FOSSIL VIVIPARIDAE (MOLLUSCA: GASTROPODA) OF THE LEVANT

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Abstract *Today there are no representatives of the freshwater family Viviparidae in the Levant but Pliocene-Pleistocene remains are abundant. This conchometric study explores their taxonomical position within the family. All Levantine fossils are here assigned to the African-Asian sub-family Bellamyinae and not to the Eurasian-N. American sub-family Viviparinae on the basis of their high apex and high conicality index. Two genera are recognized: Bellamya with three species and a new genus, Apameaus, with one species.*

Key words *Fossil, Levant, Viviparidae, Bellamya, taxonomy.*

INTRODUCTION

During the 19th century virtually all viviparid species were ranged in the genus *Viviparus* Denys de Montfort. On the basis of anatomical (e.g. genitalia, operculum) and conchological differences (e.g. ornamentation and size of the embryonic and to a lesser degree the adult shell), different genera have since been recognized and divided into two subfamilies: the Viviparinae with a Laurasian distribution (N. America and Paleartic Eurasia) and the Bellamyinae with an eastern Gondwana one (Africa and southern Asia) (Rohrbach, 1937; Vail, 1977; Boss, 1982). While this taxonomic approach is satisfactory for identifying Modern species, identification of the Plio-Pleistocene viviparid faunas that formerly occurred in the region of the Paratethyan system (brackish and freshwater lake basins in central-eastern Europe and western Asia), situated intermediately between the two respective distribution areas of both subfamilies, remains, problematic (Magyar, Geary & Müller, 1999; Müller, Geary & Magyar, 1999) . Till now the taxonomy of the often strongly ornate and highly distinctive fossil viviparid species that lived in the Paratethyan lake systems such as Palaeolake Pannon or rather its Pliocene successor the Paludina Lake (Central Europe), the Euxinian lakes (Eastern Europe and Western Asia) and in the lakes and rivers of the Levant have not been revised. Viviparids of the Levant were referred to either as *Viviparus sensu lato* (or erroneously as *Tulotoma*, a northern American genus), e.g. *Viviparus apameae* Blanckenhorn in Braun & Tchernov (1991), Tchernov (1975) and Schütt & Ortal (1993) or assigned to the African species *Bellamya unicolor* (Olivier) in Blanckenhorn & Oppenheim (1927) and Tchernov (1973, 1975). In the present paper we investigate the taxonomy of the fossil viviparids of the Levant on the basis of the characteristics of the embryonic whorl (a primary diagnostic element) in combination with quantitative conchometrics of adult shell characters.

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MATERIAL

ABBREVIATIONS USED

HUJ Hebrew University of Jerusalem
SMF Forschungsinstitut und Naturmuseum Senckenberg
P Paleontology Unit, Gent University.

Fossil Levantine material Viviparid material was collected from the following Plio-Pleistocene sites (Fig. 1).

1. 'Erq el-Ahmar, Central Jordan Valley south of Lake Kinneret (Israel). Palaeoecology and age: shallow lake that persisted *c.* 20,000-30,000 years during the Terminal Pliocene (2.0 My) (Heller & Sivan, 2002 and references therein). Material was collected by the authors in 2001 and 2004.

2. The Hula Valley, northern Jordan Valley (Israel). Palaeoecology and age: shallow lake with a continuous sedimentary record from Mid Pleistocene till Modern times. *Viviparus* remains were found during the drilling of boreholes

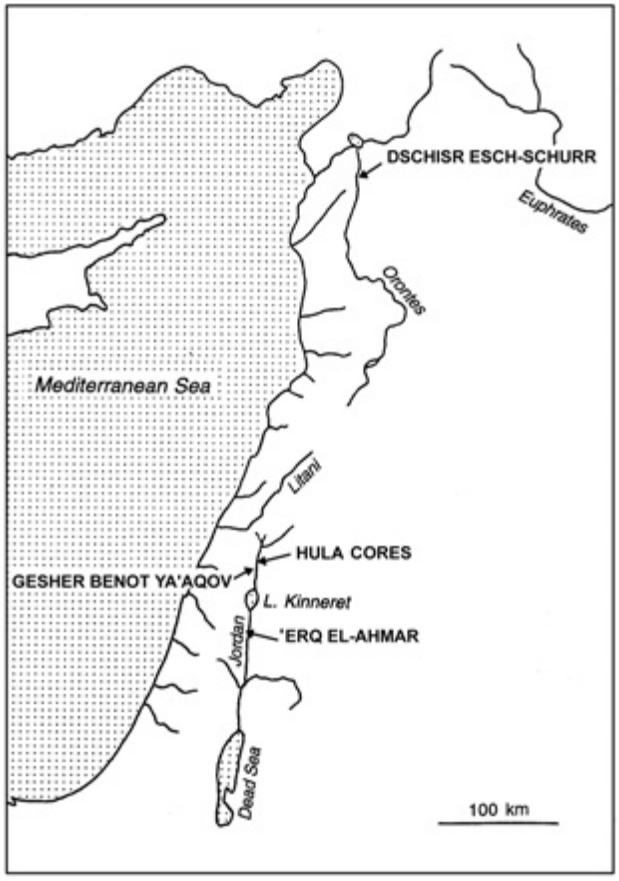

Figure 1 The Levant, with the four sites investigated in this study.

in the dried Hula swamp during the 1980's (Moshkovitz & Magaritz, 1987). Additional material was collected by the authors on the surface near Gesher Benot Ya'aqov. In the present study all Hula Valley specimens are pooled and assigned to a period of 100,000 to 780,000 yrs BP (see also Moshkovitz & Magaritz, 1987; Grossowicz, Sivan & Heller, 2003).

3. Dschisr esch-Schurr region, Orontes Valley (Syria). Palaeoecology and age: shallow lake, terminal Pliocene. Shells from this site, collected by A. Gautier (Gent University) in 1978, and by R. Kinzelbach (Senckenberg Museum) in 1990 were made available for the present study.

Modern and fossil comparative material For comparison, the following material was examined:

African specimens
Bellamya jeffreysi, Lake Malawi.
Bellamya mweruensis, Lake Mweru-Luapula.
Bellamya unicolor f. elatior, Entebbe, Lake Victoria.
Bellamya unicolor, HUJ Nile; HUJ 9028 Nile; HUJ 2658, 2658A, 8559 Lake Victoria; HUJ 39176 Palmahim Beach, Israel (origin prob. Nile); HUJ 37770 Gaza (origin prob. Nile); SMF 206915/7 Lake Victoria, near Entebbe; SMF 48536/2 Egypt; SMF 292892/4 Nile, near Cairo.
Bellamya constricta trilirata, HUJ 9033 L. Victoria, Entebbe.
Bellamya unicolor unicolor, Turkana Basin, Ethiopia, Kibish Formation, Early Holocene.
Neothauma tanganyicensis, HUJ 3295, 3294A, 3295B + Van Damme, all Lake Tanganyika.

