Early human peopling of Sicily: Evidence from the Mesolithic skeletal remains from Grotta d’Oriente

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Abstract

Background: The site of Grotta d’Oriente, Island of Favignana, Sicily has yielded the complete skeleton of an adult female (OB) dated to the Mesolithic age. The cranial morphometry of this individual can provide us with some useful information about the peopling of Sicily in the Early Holocene period.

Aim: Morphological affinities of OB and other Sicilian Mesolithic specimens were assessed to verify hypotheses concerning the early peopling of Sicily.

Subjects and methods: Craniofacial metric data were employed in a comparative analysis with European Upper Palaeolithic (UP), Mesolithic, Neolithic, and Copper/Bronze age samples, and contemporary Italians. Both a model-free and a model-bound approach were used not only to calculate craniometric distances, but also to assess the role played by gene flow and drift to produce the resulting pattern of variations and relationships.

Results: A Sicilian Mesolithic (SM) sample, including OB, resulted morphologically very close to an Italian Late UP comparative group. A general similarity among Western/Central European UP and Mesolithic groups was also detected.

Conclusion: Intense gene flow among hunter–gatherer populations accounts for close resemblances among various UP and Mesolithic groups. The beginning of a regional characterization is suggested by the morphological similarity between Italian Late UP and SM, and by decreasing gene flow among populations during the transition from the Upper Palaeolithic to the Mesolithic period.

Keywords: Sicilian Mesolithic, craniofacial morphometry, multivariate statistics

Introduction

The Upper Palaeolithic and Mesolithic human skeletal record of Sicily provides suitable evidence to study the early peopling of the island. An ancient peopling of Sicily by Homo
sapiens has been a long debated issue (D’Amore et al. 2009). Besides uncertain evidence of an Early Pleistocene peopling of the Southern coasts (Bianchini 1969), the first real definite evidence of human peopling is at the Grotta di San Teodoro (Acquedolci, Messina), a site that exhibits buried human remains and ecological evidence of human frequentation associated with a Late Epigravettian lithic industry. A recent calibrated AMS 14C dating of one sample in the collection revealed an age of 14 800 years BP (see D’Amore et al. 2009 for a discussion). After this early settlement, there are very clear indications of a progressive movement of people along the northern coast of the island, with stations at Riparo del Castello, Grotta del Cavallo (Late Upper Palaeolithic sites), Grotta Molara, Grotta dell’Uzzo, Grotta d’Oriente (Palaeo-Mesolithic sites) (see D’Amore et al. 2009 for a discussion). Recently, new industrial and ‘ecological’ evidence of Epigravettian frequentation in the western part of Sicily has been produced from preliminary excavations in Grotta Racchio (S. Vito lo Capo – Trapani; Martini et al. 2006a), in the Carboj Valley near Partanna (Trapani) (Barattolo et al. 2006); in Grotta Maltese, in the Erice countryside (Trapani) (Copat et al. 2006). Furthermore, transitional Mesolithic (and Neolithic) horizons have been preliminarily described in Grotta dell’Ucciria on Favignana Island (Trapani) (Martini et al. 2006b), in Contrada Mariano – San Cipirrello (Palermo) (Scuderi et al. 2006), in Rocchitella di Mineo (Catania) (Di Patti et al. 2006), and in Grotta d’Oriente ‘C Area’ (Trapani) (Martini et al. 2006c).

Previous and well known archaeological sites such as Levanzo island (Grotta Cala Genovesi) and the Uzzo shelter have recently produced new Mesolithic artefacts and, in the case of Uzzo, a new skeleton (Uzzo XI) (Di Salvo et al. 2008)

But what are the phylogenetic relationships between the first peopling and other successive evidences that spread towards the western cliffs in the late Palaeolithic and Mesolithic epochs?

The basic hypothesis of human Palaeolithic dispersal on the island is that of a progressive and constant dispersal of the Epigravettian culture in Sicily, with further support by other inputs from the Italian peninsula during and immediately after the glacial peak, taking advantage of the massive marine regression in the Messinian strait.

The analysis of human remains from the Palaeo-Mesolithic site of Grotta d’Oriente on the Island of Favignana (Figure 1) offers a possibility to test the hypothesis of continuing human dispersal in Sicily. Favignana is situated in the Egadi archipelago off the western corner of Sicily. During the Last Upper Palaeolithic period this small island, at the end of an emerged marine terrace, was a site of seasonal occupation for groups inhabiting the S. Vito and Mount Speciale area. Furthermore Favignana is situated at the end of a route of hunter-gatherer colonization that goes from east to west along the Tyrrenian coast.

The history of the site starts in 1969, when Giovanni Mannino, performing a surface field survey of the island, described a prehistoric site in a grotto on Montagna Grossa. The site, which is difficult to access, opens out at the base of the carbonatic cliff at 50 m above sea level.

The cave consists of a forward room (antegrotto) that leads to the actual grotto. A subsequent field survey of the forward area, performed by Mannino in 1972, described two prehistoric graves, ‘Oriente A’ and ‘Oriente B’ (OA and OB from this point) (Mannino and Thomas 2002); recently the cave has produced a third burial, as yet not described (Oriente C; Martini et al. 2006c).

OA grave has produced a fragmentary calvarium and an incomplete mandible, whereas OB brought to light a more complete skeleton. The skeletal biology of the individual has been carefully described (Di Salvo et al. 2008). The OB specimen is a female adult individual according to the criteria defined by Acsadi and Nemeskeri (1970)
and Ferembach et al. (1980). The Mesolithic age for OB has previously been established by a radiocarbon AMS dating of a gastropod shell, which has been considered as synchronous or slightly younger than OB. This dating (calibrated Marine 04, and corrected for the variation $\Delta R = 71 \pm 50$ due to the reservoir effect), falls between 8740 and 8390 years BP for the 95.4% interval, and between 8630 and 8450 years BP for the 68.2% interval, both in the Mesolithic period (Di Salvo et al. 2008). These dates have to be considered as a terminus ante quem for the OB deposition. Furthermore, in order to detect the age of Oriente B, direct AMS-$^{14}$C dating was undertaken on a rib fragment from the burial. The date was obtained from this bone at the Leibniz Laboratory for Radiometric Dating and Stable Isotope Research in Kiel is 9395 $\pm$ 45 years BP (KIA-36050) (Marcello Mannino and Michael Richards, personal communication). The burial in question is of an early Mesolithic individual, contemporary to the earliest humans buried in Grotta dell’Uzzo (Piperno 1985), but much earlier than the dated individual from Grotta Molara (OXA-534: 8600 $\pm$ 100 years BP; Gowlett et al. 1987). The OA burial, which is stratigraphically
distinct from OB, is presumably older, attributable to the Late Epigravettian period, and posterior to the terminus post quem of the occupation of the site, dated back to 12 132 ± 80 years BP (Martini et al. 2006c).

