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New morphometric parameters for assessment of body size in the fossil freshwater crab assemblage from the Acheulian site of Gesher Benot Ya'aqov, Israel

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Abstract

The faunal assemblage of Gesher Benot Ya'aqov (GBY) in the northern Jordan Valley, Israel, a waterlogged Early–Middle Pleistocene Acheulian site (0.79 Ma) correlated with Oxygen Isotope Stage (OIS) 20.2–18.2, includes over 5000 fragments (1–40 mm) of fossil freshwater crab of an undetermined species suspected to be *Potamon* sp., based on the morphology of its pincers. Most of the fragments (92.6%) were identified to crab body part, of which 74.6% are pincers. The fossil crabs of GBY demonstrate four distinct pincers, as is also typical of the present-day species in the region, *Potamon potamios*. In this study we propose for the first time a series of 22 easily measurable morphometric parameters that permit assessment of the pincer size of fossil freshwater crabs from measurable fragmented pincers (35.5% of fragments). We assume that the pincer length represents the crab body size, as in the recent species in the region. The study was restricted to GBY Area C layer V-6, which yielded 91.6% of the crab fragments found in Area C. It has been found that the measurable parameters are significantly correlated to the length of the related pincer ($r = 0.671–0.955$, $P < 0.0025$). The same parameters measured for comparison in 208 specimens of recent *Potamon potamios*, mainly from the same region, resulted in higher correlations ($r = 0.806–0.990$, $P < 0.0002$). Consequently, even if fossil crab remains are very fragmentary, it is still possible to reconstruct the body size of the crab. Regression line equations are given as an implicative tool for future assessment of the pincer size of fragmentary fossil crabs from the region.

The GBY pincer length data indicate that the broad size range seen in living populations of *Potamon potamios* also exists in the GBY fossil crabs. A minimum number of individuals (MNI) resulted in a very high density of 668 specimens (321 specimens per m^3). In cluster analyses for each of the 22 parameters, the mean of the GBY crab population measurements is consistently smaller than that of the recent crabs, in which females display intermediate values and males are the largest. However, when allometry is also taken into consideration, cluster analysis groups together the recent males and the recent females and distinctly separates them from the GBY crabs. Further allometric analyses of fossil crab populations from earlier and later prehistoric sites in the northern Jordan Valley will enable a better understanding of the significance of these differences and possible evolutionary trends in the fossil crab population's taxonomy.

Keywords: Early–Middle Pleistocene; Fossil pincer measurements; Freshwater crabs; Gesher Benot Ya'aqov, Israel; Morphometric parameters; *Potamon potamios*; Size reconstruction

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1. Introduction

Gesher Benot Ya'aqov (GBY), a waterlogged Early–Middle Pleistocene Acheulian site (0.79 Ma) in the northern Jordan Valley, Israel, consists of the sedimentary sequence of a freshwater lake and its margin deposits [4,5,7]. The sediments contain lithic assemblages consisting of thousands of in situ artifacts [8] in association with archaeobotanical and palaeontological remains [9]. There is great variability in the distribution and density of fossil remains and hominin artifacts within the different archaeological horizons of GBY. The rich molluscan and crustacean fauna from the site reflect favorable lake-margin environmental conditions and possibly human impact.

The faunal assemblage of GBY includes 5033 fragments of fossil freshwater crab remains of an undetermined species. This assemblage is unusual in both quantity and density in comparison to any assemblages of fossil freshwater crab remains from the Mediterranean region and Europe [16–18,20,22]. The abundance of the crab remains from GBY is also exceptional in the context of the preliminarily examined crab fragments from other archaeological sites along the Jordan Rift Valley of Israel ('Ubeidiya, Ohalo II and Eynan; Ashkenazi, unpublished data). Moreover, this assemblage is exceptional in view of the archaeozoology of aquatic invertebrates of the Middle East and elsewhere, particularly for such an early site as GBY. Most archaeozoological studies worldwide deal with analysis of vertebrate remains. The existing several studies of invertebrates generally deal with archaeomalacology, especially studies of marine molluscs focusing on a few genera of bivalves that tend to appear in abundance in relatively recent shell middens or were used as ornaments [15]. Studies of aquatic invertebrates, particularly arthropods (such as crabs), are even rarer and concentrate in shell middens in different regions, like the study of deFrance [3] in the Caribbean.

No measurable parameters have previously been established for size estimation or species identification of fossil freshwater crabs [2,16,18,20]. The main reason for the paucity of such methods is the rarity of material of this kind and the scarcity of large fragments among fossil crab remains (even in the excellent waterlogged conservation conditions of the GBY fossils). Evaluation of the body size and size range of specimens in a fossil population is essential for understanding the palaeoecological meaning of large assemblages of animals in a site. Different patterns of size groups will lead to different conclusions concerning the palaeoenvironment of the site during the deposition of the specimens and about the role of humans, if any, in the formation of the assemblage.

Assessment of body size in recent freshwater crab populations in the Mediterranean region and Europe is based on direct measurement of carapace length or indirect measurement of pincer length, which is correlated to carapace length [1,6,12,17]. The gonopod (reproductive organ) is the best parameter for the identification of freshwater crab species [1,19,20]. However, in fossil remains the carapace is usually broken into fragments and gonopods are rarely preserved. Pincers are the crab parts most frequently found in archaeological samples. Pincers are composed of chitin mineralized with calcium carbonate and are more heavily calcified than other parts of the exoskeleton [21].

Reconstruction of fossil crab body size from fragments requires comparable morphometric criteria that will be applicable to both fossil material and related recent freshwater crab specimens. The parameters must be easily measured features, easily distinguished, preferably with straight lines, and must show a high correlation with pincer length in both fossil and recent crab populations. In addition, in recent populations, the measured parameters must show a high correlation with carapace length and width. Carapace measurements are known to be indicative of body size in recent populations of the genus *Potamon* and the species *Potamon potamios* Olivier 1804, known from the region and from Israel [6,17].

According to the revised taxonomy of the freshwater crabs in the Mediterranean region, freshwater crabs in Israel belong to a single species, *Potamon potamios* [1]. Four different pincers (heterochely) are typical of this living freshwater crab species in the region [1,13,20]. The presence of four differently shaped pincers complicates the reconstruction of crab body size, as each of the pincers requires specific morphometric parameters that are correlated with the associated pincer length and indirectly to the carapace, which is the best parameter for evaluation of crab body size.

In cases in which fossil species are identified, the pincers can be directly correlated to carapace size in recent populations of similar species, as shown by deFrance [3]. However, for the fossil crabs of GBY, which are of undetermined species, we use the indirect methodology of pincer length as representing the crab body size. Based on the morphology of the pincers and the basal tooth of the upper right pincer, we suspect that the fossil crab belongs to the genus *Potamon*.

The pincers of several crabs, including the larger upper pincer of the chelipeds in *Potamon potamios*, have a basal tooth for crushing molluscs or other prey with protective shells. The basal tooth is large, rounded or elongated, and modified to a crushing cusp, while the opposite lower pincer has a depression that fits the basal tooth size [25]. Most of the molluscivorous crabs have dimorphic chelae of this kind, with large, heavy master chelae (with basal tooth and crushing depression) adapted for crushing, normally on the right, and more slender cutting chelae, usually on the left [11,25]. Among

291 measured *Potamon potamios* in the Dead Sea area in Israel, 79% of the population was right-handed, with no significant difference between males and females but significantly larger proportions (84%) in young specimens [6].

This study suggests 22 new comparable morphometric parameters for assessment of fossil crab size, based on measured features of whole or fragmented pincers. These parameters are potentially useful tools for understanding the significance and taphonomy of crab assemblages and for comparison of freshwater fossil populations within their entire distribution range. Measurable parameters also have potential for comparison of specimens from a wide range of periods and assessment of evolutionary trends in crab taxonomy.

2. Aim of the study

This study aims to evaluate the feasibility of applying new morphometric parameters to fragments of fossil crab pincers to enable assessment of the pincers' size and, indirectly, the specimens' body size. This aim will be achieved by applying similar morphometric parameters to samples of the recent living freshwater crab in the region (Eastern Mediterranean and Upper Jordan Rift Valley), *Potamon potamios*, which shows correlation between pincer size and carapace size. Since we assume that similar correlation between pincer size and body size exists in the fossil material of GBY, we relate to fossil pincer size as being representative of body size.