Asian specimens
Bellamya bengalensis, HUJ 1171 Bengal and India.
Bellamya dissimilis, HUJ 7390 Bengal; HUJ 7392 Madras.

European specimens
Viviparus viviparus, HUJ 231 Essex; HUJ 231C Sussex; R. Thames (all UK).
Viviparus contecta, HUJ 98, Runnemede; Wallon Bridge (all UK).

METHODS

Conchometry General measurements included (Fig. 2) shell-height (SH), minimal shell-diameter (SDs) and mouth height (MH, taken as parallel to axis of shell). From these measurements three ratios were calculated: Shell-diameter (s)/shell-height, mouth-height/shell-height and mouth-height/shell-diameters. The use of minimal (rather than maximal) shell-diameter enables the inclusion of shells with an eroded outer lip.

In addition, at whorl-height 3 mm, the following measurements were taken: width of upper suture (a); width of lower suture (b); width 1 mm below upper suture (c). From these measurements two ratios were calculated: a/b expressing expansion of the whorls, and a/c expressing their convexity.

Height of apex was taken as the height from the apex at which the shell diameter is 4 mm.

On ridged shells, the number of ridges was counted at whorl-height 3 mm. Ridge height was measured at whorl-height 6 mm, on the ridge above the suture.

Shell-height and minimal shell-diameter were measured by caliper; all other measurements were taken under the binocular microscope,

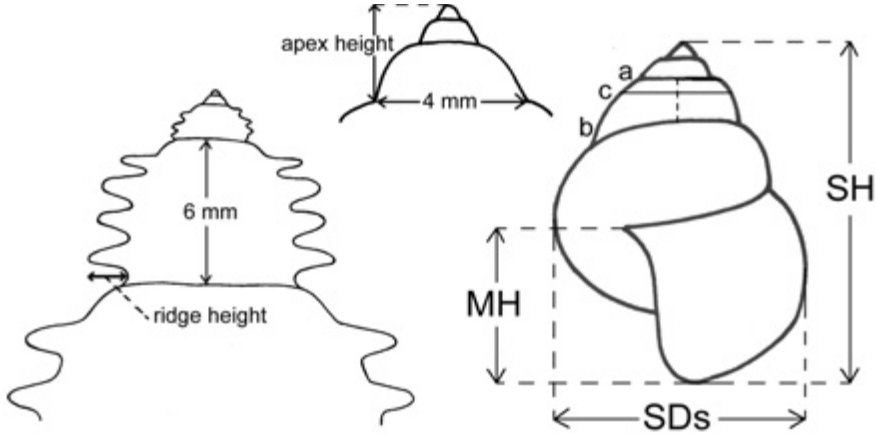

Figure 2 Conchiometrics (SH – shell-height, SDs – minimal shell-diameter, MH – mouth-height).

using an eye-piece micrometer. Shells smaller than 10mm and shell fragments were used for examining the embryonic whorl and height of apex, but excluded from other measurements.

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

SYSTEMATIC RESULTS

VIVIPARIDAE (Gray, 1847)
BELLAMYINAE Rohrbach, 1937
Genus ***Bellamya*** Jousseaume, 1886

Description *Bellamya* has a sharply pointed shell apex with a ridge and bristles (Brown, 1994, p. 46; Van Damme & Pickford, 1999). The embryonic whorl is angular, the top of the whorls being flattened and forming a distinct angle with the lower part (Fig. 3A), the body whorls may be either smooth or with different degrees of ornamentation. The carinae sometimes present in adult shells are simply a continuity of the embryonic ornamentation, which disappear when selective forces favor smooth shells.

Bellamya occurs in Africa since the Lower Miocene (19 Ma) and its many fossil African species have been described by Van Damme & Pickford (1999). Today it ranges from Egypt to South Africa, but is absent in western Central Africa. It occurs in vast numbers in those rivers, floodplains and lakes where the water is well-oxygenated and rich in organic sediments, but is absent where the water has low oxygen levels (e.g. papyrus swamps) or very low salinity (Van Damme & Pickford, 1999). As a rule river dwelling forms are smooth (to reduce tow and drag) whereas lake forms are ornamented with one or more carinae, or even ridges (to reduce predation pressures, Van Damme & Pickford, 1999). The transition between ornamented and smooth shells has probably occurred independently at different times and places.

Comparative conchometric and morphological analysis We compared the Fossil viviparids of the Levant to the viviparine genus *Viviparus* and to the African bellamyine genera *Bellamya* and *Neothauma*. *Neothauma* is characterized by a smooth and large protochonch, and a very big shell (fully grown about 60 mm high) (Brown, 1994). As the Levant material has a small protoconch and a maximum shell hight of 49.5 mm, we exclude affinity to *Neothauma*.

In Modern *Bellamya* the apex of the shell is more pointed than that of Modern *Viviparus*.

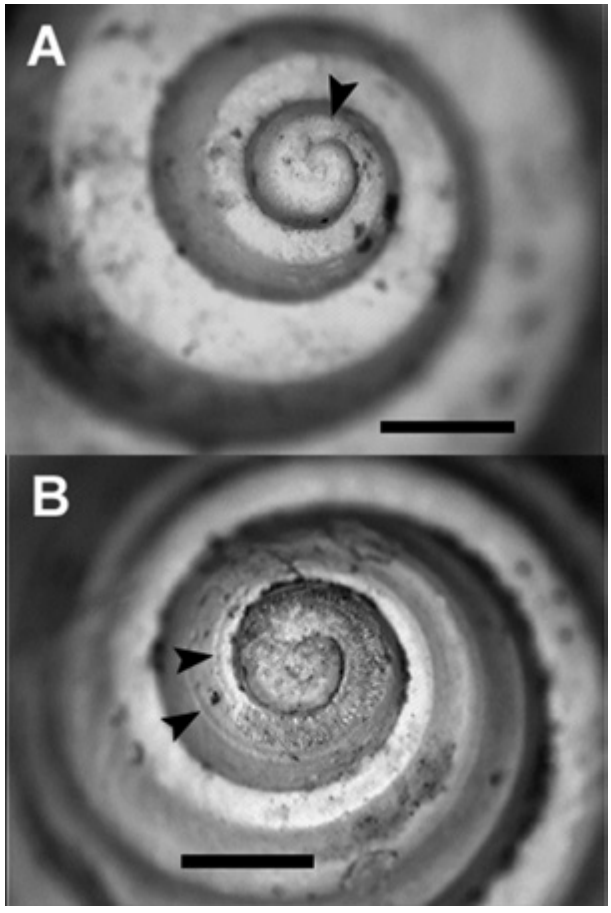

Figure 3 **A** Apex of *Bellamya* showing angular whorls. **B** Apex of *Apameaus* showing two carinae transformed into ridges. Scale bar = 1 mm.