This study intends to assess the morphological affinities of OB and other Sicilian Mesolithic specimens in order to test hypotheses concerning the peopling of Sicily during the ecological transition towards the Early Holocene period.

For this purpose, we used the OB craniofacial specimen (Figure 2) and the entire Mesolithic sample available from Sicily in a comparative analysis with other Upper Palaeolithic and Mesolithic samples from Italy and neighbouring European areas. We collected a set of craniofacial metric data and compared it to European, Italian, and Sicilian samples of different chronology/cultural assemblages, as well as to some reference samples from modern populations, for which genetic relationships are known. Multivariate techniques including $D^2$ distance analysis, partial Mantel test, cluster analysis, multidimensional scaling, R-matrix analysis, and principal coordinate analysis, were used not only to calculate craniometric distances, but also to assess the role played by gene flow and drift to produce the resulting pattern of variations and relationships. We set out to show that, if the Sicilian Mesolithic sample reveals more affinity with an earlier Sicilian Upper Palaeolithic comparative group, it is plausible that there is continuity between them in conditions of relative isolation. However, if the Mesolithic Sicilians are similarly related to both a chronologically preceding Sicilian comparative group, and to a coeval non-Sicilian comparative group, such results may support a major role of gene flow. A much greater affinity with a coeval non-Sicilian comparative group or a significant differentiation from all the groups, would support an extra-Sicilian source for the Mesolithic peopling of Sicily.

Materials and methods

Samples for comparative morphometric analysis.

Comparative analysis of OB and the available Sicilian Mesolithic sample made use of both prehistoric and recent samples. Prehistoric comparative samples were drawn mostly from literature and contained 167 specimens mainly from Western and Central European sites.

Figure 2. The cranium of Grotta d'Oriente B in norma frontalis and in norma lateralis. The scale bar is in centimetres.
Particular attention was given to include as many Italian specimens as possible, because of the geographic position of the Sicilian Mesolithic sample. The resulting data set may be affected by problems of inter-observer variability because it includes data collected by various authors. When possible, we checked for such differences by comparing values for the same specimen taken by multiple observers. Preferably, we used the values reported by the most cited authors. The entire sample was arranged into 12 groups following an archeologically based criterion (including cultural, geographical and uncalibrated chronological subdivisions (Table I; Figure 3). The full list of references for sources of metric data, chronology and cultural attribution for all the specimens can be found in D’Amore et al. (2009). The ‘Italian Late Epigravettian’ group includes 16 specimens from the Northern, Central and Southern Italian sites, as well as from Sicily, dated back to 15 000–10 000 years BP. All these specimens were considered as a single comparative group because a previous study demonstrated a close morphometric similarity among geographically separate sub-samples (D’Amore et al. 2009). This group can be considered as a Sicilian Upper Palaeolithic comparative group, which chronologically preceded the Sicilian Mesolithic group: Indeed, it also includes the San Teodoro Late Epigravettian Sicilian sample.

Table I. List of specimens arranged into the 12 prehistoric comparative groups, with abbreviations used, approximate chronological intervals (uncalibrated), and sample sizes. For references for metric data and associated absolute/relative dates and/or culture, see D’Amore et al. (2009).

<table>
<thead>
<tr>
<th>Western Europe Early Upper Palaeolithic (WEUP) (28 000–22 000 BP; n = 11)</th>
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<tbody>
<tr>
<td>Arone Candide 1, Barma Grande 1, 5, Cavigilone 1, Combe Capelle 1, Cro-Magnon 1, 2, Fanciulli 4, 5, 6, Paglicci 25</td>
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<tr>
<td>Eastern Europe Early Upper Palaeolithic (EEUP) (32 000–23 000 BP; n = 9)</td>
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<tr>
<td>Brno III, Dolni Vestonice III Kostenki 14 (Markina Gora) Mladec Predmost 3, 4, 9, 10 Sunghir 1</td>
</tr>
<tr>
<td>Italian Late Epigravettian (LEG) (15 000–10 000 BP; n = 15)</td>
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<tr>
<td>Arone Candide 2, 3, 4, 5, Ortucchio 1, Romito 2, 4, 5, 6, 7, 8, San Teodoro 1, 2, 3, Vado all’Arancio 1</td>
</tr>
<tr>
<td>French &amp; German Magdalenian (MAGD) (21 000–10 000 BP; n = 10)</td>
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<tr>
<td>Abri Pataud, Bruniquel-Abri Lafaye, Cap-Blanc, Chancelade 1, Le Bichon 1, Le Placard, Mas d’Azil, Obercassel 1, 2, Saint-Germain-la-Riviere 4</td>
</tr>
<tr>
<td>Sicilian Mesolithic (SM) (9300–8600 BP; n = 8)</td>
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<tr>
<td>Grotta d’Oriente B, Molara 2, Uzzo 1, 2, 5, 6, 7, 9</td>
</tr>
<tr>
<td>South-Central France, Corsican &amp; Alpine Mesolithic (FM) (10 000–6500 BP; n = 10)</td>
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<tr>
<td>Birsmatten-Basigrotte, Bonifacio 2, Culoz 1, 2, Gramat 1, Le Cheix 1, Montclus 1, Rochereil 1, St Rabier 5, Vatte di Zambana 1</td>
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<tr>
<td>Brittany Mesolithic (BM) (7200–6300 BP; n = 19)</td>
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<tr>
<td>Hoedic 1, 5, 6, 8, 9, Teviec 1, 2, 3, 4, 6, 7, 8, 9, 11, 13, 14, 15, 16, 18</td>
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<tr>
<td>Iberian Epi-Palaeolithic/Mesolithic (IM) (11 500–6300; n = 15)</td>
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<tr>
<td>Cabeca de Arruda 3, 6, V, Moita do Sebastiao 1, 3, 12, 19 (XVII), 20, VI (M7), XVI, Urtiaga A1, A2, B1, Roc del Migdia, El Collado 12</td>
</tr>
<tr>
<td>Southern Germany Mesolithic (GM) (7800–7400 BP; n = 12)</td>
</tr>
<tr>
<td>Hohlenstein-Stadel 1, 2, Kauftersberg, Offen-I 2, 3, 4, 8, 11, 13, 14, 15, 18, 21, 24, 25, Offen-II 2, 5</td>
</tr>
<tr>
<td>Northern Europe Mesolithic (NM) (8000–5300 BP; n = 10)</td>
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<tr>
<td>Backaskog, Bleivik, Bottendorf, Koelbjerg, Koerhuisbeek CI, Korsor Nor, Loschbour, Melby, Stora Bjers, Vedbaek</td>
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<tr>
<td>Neolithic Liguria (NEO) (7200–4500 BP; n = 30)</td>
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<tr>
<td>Arone Candide I, III, IV, V, VI, VII, XIII, T1, T2, XI, IX, VIII, X, XII, Arma del Morto II, Arma dell’Aquila II, V, Arma di Nasino 1, Bergeggi 1, I Matta 1, 2, I, III, Pollera I, VI, VIII, IV, Tara Bertrand I</td>
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<tr>
<td>Copper &amp; Bronze Age Sicily (COP/BR) (5000–3000 BP; n = 18)</td>
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<tr>
<td>Canalotto 3514A, Castelluccio 1931, 2231, 728, 729, Castiglione 726, 730, T.114-1, T.119-1, T.93-8, Chiusilla 2754, 2755, 2756, 2757, Isnello 2580, 2581, Pantalica 2225, Plemmyrion 2229</td>
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Figure 3. Geographical position of sites where sample/specimens come from, with indication of the comparative group where they have been included (see Table I for abbreviations). 1 – W: WEUP, E: EEUP; 2 – L: LEG, M: MAGD; 3 – S: SM, F: FM, B: BM; 4 – I: IM, G: GM, N: NM; 5 – N: NEO, C: COP/BR; 6 – L: Lombardy, T: Tuscany, S: Sicily, Sa: Sardinia.
We considered the cultural association of the specimens as a primary criterion, but it should be noted that the Mesolithic period cannot be univocally separated chronologically from the Upper Palaeolithic, since the oldest Mesolithic dates for certain regions overlap the most recent Epi-Palaeolithic dates from other regions. In this case, we conventionally fixed a date of 10,000 years BP (approximately at the Pleistocene/Holocene boundary) as the chronological boundary between the Upper Palaeolithic and Mesolithic groups. A similar problem concerns the separation between Mesolithic and Neolithic samples, because the neolithization process began at quite different times in diverse areas. In order to avoid controversial assemblages, our NEO group includes only individuals from different sites of Liguria, in Northern Italy, where the Early Neolithic started at ca 7200 years BP. Even in this case there may be an overlap for one or two thousand years with the Northern Europe Mesolithic period. The COP/BR group includes Sicilian individuals from both the Copper Age (ca 5000–4000 years BP) and Bronze Age (ca 4000–3000 years BP) (Di Marco 2004). This group was included in order to compare a post-Neolithic Sicilian sample, which is intermediate in age between the Sicilian Mesolithic sample and the more recent people of the island.

