height 0.48 ± 0.03 vs. 0.44 ± 0.03), has a larger mouth-height compared to shell-height (0.54 ± 0.03 vs. 0.50 ± 0.03), is more conic (0.86 ± 0.05 vs. 0.93 ± 0.05), and has significantly more ribs (11.0 ± 1.14 vs. 9.4 ± 1.1) (Table 5). Differences between *M. c. lampra* and *M. c. costata* are best seen in shells of above 19 mm shell-height and therefore, in Figure 12, only such shells are presented. In addition, the ribs of *M. c. lampra* are narrower. Consequently, *M. c. lampra* clusters separately from *M. c. costata* (Fig. 13).

M. c. lampra from the coastal plain of the southern Levant differs from that of the Jordan Valley in that it has fewer ribs, a more shallow notch, a higher rib index and it is more conic (Heller *et al.*, 2002). However, the extent of overlap between the coastal plain and Jordan Valley populations is so considerable that we consider them conspecific.

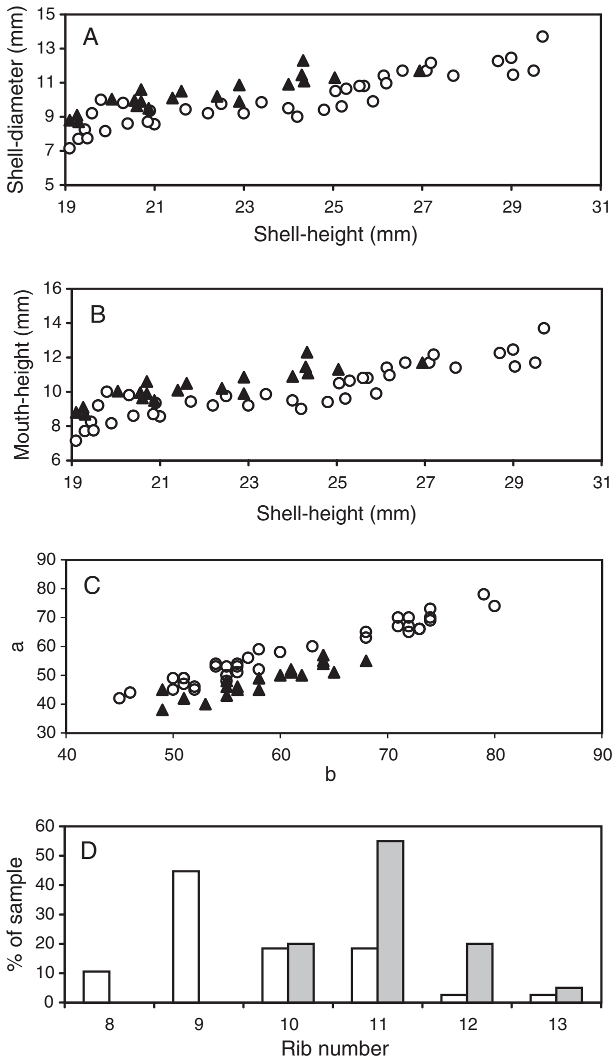

Figure 12. *Melanopsis costata lampra* from upper Jordan Valley (▲) and *M. c. costata* from Antiochia and northwards (○) (shells of at least 19.0 mm shell height). A, shell-diameter vs. shell-height. B, mouth-height vs. shell-height. C, conicality. D, rib number.

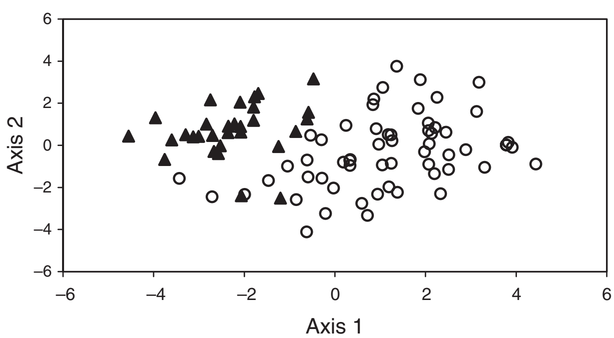

Figure 13. *Melanopsis costata lampra* (▲) and *M. c. costata* (○): PCO scores.

MELANOPSIS COSTATA JORDANICA ROTH (FIG. 10C)

Melanopsis costata var. *jordanica* Roth, 1839: 25, pl. 2, figs 12, 13.
Melanopsis jordanica, Rossmässler, 1854: 17, 905; Bandel, 2000: 176, figs 127, 128.
Melanopsis ovum Bourguignat, 1884: 143.
Melanopsis costata jordanica Roth, Heller *et al.*, 1999: 64–67, fig. 4D.

Material examined

Holotype: Melanopsis costata var. *jordanica* from 'mari Galilaeo' in ZSM.
Additional material: ISRAEL: Six sites along the shoreline of Lake Kinneret, as in Heller *et al*. (1999).

Diagnosis

Melanopsis costata jordanica differs diagnostically from *M. c. costata* in that its shell is stouter and its mouth larger. In these characters it differs also from *M. c. lampra*, though in statistically significant, not diagnostic, terms.

Description

The shell is stout. The ribs are mildly pronounced, with rounded shoulders. Shell colour varies: some are black but many others are banded, the dark bands being broad and black, the pale bands narrow and pale grey to dark brown. The last whorl of each shell has three dark bands and two pale ones. Conchometrics are in Table 5 (from Heller *et al*., 1999 and from additional data).

Distribution and habitat

The many samples of *M. c. jordanica* in the various collections we inspected are all from Lake Kinneret. One exceptional sample from Damascus (coll. Capt. Burton, BMNH) is the only record beyond Lake Kinneret. As there is no further evidence of *M. c. jordanica* in the well-collected region of Damascus, we reject Damascus as a mislabelling.

Lake Kinneret is about 21 by 12 km and frequent daily winds cause it to become wavy, choppy or stormy. Its natural salinity was once almost 400 mg/L (chlorinity) but recent diversion of haline springs from the lake has decreased salinity levels to about 200 mg/L. Within the Kinneret *M. c. jordanica* occurs along rocky shores consisting of gravel, cobble, stones and boulders, down to a depth of 5 m; it is not found on shores consisting of mud, sand and silt. Two snail-predating fish, *Barbus longiceps* (Valenciennes, 1842) and *Blennius fluviatilis* Asso, 1801, are found in Israel, mainly in Lake Kinneret, and they may perhaps exert selection on shell colours (Heller, 1979).

Synonyms

From Lake Kinneret, Bourguignat (1884) described *Melanopsis ovum*. Upon inspecting and measuring the type series of *M. ovum* (BGT 11395, $N = 11$) we find no differences between it and *M. c. jordanica*; hence we consider *M. ovum* a synonym.

Comments

As suggested by Figure 14, *M. c. jordanica* is well separated from *M. c. lampra*. Falniowski *et al*. (2002a, b), in an analysis of allozyme data, found that populations of *M. c. jordanica* cluster close to but separately from populations of *M. c. lampra*. Also, the radula of *M. c. jordanica* clusters separately from that of *M. c. lampra* (Mazan-Mamczarz *et al*., 2002).

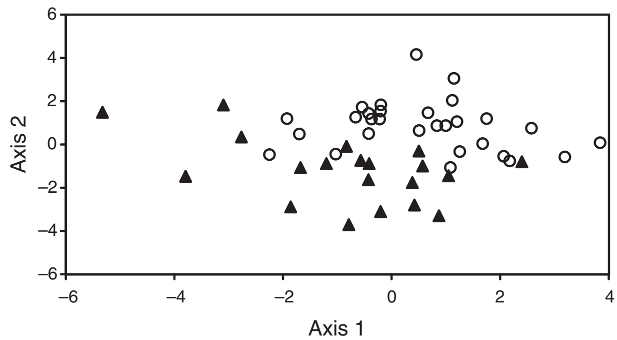

Figure 14. *Melanopsis costata jordanica* (▲) and *M. c. lampra* (○): PCO scores.

Melanopsis costata obliqua Bourguignat (Fig. 10D)

Melanopsis obliqua Bourguignat, 1884: 138.
Melanopsis eumorphia Bourguignat, 1884: 146.
Melanopsis egregia Bourguignat, 1884: 146.
Melanopsis noetlingi Bourguignat in Noetling, 1886: 817, pl. 23, fig. 6*;* Bandel, 2000: 171–2, figs 105, 106.
Melanopsis lampra, Pallary, 1939: 93–94, pl. 6, figs 45, 46.
Melanopsis costata noetlingi Bourguignat*,* Heller *et al*., 1999: 67–68, fig. 4E.

Material examined

Holotype: Melanopsis obliqua from 'Le Belus pres St. Jean d'Acre', BGT 11394.

Additional material: lower Jordan River: (BMNH 1937.12.30.10366–77, SMF 111879, 168956, NHMW 52309, Allenby Bridge (HUJ); Yarmouk River (HUJ).

Diagnosis

Melanopsis costata obliqua differs from *M. c. costata* in that in all specimens the ribs on the last whorl extend the entire length of the whorl. Each rib consists of a very prominent upper tubercle, fused to a straight, prominent, lower ridge.

Description

The shell is conic to elongate. The upper three whorls are smooth whereas the lower ones are ribbed. The ribs on the last whorl are very high and prominent, and extend the entire height of each whorl. The upper section of each rib (near the suture) consists of a very prominent upper tubercle, fused to a straight, prominent, lower ridge. The tubercle and the ridge are either continuous, or separated by a depression. Shell colour is greyish yellow to almost black. Conchometrics are in Table 5 (all material: Yarmouk and lower Jordan; $N = 63$).