We also aim to compare the range of reconstructed pincer size and allometry of the GBY fossil crab material to the size range and allometry of the recent population of *Potamon potamios*, in an attempt to achieve better understanding of the meaning and taxonomic status of the fossil assemblage. The reconstructed body size of the fossil crab assemblage will facilitate future comparison of fossil populations from a wide range of periods in other sites in the Jordan Valley, Israel, and adjacent regions.

This study is the first necessary stage for a future taphonomic study that will evaluate the reasons for the large accumulation of crabs in certain stratigraphic layers of GBY.

3. Methods

The fossil material from the GBY excavations has been stored in the Archaeozoology Laboratory in the department of Evolution Systematics and Ecology, of the Hebrew University of Jerusalem since the conclusion of the excavations in 1997. The present study is based on the stored material.

3.1. Study Methods

1. Fossil freshwater crab fragments were sorted from the samples of excavated material originating from four areas and six trenches within the site, Areas A, B, C and Jordan Bank (JB) and Trenches I–VI (Fig. 1), each representing several archaeological horizons [5,7].
2. Sorting of the fossil material is still ongoing for the excavated Areas A and B. The samples from Area JB are too small for separate analysis and the trenches yielded no fossil crabs. We analyzed available data from all layers for general information on identified fossil crab body parts.
3. In order to restrict the time span and different stratigraphic layers represented by the remains, we analyzed for morphometric parameters only data from Area C layer V-6, a mainly clay deposition layer that is so far the richest and most diverse in fossil fauna.
4. Each crab fragment was examined and identified to body part with the aid of a binocular microscope (up to 40×) and catalogued in a database that includes details of number, coordinates, crab body part, size in mm, and the measurements of the defined set of parameters.
5. All measurements were taken by use of a microscope connected to a computer with Image Analyzer software (Image Pro Plus version 4.1 for Windows), which enables accurate, scaled measurements of the enlarged feature on the computer screen.
6. Measurable parameters were selected after examination of several samples of the crab remains, thus assuring the simplicity and accuracy of the measurements. The fossil crab remains demonstrate four differently shaped pincers (upper movable and lower fixed pincers on large and small chelipeds), each requiring a different set of measurable parameters (Fig. 4a–d). Altogether we tested 22 parameters, which yielded adequate data for analysis.
7. A sample of complete pincers of each type was selected for preliminary evaluation of the correlation between the proposed parameter measurement and pincer length.
8. The revised taxonomy of recent freshwater crab populations in their entire distribution range (including Israel) assigns all populations of this crab to the species *Potamon potamios* (Olivier 1804) Decapoda, Brachyura [1]. We therefore consider all of the recent crab data that we employ here to derive from this species.
9. Morphometric parameters, similar to those measured in the fossil material, were applied to 208 recent *P. potamios* specimens from the invertebrate collection (preserved in 70% alcohol) of the Hebrew University of Jerusalem. In addition, carapace

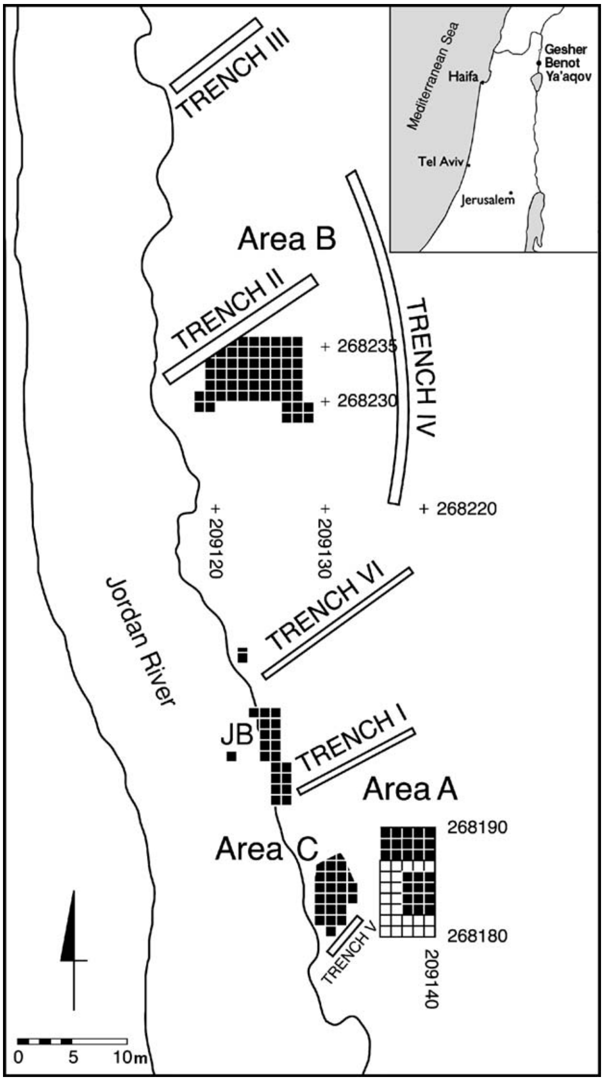

Fig. 1. Map of the excavation areas and trenches at GBY (insert: map of Israel with location of the site).

height and width were measured to confirm the correlation between carapace and pincer length in recent specimens (see Fig. 5).

10. The invertebrate collection consisted mainly of medium- to large-sized crabs (carapace width 36–50 mm). In order to supply missing size classes, we collected from several habitats in the Hula and Jordan Valley 5 to 10 specimens of each of the size classes 1–5, 6–10, 11–15, 16–20, 21–25, 26–30 and 31–35 mm, and 10 specimens with carapace width larger than 51 mm.
11. The statistical analyses (correlation, mean, standard error, regression lines and cluster analyses) were calculated using Excel and Multi-Variate Statistical Package (MVSP) software.
12. Correlation significance was calculated by application of the Bonferroni correction, as large series of correlations were examined simultaneously. According to the simple Bonferroni correction, the correlation is significant if $P<0.05/k$ (k is the number of calculated correlations).

3.2. The site

Gesher Benot Ya'aqov is located in the northern Jordan Valley, Israel (Fig. 1). Excavations at the site were carried out from 1989 to 1997 [7]. The site provides important clues to hominin lifeways and the adaptation process in the Levantine Corridor [7,10]. Evidence of human occupation at the site spans a period of ca. 100 Ka across the Matuyama–Brunhes Boundary (MBB, 0.79 Ma) magnetic polarity transition. The sedimentary sequence at GBY (35 m thick in total) consists of a freshwater lake and its fluctuating margin deposits. The strandline is reflected by coquinas and molluscan sands, which preserve the bulk of the archaeological assemblages. The conglomerates that bound the base and top of the sequence of deposits are interpreted as reflecting the strong cool/dry effects of OIS 20.2 and 18.2, respectively [4,5].

The site of GBY is characterized by rich fossil accumulations associated with beach coquina [5]. The fossil crabs of GBY were found with a large assemblage of molluscs (over 40 freshwater species), such as *Melanopsis* spp., *Theodoxus* spp. and *Viviparus* spp., which were probably predated by crabs. The recent freshwater crab of the region, *Potamon potamios*, from the Hula Valley has been observed feeding on *Melanopsis* spp. in captivity (Ashkenazi, unpublished).

The richest and most diverse fossil findings were in Area C in layer V-6, a deposit of clay ca. 1 m thick. The excavated volume of Area C layer V-6 (the layer selected for detailed analysis) is 1.39 m^3 [10].

4. Results

We present here the results of analyses of data derived from fossil crabs from GBY and recent freshwater crabs *Potamon potamios* (Olivier 1804) Decapoda, Brachyura, and from comparative analyses of both data sets.

4.1. Fossil crab material

The fossil freshwater crabs from GBY comprise 5033 fragments ranging in size between 1 and 40 mm. Most of the fossil remains were found in Area C ($n = 2972$, 59.1%), which yielded the richest archaeological assemblages of the site (Fig. 2). In Area C the archaeological horizon with the richest crab remains is layer V-6 ($n = 2722$, 91.6% of Area C fossil crabs and 54.1% of the total crab material).

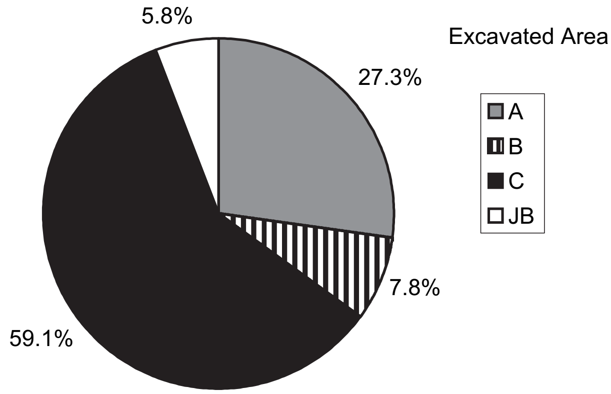

Fig. 2. Distribution of fossil freshwater crab remains within the excavated area of GBY.