Contemporary samples were included in the analyses in order to provide a morphometric variation standpoint useful both to compare and to improve the reliability of the variance–covariance matrix used in the calculation of $D^2$ distances. We collected comparative data on a set of recent populations from the skeletal collections housed in the Museo di Storia Naturale, Sezione di Antropologia ed Etnologia, of the University of Florence (D’Amore et al. 2003). These samples include 214 individuals from several Italian localities: 25 male and 25 female individuals from Milan, Bergamo, Brescia, Mantova and Pavia in Lombardy; 25 male and 25 female individuals from Florence in Tuscany; 34 male and 18 female individuals from Syracuse in Sicily; and 31 male and 31 female individuals from Cagliari, Sassari, Nuoro and Oristano in Sardinia. These samples mostly date back to the 19th century AD, with some dating back to the 18th and early 20th centuries AD; furthermore, they all came from Italian sites and belong to populations that display a large amount of genetic variation (Piazza et al. 1988; Cavalli-Sforza et al. 1994).

Craniometric data

Taking into account the technique and criteria defined by the classical treatise of Martin and Saller (1957) (cf. Braüer 1988), 10 craniofacial measurements were recorded for the Grotta d’Oriente B specimen and for the comparative prehistoric and modern crania. The measurements are: Maximum cranial length and breadth, minimum frontal breadth, basibregmatic height, upper facial height, bizygomatic breadth, orbit breadth and height, nasal breadth and height. The data for OB were collected by two of the authors (L.S. and A.M.) and were checked for inter-observer variation. Mandibular measurements are not included in this study because they are less available in comparative samples. One problem in preparing the metric data was the lack of some observations among the available measurements, because of the incompleteness of certain specimens and the different lists of measurements chosen by different authors. We estimated some measurements by a visual inspection of scaled photographs and drawings of the specimens and, for the remaining missing data, we used multiple regression estimation, mainly when one or two observations, at the most, were missing from the full selected set of measures.

Sexes were pooled to increase the sample size of the smallest groups, and original metric data were size-adjusted through the Q-standardization procedure and transformed into
Mosimann shape variables (Darroch and Mosimann 1985, Jungers et al. 1995). This step eliminates problems of sexing prehistoric individuals when uncertainty can be caused by a diachronic trend toward gracilization, differentially expressed in males and females (Henke 1987; D’Amore et al. 2007). Furthermore, sexual dimorphism in shape should affect only within-population variation, and any variation due to shape sexual dimorphism should be negligible among populations (Sardi et al. 2005).

Statistical procedures

Comparative analysis between the OB specimen plus the whole Sicilian Mesolithic sample and other groups was carried out by using two different methodological approaches, named respectively as ‘model-free’ and ‘model-bound’ (Relethford and Lees 1982).

A model-free approach involves the indirect application of models of population structure in the assessment of biological differences among populations. Usually, measures of biological similarity are used to assess overall phenotypic similarity, and to reconstruct evolutionary histories of groups, without however assessing the differential role played by evolutionary parameters such as gene flow and genetic drift (Relethford and Lees 1982, p. 116).

On the contrary, a model-bound approach involves the direct incorporation of measures of population similarity into models of population structure. This approach allows the estimation of specific evolutionary parameters such as gene flow (GF) and genetic drift (GD). When using this approach in polygenic traits analysis (such as craniofacial quantitative characters), a key assumption is that phenotypic variation is stated as an estimate of genotypic variation. In addition to an equal and additive effects model, non-genetic influences are assumed to be negligible, either because they do not exist, or because they are distributed randomly throughout a region (Relethford and Lees 1982, p. 117).

Analysis by the model-free approach made use of multivariate statistical techniques such as Mahalanobis’ distance analysis (tested for statistical significance by Rao’s and Steerneman’s methods), partial Mantel test, cluster analysis (UPGMA and neighbour-joining methods), and nonmetric multidimensional scaling (MDS).