Synonyms

M. eumorphia, *M. egregia* and *M. noetlingi* (and also the specimen from the Yarmouk named *M. lampra* by Pallary, 1939; pl. 6, figs 45, 46) all have ribs in which there is a very prominent upper tubercle, fused to a prominent, lower ridge, and on this basis we consider them synonyms of *M. c. obliqua*.

Distribution and habitat

M. c. obliqua is known from the lower Jordan Valley and the coastal plain of the southern Levant (Fig. 11). In the lower Jordan Valley, the current in the outlet of the Yarmouk is torrential and we found *M. c. obliqua* on boulders; in the lower Jordan River the current is slow and we found it on submerged vegetation. The coastal plain (Belus, today named Na'aman) is the type locality of *M. c. obliqua*; in a recent survey we did not find *M. c. obliqua* in this region (Heller *et al*., 2002).

Comparisons

General conchometrics of *M. c. obliqua* are similar to those of *M. c. costata,* but its tubercles, combined with its longer ribs, place it in a separate position. The tubercles also separate it from *M. c. lampra* and *M. c. jordanica,* which are closer to *M. c. obliqua* in geographical terms. A sample recently collected from the lower Jordan is of smaller size and is less tuberculose than specimens collected in the prepollution era of the nineteenth and early twentieth centuries.

MELANOPSIS SAULCYI BOURGUIGNAT, 1853 (FIG. 15A, TABLE 6)

Melanopsis saulcyi Bourguignat, 1853: 66, pl. 2, figs 53, 54.
Melanopsis hiera Bourguignat, 1884: 121–122.
Melanopsis jebusitica Bourguignat, 1884: 126.
Melanopsis saulcyi Bourguignat, 1853, 1884: 127; Mienis & Ortal (1994: II; Heller *et al*., 1999: 68–72, fig. 4F, G; Bandel, 2000: 176, figs 76–79, 84; Heller & Sivan, 2002b: 601–603, fig. 3E.
Melanopsis aterrima Bourguignat, 1884: 127–128.
Melanopsis faseolaria, Bourguignat, 1884: 128.
Melanopsis sancta, Bourguignat, 1884: 129.
Melanopsis cerithiopsis Bourguignat, 1884: 130–131; Pallary, 1939: 95, pl. 4, figs 18, 20, pl. 6, figs 47–50, 53, 54, 73.
Melanopsis cerithiopsis var. *curta* Bourguignat, 1884: 131, from Hula Valley ('Ain el Mellaha).
Melanopsis desertorum Bourguignat, 1884: 134–135, from Tarsous (Anatolia, the type) and Belus.
Melanopsis costata var. *luteopsis* Germain, 1921: 494, pl. 20, figs 9, 10.
Melanopsis palmyrensis Pallary, 1939: 96, pl. 6, figs 60–62.
Melanopsis praemorsa obsolete, Schütt, 1987: 66, fig. 5(3).
Not *Melanopsis* var. *obsoleta* Martens 1874: 32, pl. 5, fig. 39.
Melanopsis praemorsa bandeli Schütt, 1988: 216, fig. 7.
Melanopsis cerithiopsis Bourguignat, 1884, Mienis & Ortal, 1994: II.
Melanopsis bandeli, Bandel, 2000: 176–77, figs 80–83, 85–93, 95.

Material examined

Types: four syntypes (BGT 11358) from 'Artouse, en Syrie' (Bourguignat, 1853: 66). The type locality of *M. saulcyi*, given by Bourguignat, 1853: 66) as 'Artouse, en Syrie', is problematic, because Pallary (1939) argued that there is no such site in Syria; he suggested that the type locality should be Tartous, on the Syrian coast (Fig. 16). An inscription on the label of the type specimen also mentions Artous as being near Jericho. However, Artous (Artuz in modern maps) is a site south-west of Damascus. To conclude, within the southern Levant we could not determine the precise whereabouts of Artous, the type locality of *M. saulcyi*.
Additional material: SYRIA: vicinity of Homs (SMF 290940, 290952, 290954, 29059, NHMW 29382, 30407); Palmyra (SMF 282826, 282827, NHMW 84546). ISRAEL: coastal plain: Nahal Kishon (BMNH 20030249, NHMW 52219), Nahal Taninim (HUJ); Jordan Valley: Enot Huga, En Hanaziv, Hamat Gader (all HUJ).

Diagnosis

Melanopsis saulcyi differs from *Melanopsis c. costata* in that it has more ribs, and these are usually bumpier.

Description

The shell is usually elongate, and its mouth-height small in relation to shell-height. The 2–4 upper whorls are smooth, the 3–6 lower ones are ribbed. In most shells, the ribs descend from the suture to about the middle of the lowest whorl; in others they descend further, sometimes exceptionally so, even extending to the base of the whorl. Each rib usually consists of an upper tubercle, fused to a lower ridge. Consequently the rib normally has a waist between the tubercle and

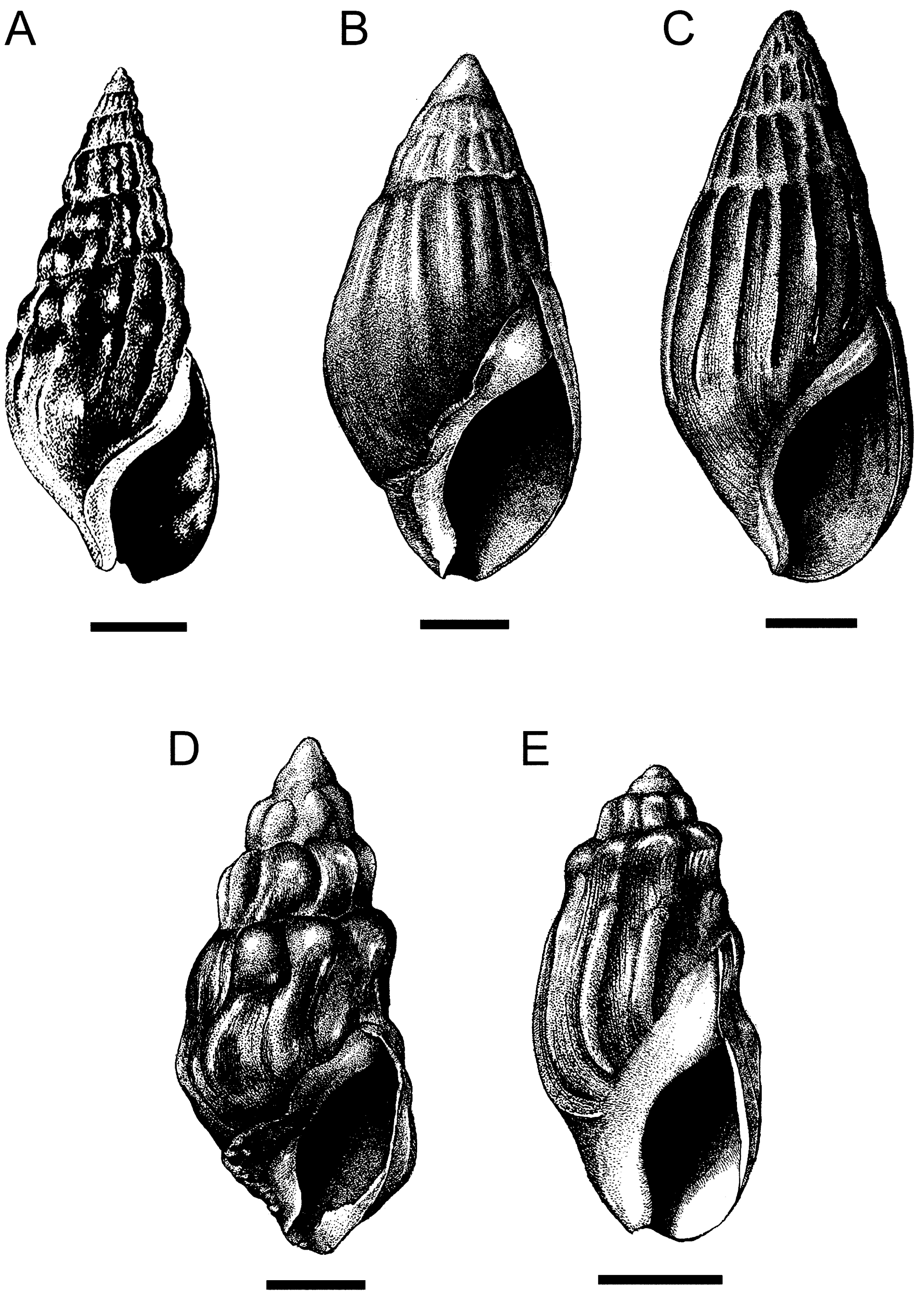

Figure 15. Ribbed *Melanopsis* of the Levant. A, *M. saulcyi.* B, *M. pachya.* C, *M. germaini.* D, *M. infracincta.* E, *M.* sp.

ridge; this waist is present in all ribbed whorls (not only in the ultimate whorl, as is sometimes the case in *M. costata*). When the ribs extend the entire height of the lower whorl this is due to the appearance of an additional ridge, beneath the previous (upper) one; eventually the two ridges fuse to a varying degree. Usually, the overall appearance of the shell is bumpy. Shell colour varies from uniform pale brown via dark brown to uniform black. On the inner lip the pale callus of the upper parietal wall merges with the white columella, so that the entire inner lip is pale. Conchometrics of *M. saulcyi* are in Table 6.