Fig. 4A presents apex height of three Modern *Bellamya* species (pooled) as compared to two Modern *Viviparus* species (pooled) and to all fossil material from the Levant (Modern species: *Bellamya unicolor, B. bengalensis, B. dissimilis, Viviparus viviparus* and *V. contecta*). In this figure Modern *Bellamya* differs from Modern *Viviparus* in its almost diagnostically higher apex. The fossil viviparids of the Levant have an apex similar to that of Modern *Bellamya* or higher. (The only *Viviparus* species which has a relatively high apex (1.9 – 2.2 mm) is *V. contecta*, but it differs from our fossil material in its high ratio SDs/SH).

Modern *Bellamya* shells differ significantly from Modern *Viviparus* also in their less expanded whorls (higher a/b), narrower shell (lower ratio shell diameter(s)/shell height) and less convex whorls (higher a/c ratio) (Fig. 4B). Consequently, *Bellamya* clusters separately from *Viviparus*, in the PCO of Fig. 4C.

During this study it was brought to our attention that also certain fossil European viviparids have a narrow apex. The question whether these European fossils should be assigned to *Viviparus* and considered a conchometric deviation from recent species, or to *Bellamya* and considered a bio-geographic extension of this genus, is beyond the scope of this present study.

Table 1 Measurements and ratios of Fossil *Bellamya* sp. of the Hula Valley (mean ± SD and range).

	Bellamya sp. n = 23
Max. Shell-height (mm)	42.7
Shell-diameter (s)/shell-height	0.69 ± 0.038 0.60 – 0.76
Mouth-height/shell-height	0.52 ± 0.042 0.44 – 0.59
Mouth-height/shell-diameter (s)	0.75 ± 0.034 0.69 – 0.84
Apex (mm)	2.35 ± 0.020 2.1 – 2.6
a/b	0.55 ± 0.025 0.52 – 0.62
a/c	0.67 ± 0.021 0.63 – 0.70
Ridges	0 - 5
Ridge height (mm)	0 – 0.10

The Levantine shells, here considered as belonging to the genus *Bellamya*, form three separate clusters in the dendrogram of Fig. 5. One group consists of smooth or slightly ribbed shells from Hula (Gesher Benot Ya'aqov); a second group consists of smooth shells from 'Erq el-Ahmar; and a third 'group' consists of the single rounded and heavily carinated shell from Hula. These three groups are described below as different species, namely *Bellamya* sp. indet., *Bellamya hulensis* sp. nov. and *Bellamya paxi* sp. nov. The species, originally described as *Viviparus apameae*, is placed in a new genus, *Apameaus*, forming a distinctly isolated cluster from *Bellamya* (Fig. 6).

Bellamya sp.
Fig. 7, Table 1

Viviparus apameae - Picard 1934: 113 (non *Viviparus apameae* Blanckenhorn, 1897)
Viviparus apameae - Tchernov 1973: 40-41, pl. 6, fig. 1 (non *Viviparus apameae* Blanckenhorn, 1897)
Bellamya apameae galileae Schütt, 1993 - Schütt &