4.2. Identified fossil crab body parts

We used *Potamon potamios* from the northern Jordan Valley as reference material for fossil crab fragment identification to body part. A total of 4659 fragments (92.6%) were identifiable to specific body part. The remaining 374 fragments (7.4%), mostly very small pieces measuring 2–4 mm, were unidentified. The percentages of identified crab body parts are presented in Table 1 and the different parts are described in Figs. 3–5. The most abundant parts among the fossil crab remains are pincers (74.6%).

4.3. Morphometric criteria and their measurements in fossil crabs

Among the GBY fossil crab fragments, only the pincers and dactylus are abundant and have measurable features. Among them, 1787 (35.5%) fragments with suitable parameters were measured. The fossil material demonstrated four different forms of pincers representing larger (the right cheliped R, in most recent specimens) and smaller (the left cheliped L) pincers. Each cheliped has upper movable (Right Up = RU and Left Up = LU) and lower fixed (Right Down = RD and Left Down = LD) pincers, which differ in morphology (Fig. 4). We defined 22 measurable parameters for pincers: 6 in RU, 7 in RD, 4 in LU and 5 in LD. In further analyses, we restricted data to Area C layer V-6 and correlated 18 of the parameters to 4 parameters of their related pincer's ventral length (v).

Table 1
The number and percentage of identified fossil crab body parts in GBY ($n = 4659$)

Crab body part	Number	%
Pincers	3474	74.6
Propodus	612	13.1
Carapace	282	6
Dactylus	129	2.8
Abdomen parts	82	1.8
Mandible (maxillipeds)	68	1.5
Sternum	6	0.1
Inner body parts	6	0.1
Total	4659	100

For description of body parts, see Figs. 3–5.

Data on different morphometric parameters of the assemblage of GBY fossil crabs are presented in Table 2. We found 1477 measurable pincers. There are more measurable pincers of the larger (R) type ($n = 1001$, 67.8%) than the smaller (L) type ($n = 476$, 32.2%). There are more pincers of the RU type ($n = 580$, 57.9%) than the RD type ($n = 421$, 42.1%) and more pincers of the LD type ($n = 271$, 56.9%) than the LU type ($n = 205$, 43.1%). The most abundant measurable part is the large basal tooth (length BT l and width BT w, 497 and 513 specimens, respectively). Similar proportions of crab pincer parts were found when Area C was considered in isolation: larger pincers (R) comprise 64.0% ($n = 795$) and the upper type RU is more abundant (59.7%). Among the smaller pincers (L) from Area C, 36% ($n = 447$), the lower form LD is more abundant (58.0%).

4.4. Regression lines and correlations between the proposed parameters and pincer length

The regression lines and correlations between the proposed morphometric parameters and their related pincer length in fossil crabs from GBY Area C layer V-6 are presented in Table 3. We tested correlation coefficients (18 parameters against their 4 length parameters) and found all to be positive at the 5% significance level, after application of the appropriate Bonferroni correction. The correlations between the parameters and the length of the upper pincer of the larger cheliped (RU) are lower than in other pincers.

4.5. Minimum number of individuals and density of the fossil crab assemblage

The differences in morphology between the four pincers were used to determine the minimum number of individuals in the examined fossil sample of GBY. The existence of four different pincers in fossil material increases the accuracy of the assessment of crab population structure and its size range, and eliminates errors in taxonomic identification by excluding species with even-shaped chelipeds. Based on the most abundant pincer among the crab fragments (RU), the minimum number of crabs in the GBY archaeological horizons is 668 specimens. Considering only Area C, the minimum number of fossil crabs is 475 specimens, of which 446 (93.9%) are from Area C layer V-6. Thus the density of fossil crabs in Area C layer V-6 is 321 crabs per m^3.

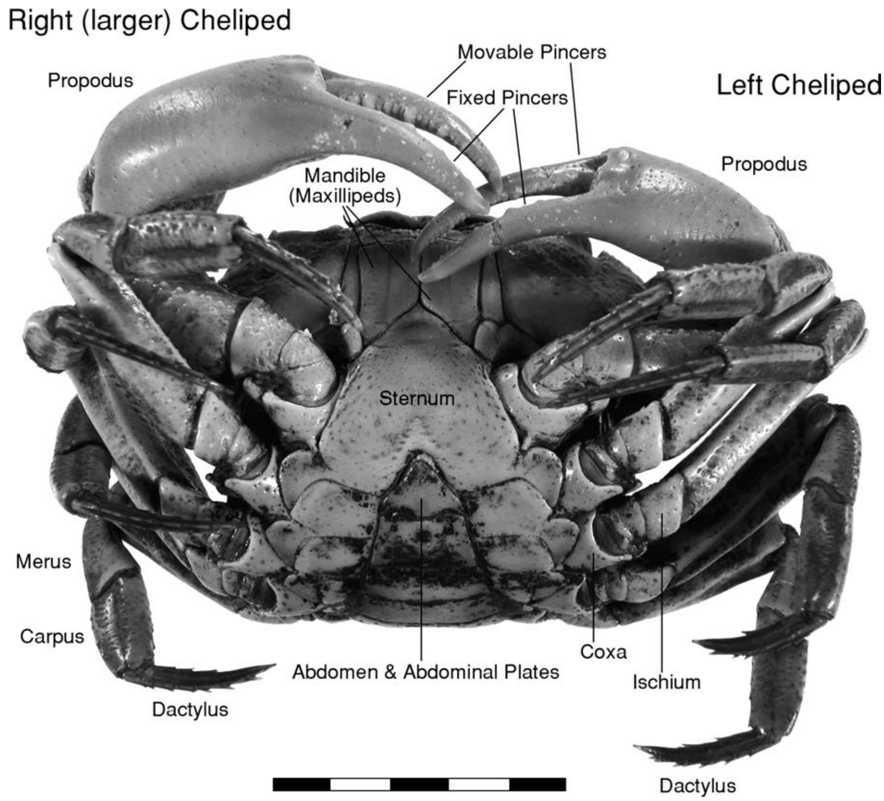

Fig. 3. Body parts of the freshwater crab *Potamon potamios*.

4.6. Measurements of Potamon potamios

Recent freshwater crabs were measured for the same parameters as the fossil crabs. In addition, the dorsal length of the upper pincer in both chelipeds (RU d and LU d, Fig. 4a and c, mostly broken in the GBY fossil material) and carapace length and width (Fig. 5, fragmented in fossil material) were measured only in recent crabs. The carapace was measured for evaluation of the correlation between the length of each pincer and carapace size. We used the entire data set (without separation of males and females), since identification of sex was not possible in the fossil material. The parameter that yielded the largest data set is the ventral length (v) of the larger movable pincer (RU v, 161 specimens). The data for measured parameters of recent freshwater crabs are presented in Table 4.

4.7. Regression lines and correlations between the proposed parameters, pincer length and body size in Potamon potamios

Regression lines and correlations between the proposed morphometric parameters and their related pincer length in recent *P. potamios* are presented in Table 5. Correlations in recent crabs were examined for the entire data set and for each sex separately to facilitate accurate comparison between the fossil (sex not identified) and recent crab data. All the correlations were significantly different from 0 ($P<0.05$). Since we examined 51 correlations simultaneously, we calculated the Bonferroni correction to improve the accuracy of the results. All correlation coefficients presented in Table 5, except for one (in females, between RU v and RU BT l), are significant at the 0.05 significance level (after applying the Bonferroni correction).

Both upper pincers (RU and LU) demonstrate a very high and significant correlation between dorsal and ventral length measurements (RU d and RU v correlation, $r = 0.990$, $P<0.0001$; LU d and LU v correlation, $r = 0.991$, $P<0.0001$). These results enable the use of either pincer length parameter (ventral or dorsal) for assessment of crab body size.

In addition, we confirmed the correlation between pincer size and crab carapace size from the same samples of recent crabs (Fig. 5, Table 6) and gave the regression lines. The high correlation between height and width of the carapace ($r = 0.997$, $P<0.0001$) allows reliable use of either of the parameters for assessment of body size.