Synonyms

Under his heading *saulcyana,* Bourguignat (1884: 75) placed six species: *saulcyi* from Artouse, Ain Soultan and Ain el Bass; *jebusitica* from near Jericho; *aterrima*

Table 6. *Melanopsis saulcyi*, conchometrics (mean ±SD and observed range): pooled data, type and synonyms. MsSL: *M. saulcyi* Southern Levant $N = 40$ (pooled); MsA: *M. saulcyi* Artrouse $N = 4$; Mpo: *M. praemorsa obsoleta* Palmyra $N = 8$ (pooled); MsH: *M. saulcyi* Homs $N = 25$ (pooled)

	MsSL	MsA	Mpo	MsH
Max. shell-height	25.6 mm	14.4 mm	13.1 mm	22.1 mm
Max. shell-diameter	12.4 mm	6.5 mm	7.4 mm	10.5 mm
Max. mouth-height	13.0 mm	8.8 mm	6.5 mm	11.7 mm
Shell-diameter/shell-height	0.44 ± 0.03/0.38–0.49	0.44 ± 0.02/0.42–0.46	0.46 ± 0.02/0.43–0.48	0.44 ± 0.03/0.39–0.50
Mouth-height/shell-height	0.50 ± 0.03/0.44–0.56	0.57 ± 0.04/0.52–0.61	0.48 ± 0.04/0.41–0.56	0.50 ± 0.02/0.46–0.55
Mouth-diameter/ mouth-height	0.43 ± 0.02/0.37–0.47	0.38 ± 0.02/0.35–0.40	0.46 ± 0.02/0.43–0.49	0.43 ± 0.02/0.40–0.47
Mouth-height/ shell-diameter	1.15 ± 0.06/1.04–1.32	1.28 ± 0.07/1.19–1.35	1.05 ± 0.08/0.93–1.18	1.15 ± 0.06/1.05–1.28
Notch-width/notch-depth	0.85 ± 0.06/0.73–1.18	0.83 ± 0.06/0.76–0.88	0.83 ± 0.04/0.77–0.89	0.88 ± 0.06/0.80–1.00
Notch-width/ mouth-diameter	0.54 ± 0.06/0.37–0.69	0.52 ± 0.08/0.45–0.61	0.50 ± 0.03/0.47–0.53	0.53 ± 0.06/0.43–0.61
e/mouth-height	0.38 ± 0.04/0.30–0.48	0.30 ±0.04/0.26–0.36	0.45 ± 0.09/0.30–0.59	0.39 ± 0.04/0.31–0.47
f/mouth-height	0.24 ± 0.03/0.18–0.28	0.20 ± 0.03/0.17–0.24	0.26 ± 0.04/0.19–0.30	0.26 ± 0.04/0.20–0.36
Conicality (a/b)	0.84 ± 0.05/0.72–0.92	0.85 ± 0.02/0.83–0.87	0.81 ± 0.04/0.74–0.85	0.88 ± 0.05/0.79–0.98
Figurativity (c/d)	0.93 ± 0.02/0.89–1.00	0.93 ± 0.02/0.90–0.94	0.95 ± 0.03/0.92–1.00	0.97 ± 0.03/0.93–1.04
Shouldering (b/c)	0.80 ± 0.03/0.74–0.90	0.79 ± 0.04/0.76–0.82	0.82 ± 0.02/0.80–0.85	0.77 ± 0.04/0.63–0.86
Number of ribs	13.1 ± 2.2/10–18	14.0 ± 2.2/11–16	13–18	10.2 ± 1.33/8–13
Rib length	2.46 ± 0.40/1–4	All 2.5	2–2.5	2.52 ± 0.56/1.5–3.5
Rib density	4.15 ± 0.90/3.0–6.0	4.75 ± 0.50/4.0–5.0	5–8	2.92 ± 0.90/2.0–4.0
2 rib width/shell-diameter	0.30 ± 0.04/0.20–0.38	0.31 ± 0.05/0.28–0.37	0.26–0.30	0.41 ± 0.07/0.28–0.58

from Ain Soultan; *faseolaria* from Ain Mallaha and Belus; *sancta* from Jordan 4 km from the Dead Sea, Ain el Placa (Hula Valley) and Ain Soultan; and *cerithiopsis* from Ain el Mallaha. We inspected Bourguignat's types of these species and as we found no significant conchometric differences among them, we consider them all as synonyms of *M. saulcyi* (as suggested also by Germain, 1921).

Melanopsis costata var. *curta*, a small shell (height 16 mm) with ribs that are not well developed and that fade out at the base of the lower whorl, was described (but not illustrated) from Lake Homs and Lake Antioch by Locard (1883) and Germain (1921). From these descriptions we find no differences between *M. c.* var. *curta*, with its small shell and ribs that fade out in the lower part of the last whorl, and a typical *M. saulcy*i; hence we consider *M. c.* var. *curta* a synonym of *M. saulcyi*. From Lake Homs and also from Jayrud, Germain (1921) described and illustrated *M. c.* var. *luteopsis*. We see no differences between *M. c.* var. *luteopsis*, with its slim shell and ribs that fade out in the lower part of the last whorl, and a typical *M. saulcy*i, so we consider it a synonym of *M. saulcyi*.

From Palmyra, Dautzenberg (1894) and Germain (1921) described *M. saulcyi* var. *obsoleta* as having a small size, slender shell and faint ribs. Schütt (1987) removed this variety from *M. saulcyi* and placed it as a separate subspecies, *M. praemorsa obsoleta*. Schütt suggested that *M. p. obsoleta* is an endemic relict of the Pliocene *Melanopsis* inhabiting the Pliocene connection between the Euphrates and the Jordan Valley via the basins of Palmyra, Qaryatain and Damascus, and that *M. cerithiopsis* Bourguignat of the Jordan Valley is its closest relative.

In a previous study (Heller *et al.*, 1999) we presented evidence that *M. cerithiopsis* is a synonym of *M. saulcyi*. Here we present conchometrics of three samples (eight specimens) of *Melanopsis* from Palmyra described as *M. p. obsoleta* by Schütt (Table 6). The shells have ribs similar to those of *M. saulcyi*, but in some of them the ribs are diffuse. The shells from Palmyra have a slightly smaller mouth than those of *M. saulcyi* from the southern Levant, giving small differences in all the ratios that include mouth-height; these differences are not diagnostic and the overlap is so great that we consider *M. p. obsoleta* a synonym of *M. saulcyi.*

From Syria (Palmyra) Pallary (1939: pl. 6, figs 62–64) described *M. palmyrensis*, which was considered by Schütt (1983, 1987, 1988: fig. 6) as *M. praemorsa obsoleta*. *M. p. obsoleta* falls within the range of *M. saulcyi*, so we consider it a synonym.

From the Kingdom of Jordan, Schütt (1988; fig. 7) described *Melanopsis praemorsa bandeli* as having a narrow shell with dense ribs that do not reach down to the base of the whorl. This description closely follows

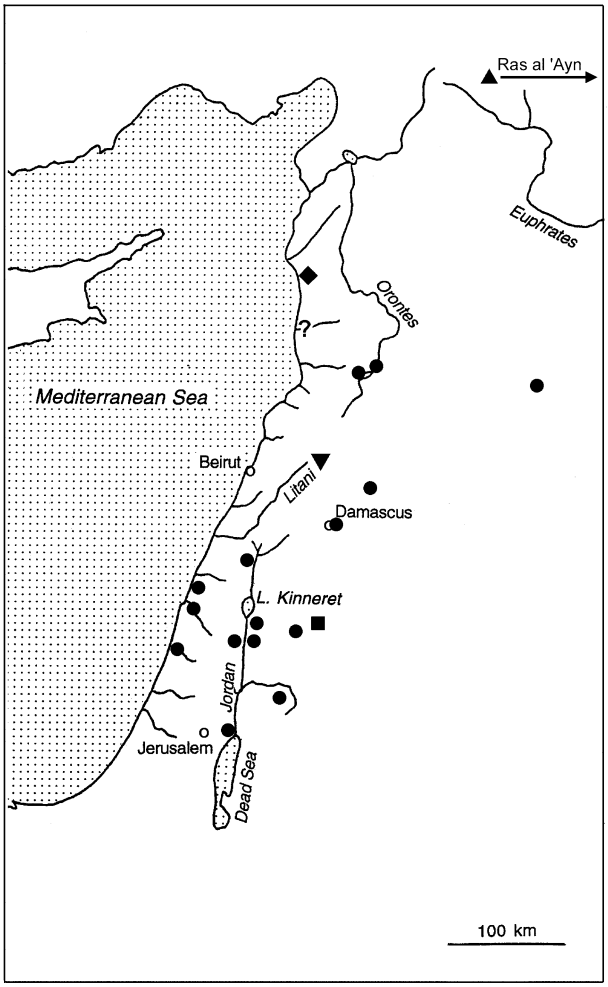

Figure 16. Distribution of *Melanopsis saulcyi* (●), *M. pachya* (■), *M. germaini* (◆), *M. infracincta* (▲) and *M.* sp. (▼) in the Levant (inspected records). **?**, type locality of *M. saulcyi* as suggested by Pallary.