Mahalanobis’ distance analysis is based on $D^2$, a classical statistic that measures dissimilarity between objects or groups of objects starting from a set of quantitative variables (Mahalanobis et al. 1949). Unlike other distance statistics, $D^2$ takes into account correlations among variables, and is highly recommended for metric traits of the skull (Albrecht 1992; Pietrusewsky 2000; Van Vark and Schaafsma 1992).

First, $D^2$ distance was calculated in order to determine to which a priori comparative group OB specimen morphologically mostly resembles, on the basis of its lowest $D^2$ distance. At the start of this analysis OB specimen was considered ‘unknown’ or ‘ungrouped’ in respect to a priori defined groups. A $D^2$ distance between an individual specimen and a sample (a comparative group) is calculated as

$$D^2 = (X - X_j)' W^{-1} (X - X_j),$$

where $X$ is the vector of measurements for the specimen, $X_j$ is the mean vector for the sample $j$, and $W$ is the pooled within-group covariance matrix (Jantz and Owsley 2001).

Van Vark and Schaafsma (1992, p. 235) recommended including one or more large reference samples (i.e. samples that are used to obtain a better estimation of the underlying covariance matrix) in a Mahalanobis distance analysis. For this reason, we have included
large modern (contemporary) samples in the comparative analyses. We also estimated the posterior probabilities that OB specimen could fall into each one of the comparative reference samples.

Then, we calculated Mahalanobis $D^2$ distance matrix on all the a priori groups including a newly created Sicilian Mesolithic (SM) group (assembling all Sicilian specimens with OB). Rao’s method (1952, p. 245) was used in order to test for statistical significance of any $D^2$ generalized distance. Van Vark and Schaafsma (1992) consider that, in actual practice, computation of $D^2$ distance can often concern samples not very representative of their original populations. In fact, sampling effects may play a very important role, particularly if the sample sizes are small in relation to the numbers of variables, for the existing risk to lose diagnostic power, biased results, and misinterpretations (Van Vark and Schaafsma 1992, p. 228). To correct such a possible bias we calculate an unbiased estimator of $D^2$, $\Delta^2$, as follows:

$$\Delta^2 = \frac{n - k - p - 1}{n - k} \cdot D^2 - \frac{n_A + n_B}{n_A \cdot n_B} \cdot p$$

where $n$ is the total sample size, $k$ is the total number of samples involved (possibly including one or more large reference samples), $p$ is the number of variables, and $n_A$ and $n_B$ are the sizes of the samples whose $D^2$ distance is calculated.

The shortest distances resulting for SM group were analysed also by means of the ‘Steerneman test’ described in Van Vark (1984) and designed to judge whether $D^2$ generalized distances among groups are significantly different (see also Van Vark et al. 1992). The statistic

$$T = \frac{\{D^2_{A,C} - D^2_{A,B} - p(n_B^{-1} - n_A^{-1})\}}{\sqrt{D^2_{B,C} + 4n_B^{-1}D^2_{A,B} + 4n_C^{-1}D^2_{A,C}}^2}$$

was calculated, where $n$ is a group size and $p$ is the number of principal components extracted from the covariance matrix such that the power of the test is maximized (Van Vark et al. 1992, p. 403). This statistic tests the null hypothesis that a distance between a pair of groups A and B (e.g. SM and Italian Late Epigravettian) is the same as that between groups A and C (e.g. SM and French Mesolithic), the alternative hypothesis being that groups A and B are either farther apart or closer together than groups A and C. If $T > 1.96$, the distance between groups A and B is significantly ($p < 0.05$) less than the distance between A and C; the opposite if $T < -1.96$. If $-1.96 < T < 1.96$, the null hypothesis is confirmed and the two distances are not significantly different.

A Mantel test was used to assess the correlation between $D^2$ morphological distance matrix obtained for the 16 groups and the matrix of the corresponding geographic distances. A significant correlation between the two matrices is expected if the gene flow was the main evolutionary factor producing the observed pattern of morphological relationships. A standard Mantel test allows for the comparison of two matrices A and B (Mantel 1967). Since our groups are also chronologically separated, a partial Mantel test was performed in order to control for a third matrix C (i.e. a temporal distance matrix). This is achieved by regressing the elements of A and B onto C, and using the residuals from the regressions as the input for a standard Mantel test (Smouse et al. 1986). A partial
Mantel test was performed with 9999 permutations through the programme zt Version 1.1, written and kindly made available on the web by E. Bonnet.

Geographic distances $D$ between all the groups were calculated as great circles, distances in kilometres according to the formula

$$D = 2R \cdot \arctan \frac{\sqrt{\text{hav}(\theta)}}{\sqrt{1 - \text{hav}(\theta)}}$$

where $\text{hav}(\theta) = \sin^2 \frac{\delta_1 - \delta_2}{2} + \cos \delta_1 \cdot \cos \delta_2 \cdot \sin^2 \frac{\alpha_1 - \alpha_2}{2}$,

where $\alpha_1$, $\delta_1$ and $\alpha_2$, $\delta_2$ are the average latitudinal and longitudinal coordinates, respectively, for groups 1 and 2, and $R$ is the radius of the Earth (6371 km) (Ramachandran et al. 2005).

Temporal distances were obtained by calculating the difference in average dating between groups.

Cluster analysis was carried out in order to represent the pattern of numerical results of the unbiased $D^2$ distance matrix in a visually interpretable form. Two different agglomerative clustering algorithms were used: the unweighted pair-group method using arithmetic average (UPGMA) (Sneath and Sokal 1973), and the neighbour-joining (NJ) method (Saitou and Nei 1987). UPGMA method returns a dendrogram where clustering of groups reflects genetic/morphological similarity among them. The NJ method produces a tree that depicts the real phylogenetic relationships between groups. The tree does not assume an evolutionary clock but a rate of ‘minimum evolution’, and is an unrooted tree. However, when using metric data, it is advisable to state an out-group that can provide an axis of polarity and a measure of derived similarity (Lockwood et al. 2004; Schillaci 2008). For this reason we have chosen to rotate NJ by the branch shared by both Early Upper Palaeolithic groups, since these are the most ancient samples in our comparison. NJ analysis was run through Phylip Version 3.6 (Felsenstein 2004).

Multidimensional scaling (Torgerson 1952; Manly 1994) was used in order to synthesize the overall information scattered within the distance matrix in a reduced number of dimensions. These dimensions are then returned in the form of axes of variation. A plot of only two dimensions should provide a graphical visualization of the overall pattern of interrelationships between individuals or samples according to their reciprocal $D^2$ distances. A result was considered within the limits of acceptability when stress was $<0.200$ (Kruskal 1964).

