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A Regional Biological Approach to the Spread of Farming in Europe

Anatolia, the Levant, South-Eastern Europe, and the Mediterranean[1]

by Ron Pinhasi and
Mark Pluciennik

This article examines the potential contribution of archaeological human skeletal material, in particular craniometric data, to interpretations of the nature of the transition to farming in Europe. The material is discussed particularly in relation to recent debates about demographic variables and processes and modern genetic frequency patterns. It is suggested that biological morphometrics enables the comparison of ancient populations on a regional basis. Analysis of the material suggests that there was considerable morphological heterogeneity among the earliest farmers of the Levant belonging to the Pre-Pottery Neolithic but that similar variability is generally not seen among the earliest mainland agriculturalists of south-eastern Europe. We propose that this may be explained by the existence of a genetic "bottleneck" among Anatolian populations and that it supports models of the largely exogenous origin of many early Neolithic populations in this region. Regional comparisons further demonstrate a biologically more complex relationship between Mesolithic and Neolithic populations in the central and western Mediterranean. The regional and chronological variability of transitions to farming is stressed, and it is pointed out that different techniques highlight different aspects of the processes involved at a range of scales and resolutions.

Ron Pinhasi is Lecturer in the School of Life and Sport Sciences, University of Surrey Roehampton, West Hill, London SW15 2SN, U.K. [r.pinhasi@roehampton.ac.uk]). Born in 1968, he was educated at Simon Fraser University (B.A., 1996), Katholieke Universiteit Leuven (M.A., 1997), and Cambridge University. He has published "A New Model for the Spread of the First Farmers in Europe" (*Documenta Praehistorica* 30), "A Biometric Study of the Affinities of Nazlet Khater: A Quantitative Analysis of the Mandible Dimensions," in *Palaeolithic Living Sites in Upper and Middle Egypt*, edited by P. M. Vermeersch (Leuven: Leuven University Press, 2003), and, with R. Foley and M. M. Lahr, "Spatial and Temporal Patterns in the Mesolithic-Neolithic Archaeological Record of Europe," in *Archaeogenetics*, edited by C. Renfrew and K. Boyle (Cambridge: McDonald Institute, 2000).

Mark Pluciennik is Director of Distance Learning and Lecturer in Archaeology at the University of Leicester (University Road, Leicester LE1 7RH, U.K. [m.pluciennik@le.ac.uk]). Born in 1953, he was educated at the University of Sheffield (B.A., 1989; Ph.D., 1994). His publications include "Radiocarbon Determinations and the Mesolithic-Neolithic Transition in Southern Italy" (*Journal of Mediterranean Archaeology* 10:115–50), "Deconstructing the Neolithic in the Mesolithic-Neolithic Transition," in *Understanding the Neolithic of North-Western Europe*, edited by Mark Edmonds and Colin Richards (Glasgow: Cruithne Press, 1998) and "The Invention of Hunter-Gatherers in Seventeenth-Century Europe" (*Archaeological Dialogues* 9[2]: 98–151).

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Recent interpretations of the Mesolithic-Neolithic transition have tended to be polarized between two dominant models. One is that of the dispersion of farmers into Europe, in which expanding Near Eastern populations replaced local hunter-gatherer bands with only a minimal-to-moderate amount of admixture. Although this model was long accepted for the "Danubian" Neolithic cultures of central Europe (e.g., Childe 1925; Clark 1965*a*, *b*; Piggott 1965), Childe especially was happy to accept a variety of possible modes of transition for Europe more generally (see Pluciennik 1999:662). However, this broadly culture-historical model was generalized by Ammerman and Cavalli-Sforza (1971, 1973) in proposing what is known as the "wave-of-advance" model, which suggested a gradual process of population expansion of farming communities northwards and westwards. The basic contention of this model was that the demographic profile of farming populations differed from that of hunter-gatherers. Population growth resulted in the expansion of local populations in all directions and at a relatively steady rate. Support for this model was based on archaeological, chronological, and geographic-distance data, and diffusion rates were calculated on the basis of geographic distances and radiocarbon dates. Subsequently, mainly genetic data were used to support arguments for this putative population expansion (e.g., Ammerman and Cavalli-Sforza 1984; Sokal, Oden, and Wilson 1991; Barbujani, Bertorelle, and Chikhi 1998; Cavalli-Sforza, Menozzi, and Piazza 1993, 1994). The strongest adherents of this view have been Renfrew (1992, 1996) and Cavalli-Sforza (1996), who have also suggested strong correlations between linguistic patterns (e.g., Indo-European language families), modes of subsistence, and modern distributions of genetic traits.

The second approach views the transition rather as a sociocultural process in which the process of Neolithization involved not so much large-scale population changes (through whatever mechanism) as the diffusion of knowledge, resources, technology, and other practices through a variety of processes. The spread of farming is seen as often gradual and not necessarily resulting in a radical break in the mobile hunting-foraging lifestyle

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(Dennell 1983:170–89; 1985; Whittle 1996, 1997). This availability-substitution-consolidation model, proposed by Zvelebil and Rowley-Conwy (1984, 1986; Zvelebil 1986), views the transition to farming as occurring at different rates and in different ways in the various regions of Europe and envisions biological and cultural continuity from the Mesolithic to the Neolithic in many areas of Europe. Archaeologists who support this model provide evidence which suggests continuity in material culture and other practices and emphasize the economic, technological, and cultural complexity of many Mesolithic societies (Zvelebil 1989, 2000; Price 2000*a*).

Zilhão (1993, 2000, 2001) has proposed a hybrid model according to which the spread of Neolithic lifeways across Europe was a punctuated process with two main pulses. The first, beginning around 6,800–6,400 uncal bp, is characterized by the spread of farming along a Danubian and a Mediterranean route. According to Zilhão the spread of farming along the first was rapid and involved the absorption of local Mesolithic groups. In sharp contrast, the spread of farming along the Mediterranean coasts was slower because of the predominance of hunter-gatherer groups in these regions. As a result, hunter-gatherer bands and a more mobile settlement system persisted along the western Mediterranean shores. This pulse of "enclave colonization" by farmers was followed by the establishment of well-defined boundaries between Mesolithic and Neolithic groups. Subsequently, a second pulse occurred after 6,000–5,500 uncal bp in which agro-pastoral economies reached northern Iberia, western France, the Low Countries, the British Isles, and Scandinavia. The spread of farming in these regions is argued to be the result of the adoption of these practices by local hunter-gatherer groups rather than an incoming wave of farmers.

There are other variants, such as van Andel and Runnels's (1995; see also Runnels and van Andel 1988) suggestion of Neolithic farmers' seeking suitable areas for "cash crops" and participating in planned colonizations of parts of Greece and Italy. However, it is fair to say that in the past five years the developing consensus among archaeologists is that the processes of transition are best described at the regional level and varied widely in context, nature, tempo, and timing across Europe (cf. Gkiasta et al. 2003). Reflecting this shift, the word "mosaic" has increasingly been invoked to describe this perceived variation (Tringham 2000:53). So far, however, little has been done in terms of comparative physical anthropology in relation to these debates (but see Lalueza Fox 1996, Jackes, Lubell, and Meiklejohn 1997*a*, and [for Iberia] Lalueza Fox and González Martín 1998). In general, genetic data are of insufficient resolution to address these issues at the regional level (but see, e.g., Bertranpetit and Cavalli-Sforza 1991). In this article a novel synthesis of biological morphometric data is analysed at the regional and interregional levels in order to address and discuss its implications for the models described above. Ultimately, the assessment of biological similarities and admixture between "hunters" and "farmers" requires the development of better understanding of morphological or other variability among all past populations.

A Regional Approach

Settlement pattern analysis was used to estimate past demographic processes of Neolithic expansion by region (Pinhasi, Foley, and Lahr 2000). *Inter alia*, analysis of the archaeological data indicates a rapid appearance of the first Neolithic occupation sites north-westwards from Anatolia into south-eastern and central Europe during the Early Holocene, from ca. 8,000 uncal BP. Subsequent dispersions of Early Neolithic occupation continued westwards and northwards largely along the main river valleys of central Europe. On the basis of these findings, a regional approach has been developed and applied to the craniometric analysis of Mesolithic and Neolithic populations. This approach emphasizes the need to examine the Mesolithic-Neolithic transition as a series of region-specific cases and a set of historical processes rather than a single generic episode (Lahr, Foley, and Pinhasi 2000).

The placement of a given specimen in a particular region was based solely on the geographic location of its associated site. The regions were defined according to a combination of geographic and archaeological criteria (archaeological cultures such as Linienbandkeramik [LBK], Impressed Ware, and the like). This regional scheme is an elaboration of similar divisions adopted in the archaeological literature (e.g., Whittle 1996). Regions 1, 5, and 6 are examined here (fig. 1). Region 1 (Turkey and the Levant) includes the place of the origins of Eurasian farming. Region 5 (south-eastern Europe) is where the earliest European Neolithic farming sites occur. Region 6 (Mediterranean Europe) is the Mediterranean zone from Greece to the Iberian Peninsula. The study of these regions thus provides an in-depth inspection of the earliest phases of the Neolithic transition in Europe. Full discussion of central and northern Europe (regions 2–4) would require more space than is available here, and for regions 7 and 8 the collection of more data will be necessary.

The skeletal data derive from fieldwork by RP, from the literature, and from the ADAMS database at the Department of Anthropology, University of Geneva, Switzerland (table 1). The sites that produced the specimens studied are depicted in figure 2. A certain degree of measurement bias in the ADAMS database due to interobserver error is to be expected given that it was compiled from various published sources and collected by different anthropologists over a period of 100 years. Nevertheless, previous analyses (Pinhasi 1996, 1998; Pinhasi, Foley, and Lahr 2000) indicate that it is possible to perform univariate and multivariate operations on data from a variety of sources and obtain meaningful results (see also Keita 1990, 1992). The number of specimens discussed from the three regions totals 231.