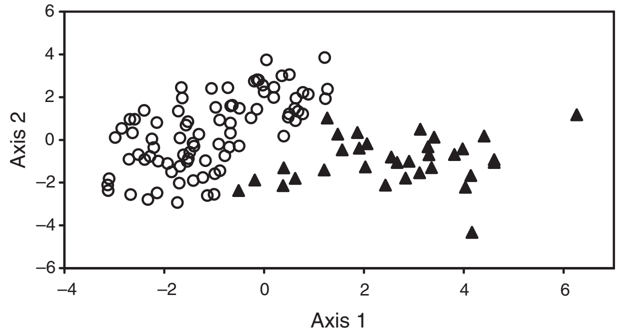

Figure 17. *Melanopsis saulcyi* (Homs and Jordan Valley pooled) (▲) and *M. costata* (*c. costata* and *c. lampra,* pooled) (○): PCO scores.

that of *M. saulcyi*. *M. bandeli* was re-described by Bandel (2000: figs 80–83, 85–93, 95), from the Kingdom of Jordan (both Recent and from fossil layers 'just before the Brackish Lisan Lake'. Bandel (2000: 177) described *M. saulcyi* as smaller and shorter than *M. bandeli* without giving any further differences between these two species. From one of his sites in the Jordan Valley, he (p.177, figs 94, 96) noted transitions between *M. bandeli* and *M. saulcyi* but observed that the majority of individuals belong to *saulcyi*. As concerns size, for *M. saulcyi* Bandel gave a shell-height of 13 mm (his figs 78, 84), whereas for *M. bandeli* he gave shell-heights of 13–20 mm (his figs 80–83, 85–93).

It is noteworthy, however, that Bourguignat (1853) described the type of *M. saulcyi* as reaching 15 mm and Roth (1855) described *M. saulcyi* as having a shell-height of 18.5 mm, both well within the range that Bandel assigned to *M. bandeli*; so too are the 13–16 mm *M. saulcyi* measured by Germain (1921: 503). A similar size range is found in *M. saulcyi* of the Jordan Valley (Heller *et al*., 1999: fig. 12). These data do not suggest a separate taxon within the shell-height range of 13 mm. We see no character with which to distinguish *M. bandeli* from *M. saulcyi*, and thus we consider it a synonym.

Distribution and habitat

M. saulcyi is widely distributed in the Levant (Fig. 16) in springs and streams, where it occurs on boulders and also on aquatic and submerged vegetation. It is our impression that, up to the beginning of the twentieth century, the original habitat of *M. saulcyi* used to be streams that border swamps; today, no swamps remain (Heller *et al*., 1999, 2002).

Comparisons

In Figure 17 *M. saulcyi* clusters separately from *M. costata*. *M. saulcyi* differs from *M. costata* mainly in its more numerous, dense and short ribs, and also in that each rib, on the penultimate whorl, has a waist (for the southern Levant the number of ribs is 13.1 ± 2.2, rib density 4.15 ± 0.90, rib length 2.46 ± 0.40). Within *M. costata,* it differs from *M. c. costata* also in that it is more conic (a/b 0.84 ± 0.05 vs. 0.93 ± 0.05), less stepped (b/c 0.80 ± 0.03 vs. 0.74 ± 0.04), has lower figurativity index (c/d 0.93 ± 0.02 vs. 1.00 ± 0.04), and a smaller ratio 2-rib width/shell-diameter. It differs from *M. c. lampra*, to which it is close in geographical terms, in its slimmer shell and smaller mouth (see Heller *et al*., 1999). All of these differences are significant, not diagnostic.

M. saulcyi falls well away from *M. costata* also in allozyme investigations, with *M. buccinoidea* scattered among both clusters (Falniowski *et al*., 2002a, b). Mazan-Mamczarz *et al*. (2002) described differences in the radula between *M. saulcyi* and *M. costata*. The sperm of *M. saulcyi* differs from that of *M. costata* in having a larger acrosome and shorter midpiece (Hodgson & Heller, 2000).

Intraspecific variability
Within *M. saulcyi,* the type specimens of *M. saulcyi* (BGT 11358) are not typical of the species: they do have numerous dense, short ribs, but they lack the bumpy appearance, and their mouth heights are large. In the Bourguignat collection, the *M. saulcyi* from Ain Sultan (BGT 11357) are more typical of *M. saulcyi*.

Samples from Homs differ from those of the Jordan Valley in that they almost always have a higher figurativity index (0.97 ± 0.03 vs. 0.93 ± 0.02), often have less ribs (10.2 ± 1.33 vs. 13.1 ± 2.2), and lower rib density (2.92 ± 0.90 vs. 4.15 ± 0.90). They further differ in that they are significantly more stepped, the ribs are wider as compared to shell-diameter (2-rib width/shell-diameter 0.41 ± 0.07 vs. 0.30 ± 0.04) (Table 6). Consequently, within *M. saulcyi* the Homs region samples cluster separately from those from the Jordan Valley (Fig. 18).

Within *M. saulcyi* of the Jordan Valley there is considerable variation in rib length; in one population (Sheluhot) they were exceptionally long (Heller *et al.*, 1999). Similar long ribs were found in the Bourguignat collection also in shells from Ain Mallaha, and named by Bourguignat as *M. cerithiopsis* (BGT 11349–50) and *M. faseolaria* (BGT 11351).

In the southern Levant hybrids were found between *M. saulcyi* and *M. buccinoidea*. As this hybridization has not resulted in the merging of the genetic pools of the two species, its occurrence does not reject the species distinctness of *M. saulcyi* and *M. buccinoidea* (Heller *et al.*, 1999, 2002; Falniowski *et al.*, 2002a, b).

Comments
Falniowski *et al.* (2002b) suggested that *M. buccinoidea*, with its high genetic variability, may be the ancestral species from which *M. saulcyi* eventually speciated, perhaps by a founder effect and the allopatric speciation of peripheral isolates.

Melanopsis pachya Pallary, 1939
(Fig. 15B, Table 7)

Melanopsis pachya Pallary, 1939: 86, pl. 5, figs 10,12.

Material examined
Types: eight syntypes (BMNH 1933.8.11.372–79) from 'Dans les Sources de Mézérib, au N. O. de Derâa (Syrie méridionale)'. Deraa is in southern Syria, on the border with the kingdom of Jordan; Mezerib is a small spring some 5 km further north-west.

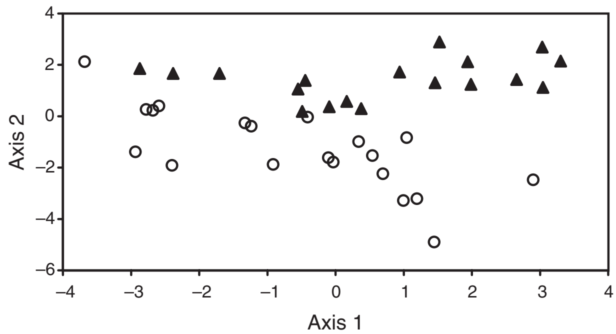

Figure 18. *Melanopsis saulcyi* from the Homs region (▲) vs. *M. saulcyi* from the Jordan Valley (○): PCO scores.

Table 7. *Melanopsis pachya,* conchometrics (mean ± SD and observed range).

Deraa $N = 8$	*M. pachya*
Max. shell-height	29.3 mm
Max. shell-diameter	16.3 mm
Max. mouth-height	14.4 mm
Shell-diameter/shell-height	0.50 ± 0.01/0.49–0.52
Mouth-height/shell-height	0.59 ± 0.02/0.59–0.62
Mouth-diameter/mouth-height	0.41 ± 0.02/0.39–0.44
Mouth-height/shell-diameter	1.15 ± 0.05/1.06–0.20
Notch-width/notch-depth	0.83 ± 0.05/0.77–0.88
Notch-width/mouth-diameter	0.51 ± 0.04/0.46–0.56
e/mouth-height	0.30 ± 0.04/0.24–0.35
f/mouth-height	0.18 ± 0.02/0.14–0.20
Conicality (a/b)	0.74 ± 0.04/0.69–0.81
Figurativity (c/d)	0.92 ± 0.02/0.87–0.95
Shouldering (b/c)	0.79 ± 0.01/0.77–0.80
Number of ribs	15.9 ± 1.57/13–17
Rib length	1.70 ± 0.67/1–2.5
Rib density	2.67 ± 0.29/2.5–3
2 rib width/shell- diameter	0.24 ± 0.03/0.22–0.28

Diagnosis
Melanopsis pachya differs from *M. costata* in that it almost always has more ribs; these usually reach only half the length of the whorl.

Description
The shell is thick and heavy. The upper whorls are eroded in all specimens available, the three lower whorls are weakly ribbed. The ribs, which descend vertically, may extend the entire height of each whorl; or, in other specimens, they may reach to about the middle of the last whorl. The upper section of each rib (near the

suture) is rounded. The inner lip is whitish. Conchometrics are in Table 7. As all shells are eroded, shell-height was calculated by adding an estimate of about 0.8 mm to the measured shell-height (this estimate was reached by comparing the *pachya* shells with non-eroded shells of other *Melanopsis* taxa of similar form).

Distribution

M. pachya is known only from the type locality (Deraa) (Fig. 16).

Comparisons

In geographical terms, *M. pachya* is close to *M. c. lampra* of the upper Jordan Valley. *M. pachya* differs from *M. c. lampra* in its rib parameters: it has more ribs (15.9 ± 1.57 vs. 11.0 ± 1.14), that are usually shorter (1.70 ± 0.67 vs. 3.55 ± 0.43) (Fig. 19A) and it has significantly lower values of the ratio 2-rib width/shell-diameter (0.24 ± 0.03 vs. 0.35 ± 0.05). It further differs from *M. c. lampra* in its significantly higher ratios of shell-diameter/shell-height, and mouth-height/shell-height; and lower mouth-diameter/mouth-height ratio and conicality index (Tables 5, 7). Consequently, *M. pachya* falls separately from *M. c. lampra*, in the PCO (Fig. 19B). *M. pachya* differs from *M. saulcyi* in that its ribs do not consist of an upper tubercle fused to a lower ridge. Consequently, the ribs do not have a waist between the tubercle and ridge.