4.8. Differences between sexes in measurements of the recent freshwater crab Potamon potamios

Data of all measured parameters of recent crabs indicate that males are larger than females. While young

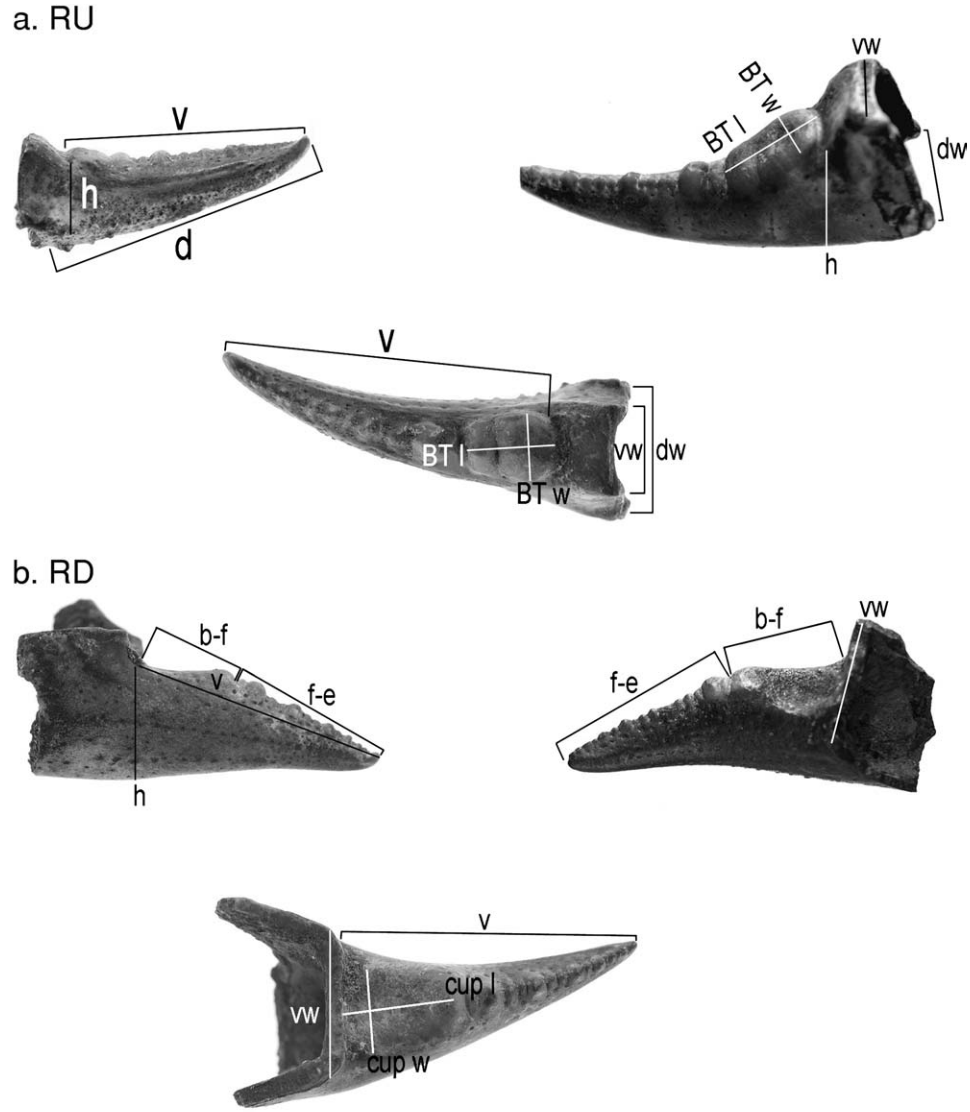

Fig. 4. Pincer types from GBY and their measurement points for measurable parameters. Pincers were photographed from different angles to show measurement points. Photographed pincers range from 15 to 22 mm and are enlarged not to scale. Measured parameters: (a) the large cheliped's movable pincer RU; (b) the large cheliped's fixed pincer RD; (c) the small cheliped's movable pincer LU; (d) the small cheliped's fixed pincer LD. Parameter measurements (all are linear lines between described points): v, ventral length, from proximal ventral ridge base to distal edge of pincer; d, dorsal length, from proximal dorsal edge between dorsal joints of movable pincer to distal edge of pincer; h, height, vertical measurement from base of ventral ridge (measurement point v) to base of pincer; vw, ventral basal ridge length; dw, distance between dorsal joints of movable pincer (round-shaped joints); BT, large basal tooth of large cheliped's movable pincer; BT l, length of basal tooth measured in longest line; BT w, width of basal tooth measured in widest line; **cup**, crushing depression in large cheliped's fixed pincer; **cup** l, length of cup measured in longest line; **cup** w, width of cup measured in widest line; b-f, length of horizontal part of fixed pincers, from base of ventral ridge to point of slanting; f-e, length of distal slanted part of fixed pincers, from point of slanting to distal edge of pincer.

males overlap with females in their size parameters, the larger range of size measurements is restricted to males. For example, the maximum carapace height in our sample of recent females is CA h = 47.57 mm, while higher carapaces (CA h = 47.72–63.41 mm, range of 15.69 mm, 25%) are found only in males. Similarly, the maximum carapace width of recent females is CA w = 59.24 mm, while wider carapaces (CA w = 59.30–77.14 mm, range of 17.84 mm, 23%) are again found only in males.

Differences between various measured parameters in each pincer of fossil and recent crabs are presented in Fig. 6 using the mean values (±standard error) of each parameter for recent males, recent females and GBY (males and females together). The mean values for the GBY population are consistently smaller for each of these measured parameters compared to those of the recent crabs. More precisely, the GBY means are the smallest, those of the recent males are the largest, while those of the recent females are always intermediate.

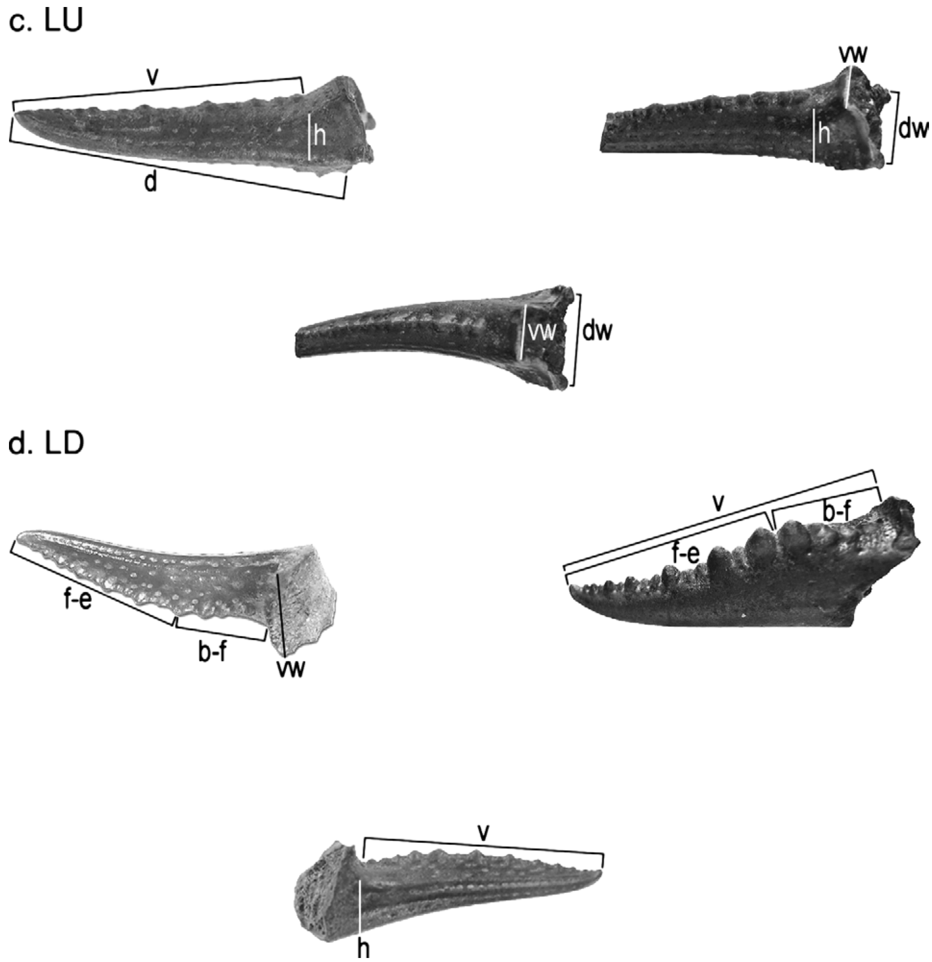

Fig. 4. (*continued*)

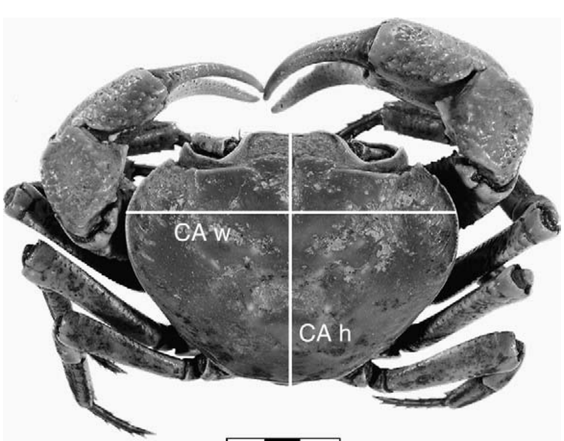

Fig. 5. Measurements of the carapace in recent crabs. Carapace height (CA h) was measured from the median frontal notch to the posterior carapace margin. Carapace width (CA w) was measured at the widest point of the upper part of the carapace.