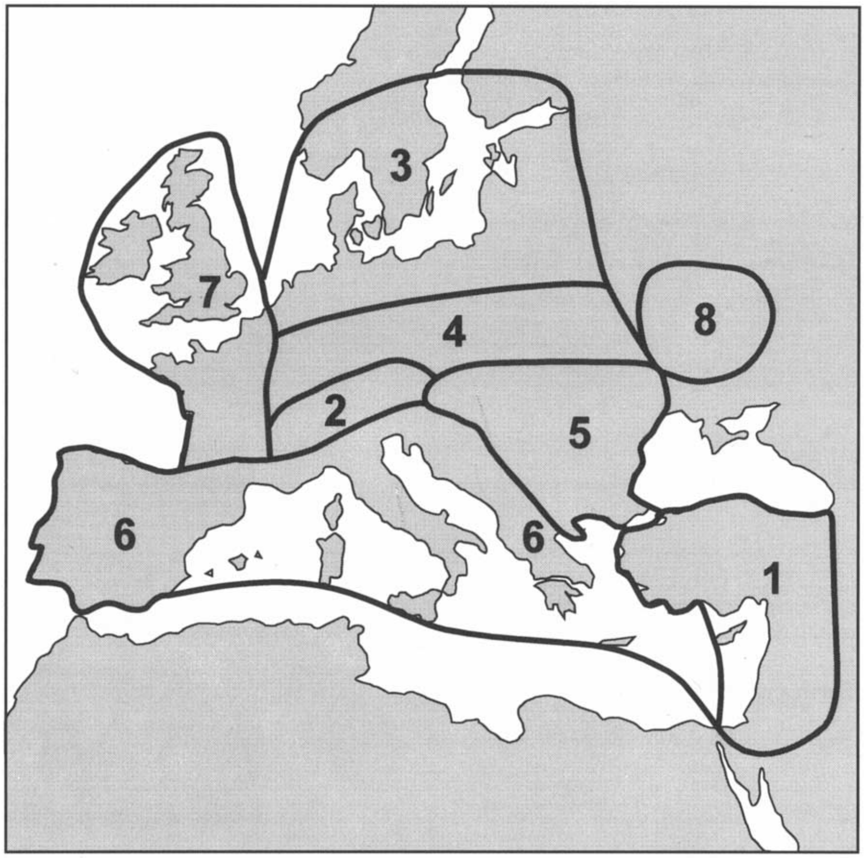

FIG. 1. *Geographical-archaeological regions.*

The Construction of Groups

Experience indicates that the pooling of specimens to form meaningful groups has a significant effect on the statistical results obtained. For this reason and others (see below) the chosen method of analysis was principal components analysis (Tabachnick and Fidell 1996). This method does not require any a priori criteria regarding the allocation of specimens to groups, and consequently the grouping criteria have no effect on the performance of the statistical analysis. In contrast, discriminant analysis requires the a priori allocation of specimens to defined groups. Groups therefore contain either specimens from a single location and archaeological period or specimens from several sites within the same archaeological period. The pooling of these specimens is based on previous analyses of Mahalanobis generalized distances as well as on the analysis of means and post-hoc analysis of variance. A selection of cranial and mandibular measurements was used (table 2). In addition, an analysis was performed on dental dimensions of specimens from region 1—the mesio-distal and bucco-lingual dimensions of the lower left canine, the first and second premolars, and the first, second, and third molars.

Missing Data and Interpolation

Neolithic crania are rarely complete. In many areas soil conditions do not favour the preservation of bony material. Thus, good series from the Neolithic period are rare in regions including Israel, Bulgaria, and Greece, and, when present, only a few single specimens have more or less complete crania. Differential preservation occurs because of physical variation among bones: parietal bones and frontal bones are usually preserved while occipital and cranial bases are often missing. Consequently, there is a systematic pattern of missing data. In most cases a specimen that is missing the cranial base is also missing some of the occipital, and the palate is disconnected. Thus high correlations exist between certain missing sets of variables (table 3). Between 30% and 40% of the specimens are missing facial dimensions and cranial height because of poor preservation.

There are several ways to treat the problem of missing data. One is to choose a small subset for which the percentage of missing data is small. Another method, commonly used for multivariate procedures, is to discard all cases for which data for one or more cells are missing. This option, however, will usually result in too small a

TABLE 1
Groups Examined by Region

Groups	Sites	*N*	Date	Period	Source/
Region 1					
Natufian	Ain-Mallaha (Eynan), Erq-El-Ahmar, Fallah (Nahal Oren), Hayonim	18	11,000	Epipalaeolithic	2
Cyprus	Khirokitia	22	7,350	PPN	1
Levant	Jericho	9	–	PPNB	2
Levant	Abu Hureyra	5	10,790	PPNB	5
Anatolia	Çayönü	8	9,360	PPNB	3
Levant	Basta	3	–	PPNB	4
Anatolia	Çatal Höyük	49	7,499	Neolithic	Ferembach (1982)
Region 5					
Greek Mesolithic	Franchthi Cave, Theopetra	5	–	Mesolithic	1, 10
Danube Gorge Mesolithic	Lepenski Vir, Vlasac	8	7,500	Mesolithic	1
Karanovo	Anza, Kasanlak, Karanovo, Jasa Tepe	7	6,500	Karanovo 1, 2	1
Körös	Deszk-Olajkut, Hódmezővásárhely, Kotacpart, Vészto-Mágori, Endröd	19	6,400	Körös	7, 8
Criş	Deszk, Gura Bacului, Sf. Gheorghe	5	6,650	Criş	1
Greek Neolithic	Theopetra, Devetaškata Peštera, Athens, B'Koybeleiki, Greek Neolithic (unknown location)	10	–	Early Neolithic, Middle/Late Neolithic	1, 10
	Nea Nikomedeia	13	8,180	Early Neolithic	1
Starčevo	Starčevo, Vinca, Lepenski Vir	10	–	Starčevo	1
Romanian Neolithic	Tîrpesti	2	6,240	Gumelnitsa	6
Region 6					
Mediterranean Mesolithic	Arene Candide, Ortucchio, San Fratello, San Teodoro	9	12,000	Mesolithic/Final LUP	1
Mediterranean Neolithic	Condeixa	20	–	Cardial	1
Mediterranean Neolithic	Finale Ligure, Salces, Arma dell'Aquila, Grotte Sicard, Maddalena, Abri de Pendimoun, Castellar	9	–	Cardial	1

SOURCES: 1, ADAMS database, Department of Anthropology, University of Geneva, Switzerland; 2, Department of Anatomy and Anthropology, University of Tel Aviv, Israel; 3, Department of Anthropology, Hacetepe University at Beytepe Campus, Turkey; 4, Department of Anatomy, Göttingen University, Germany; 5, British Museum, London, England; 6, Francis Rainer Institute of Anthropology, Bucharest, Romania; 7, Department of Anthropology, József Attila University, Budapest, Hungary; 8, Department of Anthropology, Natural History Museum, Budapest, Hungary; 9, Department of Archaeology, Institute of History, Tallinn, Estonia; 10, Department of Human Biology, University of Athens, Greece.

number of cases. A third option is to apply one of the correction/estimation parameters to the data. The preferred procedure has been to use a small set of variables which represent the main shape and size dimensions of the cranial vault, face, and mandible. This option was employed in the case of region 1 because of the small sample sizes. Missing data were estimated using the NORM V. 2.03 software package (Schafer 1999). The main elements of NORM are as follows: (1) An expectation-maximization algorithm for the efficient estimation of mean, variances, and covariances (or correlations) which uses all of the cases in the data set, including those that are partially missing; and (2) a data augmentation procedure for generating multiple imputations of missing values. NORM creates multiple imputations by a special kind of Markov-chain Monte Carlo technique that simulates random values of parameters and missing data from their posterior distribution and then provides estimates of missing values for a given specimen on the basis of its dimensions. Data were augmented using the option of imputing only once at the end of the data augmentation cycle, basing this imputation on the expectation-maximization parameters previously obtained. Each imputation run was performed using the dummy coding option, which involves a categorical variable y that takes values 1, 2, . . ., k (or any other set of k numbers). Y is the grouping variable with k values (i.e., groups). It is then taken as a set of $k-1$ dummy codes, with the result that associations between y and other variables are preserved in the imputed data sets.

The main statistical method utilized was principal components analysis, in which a large number of vari-

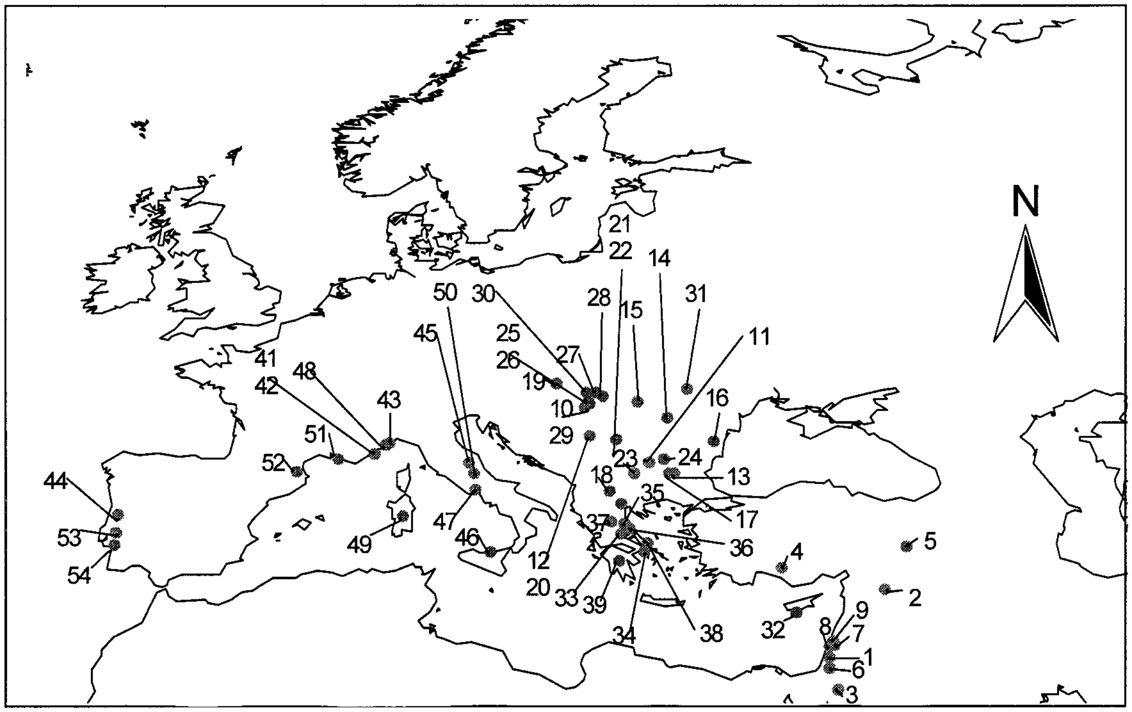

FIG. 2. *Locations of specimens used in the mean data principal components analysis.* 1, *Jericho;* 2, *Abu Hureyra;* 3, *Basta;* 4, *Çatal Höyük;* 5, *Çayönü;* 6, *Erq-El-Ahmar;* 7, *Ain Mallaha;* 8, *Nahal Oren;* 9, *Hayonim;* 10, *Deszk;* 11, *Jasa Tepe;* 12, *Vinca;* 13, *Karanovo;* 14, *Sf. Gheorghe;* 15, *Gura Bacului;* 16, *Cernavoda;* 17, *Kasanlak;* 18, *Anza;* 19, *Šturovo;* 20, *Starčevo;* 21, *Vlasac;* 22, *Lepenski Vir;* 23, *Sofia;* 24, *Devetaškata Peštera;* 25, *Kotacpart;* 26, *Hódmezővásárhely;* 27, *Endröd;* 28, *Békés-Povad;* 29, *Deszk-Olajkut;* 30, *Vészto-Mágori;* 31, *Tîrpesti;* 32, *Khirokitia;* 33, *Franchthi;* 34, *Athens;* 35, *B'Koybeleiki;* 36, *Volos;* 37, *Theopetra;* 38, *Tharounia;* 39, *Hageorgitika;* 40, *Nea Nikomedeia;* 41, *Abri de Pendimoun;* 42, *Castellar;* 43, *Finale Ligure;* 44, *Condeixa;* 45, *Maddalena;* 46, *San Teodoro;* 47, *Ortucchio;* 48, *Arene Candide;* 49, *San Fratello;* 50, *Arma dell'Aquila;* 51, *Grotte Sicard;* 52, *Salces;* 53, *Muge-Arruda;* 54, *Muge-Moita.*

ables is reduced to a smaller number of factors. The multivariate technique of the method is usually employed for the purpose of data reduction and decorrelation of the variables, but it can also be used as an tool for detecting underlying patterns or structures. In the study of region 5 discriminant analysis was also employed. The method is designed for use when two or more samples exist from potentially different populations and the researcher wishes to distinguish between them. It has two main applications. The first is interpretation of the ways in which the groups differ from each other—how well particular characteristics discriminate and which characteristics are the most powerful (Klecka 1980). The second is classification, which makes possible the prediction of group membership. The equations (canonical functions) derived combine the group characteristics in a way that allows identification of the groups which each case most closely resembles. The case under examination may be of either a known or an unknown group (Tabachnick and Fidell 1996). Both these applications were utilized.