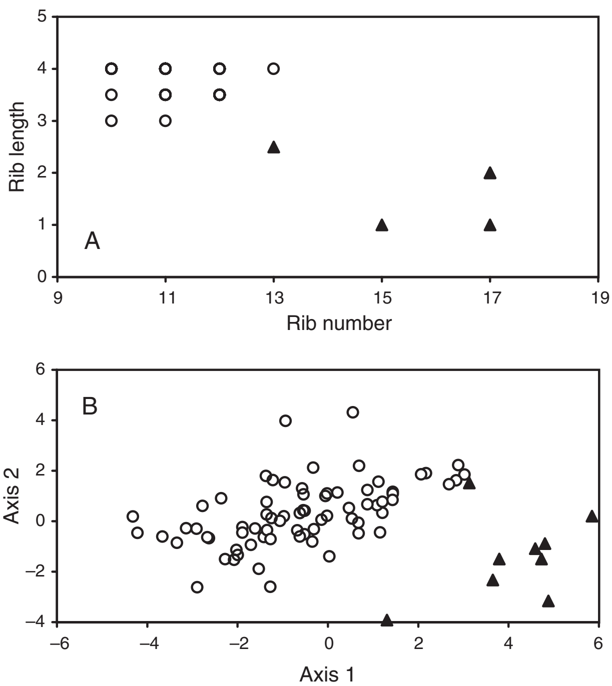

Figure 19. *Melanopsis pachya* (▲) and *M. costata lampra* (○). A, rib length vs. rib number. B, PCO scores.

MELANOPSIS GERMAINI PALLARY, 1939 (FIG. 15C, TABLE 8)

Melanopsis germaini Pallary, 1939: 93, pl. 6, figs 5–8, 14.

Material examined

Types: three syntypes in MNHN (unnumbered) from 'Sources du Nahr es Sine, au Sud de Lattaquie, sur la route de Beyrouth'.

Additional material: SYRIA: Nahr Senne: Paratype (BMNH 20030571), and five specimens (BMNH 1933.8.11.51–55) determined as *M. germaini* by Pallary; five specimens collected by Pallary, and four additional specimens in MNHN; five topotypes (NMW 1955.158. 1727); Nahr as Zirud (SMF 282739).

Diagnosis

Melanopsis germaini differs from *M. costata* in that it has at least 15 and usually 17 ribs. It differs from *M. pachya* in that it has longer ribs and is not so stout.

Description

The shell is conic. The upper whorls are eroded in all specimens, to such an extent that it is not possible to determine whether they were smooth or ribbed; the five lower whorls have well-defined, regularly spaced ribs which descend, usually vertically but sometimes with a slight curve to the right, almost the entire

Table 8. *Melanopsis germaini*, conchometrics (mean ± SD and observed range).

Nahr es Sine $N = 23$ (pooled)	*M. germaini*
Max. shell-height	29.7 mm
Max. shell-diameter	13.3 mm
Max. Mouth-height	14.7 mm
Shell-diameter/shell-height	0.47 ± 0.02/0.44–0.51
Mouth-height/shell-height	0.53 ± 0.03/0.46–0.57
Mouth-diameter/mouth-height	0.44 ± 0.02/0.40–0.48
Mouth-height/shell-diameter	1.13 ± 0.04/1.05–1.21
Notch-width/notch-depth	0.90 ± 0.07/0.77–1.00
Notch-width/mouth-diameter	0.50 ± 0.06/0.35–0.57
e/mouth-height	0.36 ± 0.04/0.28–0.42
f/mouth-height	0.23 ± 0.04/0.17–0.33
Conicality (a/b)	0.77 ± 0.05/0.66–0.84
Figurativity (c/d)	0.93 ± 0.02/0.90–0.95
Shouldering (b/c)	0.81 ± 0.02/0.78–0.84
Number of ribs	17.6 ± 2.01/15–21
Rib length	3.6 ± 0.30/3–4
Rib density	3.4 ± 0.55/2–4.5
2 rib width/shell- diameter	0.24 ± 0.04/0.18–0.31

height of the last whorl. The upper section of each rib (near the suture) is rounded. The inner lip is pale brown. Conchometrics are in Table 8.

Distribution

M. germaini is known only from its type locality, Nahr Senne (on the Syrian coast, north of Banias) (Fig. 16), and the near environment.

Comparisons

M. germaini differs diagnostically from *M. c. costata* of northern Syria (to which it is closer than other subspecies of *M. costata*, in geographical terms) in its number of ribs (17.6 ± 2.01 vs. 9.4 ± 1.1), relative rib width (2 rib width/shell-diameter 0.24 ± 0.04 vs. 0.48 ± 0.07) and conicality index (0.77 ± 0.05 vs. 0.93 ± 0.05) (Tables 5, 8 and Fig. 20A, B). It further differs significantly from *M. c. costata* in the ratios shell-diameter/shell-height, mouth-height/shell-height, figurativity, shouldering, e/mouth height, rib density and rib length. Consequently, *M. germaini* is clearly separated from *M. c. costata* in the PCO (Fig. 20C).

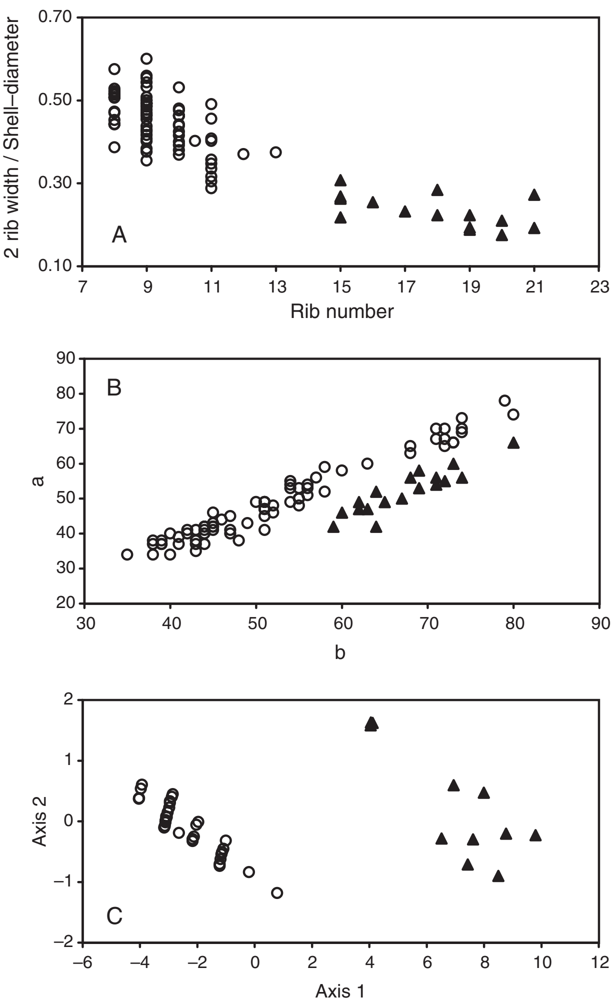

Figure 20. *Melanopsis germaini* (▲) and *M. c. costata* (○). A, 2 rib width/shell-diameter vs. number of ribs. B, conicality (a vs. b); C, PCO scores.

MELANOPSIS INFRACINCTA MARTENS, 1874 (FIG. 15D, TABLE 9)

Melanopsis costata var. *infracincta* Martens, 1874: 32, pl. 5, fig. 38.
Melanopsis (Mesopotamia) nodosa, Pallary, 1939: 98–99, pl. 4, fig. 21.
Melanopsis (Mesopotamia) mesopotamica Pallary, 1939: 99–100, pl. 5, figs 1–7.
Melanopsis (Mesopotamia) infracincta, Pallary, 1939: 103–104, pl. 4, figs 13–17.
Melanopsis (Mesopotamia) khabourensis var. *plicata* Pallary, 1939: 103–104, pl. 5, fig. 19.
Melanopsis (Mesopotamia) cheragragensis Pallary, 1939: 104–105, pl. 5, figs 8, 9, 11.

Types and type locality

'Quellen des Chabour bei Ras-el-ain'. The Khabour, in north-eastern Syria, is a tributary of the Euphrates and Ras al 'Ain' is its major source. We did not find the original types.

Table 9. *Melanopsis infracincta,* conchometrics (mean ± SD and observed range).

Ras al 'Ayn' $N = 8$	*M. infracincta*
Max. shell-height	24.3 mm
Max. shell-diameter	12.1 mm
Max. Mouth-height	11.1 mm
Shell-diameter/shell-height	0.52 ± 0.02/0.49–0.54
Mouth-height/shell-height	0.49 ± 0.03/0.45–0.53
Mouth-diameter/mouth-height	0.48 ± 0.03/0.45–0.54
Mouth-height/shell-diameter	0.95 ± 0.03/0.90–0.98
Notch-width/notch-depth	0.78 ± 0.16/0.50–0.97
Notch-width/mouth-diameter	0.48 ± 0.12/0.25–0.61
e/mouth-height	0.48 ± 0.04/0.44–0.55
f/mouth-height	0.30 ± 0.04/0.26–0.36
Conicality (a/b)	0.90 ± 0.11/0.76–1.06
Figurativity (c/d)	1.01 ± 0.05/0.94–1.08
Shouldering (b/c)	0.72 ± 0.06/0.66–0.82
Number of ribs	9.0 ± 0.93/8–11
Rib length	–
Rib density	1.63 ± 0.35/1–2
2 rib width/shell- diameter	0.44 ± 0.06/0.35–0.51

Material examined
Five specimens (BMNH 1937.12.30.293–302) and three specimens (SMF 290976), all labelled *M. infracincta* from Ras al 'Ain', Syria.