4.9. How similar are the GBY fossil crabs to recent freshwater crab Potamon potamios?

The comparative measurements of equivalent parameters in both fossil and recent crabs from the same area enabled assessment of the taxonomic similarity between the populations, based on morphology and allometry.

Comparison between fossil and recent populations indicates that the maximum pincer length of recent populations is greater by 9.8 mm (32.8% in LU v). However, when a specific structure like the basal tooth BT is considered, the fossil material includes longer (37.5%) and wider (27.9%) elements compared to the recent crabs, indicating different proportions between pincer length and basal tooth size in each population.

Comparison of ratios of measurements (the various measurements relative to the ventral ridge length for the upper movable pincers, and relative to the ventral length for the lower fixed pincers) shows that the GBY fossil crabs are not merely a smaller image of the recent *Potamon potamios*, but also differ in shape. Of 13 ratios that were compared, six are significantly different at the

Table 2
Measurable morphometric parameters in fossil crab pincers from GBY assemblage

Parameters	No. of pincers	Size range (mm)	Parameters	No. of pincers	Size range (mm)
RU pincer parameters	580		*RD pincer parameters*	421	
Ventral length (RU v)	59	2.25–28.00	Ventral length (RD v)	72	4.67–30.50
Height (RU h)	252	1.28–12.02	Height (RD h)	104	1.11–10.39
Ventral ridge (RU vw)	293	0.60–7.80	Ventral ridge (RD vw)	158	1.72–9.73
Dorsal joints distance (RU dw)	157	1.41–10.74	Crushing depression length (RD cup l)	309	1.20–11.71
Basal tooth length (RU BT l)	450	0.52–12.3	Crushing depression width (RD cup w)	269	0.89–10.40
Basal tooth width (RU BT w)	469	0.49–8.76	Base to fold (RD b-f)	160	1.80–14.89
			Fold to edge (RD f-e)	89	2.89–18.38
LU pincer parameters	205		*LD pincer parameters*	271	
Ventral length (LU v)	27	1.86–20.00	Ventral length (LD v)	59	2.25–28.00
Height (LU h)	106	1.18–7.26	Height (LD h)	106	1.28–12.30
Ventral ridge (LU vw)	137	0.96–5.28	Ventral ridge (LD vw)	118	0.96–7.79
Dorsal joints distance (LU dw)	45	1.63–8.80	Base to fold (LD b-f)	161	1.69–12.00
			Fold to edge (LD f-e)	57	1.79–13.41

For explanation of measured pincer parameters, see Fig. 4.

0.05 level and two of them (the ratio between cup w and v in RD and the ratio between f-e and v in LD) are still significant after application of the Bonferroni correction.

To improve our understanding of the differences between the populations, we performed a cluster analysis for each of the four pincers, incorporating both measurements and ratios of measurements (each standardized by the respective standard deviation). We omitted one of the characters (RD h, for which data are lacking for more than half of the pincers) and considered only pincers that yielded a full data set. Using Ward's method (squared Euclidean distances and minimum variance clustering), each of the resulting dendrograms displays a clear bifurcation into two main branches, one including the greater part of the recent pincers and the other containing the greater part of the fossil GBY pincers. A k-means clustering (with $k = 2$) analysis, which arranges the objects in two distinct clusters in order to minimize the within-cluster variability and maximize the between-cluster variability, reinforced this observation (Table 7).

The relative distances between the three populations (recent males, recent females and GBY) are demonstrated by a cluster analysis (Fig. 7) performed on the means of all 29 characters (measurements and ratios of measurements of all four pincers). Thus, although the linear measurements place the recent females in an intermediate position between GBY and the recent males (Fig. 6), when ratios between measurements are also taken into consideration the GBY fossil specimens are distinctly separated from the recent crabs.

Table 3
Regression lines and correlations between new parameters (x, in mm) and their related pincer length (v, in mm) in GBY fossil freshwater crabs

Parameter	Regression line	Correlation Coefficient	Sample Size	p-value
Pincer RU				
RU h	$v = 1.696x + 5.475$	0.569	24	0.0019
RU vw	$v = 2.578x + 4.080$	0.700	33	<0.0001
RU dw	$v = 1.925x + 3.701$	0.840	26	<0.0001
RU BT l	$v = 1.898x + 6.582$	0.671	34	<0.0001
RU BT w	$v = 3.212x + 5.341$	0.741	33	<0.0001
Pincer RD				
RD h	$v = 2.019x + 4.679$	0.870	14	<0.0001
RD vw	$v = 1.918x + 4.811$	0.855	26	<0.0001
RD b-f	$v = 1.773x + 3.200$	0.853	28	<0.0001
RD cup l	$v = 1.933x + 5.223$	0.865	29	<0.0001
RD cup w	$v = 3.673x + 4.249$	0.912	29	<0.0001
RD f-e	$v = 1.249x + 2.864$	0.924	29	<0.0001
Pincer LU				
LU h	$v = 3.413x + 2.936$	0.815	10	0.0020
LU vw	$v = 5.979x - 1.641$	0.934	10	<0.0001
LU dw	$v = 2.977x + 1.162$	0.990	6	<0.0001
Pincer LD				
LD h	$v = 2.427x + 3.238$	0.833	18	<0.0001
LD vw	$v = 3.895x - 0.173$	0.955	23	<0.0001
LD b-f	$v = 1.440x + 3.282$	0.896	31	<0.0001
LD f-e	$v = 1.478x + 1.396$	0.902	31	<0.0001

All correlation coefficients are significant at the 0.05 significance level (after applying a Bonferroni correction). For explanation of measured pincer parameters, see Fig. 4.

5. Discussion and conclusions

An unusual assemblage of fossil freshwater crabs (over 5000 fragments) in the Early–Middle Pleistocene fluctuating lake-margin Acheulian site of GBY (0.79 Ma) raises the question of the palaeoenvironmental meaning of such an accumulation. This assemblage is unique compared to other sites in the region and in the world. In the present study we make the first known attempt to extract some useful information on the palaeoenvironment by reconstructing the size of fossil freshwater crabs from fragments.

Table 4
Measurable morphometric parameters in recent *Potamon potamios*

Parameters	No. of pincers	Size range (mm)	Parameters	No. of pincers	Size range (mm)
RU pincer parameters	169		*RD pincer parameters*	168	
Dorsal length (RU d)	80	4.26–39.13	Ventral length (RD v)	147	0.75–30.73
Ventral length (RU v)	161	0.80–34.14	Height (RD h)	139	0.30–11.16
Height (RU h)	152	0.27–10.37	Crushing depression length (RD cup l)	106	0.91–10.31
Ventral ridge (RU vw)	117	0.71–7.84	Crushing depression width (RD cup w)	20	1.23–4.32
Dorsal joints distance (RU dw)	127	1.20–12.90	Base to fold (RD b-f)	104	1.17–13.58
Basal tooth length (RU BT l)	127	0.15–7.68	Fold to edge (RD f-e)	123	2.07–20.00
Basal tooth width (RU BT w)	105	0.37–6.31			
LU pincer parameters	158		*LD pincer parameters*	162	
Dorsal length (LU d)	81	3.62–34.31	Ventral length (LD v)	152	0.94–29.03
Ventral length (LU v)	141	1.06–29.79	Height (LD h)	138	0.43–7.23
Height (LU h)	138	0.44–7.98	Base to fold (LD b-f)	107	0.70–13.06
Ventral ridge (LU vw)	108	0.66–5.20	Fold to edge (LD f-e)	104	1.25–18.00
Dorsal joints distance (LU dw)	109	0.90–11.59			
Carapace	155				
Carapace height (CA h)	154	3.50–63.41			
Carapace width (CA w)	153	3.59–77.14			

For explanation of measured parameters, see Figs. 4 and 5.