The model bound approach made use of R-matrix analysis and principal coordinate analysis. An R (genetic relationship) matrix is a standardized variance–covariance matrix of population allele frequencies (Harpending and Jenkins 1973). If it is assumed that population phenotypic variances are proportional to genetic variances (Harpending and Jenkins 1973; Relethford and Blangero 1990), an R-matrix can be calculated using quantitative phenotypic traits, such as craniofacial measurements, by substituting the additive genetic covariance matrix $G$ with the product of the estimated average narrow-sense heritability $h^2$ and the phenotypic variance-covariance matrix $P$ (Cheverud 1988; Relethford and Blangero 1990; Relethford and Harpending 1994). The diagonal elements of an R-matrix, $r_{ii}$, represent the minimum genetic distance values of any population $i$ to the centroid obtained with all populations. The weighted average of all $r_{ii}$ values is a phenotypic analogue of Wright’s (1943) $Fst$, which measures the proportion of total variation and corresponds to differences among populations. Since the population samples are not contemporary $Fst$, as calculated here, cannot be considered a true measure of population structure, but rather a rough estimation of diachronic diversity, under the assumption that temporally changing selection effects are absent.
A related D (distance) matrix can be derived from an R-matrix by calculating minimum genetic distances $d_{ij}$ between any pair of populations $i$ and $j$ as

$$d_{ij} = r_i + r_j - 2r_{ij}.$$ 

R-matrix analysis was performed through the program RMET 5.0, written and kindly made available on the web by J. Relethford. The data for the 16 groups were corrected for sample size bias, and standard errors for elements of the R matrix, the distance matrix, and $Fst$ were calculated using the methods outlined by Relethford et al. (1997). An estimated average narrow-sense heritability of $h^2 = 0.55$ was assumed (Devor 1987; Relethford 1994).

A comparison of average within-group variance with the expected variance, based on the distance of each group to the centroid, was carried out in order to assess the differential amount of gene flow experienced by any group (Relethford and Blangero 1990): The greater the difference between observed and expected variances, the greater the influence of gene flow in regards to other groups.

In addition to the standard R matrix, a scaled R matrix was considered whose elements are equal to

$$g \cdot \sqrt{W_i} \cdot \sqrt{W_j} \cdot r_{ij}$$

where $g$ is the number of groups, $W_i$ and $W_j$ are the weights of groups $i$ and $j$, respectively, and $r_{ij}$ is the $ij$-th element of the R matrix. Scaling adjusts for differences in expected genetic drift and often gives a better picture of population relationships based on migration and history (Relethford and Harpending 1994; Relethford 1996). Weights are proportional to estimated population sizes. In the present study, data from census sources were used for the four recent groups; estimates in the order of $0.00183–0.02547$ people per km$^2$ were used for Upper Palaeolithic groups (Bocquet-Appel and Demars 2000; Bocquet-Appel et al. 2005); estimates in the order of $0.02–0.07$ people per km$^2$ were used for Mesolithic groups (Clark 1972); finally, estimates of $0.6$ and of $1$ people per km$^2$ were used for Neolithic and Copper/Bronze Age groups, respectively (McEvedy and Jones 1978; Ammerman and Cavalli-Sforza 1984; Cavalli-Sforza et al. 1994; Zimmermann et al. 2009). Effective population size was calculated using the geographical area (as surface in km$^2$) covered by the present-day nation (or region) where the sample/specimens’ sites are located. We assumed that such an approximation could not be so far from the reality, since the greater land exposure caused by low sea levels during Late Pleistocene and Early Holocene, might be counterbalanced by the extent of inhabited environments.

Finally, a principal coordinate analysis (Gower 1966) was performed on both the R matrix and the scaled R matrix. Like MDS, this method synthesizes the pattern of distances in a reduced number of dimensions, i.e. the first two principal coordinates. Following Harpending and Jenkins (1973), each eigenvector was scaled by the square root of its corresponding eigenvalue.

Results

*Comparative morphometric analysis by model-free approach.*

Results of the $D^2$ distance analysis (Table II) showed that OB, when analysed as an ungrouped case, produced the shortest distance ($D^2 = 9.060$) and the higher posterior
probability \( (p.p. = 0.338) \) in the comparison with the Sicilian Mesolithic group. It also produced a \( p.p. = 0.172 \) in the comparison with the Magdalenian Upper Palaeolithic group, and a \( p.p. = 0.111 \) in the comparison with the Northern Europe Mesolithic group. Any other \( p.p. \) value resulted absolutely lower.

The unbiased \( D^2 \) distance matrix calculated over the 16 comparative sample groups, showed (Table III) that SM group taken as a unit (OB specimen included) had their shortest distance values from Italian Late Epigravettian group, followed by Magdalenian, French Mesolithic and Northern Europe Mesolithic groups. All these distances were statistically significant (0.05 level), as were all the distances between SM and the other non-recent groups. SM group had its greatest distance values from the four recent groups, with the exception of the modern Sicily group.

The Steerneman statistic was computed in order to test if the distance between SM and Italian Late Epigravettian groups \( (D^2 = 3.337) \) was significantly different from that between SM and Magdalenian groups \( (D^2 = 3.991) \), from that between SM and French Mesolithic \( (D^2 = 4.035) \), and from that between SM and Northern Europe Mesolithic \( (D^2 = 4.240) \), respectively. It was \( T = 0.410 \) in the case of the first comparison, \( T = 0.411 \) in the case of the second comparison, and \( T = 0.497 \) in the case of the third comparison, implying that SM and Italian Late Epigravettian (LEG) groups are not significantly more similar to each other than SM and MAGD, or than SM and FM, or than SM and NM (at the 0.05 level). On the contrary, when we test if the distance between SM and Italian Late Epigravettian groups was significantly different from, for instance, that between SM and WEUP groups \( (D^2 = 8.707) \), or from that between SM and EEUP \( (D^2 = 10.010) \), or from that between SM and Iberian Mesolithic \( (D^2 = 10.059) \), we obtain \( T = 2.236 \), \( T = 2.369 \), and \( T = 2.688 \), respectively, implying that SM and Italian Late Epigravettian groups are significantly more similar to each other than SM and WEUP, or than SM and EEUP, or than SM and IM (at the 0.05 level of significance).