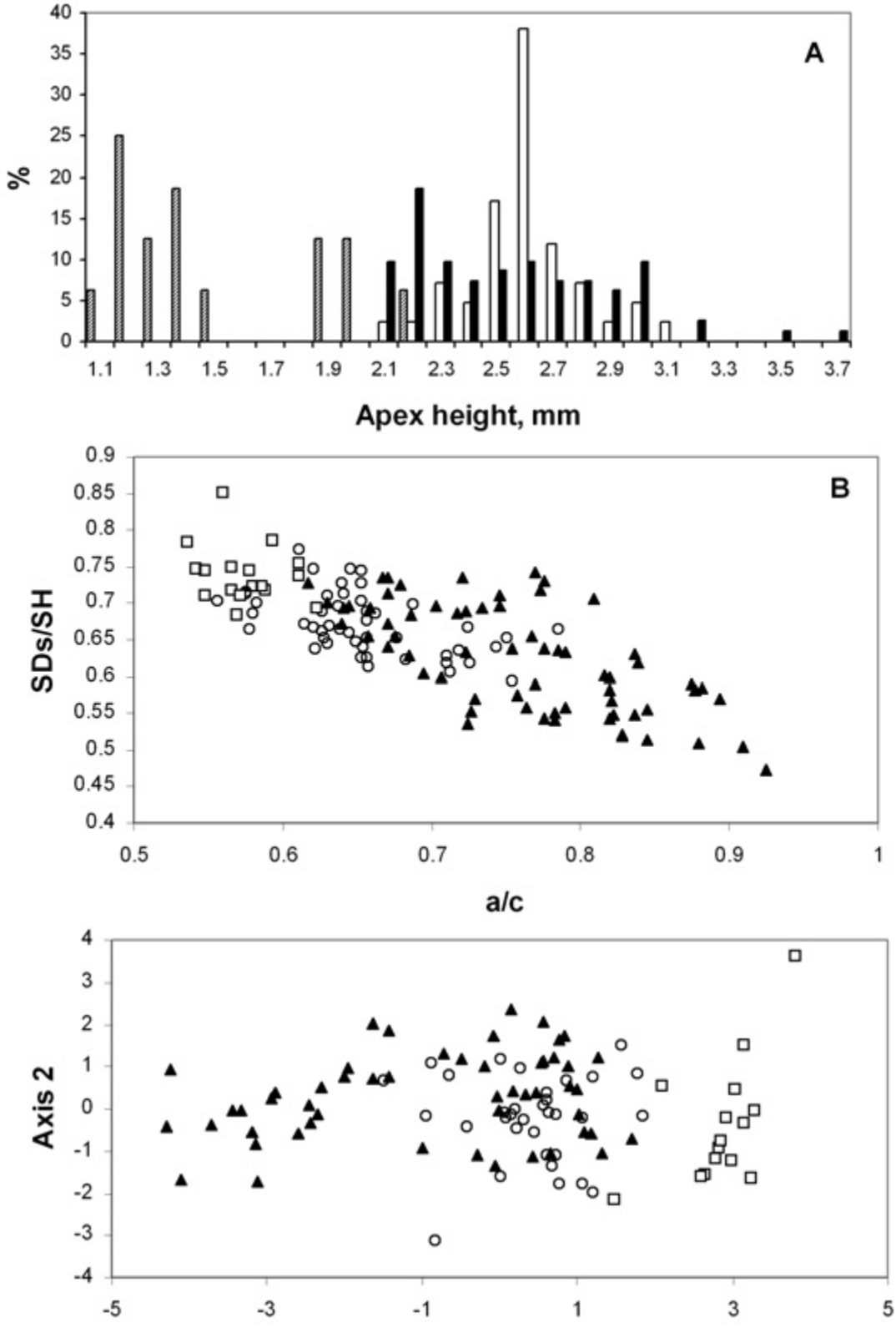

Figure 4 Shell differences between Modern *Viviparus*, Modern *Bellamya* and fossil viviparids of the Levant: A. Frequency of apex height: Modern *Bellamya* combined (white, n=34), Modern *Viviparus* combined (hatched bars, n=16), Fossils of the Levant (black bars, n=54).B. The ratio shell-diameter/shell-height versus the ratio a/c (Modern *Viviparus* open squares, Modern *Bellamya* open circles and fossil viviparids of the Levant solid triangles).C. PCO (symbols as above). (Standardized Euclidian, Axis 1: 66.8 %, Axis 2: 18.3 %)

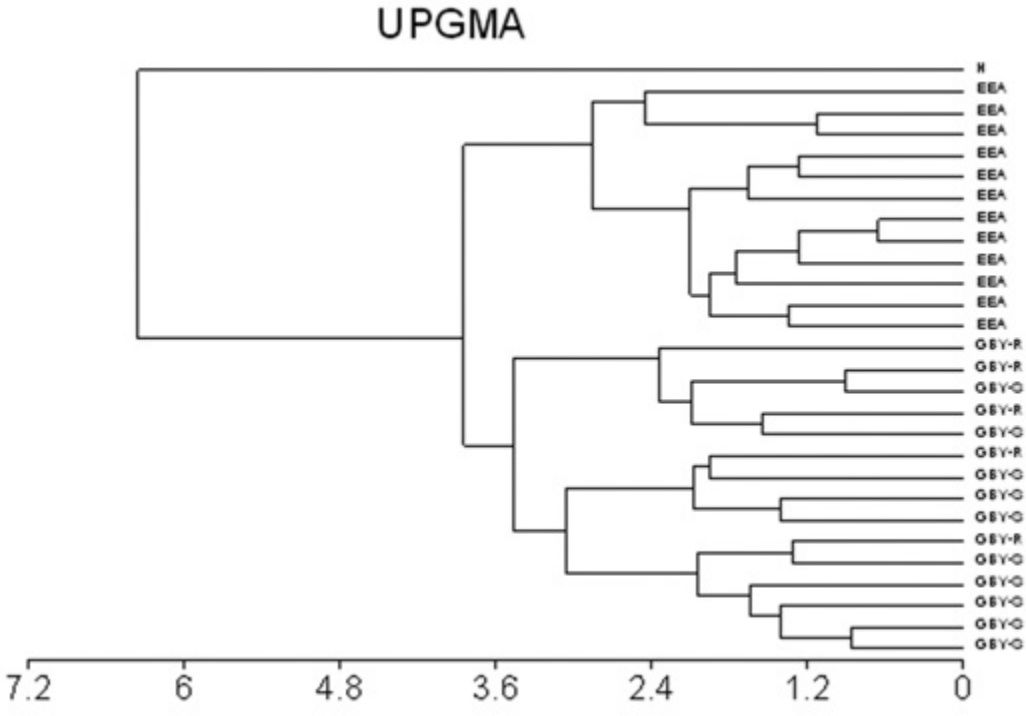

Figure 5 Dendrogram of fossil *Bellamya* specimens of the Jordan Valley. H: Hula Valley (Gesher Benot Ya'acov) heavily ribbed, EEA: 'Erq el-Ahmar (smooth), GBY-S: Hula Valley (Gesher Benot Ya'acov) smooth, GBY-R: Hula Valley (Gesher Benot Ya'acov) weakly ribbed. This figure illustrates that smooth and weakly ridged specimens from the Hula Valley do not cluster separately.

Table 2 Measurements and ratios of Modern smooth *Bellamya* species: *B. unicolor* from Africa, *B. dissimilis* from India and *B. bengalensis* from Bengal; and Modern ridged *B. constricta trilineata* from Entebbe (mean ± SD and range).

	B. unicolor n = 26	*B. dissimilis* n = 3	*B. bengalensis* n = 17	*B. constricta trilineata* n = 3
Max. Shell-height (mm)	30.3	27.8	45.6	16.2
Shell-diameter (s)/ shell-height	0.68 ± 0.045 0.59 – 0.66	0.71 0.70 – 0.72	0.67 ± 0.040 0.1 – 0.75	0.67 0.64 – 0.70
Mouth-height/shell-height	0.51 ± 0.034 0.43 – 0.58	0.52 0.50 – 0.55	0.51 ± 0.030 0.46 – 0.57	0.48 0.43 – 0.53
Mouth-height/shell-diameter (s)	0.75 ± 0.045 0.64 – 0.86	0.73 0.70 – 0.74	0.76 ± 0.037 0.66 – 0.81	0.71 0.65 – 0.74
Apex (mm)	2.60 ± 0.24 2.1 – 3.1	2.40 2.3 – 2.5	2.57 ± 0.11 2.3 – 2.8	2.5, 2.9
a/b	0.55 ± 0.037 0.50 – 0.64	0.54 0.52 – 0.56	0.53 ± 0.020 0.49 – 0.56	0.67 0.66 – 0.69
a/c	0.66 ± 0.053 0.56 – 0.75	0.64 0.62 – 0.65	0.64 ± 0.027 0.58 – 0.68	0.73 0.69 – 0.78
Spiral ridges	All 0	All 0	All 0	3.2 3 - 4
Ridge height (mm)	-	-	-	0.19 0.15 – 0.2