Animal body-size dimensions may indicate response to changes in habitat, food availability or climate, or exploitation by human or non-human predators [23]. The size distribution of the population is an excellent criterion for assessment of the habitat conditions during deposition of the fossil assemblage [14]. Moreover, the allometry of body parts and their morphology are basic parameters for identification of fossil crab taxonomy.

Eighteen of the suggested morphometric parameters are significantly correlated with their related pincer length. Consequently, even if fossil crab remains are very fragmentary and only one fragment of pincer is preserved, it is still possible to reconstruct the pincer size that we assume represents the crabs' body size, as is known for the genus *Potamon* [1,6,12,17]. Moreover, as broken pincers consist of either the proximal or the distal part, the suggested parameters are useful for size reconstruction of most of the fragments.

Pincers are the most abundant crab body parts preserved at GBY. Structures that function as teeth (mandibles and pincers in crustaceans and radula in gastropods) are denser and thicker than other body parts in order to withstand the pressures of feeding [21]. Although crab mandibles are among the dense and resistant parts, at GBY they are very scarce (1.5%) compared to the pincers (74.6%) (Table 1), for reasons that are as yet unknown. However, despite the scarcity of crab mandibles at GBY, some are complete, including the delicate projection in the lower part that usually breaks in archaeological conditions. We relate this fact to the excellent preservation conditions in the anoxic waterlogged site. The freshness of the edge of delicate structures as well as artifact edges implies that they accumulated well above the strand line, on the upper beach face [4].

Our results indicate that among the pincers, the upper and lower pincers of the larger cheliped (normally on the right) are more abundant (67.8%) than the smaller pincers (32.2%). This could be a taphonomic effect of better preservation of the larger pincers, which are more robust (higher and thicker) than those of the smaller and thinner left cheliped (see Fig. 3).

In sites like GBY where crabs have four types of pincers, the crab population size range should be calculated by using only the most abundant pincer (MNI), in order to avoid possible data replication by incorporating other pincers that might belong to the same fossil specimen. This method reduces the available data sets but is the most reliable for fossil data. The most abundant pincer (RU) length data for GBY indicate that the broad size range (small, medium and large crabs) that one sees in living populations of *Potamon potamios* in lake margins or river banks [6] is also present in the GBY populations, though with a narrower range.

The size range of length (v) of all pincer assemblages is larger in measured recent populations (0.75–34.14 mm) than in the GBY material (1.86–30.50 mm). We assume that the difference in minimum pincer length is due to the sieving procedure carried out during the excavations, in which the fossil material was passed through sieves with 2 mm mesh. However, the difference in maximum pincer length between measured natural populations and the GBY material reflects the overall smaller maximum pincer length parameters of the GBY population.

The density of crabs in Area C layer V-6, based on minimum number of individuals, seems unusually high (321 crabs per m^3) compared to the density of *Potamon potamios* in the Dead Sea area of Israel (0.1 crab per m^2)

Table 5
Regression lines and correlations between measured parameters and related pincer length in recent *Potamon potamios* from Israel

Parameter	Sex	Regression line	Correlation coefficient	Sample size	*P* value
Pincer RU					
RU v−RU d	Total	$v = 0.854x - 0.059$	0.990	80	<0.0001
	F	$v = 0.718x + 2.354$	0.952	23	<0.0001
	M	$v = 0.859x - 0.043$	0.991	54	<0.0001
RU v−RU h	Total	$v = 2.785x + 1.212$	0.936	79	<0.0001
	F	$v = 1.885x + 5.794$	0.760	23	<0.0001
	M	$v = 2.827x + 1.215$	0.934	53	<0.0001
RU v−RU vw	Total	$v = 3.394x + 2.473$	0.934	79	<0.0001
	F	$v = 2.447x + 5.824$	0.783	23	<0.0001
	M	$v = 3.344x + 3.135$	0.933	53	<0.0001
RU v−RU dw	Total	$v = 2.337x + 0.596$	0.964	80	<0.0001
	F	$v = 1.634x + 5.078$	0.858	23	<0.0001
	M	$v = 2.353x + 0.690$	0.965	54	<0.0001
RU v−RU BT l	Total	$v = 3.263x + 5.975$	0.830	82	<0.0001
	F	$v = 1.680x + 10.630$	0.565	24	0.0020 NS
	M	$v = 3.179x + 7.002$	0.835	55	<0.0001
RU v−RU BT w	Total	$v = 3.441x + 7.149$	0.821	76	<0.0001
	F	$v = 2.182x + 10.053$	0.681	23	0.0002
	M	$v = 3.339x + 8.145$	0.817	51	<0.0001
Pincer RD					
RD v−RD h	Total	$v = 2.635x + 1.120$	0.959	127	<0.0001
	F	$v = 2.186x + 2.823$	0.924	32	<0.0001
	M	$v = 2.628x + 1.682$	0.928	63	<0.0001
RD v−RD cup l	Total	$v = 2.290x + 5.493$	0.806	95	<0.0001
	F	$v = 1.785x + 6.739$	0.825	29	<0.0001
	M	$v = 2.159x + 7.067$	0.755	53	<0.0001
RD v−RD b-f	Total	$v = 2.233x + 1.300$	0.959	94	<0.0001
	F	$v = 1.531x + 5.262$	0.813	19	<0.0001
	M	$v = 2.258x + 1.360$	0.954	49	<0.0001
RD v−RD f-e	Total	$v = 1.573x + 0.255$	0.975	122	<0.0001
	F	$v = 1.343x + 2.271$	0.859	31	<0.0001
	M	$v = 1.582x + 0.213$	0.974	66	<0.0001
Pincer LU					
LU v−LU d	Total	$v = 0.874x - 0.001$	0.991	133	<0.0001
	F	$v = 0.846x + 0.472$	0.963	35	<0.0001
	M	$v = 0.864x + 0.223$	0.986	71	<0.0001
LU v−LU h	Total	$v = 3.554x + 1.697$	0.934	110	<0.0001
	F	$v = 2.733x + 4.162$	0.844	38	<0.0001
	M	$v = 3.688x + 1.413$	0.956	72	<0.0001
LU v−LU vw	Total	$v = 4.788x + 0.590$	0.944	82	<0.0001
	F	$v = 3.523x + 4.180$	0.806	26	<0.0001
	M	$v = 4.869x + 0.526$	0.958	56	<0.0001
LU v−LU dw	Total	$v = 2.667x + 1.343$	0.935	89	<0.0001
	F	$v = 1.866x + 5.091$	0.789	26	<0.0001
	M	$v = 2.714x + 1.366$	0.950	63	<0.0001
Pincer LD					
LD v−LD h	Total	$v = 3.603x + 0.150$	0.968	134	<0.0001
	F	$v = 3.269x + 1.308$	0.912	33	<0.0001
	M	$v = 3.529x + 0.622$	0.936	70	<0.0001
LD v−LD b-f	Total	$v = 2.266x + 1.286$	0.957	104	<0.0001
	F	$v = 1.383x + 6.390$	0.881	23	<0.0001
	M	$v = 2.187x + 2.078$	0.940	58	<0.0001
LD v−LD f-e	Total	$v = 1.586x + 0.084$	0.975	104	<0.0001
	F	$v = 1.085x + 4.534$	0.691	24	0.0002
	M	$v = 1.569x + 0.363$	0.972	57	<0.0001

All but one of the correlation coefficients are significant at the 0.05 significance level (after applying a Bonferroni correction). For explanation of measured pincer parameters, see Fig. 4. NS, not significant.