A partial Mantel test on morphological and geographical distance matrices (controlling for temporal distances) for all the 16 groups, resulted in a correlation coefficient \( r = -0.059 \), with \( p = 0.362 \), indicating that gene flow was not the main factor producing the pattern of
Table III. Unbiased $D^2$ distance matrix for 16 groups. Non-significant distances (at the 0.05 level) for Rao's (1952) method are in bold. See Table I for abbreviations.

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Mesolithic human remains from Favignana, Sicily
morphological similarity and that morphological variation among groups is not distributed according to a simple model of isolation-by-geographic distance. But, a partial Mantel test calculated on a subset of morphological distance matrix, including Late Upper Palaeolithic and Mesolithic groups, produced a statistically significant result, with $r = 0.519$, and $p = 0.018$, re-proposing the gene flow as the major mechanism influencing the variation among these groups, in accordance with a model of isolation-by-geographic distance.

Cluster analysis on the unbiased $D^2$ distance matrix by the UPGMA method produced a dendrogram (Figure 4A) in which the first knot is between prehistoric and recent groups with the exception of Sardinia. The more ancient branch was in turn subdivided into earlier (WEUP plus EEUP) and later prehistoric groups; the other branch depicted a pattern of variously mixed relationships among late Upper Palaeolithic, Mesolithic and more recent prehistoric groups, with tight links between the recent Sardinians and the Neolithic sample.

![Dendrogram](image)

**Figure 4.** Cluster analysis on the 16 × 16 unbiased $D^2$ distance matrix. (A) Dendrogram by UPGMA method; (B) phylogenetic tree by NJ rooted by the branch shared by both early Upper Palaeolithic groups.
from Liguria, and between the FM and BM groups. The SM group remained close to LEG, but the latter one was linked firstly to NM.

Clustering by NJ resulted in a tree (Figure 4B) where FM and BM separated first, after the root formed by both the WEUP and EEUP groups. The successive bi-partition patterning of the remaining groups distinguished late Upper Palaeolithic plus Mesolithic groups on one side, from more recent groups on the other side, with the notable exception of IM, which joined the more recent branch as a sister group. In this phylogenetic analysis, LEG and SM tied tightly to each other before joining the other late Upper Palaeolithic and Mesolithic groups.

A two-dimensional plot (Figure 5) was obtained by applying the multidimensional scaling (MDS) method to the 16 × 16 unbiased $D^2$ distance matrix. The resulting stress was 0.098. A separation between chronologically earlier and later groups was observed in the virtual ‘morphospace’ delimited by dimensions 1 and 2. The left half of the plot contained Upper Palaeolithic and Mesolithic groups, with earlier EEUP and WEUP restricted to a more peripheral position in the lower quadrant. The SM group was positioned in the upper left quadrant not far from the Italian Late Epigravettian group, but it was also very close to the Northern Europe Mesolithic group. Other adjacent groups of this area of the plot were GM, MAGD, FM and BM.

Comparative morphometric analysis by model-bound approach.

R-matrix analysis for all 16 groups, based on the 10 (size-adjusted) craniofacial traits, produced an unbiased estimate of $F_{st} = 0.103$, with a standard error (SE) = 0.008. Such an estimate is very close to other estimates for a worldwide population structure obtained with an assumed average narrow-sense heritability $h^2 = 0.55$ [e.g. $F_{st} = 0.246$, SE = 0.004 (Schillaci 2008), $F_{st} = 0.144$, no SE given (Relethford 1994), $F_{st} = 0.149$, SE = 0.001

Figure 5. Plot of dimensions 1 and 2 from MDS on the 16 × 16 unbiased $D^2$ distance matrix. See Table I for abbreviations.
(Sardi et al. 2005)], but often with a much larger set of craniofacial traits. Different subsets selected out of the original 16 groups produced different estimates of $F_{st}$ (SE): 0.106 (0.022) for the four Upper Palaeolithic groups, 0.117 (0.015) for the eight late Upper Palaeolithic plus Mesolithic groups, 0.162 (0.020) for the six Mesolithic groups, and 0.085 (0.008) for the four recent groups. These results suggest different levels of among-group variation in relation to the chronological dispersion.

An average within-group variance of 0.725 was obtained from the R-matrix analysis of the 16 groups. Comparison of observed within-group phenotypic variance for each group with the corresponding distance $r_{ii}$ to the centroid, is presented in the plot of Figure 6, where the line represents the expected variance based on the distance $r_{ii}$ assuming a balance between gene flow and genetic drift (Relethford and Blangero 1990; Sardi et al. 2005).

In fact, under this condition of balance, the distinctiveness of a population is inversely related to its phenotypic variance, and the expected variance can be calculated by the application of a multivariate extension of the Harpending–Ward model (Relethford and Blangero 1990).

The wide difference between observed and expected variances for Upper Palaeolithic and Mesolithic groups suggests that they probably underwent a greater gene flow compared to the other groups, producing a much greater amount of within-group phenotypic variation. Difference between observed and expected variances decreases from early Upper Palaeolithic groups to late Upper Palaeolithic groups, to Mesolithic groups; however some groups (i.e. MAGD, BM and, above all, IM) show a smaller difference in comparison with the other coeval groups. This could result from a greater role played by gene flow in the cumulative effect with genetic drift, or, more simply from a sampling effect. The proximity between WEUP and EEUP, and the clustering of the Mesolithic groups on one side and of the more recent groups on the other appear evident.

Figure 6. Plot of observed within-group phenotypic variance versus morphological distance $r_{ii}$ from the centroid for the 16 groups. The line indicates the regression line for expected within-group phenotypic variance according to the model described in Relethford and Blangero (1990). See Table I for abbreviations (Lomb., Lombardy; Tusc., Tuscany; Sard., Sardinia).
The D distance matrix derived from R-matrix (not shown) produced the following vicinity values for the Sicilian Mesolithic group: 0.393 from LEG, 0.428 from FM, 0.446 from MAGD, 0.515 from GM, 0.556 from BM, 0.761 from NM, and 0.872 from WEUP. These results are not dissimilar to that proposed by the $D^2$ distance matrix.

Principal coordinate analysis applied to the R-matrix produced two eigenvectors (scaled by the square root of their eigenvalues) plotted in Figure 7A. As can be seen, the resulting pattern of morphological relationships appears very similar to the pattern displayed by the MDS of Figure 5, with the Sicilian Mesolithic group appearing close enough to the Italian Late Epigravettian LEG group. But SM was closer to both the NM and GM groups than to

Figure 7. Plot of first two scaled eigenvectors from principal coordinate analysis: (A) on the 16 x 16 R-matrix (first two eigenvectors account for 74.3% of the variation); (B) on the 16 x 16 scaled R-matrix (first two eigenvectors account for 82.5% of the variation), full circles without labels mark the 12 prehistoric groups; (C) on the 8 x 8 scaled R-matrix of late Upper Palaeolithic plus Mesolithic groups only (first two eigenvectors account for 64.7% of the variation). See Table I for abbreviations.
LEG, and anyway it was also not far from MAGD, FM and BM, so giving a somewhat confusing picture of its relationships.