Region 1: Turkey and the Levant

The aims of the analysis were to assess the morphological affinities between specimens from the Pre-Pottery Neolithic B (PPNB) sites in the Levant and Anatolia (from the sites of Cayönü, Basta, Abu Hureyra, and Jericho) and to examine their similarity to specimens from Natufian sites, from Çatal Höyük, and from Khirokitia. Principal components analysis was performed on two imputed data sets, one of cranial dimensions and the other of mandibles and lower dentition. The independent performance of these analyses with different morphological complexes allowed the cross-comparison of the results and their interpretation in terms of actual morphological similarities and differences. In addition, the data sets complemented each other, as the mandibular and dental set contained data for additional specimens for which mandibles were available with no associated crania.

For the analysis of cranial dimensions from a set of

TABLE 2
Variables Utilized in the Analyses

Measurement	Howells (1973)	Martin (1957)
Cranial		
Maximum vault length	GOL	1
Vault height (basion-bregma)	BBH	17
Maximum frontal breadth	XFB	10
Maximum vault breadth (at parietals)	XPB	˜8
Bizygomatic breadth	ZYB	45
Minimum frontal breadth	MFB	9
Upper facial height (nasion-prosthion)	NPH	48
Nasal length	NLH	55
Nasal breadth	NLB	54
Orbital height	OBH	52
Mandibular		
Ramus height	RAMH	70a
Ramus breadth	RAMB	71a
Maxillary length	MAXL	68
Bigonial breadth	GONB	66
Bicondylar breadth	CONDB	65
Anterior height	ANTH	69
Dental (each tooth)		
Mesio-distal dimension	–	–
Bucco-lingual dimension	–	–

106 specimens the following set of variables was selected: maximum vault length (GOL), maximum vault breadth (XPB), bizygomatic breadth (ZYB), minimum frontal breadth (MFB), upper facial height (NPH), nasal length (NLH), nasal breadth (NLB), and orbital height (OBH). Eigenvalues and factor loadings are shown in tables 4 and 5. Figure 3 is a scatterplot of the first two components. The facial-height variables NPH and NLH and cranial-length variable GOL have high positive loadings on the first component. The facial-width variables MFB, ZYB, and XPB load highly on the second component. Orbital height (OBH) has a high positive loading on the third component. The line separates two complexes. On the left of the figure are the specimens from Khirokitia, Basta, and Abu Hureyra, ascribed to Pre-Pottery Neolithic (PPN) populations. On the right are those from the Natufian sites, Çatal Höyük, and Çayönü. The

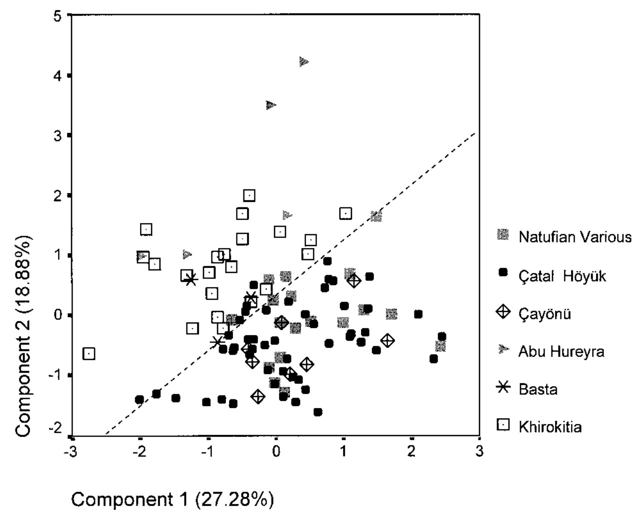

FIG. 3. *Analysis of cranial dimensions, region 1.*

PPN groups have low, average-to-wide faces and medium-to-short, wide vaults, while the Natufian–Çatal Höyük–Çayönü group has higher, narrower faces with relatively long, narrow vaults. Angel (1953) noted the peculiar "short-headedness" and paedomorphic features among the Khirokitia specimens and contended that their morphological similarities were strong evidence for inbreeding in a small island population. In addition, artificial cranial deformation was described in the case of some of the members of this population (Angel 1953, 1961) and in 3 of the 22 specimens from the studied sample (burials 41, 101, and 106). However, these three specimens fall close to the line and therefore do not appear as outliers. We may therefore conjecture that the Khirokitia sample displays some morphological similarities to the Basta and Abu Hureyra samples while possessing certain peculiarities due to a millennium or more of island habitation.

A further analysis was performed on mandibular variables—maxillary length (MAXL), ramus breadth, (RAMB), ramus height (RAMH), bigonial breadth (GONB), bicondylar breadth (CONDB), and anterior height (ANTH)—using a set of 75 specimens. Eigenvalues and factor loadings are given in tables 6 and 7. Figure

TABLE 3
Estimation of Missing Data Percentages by Variable

< 5%	10–20%	20–30%	30–40%	40–50%
GOL, XPB, MAXL, RAMH, RAMB, GONB	MFB, CONDB, ANTH, LP4MD, LP4BL, LM1MD, LM1BL, LM2MD, LM2BL	LCMD, LCBL, LP3MD, LP3BL, LM3MD, LM3BL	BBH, OBH, NPH, NLH, NLB	ZYB

NOTE: LC, lower canine; LP, lower premolar; LM, lower molar; MD, mesio-distal; BL, bucco-lingual.

TABLE 4
Eigenvalues for Cranial Dimensions, Region 1

Component	Eigenvalue	% Total Variance	Cumulative Eigenvalue	Cumulative %
1	2.18	27.28	2.18	27.28
2	1.51	18.89	3.69	46.16
3	1.45	18.15	5.14	64.31

4 is a scatterplot of the first and second components. The upper part of the scatterplot includes specimens from Abu Hureyra, some of the Natufian sites, some of the specimens from Çayönü, and some of the PPNB specimens from Neve Yam, Hatoula, and Abu Gosh in Israel. The remainder of the scatterplot includes the specimens from Basta, other PPNB specimens from Israel, some of the Natufians, and some of the specimens from Çayönü. Thus, the scatterplot shows poor discrimination between most groups with the exception of a separation between Basta and Abu Hureyra. These results are in accord with the results obtained from the cranial dimensions analysis. All variables load high on the first component, which may therefore be interpreted as describing overall mandible size. Ramus breadth and height have high positive loadings on the second component, while bigonial breadth and condylar breadth load negative. Therefore, the second component describes two contrasting mandible shapes—narrow with tall, broad rami and broad with short, narrow rami.

The third morphological complex examined consisted of the dental measurements of the lower arcade (excluding incisors)—the mesio-distal and bucco-lingual dimensions of the lower canine (LC), lower premolars 3 and 4 (LP3, LP4), and lower molars 1–3 (LM1–3). Principal components analysis was performed on the same set of 75 specimens. Eigenvalues and factor loadings are shown in tables 8 and 9. Figure 5 is a scatterplot of the first and second components. All variables load positive on the first component. In the case of the second component, however, it is the mesio-distal dimensions of the premolar and three molars which load positive while the bucco-lingual dimensions of the premolar and molars and the dimensions of the canine load negative. The specimens from Abu Hureyra are scattered in the upper left part of the scatterplot because of their negative factor loadings on the first component and high positive loadings on the second. The specimens from Jericho form a cluster in the centre right near the specimens from Basta and within the larger clusters of the Natufian and Çayönü groups. Most of the Natufian specimens show comparatively large tooth sizes. These results imply that the Abu Hureyra specimens have large mesio-distal dimensions within a small dentition (negative scores on the first component).

In summary, analysis of cranial dimensions indicates a morphological differentiation between the PPNB specimens from Basta, Abu Hureyra, and Khirokitia and those from the Natufian sites, Çatal Höyük, and Çayönü. The second and third analyses further strengthen the differentiation of Abu Hureyra from the other PPNB groups, but in these analyses the specimens from Basta are clustered with all the other groups. In all three analyses the range of morphological variability of the Natufian specimens overlaps with those of the specimens from Çayönü, Çatal Höyük, and Jericho PPN. We may therefore conclude that a considerable amount of intra- and intergroup morphological variability exists among the PPNB groups. In terms of morphology, the Natufian group is not associated with that of Basta, Abu Hureyra, and Khirokitia.

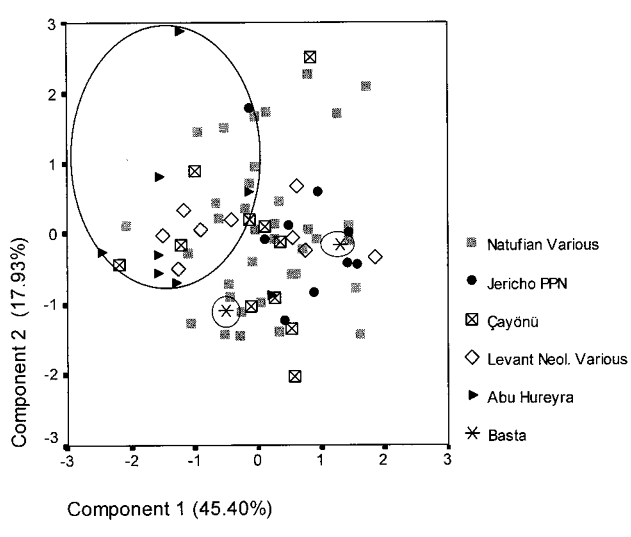

FIG. 4. *Mandibular variables, region 1.*

TABLE 5
Factor Loadings for Cranial Dimensions, Region 1

	Factor 1	Factor 2	Factor 3
GOL	0.58	−0.22	−0.15
XPB	−0.07	0.60	−0.58
ZYB	0.43	0.57	−0.49
MFB	−0.07	0.74	0.41
NPH	0.85	−0.21	0.06
NLH	0.84	0.07	0.29
NLB	0.45	0.11	−0.23
OBH	0.13	0.41	0.74

TABLE 6
Eigenvalues for Mandibular Dimensions, Region 1

Component	Eigenvalue	% of Total Variance	Cumulative Eigenvalue	Cumulative %
1	2.72	45.40	2.72	45.40
2	1.08	17.93	3.80	63.33
3	0.75	12.42	4.55	75.75

Region 5: South-Eastern Europe

The aim of the following set of analyses was to examine the similarities between local Mesolithic and Early Neolithic groups, the relationship of the Early Neolithic groups from south-eastern Europe to the Levantine and Anatolian Early Neolithic/PPNB cultures, and the degree of homogeneity among Early Neolithic specimens from south-eastern Europe.