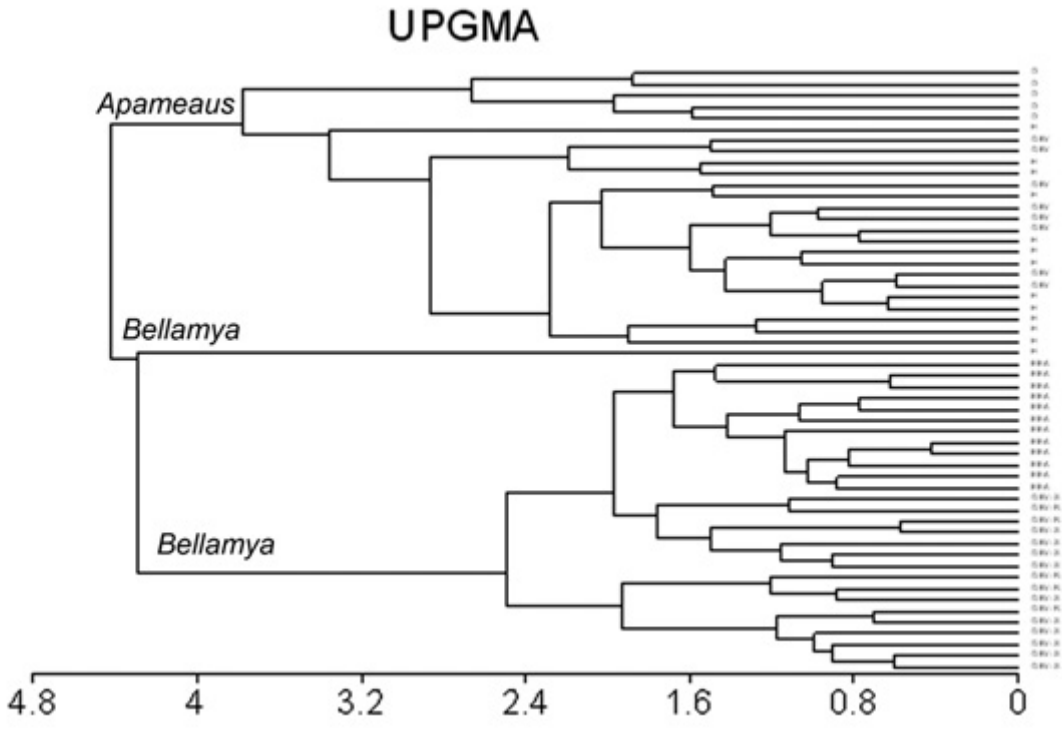

Figure 6 Dendrogram of all fossil viviparids of the Levant.

Ortal 1993: 81-82, figs. 5 –13.
(Non *Bellamya apameae galileae* Schütt, 1993 - Schütt & Ortal 1993: figs. 1-4)

Material Hula Valley: Gesher Benot Ya'aqov, on surface, eastern bank, 150 m north of bridge, leg. J. Heller 2004 (19 shells, of these we measured G1-3, G11-22); Gesher Benot Ya'aqov, different horizons, leg. R. Ortal (8 shells, G55-56, G58-60, G62-64, all measured).

Description The shell consists of convex whorls that are stepped**,** due to a slight angular contour that runs beneath the suture. A second, very faint angular contour is sometimes present on the body whorl, at about the level of the upper insertion of the mouth. The apex is pointed and the umbilicus is open. The shell is almost always smooth; sometimes it is covered with very weak spiral ridges that do not exceed 0.1 mm in ridge-height.

In the fossil material available to us 22 shells were smooth whereas 4 had shallow spiral ridges. Ridge-height on the shell with the most distinct ridges was 0.10 mm; in one shell the ridge was so indistinct that ridge-height could not be measured.

Measurements and ratios are listed in Table 1.

Distribution and age Hula Valley (Gesher Benot Ya'aqov), Mid to Upper Pleistocene.

Remarks *Bellamya* sp. is conchologically similar both to the African species *B. unicolor* (Olivier) and *B. capillata* (Frauenfeld, 1865), with a combined range extending from the Nile delta till S. Africa (Brown, 1994) and to two oriental species, *B. dissimilis* (Müller) of India, Burma and perhaps southern Iraq (near Basra, Pallary, 1939, Pl. 4 fig. 22 as *Vivipara bengalensis*) and *B. bengalensis* (Lamarck), that ranges from Bengal (see Prashad, 1928) over south-west Iran (Mansoorian, 2001) to southern Mesopotamia (west of Basra) (Bănărescu 1991: 1077; Plaziat & Younis, 2005, Pl. 3 figs. 13-18) (Table 2). The close similarity between African and Indian *Bellamya* species was noted already by Prashad (1928), who further commented that both groups may develop keels and ridges. He described *B. bengalensis* as differing from both *B. dissimilis* and *B. unicolor* by the color bands on its shell (a character we do not expect to be preserved in fossils). We did not find conchometric differences between *B. unicolor, B. dissimilis and B. bengalensis*, or between any of these species and the fossil *Bellamya* sp. of Hula Valley. Consequently, it is impossible to assign

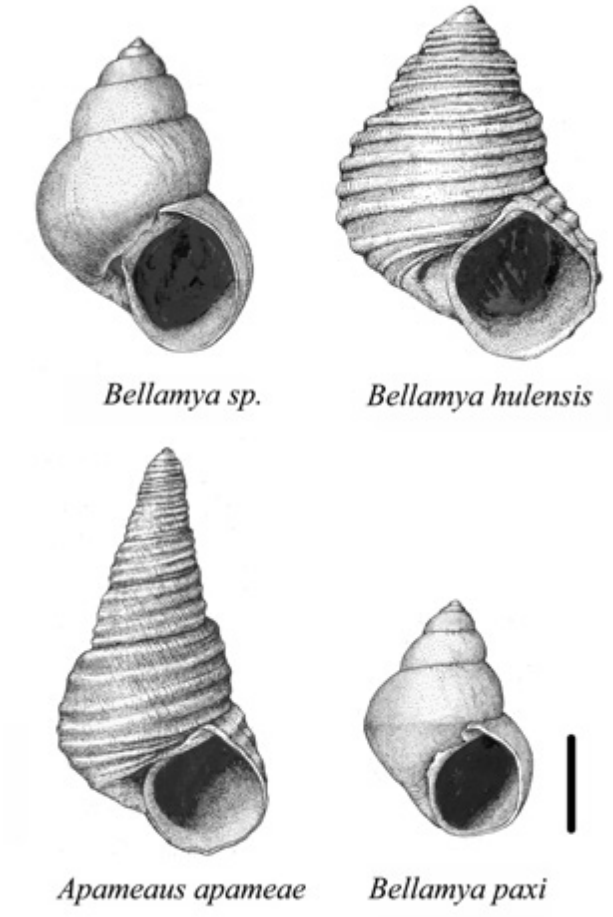

Figure 7 Fossil viviparid species of the Levant. Scale bar = 1 cm.

the fossil *Bellamya* specimens of the Hula Valley to one of these Modern species. This taxonomic uncertainty renders statements concerning zoogeographic affinities impossible, i.e. whether these shells represent an African invasion northwards from the Nile (as suggested by Tchernov, 1975 and by Schütt & Ortal, 1993) or an Asian invasion westwards from the Euphrates-Tigris.