In order to obtain a clear picture of the overall relationships among groups, a scaled R matrix was calculated by adjusting for possible differences in expected genetic drift (Relethford and Harpending 1994; Relethford 1996). Weights for groups were proportional to the estimated population sizes described in the Methods section. The plot of the first two eigenvectors obtained by scaled R-matrix (Figure 7B) presented a picture where all the prehistoric groups appeared in close proximity with each other, whereas the four recent groups revealed a major differentiation. This result suggests that the clear-cut separation between more ancient and more recent groups, and the high among-group variation observable in prehistoric groups, could be actually the product of genetic drift acting in condition of low population size. Therefore, a principal coordinate analysis was performed on the scaled R-matrix of the eight late Upper Palaeolithic plus Mesolithic groups only, in order to assess their true relationships after removing the effect of the drift. The first two eigenvectors produced the plot presented in Figure 7C. Here, the close relationship between LEG and SM appeared much clearer. The proximity between LEG and MAGD on one side, and between FM and BM on the other, appeared also evident, as well as the more distant position assumed by GM, NM and, above all, IM.

Discussion

A basic interpretation of the first peopling of Sicily, starting from the first certain evidence of anatomically modern Homo sapiens at San Teodoro (Late Epigravettian 14.800 BP) considers an east–west, and an east–south migration along ecologically sustainable coastal lines that distributed the Epigravettian peoples throughout the island (Mussi et al. 1989; Guidi and Piperno 2005). Sicily is a large island with a complicated internal orography, and a central area characterized by evaporite rocks of Messinian origin (from the Miocene Salinity Crisis). These features affected the prehistoric differential distribution of people along the coasts, with sporadic evidence of colonization of internal areas, suitable for hunting and gathering.

Early Holocene Mesolithic hunter–gatherers could be the result of local evolution of Palaeolithic individuals who migrated to the island during the Late Pleistocene or be the fruit of the overlapping of different and more recent migrations. In the first case Palaeolithic gene flow from the Italian peninsula could have been the primer of human distribution on the island, producing a relatively uniform local characterization, as a result of similar ecological scenarios. Palaeolithic hunter–gatherers could represent the effective genetic base of ancient Sicily while Mesolithics represent a cultural transition. In the second case a relatively different gene flow (Mesolithic) could have contributed different people, their evolution inside the island having been shaped by the same ecological pressures.

Cranial morphometry and statistical multivariate approach are considered a valuable tool to investigate phylogenetic relationships in human populations (D’Amore et al. 2009).

The cranial specimen of a Mesolithic individual from Favignana island (Egadi archipelago, Western Sicily) gave us the possibility to test different hypotheses on the ancient peopling of Sicily.

Favignana is now a small carbonatic island on the Trapani coast. At the glacial peak (18 000 years BP) it was at the end of a peninsula starting from the western carbonatic plateau of the region; this geographical situation could have been favourable for seasonal visiting, and presumably Palaeo-Mesolithic populations travelled intensively in the area. Furthermore, the Uzzo and S. Vito lo Capo archaeological contexts (Piperno
1985; Martini et al. 2006a), and surface findings of lithics from Monte Speziale, and Monte Passo del Lupo (L. Sineo, unpublished data), clearly indicate that this part of Sicily became an area of regular occupation during the Mesolithic period.

The Grotta d’Oriente in the island of Favignana was presumably used as a burial site in the Upper Palaeolithic and Mesolithic periods. In fact the site produced three individuals with different chronological ages (Martini et al. 2006c; Di Salvo et al. 2008), and archaeological evidence of seasonal living. Our attention was focused on the individual identified as Oriente B (OB) because of skeletal completeness and cranial integrity.

OB is a Mesolithic individual according to a direct dating of 9338 years BP (M. Mannino and M. Richards, personal communication) and a previous indirect dating, based on accompanying gastropods, that positioned the OB within a younger Mesolithic interval of 8740–8390 years BP.

The short $D^2$ distance obtained in this work in comparison with other Sicilian Mesolithic individuals, portrays OB as a typical representative of a Sicilian Mesolithic population.

Considering the proximity indicated by the Mahalanobis test, and in order to obtain a numerically more evident ‘Sicilian’ sample, we created a Sicilian Mesolithic (SM) grouping. This grouping, containing the OB individual, demonstrated a close morphological relationship with a broad Late Palaeolithic–Mesolithic Western and Central European continental stock (Late Epigravettian, Magdalenian, and Southern French and German Mesolithic samples); this could be a result of a continental Europe origin of the Epigravettian peoples of prehistoric Sicily, that evolved, in demographic continuity, into the Mesolithic population. This does not imply that Sicily became an isolated population cluster: Gene flow from the Italian peninsula was presumably frequent, and probably contributed actively to cultural transition. Mesolithic Italy itself presumably received repeated gene flow from continental Europe, but unfortunately we are not able to compare Mesolithic Sicily with Mesolithic Italy, because a continental Italian Mesolithic comparative sample is unavailable at the present.

The diffusion of Late Epigravettian lithic industry in Sicily starting 15 000 years BP may indicate a significant increase in population size (a demographic event usually acknowledged for the period after the end of Last Glacial Maximum; Gamble et al. 2006). Indirect (based on mitochondrial molecular clock) evidence indicates that in the Late Upper Palaeolithic, Europe experienced a pulsating demographic increase (Bocquet-Appel et al. 2005). Interestingly, this demographic explosion coincided with the Würm glacial peak and could relate to the increase and successive release of humanity from glacial refuges. The morphological uniformity of Upper Palaeolithic peoples could have not only an ecological explanation but also a genetic explanation after a bottle-neck event. Henke (1989) asserted that the craniofacial morphological homogeneity detected for Upper Palaeolithic and Early Mesolithic European populations was caused by long-distance high gene flow between different groups. Intensive gene flow might have been necessary among prehistoric bands to avoid extinction because of low population density (Bocquet-Appel 1985; Bocquet-Appel et al. 2005); in addition, mobility was the preferred solution to local resource scarcity.