The analysis examines the relationship between Early Neolithic specimens from Cyprus, Greece, and Anatolia and Late Upper Palaeolithic and Mesolithic specimens from Italy, Greece (Mediterranean Mesolithic), and the Danube Gorge (Vlasac and Lepenski Vir Mesolithic). The set of variables selected is similar to that used for region 1, with nasal dimensions being replaced by cranial height (BBH) in order to minimize the number of cases excluded because of missing data. The factor loadings are given in table 10. Figure 6 depicts the scatterplot of the individual factor scores on the first and second components. All factor loadings, with the exception of orbital height (OBH), which has a small negative loading, are positive on the first component. High loadings on the second component are for OBH (0.93) and upper facial height (NPH) (0.56). The first component therefore differentiates mainly according to the size of the vault. The figure indicates a separation between the two Mesolithic groups, on the one hand, and the majority of the Neolithic specimens, on the other. This is achieved by the first component, with Mesolithic specimens having positive loadings while most Neolithic specimens have negative loadings. The main exceptions are the two Mesolithic specimens from Ortucchio and some specimens from Çatal Höyük, which have, respectively, small and large sizes. The Mediterranean Mesolithic specimens have low faces and low orbits and therefore negative scores on the second component. The Mesolithic specimens from Franchthi Cave in Greece are not associated with any of the Nea Nikomedeia specimens. The Greek Neolithic group shows variability, with specimens such as Athens-Agora, Hageorgitika, and Volos 2 and 3 close to the Greek Mesolithic cluster. The specimens from the South-East European Early Neolithic group vary in their factor scores and do not form a distinct cluster.

A discriminant analysis was performed on the same set (tables 11, 12, and 13), using the variables GOL, XPB, ZYB, NPH, NLH, NLB, and OBH. The first part of the analysis examined the distribution of specimens from the seven groups in relation to each other and the location of group centroids in the discriminant space of the first and second functions (fig. 7). The main observation is the separation of Khirokitia from all the other groups analysed. The Khirokitia centroid and associated specimens are clustered in the lower part of the graph and therefore separated by their high negative values on the second function. The Mediterranean Mesolithic specimens cluster in the upper right, with the centroid close to those of the Danube Gorge Mesolithic and Neolithic groups. The centroids of Çatal Höyük (group 4) and Körös (group 6) are very close to each other, while the centroid of Nea Nikomedeia is to the left. It is therefore possible to argue for a pattern of discrimination between three main clusters: Khirokitia, Mediterranean Mesolithic, and all others. The Çatal Höyük, Nea Ni-

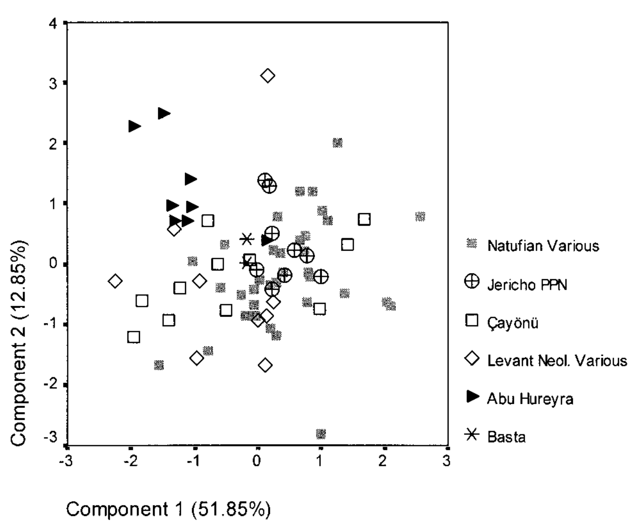

FIG. 5. *Dental dimensions, region 1.*

TABLE 7
Factor Loadings for Mandibular Dimensions, Region 1

	Factor 1	Factor 2
MAXL	0.69	0.25
RAMB	0.48	0.66
RAMH	0.62	0.37
GONB	0.65	−0.57
CONDB	0.80	−0.32
ANTH	0.76	−0.12

TABLE 8
Eigenvalues for Dental Dimensions, Region 1

Component	Eigenvalue	% of Total Variance	Cumulative Eigenvalue	Cumulative %
1	6.22	51.85	6.22	51.85
2	1.54	12.85	7.76	64.70

komedeia, and Körös specimens fall farther to the left (many have negative scores on the first function).

A further analysis involved attribution of individual specimens to groups. This analysis included all groups plus an additional group of Early Neolithic specimens for which posterior probabilities were recorded but not selected (group 8). The results are shown in table 14. Sixty percent of the cases were correctly classified. Classification was 100% accurate for Khirokitia (group 1) and 91% in the case of Mediterranean Mesolithic (group 3), confirming their distinctiveness. Among the Nea Nikomedeia specimens (group 7), 61.5% were correctly classified: misattribution occurred for other Early Neolithic groups (4, 5, and 6). Among the Danube Gorge Mesolithic (group 2) 58.3% of the cases were correctly attributed. Among the Çatal Höyük specimens, misattribution was widely distributed. Of the Körös specimens (group 6) 50% of the cases were correctly classified, and for other Early Neolithic groups the percentage of correct classifications was even lower. We therefore see a much higher degree of misattribution occurring with specimens from the Early Neolithic groups. Discrimination between the Khirokitia specimens and the Mediterranean Mesolithic and Early Neolithic groups is clear, but

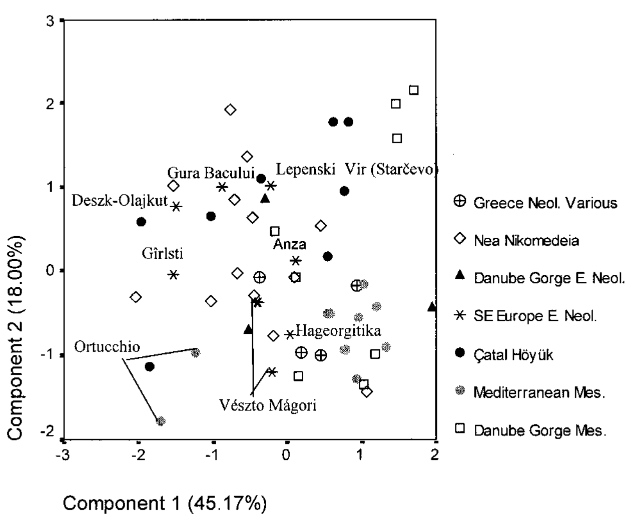

FIG. 6. *Principal components analysis of Early Neolithic specimens from Cyprus, Greece, and Anatolia and Late Upper Paleolithic and Mesolithic specimens from Italy, Greece, and the Danube Gorge.*

separation between the Danube Gorge Mesolithic specimens and those from other groups is not.

In many parts of south-eastern and central Europe Mesolithic groups appear to have had generally low population densities, and the archaeological data suggest that the dispersal of the Early Neolithic was often relatively rapid and extensive. If the spread occurred via expanding farming populations, minimal admixture with local hunter-gatherers might be predicted. The analyses support a degree of biological discontinuity between the Late Upper Palaeolithic/Mesolithic groups and those of the Early Neolithic and marked discrimination between the Khirokitia specimens and those from other Neolithic Greek groups. The PPNB specimens from Basta, Çayönü, and Abu Hureyra are generally in an intermediate position. The Çatal Höyük population resembles the Early Neolithic specimens from Greece rather than those from Cayönü. Many specimens from Early Neolithic sites in south-eastern Europe cluster together. Anza, Jasa Tepe, Karanovo, and Kasanlak cluster with Volos 1 and B'Koybeleiki 1 and 2. Morphometrically, Çatal Höyük specimens are much closer to the South-East European Neolithic examples than to those of other Anatolian/Levantine Early Neolithic groups. There is notable heterogeneity within and between Levantine PPN groups and a lack of affinity between these groups and the South-East European groups. The position of the Khirokitia group as an outlier is confirmed. If this latter is considered related to those of the PPNB cultures of the Levant, then its outlier status further strengthens the hypothesis of a high degree of biological heterogeneity among people of PPN culture groups.

TABLE 9
Factor Loadings for Dental Dimensions, Region 1

	Factor 1	Factor 2
LCMD	0.76	−0.15
LCBL	0.73	−0.33
LP3MD	0.54	0.58
LP3BL	0.71	−0.43
LP4MD	0.46	0.75
LP4BL	0.67	−0.25
LM1MD	0.73	0.29
LM1BL	0.83	−0.16
LM2MD	0.68	0.13
LM2BL	0.89	−0.15
LM3MD	0.69	0.34
LM3BL	0.86	−0.12

TABLE 10
Factor Loadings for Cranial Dimensions, Region 5

	Factor 1	Factor 2
GOL	0.78	0.02
BBH	0.78	−0.05
XPB	0.63	0.11
NPH	0.66	0.56
OBH	−0.18	0.93
ZYB	0.83	−0.25
MFB	0.63	−0.07

Region 6: Mediterranean France, Italy, and Greece

Archaeological evidence suggests that the Mesolithic/Neolithic transition in the western Mediterranean region was a complex and diverse process. Part of this complexity is due to this region's large size and physical and ecological diversity. There is therefore no reason to assume that a single model will cover processes involving northern Italy, the Iberian Peninsula, and islands such as Sardinia and Corsica. Many have argued for a delayed and selective spread of Neolithic traits in most of the western Mediterranean (e.g., Lewthwaite 1986*a*, *b*; but see also Zilhão 1993). The majority of secure dates are from the early part of the seventh millennium BP (Pluciennik 1997; Zilhão 2000, 2001), implying a gap of at least 1,000 years between the Early Neolithic in the Balkans and northern Greece and that in the western Mediterranean.

Seventy-two specimens from six groups were analysed (tables 15 and 16). The Cardial Neolithic is represented by two groups, one containing specimens from various sites (group 1) and the second coming from Condeixa in Portugal (group 2). Nea Nikomedeia, of secure Early Neolithic occupation, constitutes group 3. The South-East European group (group 4) contains various specimens from Early Neolithic sites of the Çris, Anza, and Karanovo cultures of the Balkans and southern Hungary. Çatal Höyük specimens make up group 5. The Mediterranean Mesolithic (group 6) includes specimens from Franchthi Cave, Arene Candide, Ortucchio, San Fratello, San Teodoro, and several other final Late Upper Palaeolithic and Mesolithic sites.

The first analysis was performed on 72 specimens from the above set using the following variables: GOL, XPB, MFB, BBH, NPH, NLB, NLH, and OBH. No separation was achieved between the Mesolithic and Neolithic groups (fig. 8), suggesting marked heterogeneity.

Subsequently 22 groups were selected so that each represented a single site (table 17) and a further analysis was performed on mean data. The variable set included GOL, XPB, MFB, ZYB, NPH, NLH, NLB, and OBH. The effects of sample size and sexual dimorphism on mean values were evaluated by performing additional analyses on individual females and individual males from the same data set (tables 18 and 19). As expected, there are some differences in averages between means, individual females, and individual males. However, the standard deviations of the mean values are either similar to or smaller than the standard deviations of the values for males and females, indicating that the effects of averaging and pooling the samples in the formation of means did not inflate the variance. In fact, eigenvalues and cumulative variance by factor are almost identical in magnitude to those obtained in the above factor analysis. With the exception of NLB, all the variables load highly on the first factor. The highest positive loading on the

TABLE 11
Site Names, Codes, and Sample Sizes for Discriminant Analysis

Site	Code	*N*
Khirokitia	1	4
Vlasac Mesolithic	2	12
Franchthi Cave	3	2
Ortucchio	3	2
San Fratello	3	3
San Teodoro	3	2
Kilada	3	1
Theopetra	3	1
Çatal Höyük	4	11
Lepenski Vir Neolithic	5	3
Vlasac Neolithic	5	3
Vészto-Mágori	6	6
Deszk-Olajkut	6	2
Nea Nikomedeia	7	13
Tîrpesti[a]	8	1
Cascioarele[a]	8	1
Gîrlsti[a]	8	2
Kasanlak[a]	8	1
Gura Baciului[a]	8	1

[a]Included only in the classification analysis.