Diagnosis
Melanopsis infracincta differs from *M. c. costata* in that it has diagnostically higher values of the ratio shell-diameter/shell-height and a significantly higher mouth-height/shell-diameter.

Description
The shell is elongate and its overall appearance is knobby. The upper whorls are eroded in all specimens, to such an extent that it is not possible to determine whether they were smooth or ribbed; the four to five lower whorls have elaborate ribs which descend, either vertically or diagonally to the left. The upper section of each rib (near the suture) consists of a huge tubercle that may reach gigantic size. Beneath it and fused to it, a narrow ridge extends downwards. This ridge may expand considerably in its lower part to form a lower tubercle, which may be subequal in size to the upper tubercle. On the lowermost whorl a pronounced ridge starts above the columella, curves downward flanking the columella to the left and terminates as the notch. A second ridge starts near the callus, curves downward around the whorl and terminates on the lower part of the upper lip. Shell colour is black or dark brown to greyish yellow. Conchometrics are in Table 9.

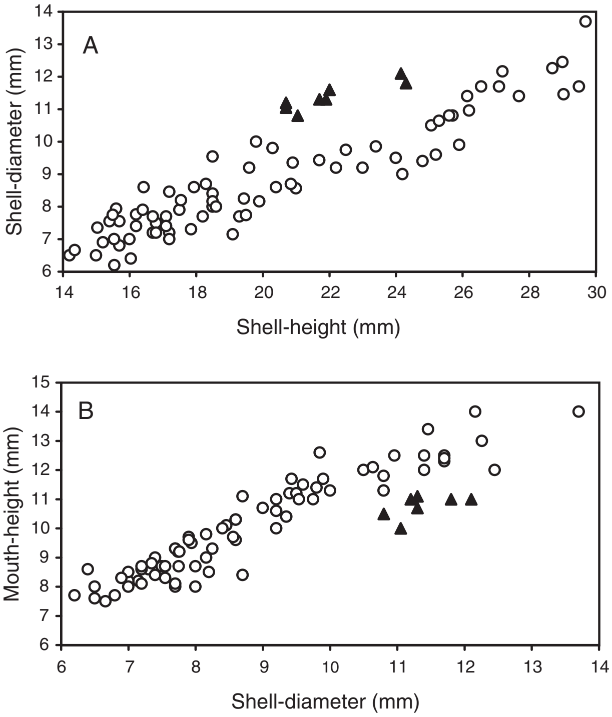

Figure 21. *Melanopsis infracincta* (▲) and *M. c. costata* (○). A, shell-diameter vs. shell-height. B, mouth-height vs. shell-diameter.

Synonyms
Melanopsis arrousiana and *M. stolliana*, two further species described by Pallary (1939) from 'Ain Arous' (his pl. 5, figs 22–25, 44–48) are probably synonyms of *M. infracincta*.

Melanopsis (Mesopotamia) khabourensis var. *dolichosoma* Pallary is characterized by upper whorls with vertical ribs, and lower whorls that are smooth. We consider *dolichosoma* an intermediate, perhaps a hybrid, between *M. khabourensis* and *M. infracincta*.

Schütt & Sesen (1989) suggested that *M. infracincta* and *M. khabourensis* may 'belong to *Melanopsis nodosa* Férussac' which they considered a highly variable species. *M. infracincta* is indeed similar to *M. nodosa* in its complexity of rib structure; the precise relations between these two species are beyond the scope of this study.

Distribution
M. infracincta is known from its type locality, Ras al 'Ayn on the Khabur'. It is also known from 'Ain ar Arous', the type locality of *M. mesopotamica*, and from Tell Abiad near Nahr Balik, the type locality of *M. cheragragensis*. All of these localities are from tributaries of the Euphrates, in north-eastern Syria.

Comparisons
In its bumpy appearance, *M. infracincta* differs from all other ribbed species here described. However, bumpiness is difficult to express in quantitative terms by the tools available to us. In the conchometric terms of this study, *M. infracincta* differs from *M. c. costata* in that it is almost diagnostically stouter (shell-diameter/shell-height 0.52 ± 0.02 vs. 0.44 ± 0.03) and the mouth is smaller relative to shell diameter (0.95 ± 0.03 vs. 1.12 ± 0.07) (Tables 5, 9 and Fig. 21A, B). Further, *M. infracincta* has significantly higher ratios of mouth-diameter/mouth-height, e/mouth-height, f/mouth-height and its ribs are less dense.

For the *Melanopsis* of Mesopotamia, Pallary (1939) established a separate section *Mesopotamia*, characterized by the presence of two distinct ridges at the base of the lowermost whorl that terminate on the left of the columella. He commented that *Mesopotamia* seems very close to a fossil group of melanopsids, *Melanoptychya*.

MELANOPSIS SP.
(FIG. 15E, TABLE 10)

A sample of six shells (NHMW 15826) are labelled '*costata*, Ras-el-Ain, near Baalbek, Syria. Leg. Dr F. Käufel; Walter Klemm collection'. These shells differ from *Melanopsis costata* in their larger mouth-height, and in that each rib has an upper tubercle, which tends to fuse with neighbouring tubercles, so as to form a pronounced ring. The three upper whorls are smooth, the three lower whorls are ribbed. Ribs extend the entire height of each whorl and descend vertically. The upper section of each rib (near the suture) consists of a pronounced tubercle, from which a low ridge extends vertically, until it reaches a lower tubercle; from here a thick, well-developed ridge extends downward, to the mouth. Strong ridges extend from one upper tubercle to the next, thereby forming a thick, 'articulate' ring, immediately beneath the suture. The overall appearance of the body whorl is as consisting of a ring, beneath which there is an indentation, beneath which ribs emerge from prominent tubercles and extend downward to the mouth. In the mouth, the anal slot is exceptionally long and narrow, expanding somewhat in the upper part. Shell colour is horny brown to black, the callus and inner lip are white. Conchometrics ($N = 6$) are in Table 10.

Melanopsis sp. is so closely similar to *M. letourneuxi* Bourguignat from northern Africa (BMNH 1937.12.30.10.113–18, 1937.12.30.10.28–32 and 1937.12.30.10.35–40) as to suggest that it may perhaps be conspecific and mislabelled as to its locality.

Table 10. *Melanopsis* sp., conchometrics (mean ± SD and observed range).

Baalbek $N = 6$	*M.* sp.?
Max. shell-height	18.0 mm
Max. shell-diameter	9.6 mm
Max. Mouth-height	12.5 mm
Shell-diameter/shell-height	0.50 ± 0.02/0.48–0.53
Mouth-height/shell-height	0.67 ± 0.04/0.61–0.71
Mouth-diameter/mouth-height	0.39 ± 0.01/0.38–0.41
Mouth-height/shell-diameter	1.33 ± 0.05/1.26–1.40
Notch-width/notch-depth	0.76 ± 0.04/0.69–0.81
Notch-width/mouth-diameter	0.58 ± 0.03/0.55–0.60
e/mouth-height	0.29 ± 0.05/0.21–0.37
f/mouth-height	0.15 ± 0.02/0.11–0.18
Conicality (a/b)	0.89 ± 0.06/0.83–0.97
Figurativity (c/d)	0.95 ± 0.05/0.88–1.02
Shouldering (b/c)	0.68 ± 0.07/0.59–0.76
Number of ribs	8.2 ± 0.41/8–9
Rib length	3.92 ± 0.20/3.5–4
Rib density	2.50 ± 0.32/2.5–3
2 rib width/shell-diameter	0.44 ± 0.03/0.39–0.46

DISCUSSION

From this conchometric study we conclude that ten *Melanopsis* species occur in the Levant, one of which consists of four subspecies. This conclusion disagrees with that of Glaubrecht (1993, 1996, 1999) who suggested only two taxa (*Melanopsis praemorsa costata* and *M. p. buccinoidea*; while Glaubrecht (1993) figured *nodosa* as a separate taxon he considered it identical with *costata*, its separate name reflecting mere convention). This disagreement is so considerable that it merits detailed discussion.

In seeking natural groups within *Melanopsis* one must determine where intraspecific variability stops and where a discernible gap starts, between natural groupings. This requires covering as many populations, collecting as many snails, making as many measurements and using as many characters as possible. One effective tool to achieve this is molecular taxonomy, which enables reconstruction of phylogenetic trees; another is conchometrics, which enables comparison with fossils. The present study, because it is based upon museum collections, is constrained to conchometrics.

Glaubrecht (1993: 71, 82) commented that to describe different species on grounds of the shell alone is consistent with neither modern systematics nor any contemporary biological concept. This comment may perhaps refer to studies in which only standard conchometrics are used, as these may, in some gastropod genera, contain limited information. However, standard conchometrics may be enriched by nonstandard measurements.