Bellamya hulensis sp. nov.
Fig. 7. Table 3

Holotype and type locality Israel: Hula core L-12, #27, 120 m (HUJ 9715).

Paratypes Israel: Hula core 08, # 34 (HUJ 9716, one damaged juvenile specimen, shell-height approximately 11.5 mm, apex 2.7 mm).

Material examined Type material

Diagnosis *Bellamya hulensis* differs from *Bellamya* sp. in that it has heavy carinae that are 0.5 mm high.

Description The shell consists of convex whorls that are covered with strong spiral ridges. The ultimate whorl has nine such ridges, of which four are above the point of insertion of the mouth. The lower ridges of the ultimate whorl, surrounding the narrowly open umbilicus, are less pronounced than the upper ones. The apex is pointed. The aperture is rounded.

Measurements and ratios of the type specimen are listed in Table 3.

Distribution and age *Bellamya hulensis* is known only from the type locality, Mid Pleistocene.

Remarks In his description of Modern *Bellamya unicolor*, Brown (1994, p. 46) mentioned that lake populations have a higher spire but no particular ornamentation. None of the *B. unicolor* specimens we examined is carinate. Of the 18 African species Brown recognizes, only three (all endemic to L. Victoria) possess spiral ridges: *B. monardi* Haas has very fine ridges; *B. costulata* (Martens) has ridges of varying strength but still fine while *B. constricta* (Martens), the smallest species in the genus, has more pronounced thicker ridges but a conical shell (Table 2). Since *Bellamya hulensis* is identical in size, general form and shell ratios with other representatives of the genus *Bellamya* we consider it to belong to this genus. The marked spiral ornamentation makes it a clearly distinctive species within the genus.

Bellamya paxi sp. nov.
Fig. 7. Table 4

Viviparus unicolor (Olivier, 1804) – Tchernov 1975: 14-15, pl. 1, fig. 2
Viviparus unicolor (Olivier, 1804) - Schütt & Ortal 1993: 82.

Holotype and type locality Israel: 'Erq el-Ahmar (HUJ 9711, leg. J. Heller & F. Ben-Ami 4.07.2004).

Paratypes Israel: 'Erq el-Ahmar, boulder cliff : HUJ 9712, leg. J. Heller & F. Ben-Ami 4.07.2004 (21 shells, of these we measured 7), HUJ 9713, leg. J. Heller & F. Ben-Ami 25.07.2001 (4 shells, of these we measured 3), Western shovel road

Table 3 Measurements of the type specimen of Fossil *Bellamya hulensis* (HUJ 9715) from the Hula Valley.

	B. hulensis
Shell-height (mm)	36.8
Shell-diameter (s)/shell-height	0.73
Mouth-height/shell-height	0.53
Mouth-height/shell-diameter (s)	0.72
Apex (mm)	2.2
a/b	0.51
a/c	0.62
Spiral ridges	4
Ridge height (mm)	0.5

Table 4 Measurements and ratios of the type material of Fossil *Bellamya paxi* of 'Erq el-Ahmar (mean ± SD and range).

	B. paxi n = 13
Shell-height (mm)	26.0
Shell-diameter (s)/shell-height	0.69 ± 0.036 0.63 – 0.74
Mouth-height/shell-height	0.54 ± 0.024 0.50 – 0.58
Mouth-height/shell-diameter (s)	0.77 ± 0.025 0.74 – 0.82
Apex (mm)	2.21 ± 0.104 2.1 – 2.4
a/b	0.61 ± 0.020 0.57 – 0.64
a/c	0.74 ± 0.022 0.72 – 0.78
Spiral ridges	All 0

(HUJ 9714, leg. R. Ortal 1990, 7 shells, of these we measured 3).

Material examined Type material.

Diagnosis *Bellamya paxi* differs diagnostically from *Bellamya* sp. (and hence from *B. unicolor-capillata* and *B. bengalensis-dissimilis*) in that the a/c ratio is 0.72 – 0.78 as opposed to 0.63 – 0.70 in *Bellamya* sp. (Tables 1, 4; Fig. 8).

Bellamya paxi differs from *B. hulensis* in that it is smooth.

Description The shell consists of smooth whorls that are conical. A distinct angular contour is present on the body whorl, at about the level of the upper insertion of the mouth. There is no angular contour beneath the suture and there are no spiral ridges. Measurements and ratios are listed in Table 4.

Distribution and age Only known from the type locality ('Erq el-Ahmar), Late Pliocene.

Remarks In *Bellamya paxi* the whorls are less expanded than in *Bellamya* sp. or in *B. unicolor* (etc.). This is expressed in smaller values of the a/b ratio. In addition, the whorls are less convex and there is no angular contour immediately beneath the suture. This is expressed in significantly smaller values of the a/c ratio (Fig. 8). Further, the mid-whorl angular contour of the body whorl of *Bellamya paxi* is more distinct than in *Bellamya* sp. Also, the umbilicus in *B. paxi* is partly or completely covered whereas in *Bellamya* sp. it is open. Finally, *Bellamya paxi* reaches a shell height of only 26 mm while *Bellamya* sp. with a size of 42.7 mm is almost twice as large.

In the dendrogram (Fig. 5), *Bellamya paxi* specimens are completely separated from *B. sp.* and from *B. hulensis*.

Apameaus genus nov.

Diagnosis *Apameaus* differs from *Bellamya* in that the embryonic whorl is large and rounded with an ornamentation consisting of two or three distinct carinae, but with no distinct angle. These carinae always transform below the embryonic whorl into 3-5 massive ridges (Fig. 3B).

Comparisons The dendrogram of Fig. 6 shows the separation of *Apameaus* from *Bellamya*. The uppermost cluster includes all *Apameaus* shells from Orontes, all the conic, ridged shells from the Hula cores and nine conic, ridged shells from Gesher Benot Ya'aqov. Isolated and intermediate is the one ridged shell from Hula, described above as *Bellamya hulensis* (because of its distinct ridges, in the dendrogram it falls somewhat close to *Apameaus*; in most other characteristics it is close to the other *Bellamya* species, Tables 1,3,4). A third group comprises *Bellamya sp.* specimens from Gesher Benot and *B. paxi* from 'Erq el Ahmar.