Table 6
Regression lines and correlations between carapace size (CA h: height; CA w: width) and between carapace height (CA h) and pincer length in recent *Potamon potamios* (total sample and sex groups)

Parameter	Sex	Regression line	Correlation coefficient	Sample size	P value
CA h–CA w	Total	$CAh = 0.793x + 0.440$	0.997	149	<0.0001*
	F	$CAh = 0.771x + 1.118$	0.990	38	<0.0001*
	M	$CAh = 0.816x - 0.616$	0.992	80	<0.0001*
	Y	$CAh = 0.746x + 1.155$	0.984	31	<0.0001*
CA h–RU v	Total	$CAh = 1.874x + 6.179$	0.977	135	<0.0001*
	F	$CAh = 1.990x + 6.601$	0.964	37	<0.0001*
	M	$CAh = 1.711x + 8.764$	0.972	77	<0.0001*
	Y	$CAh = 2.424x + 1.476$	0.972	19	<0.0001*
CA h–RD v	Total	$CAh = 2.036x + 6.062$	0.975	123	<0.0001*
	F	$CAh = 2.141x + 6.706$	0.959	35	<0.0001*
	M	$CAh = 1.829x + 9.288$	0.967	70	<0.0001*
	Y	$CAh = 2.572x + 1.304$	0.974	18	<0.0001*
CA h–LU v	Total	$CAh = 2.120x + 5.066$	0.975	128	<0.0001*
	F	$CAh = 2.261x + 4.961$	0.950	36	<0.0001*
	M	$CAh = 1.927x + 7.951$	0.966	72	<0.0001*
	Y	$CAh = 2.468x + 1.253$	0.967	19	<0.0001*
CA h–LD v	Total	$CAh = 2.275x + 5.140$	0.977	133	<0.0001*
	F	$CAh = 2.308x + 6.851$	0.933	35	<0.0001*
	M	$CAh = 2.067x + 8.075$	0.973	77	<0.0001*
	Y	$CAh = 2.567x + 1.315$	0.966	20	<0.0001*

Significant correlations obtained by the Bonferroni correction are marked with an asterisk. For explanation of measured parameters, see Figs. 4 and 5.

[6]. Although the time span of the examined layer at GBY is as yet unknown, the assemblage is unusually dense compared to natural populations, other layers of GBY (Fig. 2) and other assemblages from Upper Jordan Valley sites (Ashkenazi, unpublished). Further analyses of the spatial distribution and clusters of individual size classes, as well as the distribution of apparently burned crab fragments, with the aid of GIS mapping will examine whether the remains reflect a taphonomic effect on the GBY crab assemblages [10].

The good preservation conditions of crabs in Area C layer V-6 may reflect a taphonomic effect of preservation of burrowing-type crabs. This has been demonstrated for Late Cretaceous burrowing-type crabs (Decapoda, Brachyura), which were better preserved in a massive oyster bed than in the underlying 1 m of light gray sandstone, in which carapaces (assumed to be exuviae) were badly preserved [24].

Apart from the study on *Potamon potamios* in an oasis in the Dead Sea region [6], there are no reference works on large-scale fossil crab measurements in the Mediterranean region. In recent crabs from the Hula Valley (measured in this study) we found a very high and significant correlation between dorsal and ventral length measurements of both movable pincers, enabling the use of either parameter for assessment of crab body size. Similar results were obtained for the correlation between carapace width and height. Carapace height was preferred and is recommended for further measurements, as the measurement points are obvious, thus minimizing errors (Fig. 5). Moreover, carapace height is the parameter that is least susceptible to growth variation with sexual maturation [12].

All correlations between the proposed morphometric parameters and their related pincer in the fossil material were significant (Table 3). Although significant, the correlation of pincer length with the height of large movable pincers (RU h) is lower than the other results. This parameter is difficult to measure, due to variability in the shape of the pincers. Some of the pincers are rounded, while others have a sharper angle; the exact point for measurement is more difficult to define in rounded pincers and consequently this measurement is less accurate. Lower correlations also occur between the length of the upper pincer of the larger cheliped (RU) and its related parameters. These results are probably due to morphological variability in this pincer. We identified two types of large basal tooth (BT), one large and rounded and the other large and oval with two peaks. In addition, the maximum width and length of the basal tooth exceed by about 30% the dimensions in recent populations, despite the longer pincers found in recent populations. Further understanding of the reasons for these morphological differences requires examination of similar crab remains from different Jordan Valley sites that predate and postdate the GBY assemblage. Despite the morphological variability in several parameters, the regression lines provided for the relations between the parameters and pincer size (Table 3 for fossil and Table 5 for recent crabs) are valuable tools for assessment of crab pincer size (and indirectly crab size) from small fossil fragments in archaeological sites in the region.

The consistent results of the comparison of measured parameter means for pincers (±standard error) presented in Fig. 6 display a difference in size between GBY

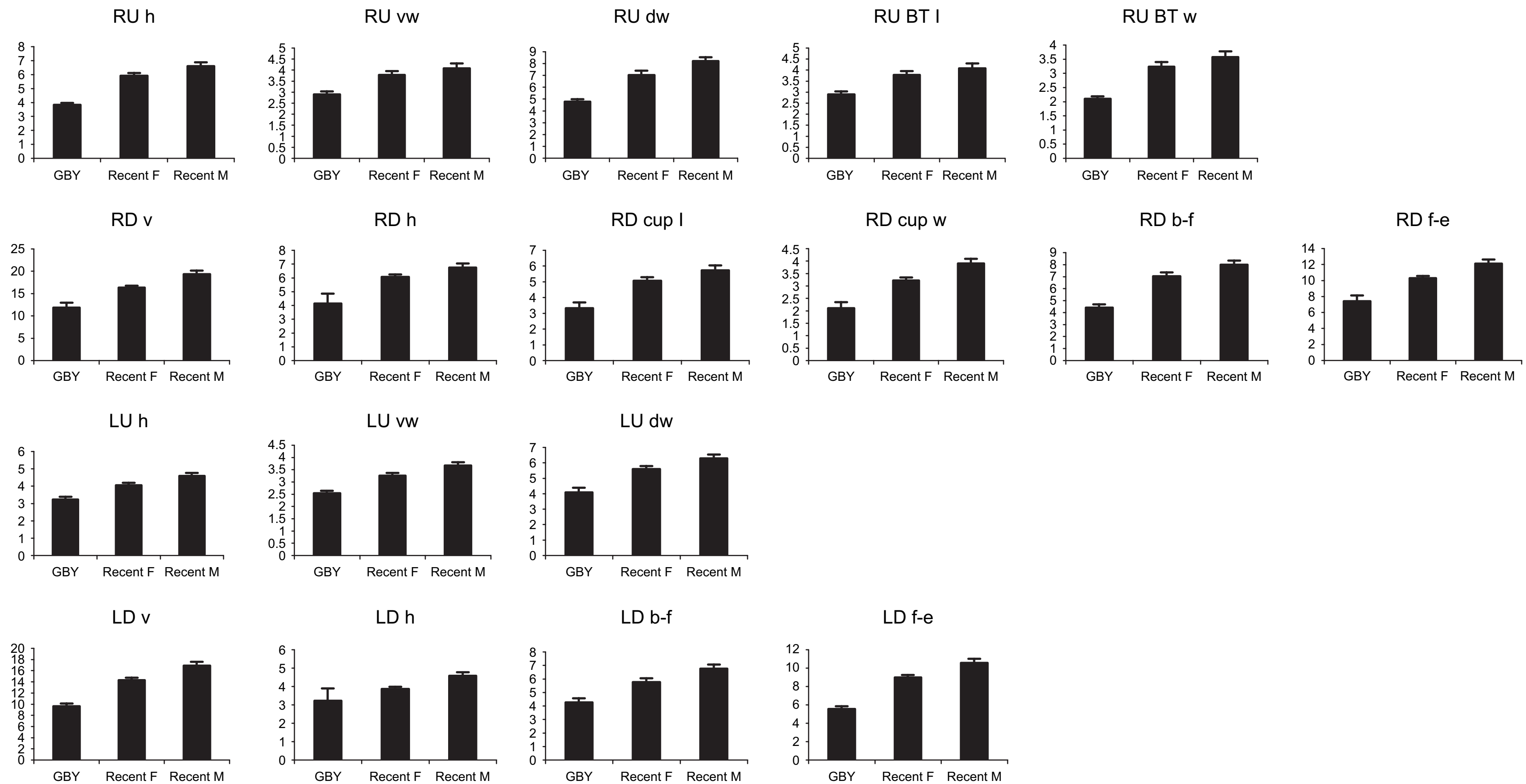

Fig. 6. The means (±standard error) of the various pincer parameter measurements taken for the three populations: recent males, recent females and the fossil GBY remains (males and females together). For description of parameters, see Fig. 4.