TABLE 12
Wilks's Lambda

Test of Function(s)	Wilks's Lambda	Chi-square	df	*p*
1 through 6	0.12	119.80	42	.000
2 through 6	0.31	66.87	30	.000

TABLE 13
Structure Matrix

	Function	Function 2
ZYB	0.68[a]	−0.01
GOL	0.43	0.59[a]
NPH	0.06	0.29
NLH	0.37	0.05
XPB	0.14	−0.39
NLB	−0.17	0.18
OBH	−0.18	0.07

[a]Largest absolute correlation between each variable and any discriminant function.

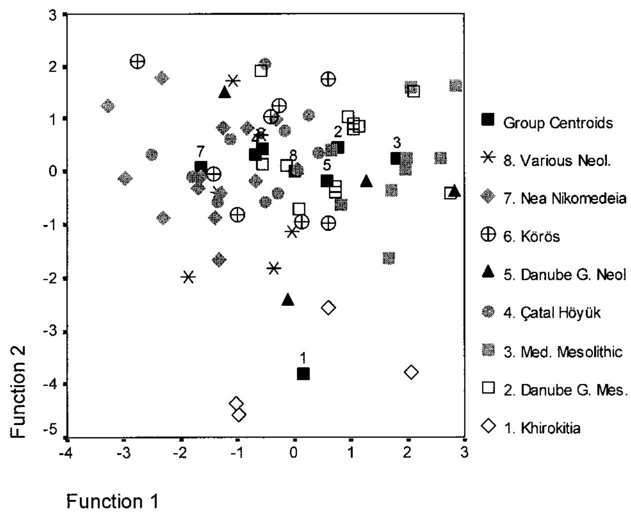

FIG. 7. *First and second discriminant analysis functions for the Early Neolithic specimens from Cyprus, Greece, and Anatolia and the Late Upper Paleolithic and Mesolithic specimens from Italy, Greece, and the Danube Gorge.*

second factor is for NLB (0.91) and the highest loading is for ZYB (−0.39). The highest positive loadings on the third component are GOL (0.43) and OBH (0.38) and the highest negative loadings are MFB (−0.68), and XPB (−0.55). We can therefore deduce that the first component accounts for general size while the second is mainly sensitive to nasal breadth. The third component is mostly a reflection of variations in frontal and parietal breadth.

Figure 9 illustrates the positions of the groups in the two-dimensional space of the first two components. Pronounced variability is evident in the distribution of Cardial Neolithic specimens, with specimens from two sites at the top of the scatterplot but those from Grotte Sicard at the bottom. Variability is mostly along the second axis and thus in morphological terms mainly reflects variation in nasal breadth among the Cardial groups. The Early Neolithic specimens from region 1 cluster in the centre of the plot. The Mediterranean Mesolithic specimens are in the lower portion of the graph, with variation seen mainly in the first component and reflecting general size.

TABLE 14
Summary of the Classification Results

	Predicted Group Membership							
	1	2	3	4	5	6	7	Total
1 Khirokitia	4	0	0	0	0	0	0	4
2 Danube Mesolithic	0	7	2	1	1	1	0	12
3 Mediterranean Mesolithic	0	0	10	0	0	1	0	11
4 Çatal Höyük	0	1	1	4	2	1	2	11
5 Danube Neolithic	1	1	1	0	2	0	1	6
6 Körös	0	0	1	0	1	4	2	8
7 Nea Nikomedeia	0	0	0	4	0	1	8	13
8 Early Neolithic, various	0	0	0	2	1	1	0	4

TABLE 15
Groups and Codes for Principal Components Analysis, Region 6

Group	Period	Code
Cardial-various	Cardial	1
Cardial-Condeixa	Cardial	2
Nea Nikomedeia	Early Neolithic	3
South-Eastern Europe-various	Early Neolithic	4
Çatal Höyük	Early Neolithic	5
Mediterranean Mesolithic	Mesolithic	6

Our initial questions had to do with regional Mesolithic–Early Neolithic morphological affinities. The results display great heterogeneity among the Cardial Neolithic groups, with Cardial specimens morphologically associated with both Early Neolithic and Mesolithic groups, and show that, in this region at least, cultural groupings do not map neatly onto biological populations. The lack of a satisfactory sample size and geographic coverage for Mediterranean Early Neolithic specimens precludes closer examination of potential specific areas of admixture (but see Lalueza Fox 1996, Jackes, Lubell, and Meiklejohn 1997*a*). Our current analysis suggests, if anything, great variability in biological (and potentially other) relationships and processes within and between the various groups.

Reassessing the Models for the Spread of Farming

We have argued that in terms of cranial morphometrics Neolithic populations can be shown to vary by both period and geographic location. The earliest farming populations in Anatolia and the Near East differed significantly from each other, suggesting the possibility that only a bottleneck population from the former region dis-

TABLE 16
Factor Loadings for Cranial Dimensions, Region 6

	Factor 1	Factor 2
GOL	0.79	−0.15
BBH	0.76	−0.39
XPB	0.42	0.16
MFB	0.55	−0.27
NPH	0.78	0.27
NLH	0.77	0.38
NLB	0.34	−0.56
OBH	0.28	0.70

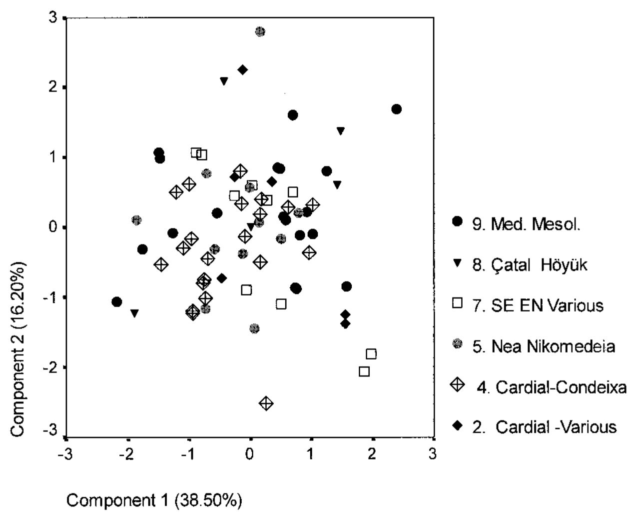

FIG. 8. *First two components of the first principal components analysis of cranial morphometrics from region 6.*

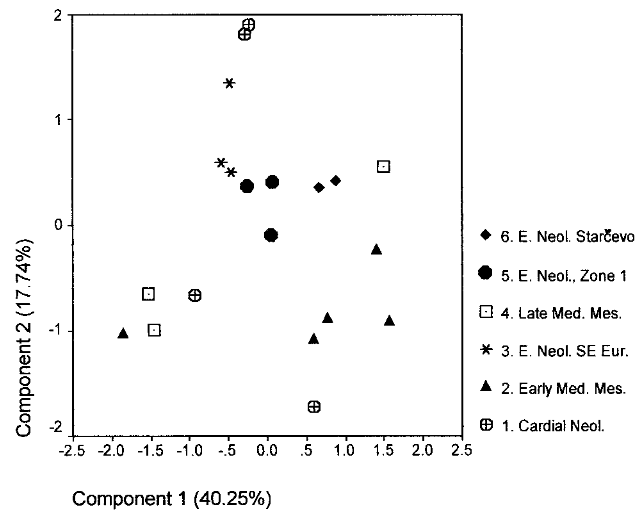

FIG. 9. *First two components of principal components analysis on mean data of cranial morphometrics from region 6. Each point represents a single site.*

persed into Europe. There is a lack of secure archaeological evidence for direct local cultural continuity between the Mesolithic and Neolithic at many of the sites considered. The results of the principal components analysis may partly support this discontinuity hypothesis in biological terms. Specimens from Levantine Jericho (PPNB), Basta (PPNB), Abu Hureyra (PPNB), Cypriot Khirokitia ("pre-pottery"), and Çayönü (PPNA) demonstrate a fair degree of morphological heterogeneity within and between the region 1 groups. This pattern among the Early Levantine and Anatolian populations contrasts with the apparent homogeneity of Early Neolithic groups from south-eastern Europe and Çatal Höyük (Pinhasi 2003). This is supported by the univariate

TABLE 17
Groups Analysed in Mean Data Analysis, Regions 1–6

Location	*N*[a]	Date (bp)	Latitude (N)[b]	Longitude (E)[b]	Period	Code
Arma dell'Aquila II	3	–	42.37	13.37	Cardial	1
Condeixa	60	–	40.06	−8.30	Cardial	1
Finale Ligure	3	–	44.12	8.18	Cardial	1
Grotte Sicard	3	–	43.24	5.12	Cardial	1
Arene Candide	3	–	38.33	16.12	Early Mesolithic	2
Franchthi Cave	3	–	39.00	22.30	Early Mesolithic	2
Ortucchio	3	12,500	41.54	13.42	Early Mesolithic	2
San Fratello	4	12,003	38.00	14.36	Early Mesolithic	2
San Teodoro	4	–	42.00	13.30	Early Mesolithic	2
Nea Nikomedeia	11	8,180	40.65	22.30	Early Neolithic	3
Vészto-Mágori	7	6,200	46.94	20.23	Körös	3
Tîrpesti	4	6,240	47.17	26.33	Pre-Cucuteni	3
Lepenski Vir Mesolithic	15	7,313	44.33	22.03	Late Mesolithic	4
Muge–Arruda	10	–	39.06	8.42	Late Mesolithic	4
Muge–Moita	14	–	38.37	8.58	Late Mesolithic	4
Çatal Höyük	50	7,499	37.10	32.13	Early Neolithic	5
Çayönü	9	9,360	38.23	39.65	PPN	5
Khirokitia	21	7,368	34.54	33.00	PPN	5
Anza	3	–	41.39	21.58	Starčevo	6
Lepenski Vir Early Neolithic	23	–	44.33	22.03	Starčevo	6
Šturovo	5	–	47.47	18.42	Starčevo	6
Vinca Neolithic	9	–	44.48	20.36	Starčevo	6

[a]Sample sizes are given prior to the casewise exclusion due to missing values.
[b]All entries are in decimal notation. All latitude values are positive (Northern Hemisphere). Positive longitude is in the north-east quadrant and negative longitude is in the north-west quadrant.

and Mahalanobis-distance analyses (not included here), is unlikely to have been affected by small sample sizes, and would appear to support a version of the wave-of-advance model. However, these statistics contrast with the strictly archaeological evidence, which indicates different modes of Early Neolithic settlement and Neolithic expansion occurring in Crete, Cyprus, the Aegean, and different regions of Greece, European Turkey, and elsewhere in south-eastern Europe, for example (Broodbank and Strasser 1991; Chapman 1994; Halstead 1996; Price 2000*b*:7–9; Tringham 2000). This suggests that different processes (demographic, biological, and cultural) should not be assumed to be in a constant relationship. A closer examination of the analyses also cautions against accepting the wave-of-advance model wholesale. This model explains observed south-east-to-north-west genetic and chronological clines in terms of increasing mixing between initially differentiated local Mesolithic and incoming farming populations. One would expect to detect a similar clinal pattern from the craniometric data, but the analyses show a lack of morphological differentiation related to geographic distance. Biological admixture is easier to argue for in the case of the western Mediterranean and less so in the case of Anatolia and south-eastern Europe, but with significant exceptions.