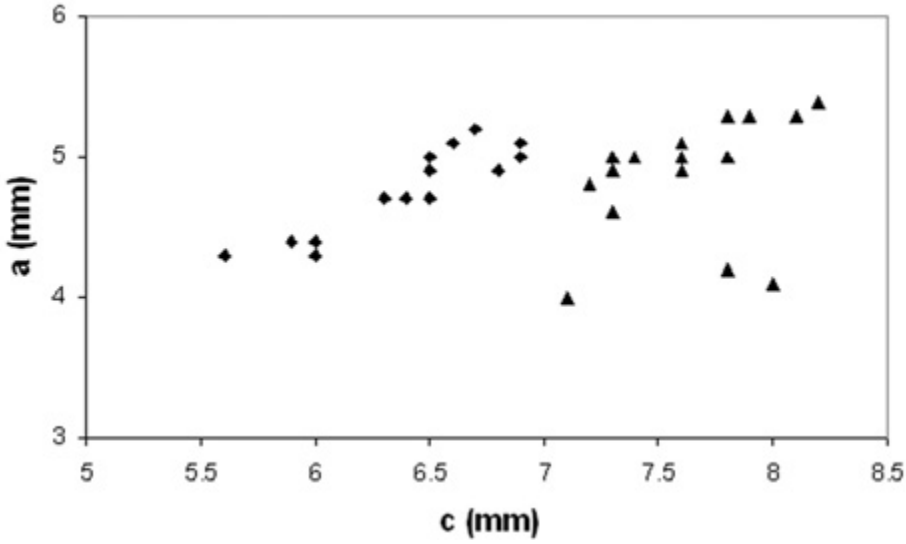

Figure 8 *Bellamya paxi* (rhombs) as compared to *Bellamya* sp. (triangles): a versus c.

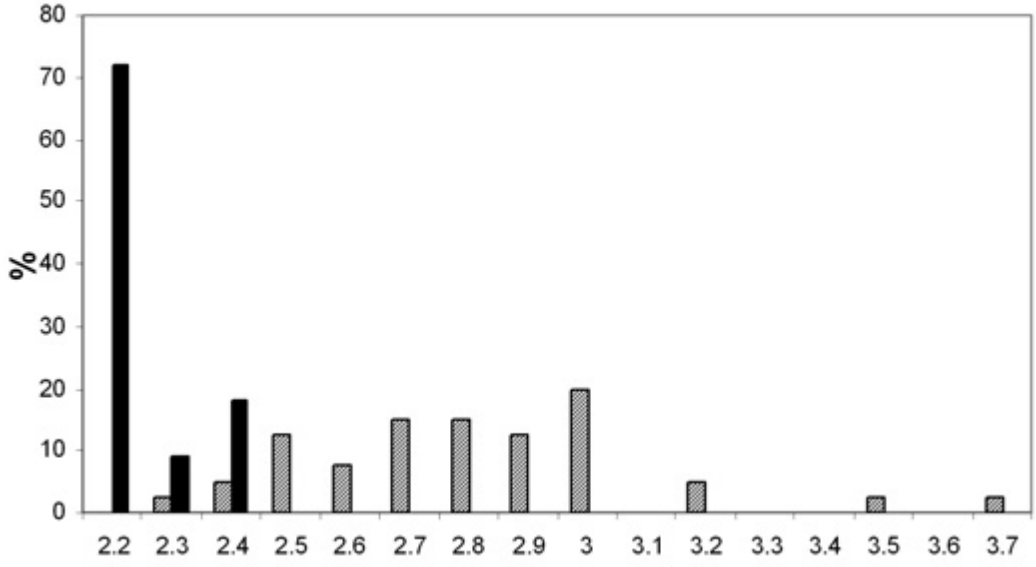

Figure 9 Frequency of apex height: *Apameaus apameae apameae* (black, n=40), *A. a. galileae* (hatched, n=20).

The description of the genus *Apameaus* is given below under the description of its only species, *Apameaus apamea*.

Apameaus apameae (Blanckenhorn, 1897)
Fig. 7, Table 5

*Paludina (*sg. *Tulotoma) apameae* Blanckenhorn, 1897: 103-105, pl. 8, figs 9-14.
Vivipara syriaca Pallary, 1930 – Pallary 1939: 78, fig. 8.
Viviparus apameae Blanckenhorn, 1897 - Schütt 1988: 134, pl. 2 fig. 11.
Viviparus apameae galileae Schütt, 1993 - Schütt & Ortal 1993: 81-82, pl. 1, figs 1-4.
(non *Viviparus apameae galileae* Schütt, 1993 - Schütt & Ortal 1993, pl. 1, figs 5-13).

Material examined **Israel** Hula Valley: Hula cores, Trench L 08 at different levels (n=90, of these measured H2-5, H7, H12-14, H18-19, H23-24, H27, H29, H34-35, H39, H47); Gesher Benot Ya'acov, on surface, eastern bank, 150 m north of bridge, leg. J. Heller (6 shells, of these measured G4-8); Gesher Benot Ya'acov, different horizons, leg. R. Ortal (5 shells, G52-54, G57, G61, all measured).

Syria Orontes: "Pliozean, untere Tonbank der Pliozeanschiften am Westufer des Orontes, 12 km S. of Gisser-as Sugur" (SMF 307193, one specimen). Archaeological site of Apamea, limestone and fossil shells from nearby Pliocene deposits

Table 5 Measurements and ratios of Fossil *Apameaus apameae apameae* from the Orontes and *A. a. galileae* from the Hula Valley (mean ± SD and range).

	A. apameae apameae n=20	*A. apameae galileae* n=33	All *A. apameae* n=53
Max. shell-height (mm)	40.5	49.5	49.5
Shell-diameter (s)/shell-height	0.56 ± 0.022 0.52 – 0.60	0.58 ± 0.049 0.47 – 0.68	0.58 ± 0.045 0.47 – 0.68
Mouth-height/shell-height	0.44 ± 0.020 0.41 – 0.48	0.42 ± 0.042 0.34 – 0.60	0.43 ± 0.038 0.34 – 0.50
Mouth-height/shell-diameter (s)	0.79 ± 0.035 0.72 – 0.84	0.75 ± 0.032 0.69 – 0.83	0.76 ± 0.037 0.69 – 0.84
Apex (mm)	2.25 ± 0.082 2.2 – 2.4	2.81 ± 0.26 2.4 – 3.7	2.66 ± 0.34 2.2 – 3.7
a/b	0.67 ± 0.042 0.62 – 0.74	0.71 ± 0.044 0.64 – 0.80	0.70 ± 0.047 0.62 – 0.80
a/c	0.78 ± 0.056 0.71 – 0.89	0.83 ± 0.046 0.76 – 0.92	0.81 ± 0.054 0.71 – 0.92
Spiral ridges	3.27 ± 0.38 3 - 4	4.12 ± 0.53 3 - 5	3.72 ± 0.66 3 - 5
Ridge Height (mm)	0.36 ± 0.111 0.25 – 0.50	0.18 ± 0.067 0.05 – 0.30	0.21 ± 0.101 0.05 – 0.50

used as building layer (P2372, 26 shells, of these 19 measured).