In a previous study of *Melanopsis* of the Jordan Valley, species-level taxonomy was first deciphered by combining standard with nonstandard conchometrics (shell-height, shell-diameter, mouth-diameter and presence/absence of ribs; with shouldering, figurativity, conicality, notch dimensions, rib number, length, shape, height and waviness). Four species were found (*buccinoidea, costata, saulcyi* and *meiostoma*). Of these, *costata* was found to consist of three subspecies, and *buccinoidea* was found to interbreed with *costata* and *saulcyi* (Heller *et al*., 1999; Heller & Sivan, 2000).

Next, to explore the extent to which this conchometrics-based taxonomy is congruent with other taxonomic tools, the Jordan Valley *Melanopsis* were analysed critically using another taxonomic tool, electrophoresis. Falniowski *et al*. (2002a, b) found (with the exception of *meiostoma*) that isozymes reveal the same natural groupings found in the conchometric study: three very close but distinct biological units, one of which, *costata,* consists of two subspecies; the other, *buccinoidea*, hybridizes with other species.

To further evaluate conchometric taxonomy, the Jordan Valley *Melanopsis* were analysed using another taxonomic tool, sperm morphology. Hodgson & Heller (2000) found significant differences in the sperm of the four 'conchometric species' (in this character, in contrast to electrophoresis, the distinctness of *meiostoma* was confirmed). Also, examination of the radula yielded results broadly congruent with the conchometric taxa (again supporting the distinctness of *meiostoma*; see Mazan-Mamczarz *et al*., 2002). The fact that the isozymes, sperm and radula broadly confirm conclusions reached from conchometrics suggests that the taxonomic ranking of conchometrically different populations of *Melanopsis* as separate taxa, if based on numerous samples and characters, may be reliable.

Encouraged by this broad support for use of the shell, we extended the geographical range of our research and applied conchometrics to *Melanopsis* of the entire Levant. *M. germaini* was found to differ from *M. costata* in its more numerous ribs, *M. pachya* in its shorter ribs, *M. saulcyi* in its bumpy ribs, and *M. infracincta* in that each rib has huge tubercles. Among species without ribs, *M. ammonis* was found to differ from *buccinoidea* (of the nearby Jordan Valley) in its more narrow shell, *M. dircaena* in being more stepped, *khabourensis* in its broader columella and *meiostoma* in its smaller mouth.

The shell was thus found to contain a wealth of information, revealed via the addition of nonstandard measurements to standard ones. Accordingly, we consider conchometrics a worthy systematic tool for intrageneric taxonomy. While in certain freshwater pulmonate snails the shell is neither a consistent character nor taxonomically diagnostic (Britton & McMahon, 2004) in *Melanopsis* it is definitely not 'an antiquated systematic concept that unfortunately long prevailed in malacology' (Glaubrecht, 1993: 81). To conclude, one source of the disagreement between conclusions reached in this present study and those of Glaubrecht is in our more detailed use of conchometrics.

Another source of disagreement concerns the evaluation of data derived from the radula. Glaubrecht (1993) gave priority to the radula over the shell in *Melanopsis* taxonomy. He found variability of the radula formula over broad areas on the one hand, and nearly identical dentitions in widely separate populations on the other; this led him to conclude that all circum-Mediterranean *Melanopsis* should be assigned to one group. There is, however, no reason why, in the taxonomy of *Melanopsis,* similarities in the radula should be given more weight than differences in the shell, nor is there a reason why different closely related species should not have a similar radula. Further, in taxonomic use of the radula one should, beyond recording variability, seek gaps in the data.

In *Melanopsis* of the western Mediterranean there is indeed evidence for gaps in the formula of the radula even in Glaubrecht's own data, in that *M. cariosa* has five cusps of the rachidian tooth vs. seven in *M. tricarinata* (Glaubrecht, 1993: table 5; Glaubrecht, 1996: table 2). As concerns the eastern Mediterranean Mazan-Mamczarz *et al*. (2002) found considerable differences between *M. meiostoma* and other neighbouring species. Thus, as pointed out by Reid & Mak, (1999), radular characters must be used with caution in taxonomic studies. We do not accept the generalization that 'conchology provides very unreliable taxonomic characters in freshwater molluscs, compared to soft tissue and radula features' (Glaubrecht, 1993: 71).

Though most shells of this study fall into clearly distinct species, intermediates are found throughout the Levant and the precise conchometric limits of some species are somewhat hazy. In the Jordan Valley, where we collected personally, we found that *buccinoidea* and *costata* generally remain distinct; but in zones of contact intermediate hybrids were found, at low frequencies and over distances of no more than a few hundred metres. These contact zones are connected to a major ecotone, from gently running stream outlets, inhabited by *buccinoidea*, into the choppy and wavy Lake Kinneret, inhabited by *costata* (Heller *et al*., 1999). Also at two Pleistocene sites of the Jordan Valley, *buccinoidea-costata* hybrids were found (Heller & Sivan, 2002a).

This Pleistocene-Recent chain of hybrids indicates that *costata* and *buccinoidea* of the Jordan Valley have been living together side by side in the same water bodies of the Levant for 1.4 Myr at least; and though they have been (continuously?) hybridizing since the early mid-Pleistocene, this hybridization has not resulted in merging of their genetic pools. The 1.4 Myr old fossil hybrids may be the earliest direct evidence available among molluscs of hybridization in nature, that is still going on today in the same region and aquatic system, among the same species. The *Melanopsis* hybrid populations may perhaps act as filters that prevent the introgression of most genes, but allow others to disperse into the range of the parent species (Heller & Sivan, 2002a).

In regions beyond the Jordan Valley (and the coastal plain of Israel) where we used only museum material and did not collect personally, the intermediates found may represent either gradual transition from one species into another, or hybridization. As evidence for gradual transition, one would expect one taxon in one region, intermediate forms in transitional regions and another taxon in another region. On the other hand, a situation in which intermediates occur repeatedly in various regions would suggest (repeated) hybridization.

Throughout the Levant, the scattered distribution of the *buccinoidea–costata* intermediates suggests that they are hybrids. In addition to *buccinoidea–*

costata, intermediates were found between *M. buccinoidea* and *M. saulcyi*; *M. khabourensis* and *M. infracincta;* and *M. costata and M. dircaena.* Following the *buccinoidea–costata* evidence, we consider all these intermediates to be hybrids.

Another source of disagreement between our conclusions and those of Glaubrecht concerns matters of concept and terminology. Glaubrecht (1993) noted that the smooth and ribbed forms of *Melanopsis* intergrade when they come into contact at a given location, 'as is expected for subspecies' (p. 66). If the term 'subspecies' refers to taxa that are isolated to such a poor extent that they hybridize, then (in restricting ourselves, at this point of the discussion, to the taxa of the Jordan Valley where we collected personally) *costata*, *buccinoidea* and *saulcyi*, since they frequently hybridize, could be ranked as subspecies. In the present study, however, the term subspecies refers to intraspecific variation on a geographical basis (see Mayr, 1969: 41–42) whereas hybridization refers to those cases in which reproductive barriers fail between valid species. Consequently, as *costata*, *buccinoidea* and *saulcyi* have mosaic distributions within the same geographical region; and as, in spite of hybridization, very many populations consist of either pure smooth or pure ribbed shells, we rank them as species – which may interbreed to a certain extent at sites where they come into contact.

From the question of species vs. subspecies we now come to the question of subspecies not mentioned by Glaubrecht (1993, 1996, 1999) but recognized in this present study (*M. c. costata*, *M. c. lampra*, *M. c. jordani* and *M. c. obliqua*). The term 'subspecies' as expressing geographical intraspecific variation is not sharply defined: there is no definition of the size of a geographical area that entitles local variation to the rank of subspecies; and there is no current definition as to how significant the intraspecific differences should be. We are speaking of a continuum. At one end there are fully separate species with large distribution areas, clearly differentiated; when inspecting a specimen it will almost always be absolutely clear which species it belongs to. At the other end there is variation within the same species (genetic pool) when two close populations differ to such a slight extent that, when inspecting a specimen from any of these populations, it will almost never be clear whether it comes from one population or another.

A subspecies is somewhere in between: when inspecting a certain specimen from any of these populations one can sometimes tell that it comes from one population, not from the other. In an early attempt to quantify the term Mayr (1969: 190) suggested that a subspecies is valid if 75% of its individuals differ from 97% of the individuals of a previously recognized subspecies. However, few use this formula today (including Mayr himself in later publications, see Mayr & Ashlock, 1991: 96–98).

Formal taxonomy should express intraspecific variation as closely as possible and if, within a species, populations of a given geographical area differ considerably from those of other areas, then they should be given a different formal name. Consequently, we assign the four geographical forms of *M. costata* to different subspecies.

Glaubrecht (1993) suggested that the many circum-Mediterranean taxa of *Melanopsis* combine to form a superspecies. He further suggested that the smooth form of *Melanopsis* is plesiomorphic whereas ribbed forms (including *costata*) appeared only during the Miocene (Glaubrecht, 1999). However, Neubert (1998: 353) argued that the term 'superspecies' refers to a monophyletic entity composed of allopatric taxa in different geographical regions, while Bandel (2000) argued that Glaubrecht, in suggesting that ribbed forms appeared only during the Miocene, did not take into account the full evidence of the fossil record.

We found that, in the Levant, within a radius of 5 km from Lake Kinneret there are six taxa (*M. c. lampra*, *M. c. jordani*, *M. c. obliqua, M. buccinoidea*, *M. meiostoma* and *M. saulcyi*) – not a distribution pattern that falls easily within the definition of allopatry. Therefore we join Neubert (1998) and Bandel (2000) in not applying the term superspecies to *Melanopsis*. The oldest *Melanopsis* fossils in the Levant date from the Pliocene (Blanckenhorn, 1897; Heller & Sivan, 2002b) so they do not contribute direct evidence to discussions concerning ribbed vs. smooth forms during the Miocene, an earlier period in the history of the genus.