Table 7
Results for the k-means clustering of fossil crabs from GBY and recent crabs ($k = 2$). The P values were obtained by the two-tailed Fisher's exact test

	GBY	Recent	Total
LD[a]			
Cluster 1	30	15	45
Cluster 2	3	71	74
Total	33	86	119
LU[b]			
Cluster 1	14	13	27
Cluster 2	6	72	78
Total	20	85	105
RD[c]			
Cluster 1	15	12	27
Cluster 2	3	45	48
Total	18	57	75
RU[d]			
Cluster 1	40	14	54
Cluster 2	14	63	77
Total	54	77	131

[a] In Cluster 1, 90.91% of GBY; in Cluster 2, 82.56% of recent crabs ($P = 8.6\times10^{-14}$).
[b] In Cluster 1, 70.00% of GBY; in Cluster 2, 84.71% of recent crabs ($P = 3.5\times10^{-6}$).
[c] In Cluster 1, 83.33% of GBY; in Cluster 2, 78.95% of recent crabs ($P = 3.3\times10^{-6}$).
[d] In Cluster 1, 74.07% of GBY; in Cluster 2, 81.82% of recent crabs ($P = 1.2\times10^{-10}$).

fossil crabs and recent crabs. While in the recent crabs *Potamon potamios* there are size differences between males (larger) and females (smaller), as expected for this species [1,6], our cluster analysis placed both recent males and recent females close together, in clear separation from the GBY fossil crabs (Fig. 7). This clear-cut distinction stems not only from differences in pincer size, but also from differences in pincer morphology. Further examination of the ratios of the measurements indicated significant differences between GBY and recent populations in 8 out of 13 ratios, reinforcing the assumption that the fossil and recent populations differ both in size and in pincer morphology. Morphologic differences earlier led to definition of at least 10 subspecies of *Potamon potamios* [20]. The revised taxonomy and zoogeography of this species from Europe, North Africa and the Middle East amalgamated all *Potamon* spp. from the area in *P. potamios* [1]. This new concept has not yet been evaluated by comparative genetic work on the DNA of individuals from the distribution range. At this stage of the study we are unable to conclude whether the morphometric differences between the pincers of GBY fossil crabs and recent Hula Valley crabs are due to different environmental conditions, different diet (ability to crush molluscs), anthropogenic effect [15] or taxonomic differences.

The use of the new method with measurable parameters for comparisons of the GBY fossil crab population with crab remains from other sites in the Jordan Rift Valley (the earlier site of ‘Ubeidiya, ca. 1.4 Ma, and the Upper Pleistocene sites of Ohalo II, ca. 0.023 Ma, and Eynan, ca. 0.013 Ma), as well as present crab populations, will enable better insight into the reasons for the significantly different morphometric parameters and evolutionary trends of crabs in sites predating and postdating GBY.

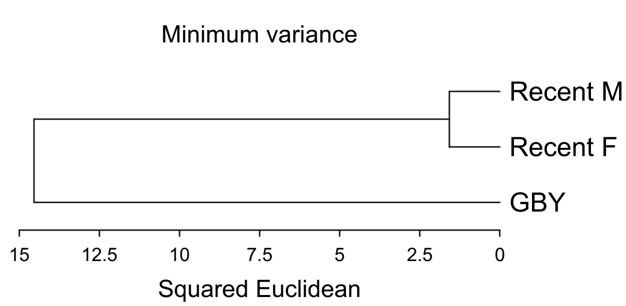

Fig. 7. Clustering of the three populations, fossils from GBY, recent males and recent females, using Ward's method (performed on the population means of all 29 characters, measurements and ratios of measurements of all four pincers).

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References

[1] D. Brandis, V. Storch, M. Türkay, Taxonomy and zoogeography of freshwater crabs of Europe, North Africa, and the Middle East, Senckenbergiana Biologica 80 (2000) 5–56.
[2] G.A. Bishop, R.M. Feldmann, F.J. Vega, The Dakoticancridae (Decapoda, Brachyura) from the Late Cretaceous of North America and Mexico, Contributions to Zoology 67 (1998) 237–255.
[3] S.D. deFrance, Saladoid and ostionoid subsistence adaptations: zooarchaeological data from coastal occupation on Puerto Rico,

in: P.E. Siegel (Ed.), Early Ceramic Population Lifeways and Adaptive Strategies in the Caribbean, BAR International Series, 506, BAR, Oxford, 1989, pp. 57–77.

[4] C.S. Feibel, Archaeological sediments in lake margin environments, in: J.K. Stein, W.R. Farrand (Eds.), Sediments in Archaeological Context, The University of Utah Press, Salt Lake City, 2001, pp. 127–148.

[5] C.S. Feibel, Quaternary lake margins of the Levant Rift Valley, in: N. Goren-Inbar, J.D. Speth (Eds.), Human Paleoecology in the Levantine Corridor, Oxbow Books, Oxford, 2004.

[6] F. Gherardi, F. Micheli, Relative growth and population structure of the freshwater crab, *Potamon potamios palestinensis*, in the Dead Sea area (Israel), Israel Journal of Zoology 36 (1989) 133–145.

[7] N. Goren-Inbar, C.S. Feibel, K.L. Verosub, Y. Melamed, M.E. Kislev, E. Tchernov, E. Saragusti, Pleistocene milestones on the out-of-Africa corridor at Gesher Benot Ya'aqov, Israel, Science 289 (2000) 944–947.

[8] N. Goren-Inbar, E. Werker, C.S. Feibel, Acheulian Site of Gesher Benot Ya'aqov: The Wood Assemblage, Oxbow Books, Oxford, 2002.

[9] N. Goren-Inbar, G. Sharon, Y. Melamed, M.E. Kislev, Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel, Proceedings of the National Academy of Sciences USA 99 (2002) 2455–2460.

[10] N. Goren-Inbar, N. Alperson, M.E. Kislev, O. Simchoni, Y. Melamed, A. Ben-Nun, E. Werker, Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel, Science 304 (2004) 725–727.

[11] P.V. Hamilton, Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae), Bulletin of Marine Science 26 (1976) 403–409.

[12] R.G. Hartnoll, Evolution, systematics, and geographical distribution, in: W.W. Burggren, B.R. McMahon (Eds.), Biology of Land Crabs, Cambridge University Press, Cambridge, 1988, pp. 6–54.

[13] R.G. Hartnoll, A.D. Bryant, Size-frequency distributions in decapod crustacean — the quick, the dead, and the cast-offs, Journal of Crustacean Biology 10 (1990) 14–19.

[14] A. Jerardino, R. Navarro, Cape Rock Lobster (*Jasus lalandii*) remains from South Africa west coast shell middens: preservational factors and possible bias, Journal of Archaeological Science 29 (2002) 993–999.

[15] R.J. Losey, S.B. Yamada, L. Largaespada, Late-Holocene Dungeness crab (*Cancer magister*) harvest at an Oregon coast estuary, Journal of Archaeological Science 31 (2004) 1603–1612.

[16] H. Mienis, Molluscs from the excavation of Tel Kabri (with an appendix dealing with crustaceans found at the site), Triton 7 (2003) 28–37.

[17] G. Pretzmann, Schetren und Scherenbezahnung bei *Potamon* (Crustacea Decapoda), Annals of Natural History Museum of Wien 75 (1971) 489–493.

[18] G. Pretzmann, Some fossil chelae of river crabs and the distribution of *Potamon* in the Eastern Mediterranean and Western Asia, Thalassia Jugoslavica 8 (1972) 71–73.

[19] G. Pretzmann, A contribution to a historic analysis of Mediterranean freshwater decapods chorology. Symposion on Decapoda Mediterranea, Barcelona, 1985, Inv. Pesqu. 51 (Suppl. 1) (1987) 17–25.

[20] G. Pretzmann, Speciation trends in Potamids, Bios (Macedonia, Greece), Proceedings of the Fourth Colloquium Crustacea Decapoda Mediterranea, Aristotle University, Thessaloniki, 1993.

[21] E.J. Reitz, E.S. Wing, Zooarchaeology, Cambridge University Press, Cambridge, 1999.

[22] W.L. Schmitt, Crustaceans, University of Michigan, 1965.

[23] W.J. Sutherland, Evolution and fisheries, Nature 344 (1990) 814–815.

[24] F.J. Vega, R.M. Feldmann, Fossil crabs (Crustacea, Decapoda) from the Maastrichtian Difunta Group, North-eastern Mexico, Annals Carnegie Museum 60 (1991) 163–177.

[25] G.J. Vermeij, Patterns in crab claw size: the geography of crushing, Systematic Zoology 26 (1977) 138–151.