Description The shell is large, its spire high and its apex sharply pointed. The whorls are flat (rather than convex), strongly elongated and have pronounced spiral ridges. The aperture is rounded. The umbilicus is narrow, and partly or completely covered. Measurements and ratios are listed in Table 5.

Distribution and age Late Pliocene of the Orontes Valley and Mid Pleistocene of the Hula Valley.

Comparisons and Remarks *Apameaus* differs both from *Viviparus* and *Bellamya*. Because of the high apex we assign it to Bellamyinae rather than to Viviparinae.

Apameaus apameae differs diagnostically from ridged specimens of *Bellamya* sp. in that it is more slender (smaller shell-diameter (s)/shell-height), has more pronounced spiral ridges (higher ridge-height) and more conic whorls (higher ratio a/b); it further differs in that it has a significantly higher ratio a/c and a smaller mouth (smaller mouth-height/shell-height) (Tables 1, 5).

Apameaus apameae differs from *Bellamya hulensis*, which also has pronounced spiral ridges, in that it has a diagnostically narrower shell with more conic whorls (lower ratios of shell-diameter (s)/shell-height, higher ratios a/b and a/c) (Tables 3, 5; Fig 5).

Vivipara pauli Brusina, as illustrated by Brusina (1897, Pl. 12, figs 27-28) from the Pliocene Palaeolake Paludina in Slovenia, is also ridged, thus superficially similar to *Apameaus apameae*. However, *A. apameae* differs from *V. pauli* in that its apex is sharply pointed, its whorls are less conic and its sutures are less impressed. It is possible that the shells illustrated by Brusina were eroded at the apex.

Among Modern viviparids there are carinate species in the genus *Bellamya* from Africa. One of these species, *B. constricta trilirata*, is much smaller than *Apameaus apameae*, but is close to it in many characters (Tables 2, 5). As mentioned

above, an ornamentation on the postembryonic shell consisting of one or more ridges evolved in the genus *Bellamya* several times independently. On the first postembryonic whorl the ridge is usually faint and single forming a continuation of the single carina present on the embryonic shell (Fig. 3A). It is only on the following whorls and in particular on the body whorl that several distinct ridges appear. This ornamentation is rather exceptional and does not constitute a basic characteristic of the genus, most *Bellamya* species being smooth (even in the few ridge-bearing forms this ornamentation is highly variable). In *Apameaus* the presence of several heavy ridges on the postembryonic shell appears to be a typical highly consistent trait and this ornamentation is a continuation of the 2 or 3 carinae (instead of a single one in *Bellamya*) that are present on the protochonch (Fig. 3B).

Tchernov (1975) suggested that *apameae* originated in the Orontes during the Miocene, where it became extinct towards the end of the Neogene. He described as *Viviparus apameae* (1975, pl. 1, fig. 3) a small, ridged shell from 'Erq el Ahmar. This specimen is so small (shell height 3 mm) that we could not assign it to any species. Schütt (1988, pl. 2, fig. 11) offers a good photograph of *apameae*, from near the type locality.

Apameaus apameae apameae (Blanckenhorn, 1897)

Diagnosis In the type subspecies the apex never exceeds 2.4 mm, and is usually less (Fig. 9).

Apameaus apameae galileae (Schütt & Ortal, 1993)

Diagnosis This subspecies differs from the type subspecies in that the apex is 2.5 mm or more (Fig. 9).

Comments Schütt & Ortal (1993) assigned *apameae* of the Hula Valley to *B. apameae galileae*, a subspecies that, they suggested, differs from *B. apameae apameae* of the Orontes in that the shell is not thick and not sclarid, the apex is pointed rather than blunt, the profile of the spire is convex to equal rather than concave turreted, and the last whorl has over ten weak ridges rather than less than ten strong ones. Our measurements of the *B. a. apameae* specimens inspected by Schütt & Ortal (1993) and 19 additional specimens, as compared to 20 specimens from the Orontes, reveal that they are identical in all conchometric characters except ridge height, which in the Hula specimens is lower; and apex height which is higher (Table 5). However, also in these characters there is overlap.

Tchernov (1975) mentioned that large specimens of *A. apameae* were drilled out of Neogene sediments from the bottom of the Sea of Galilee; but we were unable to trace these specimens.

DISCUSSION & CONCLUSIONS

In this study all the fossil viviparids of the Levant were assigned to the sub-family Bellamyinae, representatives of which are found as well in Africa as in the Far East since the Middle Miocene (Van Damme & Pickford 1999, Songtham *et al*. 2005). Bellamyinae may well have occurred also in the Middle Pliocene lacustrine deposits of Rhodes, where they have become extinct. Willmann (1981) assigned the Rhodes viviparids to *Viviparus* without studying the embryonic whorls. It is possible that part of the shells illustrated by Willmann should be assigned to Bellamyinae and for that matter other '*Viviparus*' species from the Parathethys region but this question is beyond the scope of this present study.

Representatives of the Bellamyinae could have invaded the Levant and the whole Paratethys region from Africa when that continent and Eurasia were joined in the Miocene during a period when the Red Sea was still a closed rift valley (Tchernov, 1988) and the Arabian Peninsula still had a diversified African freshwater fauna. Possibly not a single Miocene but also later invasions from the nearby Nile occurred during the Pleistocene (Schütt and Ortal, 1993). A second possibility is that Bellamyinae of Asian origin extended westwards into the Levant from the Euphrates-Tigris area. Finally it can certainly not been excluded that the Levant was invaded from both directions.

The new genus *Apameaus* is endemic to the Levant, and has been found only in the Pliocene of the Orontes, and the Early till Middle Pleistocene of the upper Jordan Valley. It is plausible that this genus evolved in the Orontes and subsequently extended its range southwards to the upper Jordan Valley.

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