Melanopsis is a difficult genus subject to considerable controversy, and taxonomic analysis may falter if we fail to capture those delicate points where intraspecific variation ends and interspecific gaps begin. This calls for a cautious, step-by-step approach: first to study populations from one small region and only later to extend research into further nearby regions, reshuffling the groups and adjusting the nomenclature as one goes along. We hope this present taxonomic analysis of *Melanopsis* of the Levant may provide a basis for future comparisons with *Melanopsis* of other circum-Mediterranean regions.

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REFERENCES

Altman Z, Ritte U. 1996. The same gene pool is shared by two distinct morphs of the freshwater snail *Melanopsis* from the Sea of Galilee. *Israel Journal of Zoology* **42:** 443–448.

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 des Geologisch-Paläontologisches Institut des Universität Hamburg* **84:** 131–208.

Bandel K, Salameh E. 1981. Hydrochemical and hydrobiological research of the pollution of the waters of the Amman Zerka area (Jordan). *Schriften der Deutschen Gesellschaft für Technische Zusammenarbeit* **94:** 1–60.

Bilgin FH. 1983 (1986). Taxonomical studies on *Melanopsis costata* ssp. (Gastropoda–Prosobranchia). *Proceedings of the 8th International Malacological Congress, Budapest 25–26.*

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

Bourguignat JR. 1853. *Catalogue raisonné des mollusques terrestres et fluviatiles recueillis par M. F. de Saulcy pendant son voyage en Orient*. Paris: Gide & Baudry.

Bourguignat JR. 1884. Histoire des mélaniens du système européen. *Annales Malacologie* **2:** 1–168.

Britton DK, McMahon RF. 2004. Environmentally and genetically induced shell shape variation in the freshwater pond snail *Pysella* (*Pysella*) *virgata* (Gould, 1855). *American Malacological Bulletin* **19:** 93–100.

Burch JB. 1985. *Handbook on schistomiasis and other snail-mediated diseases in Jordan*. Ann Arbor, MI: University of Michigan.

Burch JB, Bruce JI, Amr Z. 1989. Schistomiasis and malacology in Jordan. *Journal of Medical and Applied Malacology* **1:** 139–164.

Dautzenberg P. 1894. Liste des mollusques terrestres et fluviatiles recueillis par M. Th. Barrois en Palestine et en Syrie. *Revue Biologique du Nord de la France* **6:** 1–21.

Falniowski A, Heller J, Szarowska M, Mazan-Mamczarz K. 2002a. Allozymic taxonomy within the genus *Melanopsis* (Gastropoda: Cerithiaca) in Israel: a case in which slight differences are congruent. *Malacologia* **44:** 307–324.

Falniowski A, Heller J, Mazan K, Szarowska M. 2002b. Genetic structure of populations of the closely related species of *Melanopsis* (Gastropoda: Cerithiacea) in Israel. *Journal of Zoological Systematics and Evolutionary Research* **40:** 92–104.

Germain L. 1921. *Mollusques terrestres et fluviatiles de Syrie*. 2 Vols. Paris: Bailliere et Fils.

Glaubrecht M. 1993. Mapping the diversity: geographical distribution of the freshwater snail *Melanopsis* (Gastropoda: ?Cerithioidea: Melanopsidae) with focus on its systematics in the Mediterranean basin. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **90:** 41–97.

Glaubrecht M. 1996. Evolutionsökologie und Systematik am Beispiel von Süss- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien. *Palaontologische Befunde und Historische Zoogeographie*. Leiden: Backhuys.

Glaubrecht M. 1999. A look back in time – toward an historical biogeography as a synthesis of systematic and geologic patterns outlined with limnic gastropods. *Zoology* **102:** 127–147.

Heller J. 1979. Visual versus non-visual selection of shell colour in an Israeli freshwater snail. *Oecologia* **44:** 98–104.

Heller J. 2001. Near east ecosystems, animal diversiy. In: Levin SA, ed. *Encyclopedia of biodiversity*, 4. San Diego: Academic Press, 329–352.

Heller J, Abotbol A. 1997. Litter shredding in a desert oasis by the snail *Melanopsis praemorsa*. *Hydrobiologia* **344:** 65–73.

Heller J, Sivan N. 2000. A new species of *Melanopsis* from the Golan Heights, southern Levant (Gastropoda: Melanopsidae). *Journal of Conchology* **37:** 1–5.

Heller J, Sivan N. 2001. *Melanopsis* from the mid-Pleistocene site of Gesher Benot Ya'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:** 607–626.

Heller J, Sivan N, Ben-Ami F. 2002. Systematics of *Melanopsis* from the coastal plain of Israel (Gastropoda: Cerithiodea). *Journal of Conchology* **37:** 589–606.

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.

Hodgson AN, Heller J. 1997. A preliminary investigation of spermatid/sertoli cell association in a freshwater gastropod mollusk. *Journal of Reproduction and Development* **43** (Suppl.)**:** 79–80.

Hodgson AN, Heller J. 2000. Spermatozoon structure and spermiogenesis in four species of *Melanopsis* (Gastropoda, Prosobranchia, Cerithiodea) from Israel. *Invertebrate Reproduction and Development* **37:** 185–200.

Issel A. 1866. Catalogo molluschi raccolti dalla Missione Italiana in Persia aggiuntavi la descrizione delle specie nuove o poco note. *Memoria di Accademia Reale Societe, Torino, Serie* **2** (23): 1866.

Locard A. 1883. *Malacologie des Lacs Tibériade, d'Antioch et d'Homs.* Lyon: Henri Georg.

von Martens E. 1874. *Ueber Vorderasiatische Conchylien nach den Sammlungen des Prof. Hausknecht*. Cassel: Theodor Fischer

Mayr E. 1969. *Principles of systematic zoology*. New York: McGraw-Hill.

Mayr E, Ashlock P. 1991. *Principles of systematic zoology*. New York: McGraw-Hill.

Mazan-Mamczarz K, Heller J, Szwarowska M. 2002. Differences in the radula of the genus *Melanopsis* in the Jordan Valley, Israel. *Malakologische Abhandlungen Staatliches Museum für Tierkunde Dresden* **20:** 219–234.

Mienis H. 1983. A preliminary checklist of the freshwater molluscs of Israel and administered areas. *Levantina* **47:** 543–550.

Mienis H, Ortal R. 1994. *The names of the inland aquatic and terrestrial molluscs of Israel (including the categories of threatened species).* Jerusalem Nature Reserves Authority, supplement 2.

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.

Noetling F. 1886. Ueber die Lagerungsverhältnisse einer quartären Fauna im Gebiete des Jordanthals. *Zeitschrift der Deutschen Geologischen Gesellschaft* **38:** 807–823.

Olivier GA. 1801. *Voyage dans l'Empire Ottoman, l'Egypte et la Perse*, Vol. 1. Paris: Agasse.

Olivier GA. 1804. *Voyage dans l'Empire Ottoman, l'Egypte et la Perse*, Vol. 2. Paris: Agasse.

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

Pérès JM. 1946. Contribution à l'étude de *Melanopsis*. *Journal de Conchologie* **86:** 109–174.

Raanan M. 1986. The systematics and ecological evolution of the genus Melanopsis in Lake Kinneret. PhD Dissertation, Hebrew University, Jerusalem (Hebrew, English summary).

Radev V, Kanev I, Nollen PM, Gold D. 1999. Life history and identification of *Philophthalamus lucipetus* from Israel. *Journal of Parasitology* **85:** 291–294.

Reid DG, Mak TM. 1999. Indirect evidence for ecophenotypic plasticity in radular dentition of *Littoraria* species (Gastropoda: Littorinidae). *Journal of Molluscan Studies* **65:** 355–370.

Rossmässler EA. 1854. *Iconographie der Land- und Süsswasser-Mollusken Europas's, mit vorzüglicher Berücksichtigung europäischen noch nicht abgebildeten Arten*. Leipzig.

Roth JR. 1839. *Molluscorum species*. München.

Roth JR. 1855. Spicilegum molluscorum terries orientalis provinciae Mediterranensis peculiarum. *Malakozoologiscke Blätter* **2:** 17–58.

Schütt H. 1983. Die Molluskenfauna der Süssgewässer im Einzugsgebiet des Orontes unter Berücksichtigung benachbarter Fluss systeme. *Archiv für Molluskenkunde* **113:** 17–91.

Schütt H. 1987. The molluscs of the oasis Palmyra. In: Krupp F, Schneider W, Kinzelbach R, eds. *Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985.* TAVO A 28, 215–219.

Schütt H. 1988. Über eine reliktare *Melanopsis* aus Jordanien (Ein Beitrag zur Kenntnis der Rassenbildung durch geographische Isolation). *Annalen des Naturhistorischen Museums in Wien* **90:** 215–219.

Schütt H, Sesen R. 1989. The freshwater molluscs of Ceylanpinar. *Zoology in the Middle East* **3:** 55–58.

Tchernov E. 1975. The mollusks of the Sea of Galilee. *Malacologia* **15:** 147–184.

Tillier S, Mordan P. 1983. The conchological collections of Bruguière and Olivier from the Ottoman Empire (1792–1798). *Journal of Conchology* **31:** 153–160.

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