A model largely driven by demographic expansion predicts farmers' becoming increasingly morphologically differentiated from the original stock population through time. This assumption is based on straightforward models of stochastic change due to drift and a series of founder effects (see Wright 1951, 1969; Konigsberg 1990*a*, *b*; Relethford 1991, 1996; Barbujani, Sokal, and Oden 1995). Sokal, Oden, and Wilson (1991) have pointed out that persistent demic diffusion originating from a single source population and repeated migrations by culturally different groups along established corridors will leave similar indistinguishable marks on gene-frequency surfaces. Thus Cavalli-Sforza, Menozzi, and Piazza's (1994) claim that the synthetic map of the first component indicates a south-east-to-north-west genetic cline across Europe as the outcome of demic diffusion is tenuous.

Results from this study do, however, support the hypothesis of a genetic bottleneck from a local centre of origin somewhere in the central Anatolian Plateau, suggested by the similarities between Çatal Höyük and Early Neolithic mainland Greek and South-East European groups. Thus, even under the model of a predominantly demic diffusion, these results stress the need to differentiate between the various sites and their associated populations in the presumed centre of origin. The appearance of Neolithic levels in sites such as Khirokitia in Cyprus and Knossos level X in Crete may represent the spread of people from a Levantine pre-pottery culture which began about 10,000 uncal BP and reached Cyprus, Crete, and perhaps mainland Greece between 8,500 and 7,500 uncal BP. This is the argument made by Perlès (2001), who differentiates between "Initial Neolithic" and "Early Neolithic" phases in Greece. The former consist of the "pre-pottery" layers of sites such as Argissa, Sesklo, Soufli Magoula, and Franchthi Cave in mainland Greece and Knossos on Crete. Perlès argues that the lack of overlap between the C^{14} distributions for these periods implies the existence of two distinct occupation phases, dating to around 7,900 uncal BP for the Initial Neolithic and about 7,650 uncal BP for the Early Neolithic. She argues that the initial phase relates to sites which share many similarities with the "pre-pottery" sites of Anatolia and the Levant. However, Kotsakis (2002) has criticized approaches like this one that ultimately depend upon transhistorical concepts of singular cultural identities for both indigenous foragers and colonizing farmers.

TABLE 19
Factor Loadings of Mean Data Analysis

	Component		
	1	2	3
GOL	0.60	0.24	0.43
XPB	0.71	0.15	−0.55
ZYB	0.75	−0.39	−0.14
MFB	0.50	0.40	−0.68
NPH	0.73	−0.21	0.22
NLH	0.84	−0.20	0.27
NLB	−0.01	0.91	0.19
OBH	0.53	0.32	0.38

TABLE 18
Means and Standard Deviations for Mean Data and Individual Data by Sex

	Mean			Standard Deviation		
	Mean (N = 20)	Females (N = 39)	Males (N = 49)	Mean	Females	Males
GOL	185.51	176.81	186.93	6.62	5.61	6.87
XPB	138.69	135.53	139.36	3.91	4.78	6.13
ZYB	130.17	121.31	129.73	8.11	6.35	8.50
MFB	95.20	93.14	97.03	3.12	4.36	3.99
NPH	66.18	64.47	67.37	3.08	3.96	3.90
NLH	49.45	46.77	49.39	2.19	3.00	3.48
NLB	24.58	23.61	24.82	1.22	1.91	1.95
OBH	31.53	31.03	31.78	1.34	2.07	1.87

Ammerman and Cavalli-Sforza have also been criticized for disregarding the effects of geography (van Andel and Runnels 1995, Barbujani 2000). The physical factors may include the Aegean, Adriatic, and Tyrrhenian Seas and the Alps. If one adds a presumed preference for fertile soils, river valleys, and water sources, then the paths by which early farmers dispersed will look much less like radial logistic dispersion from an original centre. Moreover, such ecological preferences and geographic boundaries cannot simply be taken into account by modifying existing formulas for dispersion rates but require qualitative anthropological approaches. Van Andel and Runnels (1995) have therefore suggested a two-phase colonization model. They contend that, though sea travel was clearly possible, the Aegean Sea may initially be regarded as a barrier, creating a bottleneck that limited the number of migrants. At the initial stage, colonists perhaps from the Levant arrived early and almost simultaneously on Crete, at Franchthi, and in Thessaly but probably only in small numbers. In the second step, migrating farmers, possibly from central Anatolia, reached the northern part of Greece as well as Macedonia and Thrace. Van Andel and Runnels assert that the lengths of the steps and the intervals between them were dictated by geography and by population growth in each of a slowly increasing number of parent areas (but see Zvelebil 2000:74). While there are problems with some of the earliest Neolithic occupation C^{14} dates in Greece, the current findings could be argued partly to support this view. The first dispersion event by sea route was part of the expansion of a late "pre-pottery" culture which prevailed in Anatolia and the Levant and reached Crete, Cyprus, and the southern Peloponnese from around 8,500 uncal BP. The second dispersion event originated from central Anatolia approximately a millennium later, and Anatolian migrants appeared in Thessaly and rapidly spread across south-eastern and central Europe.

Assessing the Results in the Context of Genetic Studies

There is no consensus among geneticists regarding the origin of the first Europeans and what one may infer from the geographic distribution of various genetic markers (Brown and Pluciennik 2001). There is an apparent discrepancy between the results of mtDNA (Richards et al. 1996, 2000; Wilkinson-Herbots et al. 1996) and Y-chromosome (Semino et al. 2000) studies, which suggest a Palaeolithic ancestry for modern European populations, and the findings from studies of nuclear DNA (Chikhi et al. 1998*a*, *b*, 2002) and classical markers (Menozzi, Piazza, and Cavalli-Sforza 1978, Cavalli-Sforza, Menozzi, and Piazza 1993), which suggest population replacement by incoming Near Eastern farmers during the Neolithic. The main point of contention is that a clinal distribution is apparent only in the study of the classical markers, which are mainly immunological (from HLA loci) and therefore more likely to be affected by selective factors (Fix 1999). This incompatibility can be explained if one accepts that the gene pool of all modern European populations is a regionally varied mixture of different percentages of "Palaeolithic" and "Neolithic" ancestral contributions. This supposition is supported by evidence from mtDNA (Richards et al. 1996, 1998, 2000) and Y-chromosome studies (Semino et al. 1996, 2000). Interestingly, many geneticists would now agree that the "external" component—of whatever ultimate derivation—now accounts for a minority of the patterning, perhaps 10–20%, and that this may well represent the proportion of genetic and perhaps numerical demographic contribution which can be ascribed to incoming farming groups (Sykes 1999; Price 2000*a*:305; but see Chikhi et al. 1998*b*, 2002; Richards et al. 2000).

Many geneticists have been little concerned with the complexity of historical processes and the implications for the interpretation of observed genetic patterns, showing a marked tendency to equate and conflate cultural and biological populations (see Pluciennik 1996; McEachern 2000; Zvelebil 2000:72–73). Perhaps this is partly a function of a mismatch between the chronological and geographical resolution needed to interpret regionally variable sociocultural processes and that available through modern genetic data. A major problem is that regional variations in selective pressures, founder effects, and biological interactions between "hunter" and "farmer" groups could nevertheless result in a similar overall clinal pattern. Other processes such as "isolation-by-distance" migratory events without admixture and gradual dispersion with admixture can result in similar geographic distributions of gene frequencies (Barbujani, Sokal, and Oden 1995; Barbujani and Bertorelle 2001; Fix 1999; Sokal 1991; Zvelebil 2000:69–73). The association of modern gene-frequency distributions with historical events of expansion and migration is ambiguous and problematic. As Barbujani and Bertorelle (2001:22) point out, "A cline or gradient, for example, may reflect adaptation to variable environments, or a population expansion at one moment in time, or continuous gene flow between groups that initially differed in allele frequencies." Simulation studies carried out by Fix (1996, 1997; see also 1999) indicate that weak temporal selection can replicate the clinal pattern of gene frequencies observed by Cavalli-Sforza and his team. Thus, at present none of the genetic analyses can detect more constrained and particularistic mobility and admixture patterns. These patterns can be revealed only by the incorporation of non-genetic information.

Barbujani and Bertorelle (2001:23) assert that the dichotomy between Palaeolithic and Neolithic ancestry for European populations may be in fact artificial, since the direction of both Palaeolithic and Neolithic clines excludes any Mesolithic process of indigenous acculturation:

> To understand for good whether the European gene pool derives from Palaeolithic or Neolithic ancestors, one should type individuals who lived, respec-

tively, in Europe and in the Near East, say 15,000 years ago. Should these groups prove genetically different, one could infer a Palaeolithic origin of the modern gene pool from a closer similarity between modern and ancient European, and a Neolithic origin from a closer similarity between modern Europeans and the ancient inhabitants of the Near East.

Analysis of morphological variability in the Near East and Europe (here and in Pinhasi 2003) suggests that the Epipalaeolithic populations from the Natufian Levant were noticeably different to the Mesolithic populations described from the Danube Gorge, the western Mediterranean, and central Europe. No close similarities were observed between Early Neolithic and Mesolithic European groups in any of the regions studied, with the possible exception of Mediterranean Europe. However, neither were clear affinities observed between Epipalaeolithic Near Eastern groups and any other Neolithic or Mesolithic groups. These results support a third scenario—that the Epipalaeolithic population from which the first Anatolian farmers descended has yet to be discovered, as there are at present no skeletons and meagre evidence for Epipalaeolithic occupation in Anatolia. Some argue that there is little archaeological or biological evidence to support local continuity between Epipalaeolithic and the "pre-pottery" Neolithic in the Levant (I. Hershkovitz, personal communication), but the picture is complex. Some archaeologists use the PPNA as a purely chronological division, incorporating geographically differentiated forager groups (Khiamian, Mureybetian, and perhaps Harifian) as well as those with some cultivation (Sultanian) (Bar-Yosef and Belfer-Cohen 1992). Byrd (1992) argues for both colonization by expanding farming groups and adoption of agricultural resources occurring within the Levant and farther afield during the PPNA and PPNB phases. Use of domesticated caprines, beginning in the late PPNB, underwent similar diffusion (Harris 1996:554–57). This scenario presents many opportunities for biological bottlenecks and complex patterns of distribution of biological (including genetic) characteristics for humans, plants, and animals. The observed variability between Levantine and European Epipalaeolithic/Mesolithic groups should be studied in relation to their predecessor Upper Palaeolithic populations. Genetic studies arguing for an Upper Palaeolithic ancestry of modern European populations need to consider population bottlenecks and segregation during the Late Glacial period, which can perhaps account for the morphological variability seen in the Mesolithic.