According to bio-archaeological evidences, prehistoric European populations might have had a low population density. Archaeological testing for physical evidence of a hypothesized population increase in the Late Pleistocene period is challenged by the visibility of the sites, the recovery techniques, and errors in estimating the number of humans at a given time (Bar-Yosef 2001). The final part of the Pleistocene and transition to the Holocene period was characterized by increasing climate stability that created opportunities for hunter-gatherer groups distributed in the Italian peninsula (and appendices) to cyclically occupy areas in a move towards a mobile-forager/semi-sedentary ecology.
Population estimates for late Mesolithic period are in the order of 0.02–0.07 people per km² (Clark 1972, quoted in Cavalli-Sforza et al. 1994). Our data, having indicated morphometric resemblances among all Mesolithic samples from various geographical areas, and the results of a partial Mantel test applied to Late Upper Palaeolithic and Mesolithic groups, are in good accordance with a hypothesis of a large-scale gene flow network between numerically limited groups. In fact there is neither evidence nor a hypothesis of an initial higher population density in Sicily and our results prove that gene flow with the populations of the Italian peninsular was not rare during the last part of Late Pleistocene. But population pressure in southern regions (a sort of release of isolation) could have been intense at the end of glacial peak. In our opinion, in the Final Pleistocene period, crossing the Strait of Messina to reach Sicily did not represent a problematic task for humans. The Strait of Messina during the late Glacial period was geologically very different. Evidence indicates that the sea level was nearly 90 m lower than the present day, and a large emerged ridge connected the plateau of Calabria to the Ionic coast of Sicily (Antonioli et al. 2006a,b). The possibility of this overland passage persisted even later. A thin sea corridor was present, and the sea level from about 13 000–11 000 years BP was presumably 50 m lower than the present situation. Moreover, we know that humans were potentially able to develop a nautical technology to cross substantial stretches of open sea, at least since the time when they colonized Australia, roughly 60 000 years ago (Roberts and Jones 2001).

Late Epigravettian people colonized the Tyrrhenian coastal sites in an ecologically dynamic period, and might have faced rapid and drastic ecological changes. In the last Würm stadial (between 13 000 and 10 000 years BP) the area was characterized by a cool and arid climate (Older Dryas stadial period – s.p.), with a steppe-like ecology (Zanchetta et al. 2006), followed by a progressive appearance of trees (Bolling – s.p.) and then by transition towards a wooded ecology (Allerød – s.p.), and finally to a new arid steppe appearance (Younger Dryas – s.p.). Consequently, the Sicilian Mesolithics, who lived during the first stage of the postglacial (Boreal) in the Early Holocene (between 10 000 and 8000 years BP), experienced ecological changing conditions characterized by increasing average temperatures and aridity of the climate, with repercussions on faunal representation and human foraging that has been well interpreted in Uzzo archaeology (Piperno 1985).

We have made evaluations on population density and population size in order to assess the possible role of drift in shaping marginal groups. Further analysis in order to define the role of gene flow and genetic drift indicates that Mesolithic humanity maintained a high rate of gene flow with the effect of a relevant uniformity, with the exception of IM. The tendency of IM (already demonstrated with MDS) is the response to a drift of this group. The different position in the morphospace of MDS of strictly related NEO/Copper/Bronze humanity, indicates that, on the contrary, the divergence of these groups is constructed from successive and different population contributions, and presumably on a higher population size. Mesolithic homogeneity can be explained to a certain degree by gene flow (Figure 6; Figure 7A,C). The OB sample demonstrates its relationship to the LEG group, and to the European Mesolithics; the Sicilian Mesolithics, demonstrate in all the approaches a strong relationship with the core of the Italian Late Epigravettians. This could be the consequence of coalescence related to the late colonization of the island – that different evidences indicate to be not earlier than 18 000–14 000 BP.

The spreading of hunter–gatherer groups not maintaining a high gene flow could lead to the genetic drift phenomena and a geographical clustering. In fact, genetic drift is the major course of differentiation between populations. It is a phenomenon that assumes great...
importance in small reproducing groups, such as in prehistoric times. In a condition of
drift the transmission of traits is a random process, leading to the rapid
fixation of characteristics.

The gene flow–driven clustering of Prehistoric samples, in contrast to modern comparative
samples, is evident (Figure 7B). This comparison puts in evidence the issue of the dimension
of populations. Modern samples, deriving from large populations, historically shaped in their
genetics, have high variability and appear differently clustered to the periphery of the
distribution.

Palaeo-Mesolithics are morphologically conservative in the entire European sample
analysed (Figure 7), but the principal coordinate analysis confirms their relative relationship
as previously indicated by MDS. After performing the gene flow/drift test the Sicilian
Mesolithics still remain strictly related to LEG and to a more ancient continental group of
the Magdalenians, thus indicating a cline continuity that ties together Central Europe, the
Italian Peninsula and Sicily. Other Mesolithics, geographically isolated in Brittany, Spain,
Germany, Northern Europe and France, appear to be definitely different.

On the other hand, all analysis indicates the beginning of a regional characterization,
probably influenced by drift, that is suggested by the greater morphological resemblance
between Late Epigravettians and Mesolithic Sicilians.

Conclusions

Different evidences suggest that the settlement of Sicily started only in the last part of
Pleistocene period, during the diffusion of Late Epigravettians. This period, distinguished by
the increasing size of hunter–gatherer populations after the end of Last Glacial Maximum,
was still characterized by a relatively low population density and gene flow rate. Continuous
gene flow probably caused the overall morphometric homogeneity between European
human bands that can be seen in this analysis.

The results of the comparative morphometric analysis of OB individual, and the Sicilian
Mesolithic sample, demonstrate both a continuing gene flow – indicated by the morpho-
logical resemblance between European Late Epigravettians and Mesolithic Sicilians – and
the beginning of a regional characterization, presumably as a consequence of a progressive
reduction of gene flow among populations with a new level of social organization. The
Mesolithic transition could have been the engine for a progressive increase of a sedentary
and a short-lived local typology. Overall, bio-archaeological evidence from several European
sites reveals a significant increase in population density for the entire Mesolithic period. This
was connected to a transition in social complexity that led to a progressive change in the level
of social organization, from band level to an incipient tribal level, with the development of
more frequent endogamy, a decrease in mobility and an increase in cultural regionalization
(Constandse-Westermann and Newell 1989). This was plausibly the case also for the Sicilian
Mesolithic populations.

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All authors contributed to the research: G.D. planned and performed statistical analysis; R.D., A.M. and L.S. performed skeletal analysis and collected measures and anthropological parameters; G.D., S.D. and L.S. analysed data; G.D. and L.S. designed the research and wrote the paper.

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