Özdoğan (1995, 1996, 1997) has proposed that the Early Neolithic cultures of Anatolia be considered as two distinct entities: the Neolithic of south-eastern Anatolia, typified by Çayönü and related to the Mesopotamian-Levantine tradition, and an "indigenous" Neolithic of the Anatolian plateau, typified by Çatal Höyük. If these archaeological cultures represented geographically persistent biological populations, one would expect to see more similarities between specimens from Çayönü and the Natufian sites than between the latter and Çatal Höyük. However, results of the principal components analyses for region 1 indicate an overlap in morphological variability between Natufian, Çatal Höyük, and Çayönü specimens, while those from Abu Hureyra and Basta, both Levantine PPN sites, are outliers. There is therefore no unequivocal evidence from biological morphometrics for local continuity between Natufian specimens and any of those from the Anatolian or Levantine PPN cultures. Statistical analysis of the Levantine populations indicates no obvious biological continuity between Natufian groups and their successors—either the first Neolithic cultures of the PPNA or subsequently between the PPNA and the PPNB. The various Natufian groups themselves are characterized by a high degree of morphological variability. It is possible that one of these groups became agriculture-dependent at some stage and that, under such a scenario, we are looking at some form of genetic bottleneck. One of the most intriguing results is the high degree of variability among the PPN "Initial Neolithic" groups from the Levant and Anatolia. It is possible that these early farmers had separate biological lineages and that the spread of agriculture was mainly due to the diffusion of knowledge and technological aspects across the Near East and Anatolia (cf. Byrd 1992). The existence of diverse Early Neolithic groups in this region is perhaps not surprising given that agriculture existed in this region for 2,000 years or more before the first spread of farming into Europe.

Immediately beyond the zone of Anatolia and the Near East, a striking amount of morphological similarity is found between populations. The first farmers from Nea Nikomedeia and other Greek Neolithic sites are morphologically similar to the first farmers from Çatal Höyük and to the specimens from the Körös and Starčevo cultures and from the first LBK groups of central Europe (Pinhasi 2003) and show no similarity to the Mesolithic specimens from Franchthi Cave. In the western Mediterranean the picture is more obscure, with heterogeneity among the Cardial Neolithic groups and the absence of a strong pattern of differentiation between Mesolithic and Neolithic groups. It is therefore plausible that dispersion within the northern Mediterranean area was both more gradual and more varied in nature, with the possibility of more biological admixture (Simoni et al. 1999). A recent analysis of more than 2,600 European mtDNA sequences which indicates significant east-to-west clinal variation around the Mediterranean but not farther north may support this suggestion: according to Simoni et al. (2000:275) "a simple demographic expansion from the Levant is easy to reconcile with the gradients observed at many nuclear loci but it is not easy to link with the fact that mitochondrial variation is clinal only in southern Europe." They suggest that greater gene flow occurred within the Mediterranean region than across the northern part of the continent.

Conclusions

This article has examined just one aspect of the complex set of events which gave rise to the appearance of agriculture across Europe. Analysis of the available craniometric data in conjunction with data from nuclear-DNA and Y-chromosome genetic markers across Europe using spatial autocorrelation statistics would allow a more regionally and chronologically nuanced biological approach to the spread of farming in Europe that is too often missing from studies of genetic markers. Ancient-DNA studies which focus on affinities and similarities between and among the Mesolithic and Neolithic populations in Europe, Anatolia, and the Near East may eventually refine our understanding of dispersion and migration events and subsequent processes. More secure C^{14} dates from Anatolia and south-eastern Europe and further surveys and excavations in western Anatolia, European Turkey, Macedonia, and Thrace are required (M. Özdoğan, personal communication). However, neither skeletal nor genetic nor archaeological data alone will provide "solutions" to questions about the nature of the Mesolithic-Neolithic transition. Different data sets address a variety of processes at different scales and chronological and geographical resolutions (see Bentley, Chikhi, and Price 2003). The fullest interpretations need to take into account social, biological, demographic, and cultural processes which the available evidence suggests were historically and regionally variable. The results of the craniometric analysis of skeletal populations described here provide strong support for treating the Mesolithic-Neolithic transition as several historical events rather than as a single demographically driven episode of gradual logistic growth. Our findings tend to support those who argue for marked regional diversity in the nature of the spread of Neolithic characteristics. The data examined here suggest three main conclusions. First, they point to the prevalence of a biologically heterogeneous PPN culture which existed for two millennia in the Levant, Anatolia, and Cyprus and possibly extended farther west to other parts of the Mediterranean. Secondly, they support the idea that the first *colonizing* farmers of mainland Europe originated from central Anatolia, as biologically exemplified by Çatal Höyük, and entered south-eastern Europe through western Anatolia. The remarkable homogeneity among some Early Neolithic specimens from south-eastern Europe and those from Çatal Höyük implies little biological interaction among many of these initial farming groups and local hunter-gatherers. Finally, the results suggest that little admixture between local hunters and incoming farmers occurred in south-eastern Europe. This dispersal pattern contrasts with that for the western Mediterranean region, where the spread of farming was generally more gradual and seems to be less a simple case of Neolithic demic dispersion than a more gradual and complex demographic process.

Comments

ALEX BENTLEY
Institute of Archaeology, University College London, 31-34 Gordon Square, London WC1H 0PY, U.K. (r.bentley@ucl.ac.uk). 26 IV 04

For a century now, much of the progress in the investigation of the demographic origins of the Neolithic transition in Europe has been made by those who have uncovered the archaeological evidence, provided radiocarbon dates, and (more recently) discovered geographic patterns among the genes of modern populations. At this point in our knowledge, the way forward needs to involve direct evidence from the skeletons of the participants who lived millennia ago. For this reason, I applaud this paper for presenting new, thought-provoking skeletal data and assimilation of other data sets. By presenting the multivariate data in the relatively direct format of principal-component plots, Pinhasi and Pluciennik give readers the exciting opportunity to investigate the patterns independently and draw conclusions. This is a very valuable contribution indeed.

Interpreting multivariate data always involves some subjectivity, and a pleasure of reading this paper is considering its meaning. In fact, I acknowledge a degree of subjectivity in my own interpretation of the strontium isotope evidence that Douglas Price and I have collected, which I believe to be evidence for forager females' marrying into early farmer settlements (Bentley et al. 2002, 2003) whereas my own colleague favors the identified Neolithic migrants' coming from other Neolithic agricultural settlements (Price et al. 2001, Bentley et al. 2002). In anticipation of enjoyable debate, then, I submit that, while a bottleneck among Anatolian populations and a largely exogenous origin of Neolithic populations in southeastern Europe are certainly possible, the data as Pinhasi and Pluciennik have presented them do not unequivocally support these conclusions.

Regarding a bottleneck among Anatolian groups, it is claimed in different parts of paper that (1) the Natufian specimens overlap with those from Çayönü, Çatal Höyük, and Jericho PPN, (2) Çatal Höyük resembles specimens from Early Neolithic Greece rather than those from Çayönü, and (3) the Çatal Höyük group is closer to the southeastern European Neolithic specimens than to the Anatolian/Levantine Early Neolithic groups. Not only do these statements seem contradictory, but the figures give us little opportunity to evaluate them. Only in figure 3 are Çayönü and Çatal Höyük actually compared, and there the two groups overlap each other as well as overlapping the Jericho and Natufian specimens, so I do not understand why Çatal Höyük is said not to resemble Çayönü or the Levantine Neolithic. Also, in figure 3 the spread in principal-component 1 scores among Çatal Höyük specimens appears larger than for any other group shown (including the various Natufian ones), which seems not to reflect the "remarkable homogeneity" among the Çatal Höyük population that Pinhasi and Pluciennik describe.

I also do not see in these data a clear separation between Mesolithic and Neolithic groups. In figure 6, for example, I count at least 10 of the 30-odd Neolithic points on the positive side of the plot, which leave a rather unconvincing majority of the Neolithic specimens with negative loadings. Also, it is claimed that the Danube Gorge Mesolithic specimens are separate from the Natufian group, but I cannot find a plot on which those two groups are compared. It is further claimed that there are no close similarities between any of the Early Neolithic and Mesolithic groups studied, but in figure 7 the Danube Mesolithic and Danube Neolithic groups clearly overlap, with group centroids quite close together, and in figure 8 there appears to be considerable overlap between Çatal Höyük and the Mediterranean Mesolithic groups.

These contrary interpretations come from my independent viewing of the researchers' plots, which would have been easier had *all* the samples been analyzed together and presented on one plot. However, let me again congratulate them on collecting this extensive data set and in fact using it to argue for my own belief about the Neolithic expansion. One of the striking aspects about the data is the presence of clear outlier groups, including the Khirokitia group (fig. 3) and the heterogeneous Cardial groups (fig. 9) they refer to and, I would add, the Nea Nikomedeia group (fig. 7). These outlier groups may reflect founder effects that we would expect from separate maritime colonization events to Cyprus and the northern Mediterranean (cf. Zilhão 2001) and potentially, in the case of Nea Nikomedeia, from small groups of land colonists. Many of these small groups of migrant farmers would have found themselves isolated at least for some time, and through opportunity or survival necessity they would have traded with and possibly intermarried with Mesolithic groups (e.g., Bentley et al. 2003, Price 2000*a*, Zilhão 2000, Zvelebil 2000). In other words, I think Pinhasi and Pluciennik have given us a useful new data set from which we can all draw our own conclusions, discuss them, and gain a better understanding of the complexity of the Neolithic transition.

JEAN-PIERRE BOCQUET-APPEL
CNRS, UPR 2147, 44, rue de l'Amiral Mouchez, 75014 Paris, France (bocquet-appel@ivry.cnrs.fr). 27 IV 04

Pinhasi and Pluciennik have gathered palaeoanthropological data and subdivided them into three chrono-regional groups in order to test the homogeneity or heterogeneity of the populating process associated with the spread of Neolithic from the Levant. They underline the contradictions between patterns observed from genetic data and the ad hoc explanations given by population geneticists. They believe that their data show a chrono-regional pattern of Neolithicization. Although the data are unfortunately sparse, this is a useful attempt to inject morphological data into a debate that tends to be monopolized by population geneticists who often seem to ignore each other when their conclusions do not converge. Unlike the morphometric data, which are well dated, the genetic data are like a bag of marbles. The marbles themselves say nothing about the cause of their arrangement in the bag. What provides an explanation for the way they are arranged is the model of interpretation. As we know, the fit of a model to the data is not proof of its reality. Almost every new genetic variant that appears has its model. From an academic point of view, there are issues at stake here that are not only scientific but also financial. I welcome the argument for the ambiguity of genetic patterns relating to the identification of generating processes and the existence of contradictory patterns in historical perspective (traditional markers versus mtDNA and Y chromosome, Neolithic versus Upper Palaeolithic explanations) and the great interest for this debate of morphological data. The morphometric data produce the same pattern of geographical differentiation as is observed on a worldwide scale in the genetic data (Froment 1992).

Nevertheless, certain weaknesses of the approach should not be underestimated. These are primarily due to the scarcity of information, about which Pinhasi and Pluciennik can do very little. This is apparent in their principal components analysis. For example, the data are represented by values of absolute measurements. We know that the first discriminating factor in any population is sexual dimorphism (females are smaller than males). With the small sample size with which the researchers are working (for instance, in table 9, region 6, 5–11 for 22 sites and 30 for only 2 sites), just one female or male more or less in one of the groups would certainly be enough to modify the variances within and between them as well as the values for the axes (mainly axis 1). Again, in region 6, if the sample size for each site point is plotted, the variability pattern of the group averages roughly corresponds to group sizes, with "large" groups (Catal Höyük, 50; Condeixa, 60) in the barycentre of the graph and "small" groups (Final Ligurian, 3; Grotte Sicard, 3) on the periphery. It seems to me that this is not entirely a matter of chance. Estimates of group means are better at the centre and poor towards the periphery because of their sample size. This point must be mentioned especially because the genetic data employed in the paper were generally sampled from groups of several tens of individuals. In their analysis of the spatial autocorrelation of historical craniometric data—which Pinhasi and Pluciennik also seek to perform—Sokal and Uytterschaut (1987) exclude from their data the point where the sample sizes were 30. The stability of the population patterns observed by Pinhasi and Pluciennik in their morphometric data, given the very small sample size of their samples, could easily be tested by simulation (for example, with Howells's [1973] data, available in the ADAM database). This would considerably strengthen their conclusions. Another point that may weaken their approach is their device of subdividing the data into regions in order to demonstrate the existence of a historical process on a regional rather than a continental scale. It should be remembered that a random change perceived on a local or regional scale may be in fact clinal on a continental scale and conversely (Bocquet-Appel 1996). It would be desirable to analyse these data from the continental to the regional, for there is always a bias in favour of the scale of definition chosen by the researchers.

There were certainly several different regional processes at work in the spread of Neolithic, but they did not occur independently. Rather, they started in the same geographical area of the Fertile Crescent and everywhere helped to satisfy the same need for greater food security. One of the great merits of Ammerman and Cavalli-Sforza's (1971) work is to have provided a global demographic explanation at a continental scale, an ancestor of today's globalization, whereas in the 1970s, for mainstream archaeologists everything nearly always stemmed from the local.

Undoubtedly, the new frontier is now to estimate the differentiation of the rate of cultural change continuously on the map, its speed, and the rate of inbreeding between local (supposed sedentary farmers) and non-local (supposed mobile foragers), using strontium isotope techniques (Bentley, Chiki, and Price 2003). Pinhasi and Pluciennik's craniometric data should hold part of the answer. In any case, they have attempted to make a great deal from relatively little—which is much better than the reverse—with all the innovative temerity and the disadvantages associated with such an approach.

DAVID BULBECK
School of Archaeology and Anthropology, Australian National University, Canberra, ACT 2600, Australia (david.bulbeck@anu.edu.au). 16 V 04

This article is an exercise in the art of interpreting ambiguous multivariate statistical results rather than the science of rigorous testing of hypotheses and clear presentation of the results. Further, while there are some conclusions that the analyses presented suggest, they often differ from the inferences drawn by the authors.

One outstanding result, as noted by the authors, is the distinctive status of the PPNB Abu Hureyra sample (figs. 3–5). However, their discussion strangely extends this finding to the Basta sample ("results of the principal components analyses [indicate that specimens] from Abu Hureyra and Basta, both Levantine PPN sites, are outliers"). While none of the Basta specimens falls within the Abu Hureyra range of variation on any plot, at least one of them falls within the range of variation of all the other samples on every plot, with the sole exception of the Çayönü range of variation in figure 3. Only Abu Hureyra and, to a lesser degree, the island-bound sample from Khirokitia (on Cyprus) diverge noticeably from the other samples. On Pinhasi and Pluciennik's evidence, it could be reasonably inferred that by around 10,000 years ago a quite homogeneous population stretched from the southern Levant (Basta) to Anatolia (Çayönü), with the sole exception of Abu Hureyra. This might suggest that any genetic bottleneck that had the effect of diminishing metrical variability in the region would date to the Pleistocene, not the Holocene as is claimed here.

Figures 4–6, 8, and 9 all include a first component interpreted as essentially size but also reflecting sex. Surprisingly, Pinhasi and Pluciennik discuss the potential effects of sexual dimorphism with reference to the magnitude of total variance but not to the separation between specimens on their principal components plots. While the full effect of sex on the size components could be gauged only by those with access to the original data, the data in table 18 suggest that male craniometric averages are about 3–7% greater than corresponding female averages (the exact figures may differ, especially as in the case of two variables—ZYB and NLH—the reported average for the two sexes together is mysteriously larger than that for either sex). However, I suspect that, if the sex of each specimen in figures 4–6, 8, and 9 were disclosed, there would be a clear predominance of females to the left side of the graphs and males to the right. If so, differences between the samples (independent of differences in their sexual composition) would be better represented by plotting the specimens on principal components 2 and 3 rather than on 1 and 2.

Irrespective of this sexual dimorphism problem, Pinhasi and Pluciennik additionally draw inferences unsupported by their own graphs. For instance, with figure 6 we are advised that "the Mesolithic specimens from Franchthi Cave in Greece are not associated with any of the Nea Nikomedeia specimens," but one of the latter is represented by a diamond in the far bottom-right of the graph and would therefore be more closely associated with all of the Franchthi specimens than with any other Nea Nikomedeia specimen. With figure 9 we are told that "the Mediterranean Mesolithic specimens are in the lower portion of the graph," but this is true specifically of the Early Mediterranean Mesolithic specimens, which on principal component 2 are separated from 10 out of 12 of the Neolithic specimens (with Late Mediterranean Mesolithic specimens intermediate, suggesting a transitional morphology). In addition, the claim that "the Çatal Höyük population resembles the Early Neolithic specimens from Greece rather than those from Çayönü" is hard to sustain, as not one analysis presented directly compares these three groups and in the single analysis that directly compares Çayönü and Çatal Höyük (fig. 3) the Çayönü specimens are entirely included within the Çatal Höyük range of variation.

Even if the methodological and inferential problems noted above were remedied, the benefits of this line of analysis could be queried. The cranial measurements available to Pinhasi and Pluciennik from published sources (table 2) exclude many that would be regarded as critical in modern craniometry (e.g., subtenses); execution of the analyses compels them to estimate a substantial proportion of missing measurements, based on a not particularly diagnostic battery of measurements in the first place; and principal components plots accounting for only ca. 50–60% of total variation, much of which may be size-related sexual dimorphism, hardly justify placing great store in informal, intuitive interpretations of the significance of the specimens' placement on these plots. Thus, commentary on their lengthy introduction and discussion would be superfluous, as their study seemingly offers little for understanding the Neolithic transition in the Asia Minor/southern Europe region.

CATHERINE PERLÈS
Préhistoire et Technologie, MAE, 21 allée de l'Université, F-92093 Nanterre Cedex, France (perles@mae.u.paris10.fr). 21 V 04

Discussion of the biological aspects of the spread of farming populations within the Near East and from the Near East to Europe has in the past few decades been dominated by genetic analyses of modern populations. It is therefore of great interest to have data on the past populations themselves on a scale comparable to that of genetic studies. "Did they look alike?" is indeed the basic question archaeologists want to ask when they are suggesting, from archaeological data, either cultural continuity or discontinuity in a given region.

Pinhasi and Pluciennik's answer to this question varies from region to region, sometimes in more or less expected ways (the homogeneity of the Starčevo, Körös, and LBK groups and the discontinuity between the Mesolithic and Neolithic specimens in Eastern Europe, for instance) and sometimes in totally unexpected ones. This is the case, in particular, when the conclusion is reached that no clear affinities are observed between the Epipaleolithic (Natufian) groups and any other Neolithic or Mesolithic groups. This clearly raises severe problems vis-à-vis the archaeological data, as do many other results of this study. Indeed, an archaeologist would want to discuss and sometimes challenge almost every paragraph of this thought-provoking paper. Rather than going into detail, I would like to underline what is, in my opinion, both the strength and the weakness of this study—its scale. A vast geographic and chronological scale was indeed necessary if the results were to be compared with those of genetic analyses, but achieving it has meant relying on a mix of heterogeneous sources, often with very small samples and only superficial discussion of their contexts.

Jericho offers a good example of these problems: 254 skeletons (with and without skulls) were recovered from the PPNA and 232 from the PPNB, plus 85 isolated or cached skulls. In addition, previous anthropological studies claimed that two morphologically distinct components were represented in the PPNB, one of local origin and one of more northern origin (Kurth and Röhrer-Ertl 1981). With only PPNB specimens considered in this study, these problems could clearly not be approached, and the representativeness of the sample is highly questionable. Similarly, the Basta PPNB is presented as an unexpected outlier, but this is based on three specimens only. As for the "Greek Neolithic," it contains an odd mix of Greek and non-Greek sites, as though it could be assumed a priori that all southeastern Neolithic farmers had a single origin.

In conclusion, one can only welcome an approach that attempts to integrate physical biology, archaeology, and genetics, but analyses should at first proceed on a smaller geographical scale, with larger and more reliable samples. The project would also benefit from the inclusion of archaeologists capable of discussing the specific problems raised by each site and region considered.

JOÃO ZILHÃO
Departamento de História, Faculdade de Letras de Lisboa, 1600-214 Lisboa, Portugal (joao.zilhao@netcabo.pt). 23 V 04

Pinhasi and Pluciennik argue that in south-eastern Europe the introduction of farming is related to colonization from Central Anatolia, with little admixture between local hunters and immigrating agriculturalists, and that in the western Mediterranean the process was more gradual and complex, possibly involving a higher level of biological admixture. They point out, however, that these conclusions are affected by the unsatisfactory nature of the western Mediterranean sample. Since their single source for the region is the University of Geneva's ADAM database (http://ianthro.unige.ch/lp/ADAM/page1p.html), the latter's shortcomings greatly limit the validity of the conclusions.

For instance, Pinhasi and Pluciennik consider the "Condeixa" sample (ADAM-302; 159 skeletons) as Cardial. It is true that a very small Cardial component exists among the ceramics from this cave site (the Covão d'Almeida, at Eira-Pedrinha [Jorge 1979, Vilaça 1988, Zilhão 2000]). The artifactual material associated with the human remains, however, suggests that for the most part they date to the later Neolithic and the Metal Ages (see Jackes, Lubell, and Meiklejohn 1997*b* and http://intarch.ac.uk/antiquity/jackes/craniometry.html), and in fact ADAM cautions that this is a "Cardial to Bell Beaker" sample. Since the 20 individuals retained in the study represent 70% of the sample for the Mediterranean Neolithic, the "great heterogeneity" of the "Cardial" group may well be a simple consequence of the fact that it is largely made up of Copper or Bronze Age people.

Madalena di Muccio (ADAM-722; one skeleton), a settlement site from the "Central Adriatic Impressed Ware Culture," contained only "scattered human bone remains" (Cremonesi et al. 1998); the dating of that skeleton is therefore open to question. At "Finale Ligure" (presumably Arene Candide, ADAM-214; 16 skeletons) only the burial of an individual in fetal position may relate to early Neolithic uses of the site (Bagolini and Pedrotti 1998); the ca. 30 other tombs excavated here date to the Middle Neolithic Vaso a Bocca Quadrata culture, dated to ca. 5,700–6,000 BP. It is also to this culture or even a later one that Bagolini and Pedrotti relate the burials from Arma dell'Aquila (ADAM-213; five skeletons), a nearby Ligurian site (misplaced in fig. 1). In fact, ADAM lists this material as "Cardial/Uncertain."

"Pendimoun" and "Castellar" must represent the Abri Pendimoun at Castellar (ADAM-114; one skeleton), where, apart from the material in the database, recent work has yielded two similar individual burials in identical stratigraphic positions, suggesting that these are indeed Cardial inhumations in pits excavated in the underlying Impressa levels (Binder et al. 1993). At the Grotte Sicard (ADAM-314; two skeletons), a single level contains unassociated human skeletal material from successive burial episodes and some pottery decorated in a style suggesting a late Cardial or Epicardial date, but this level also contains an incineration context ascribed to the Bronze Age (Escalon de Fonton 1956); thus, the inhumations may have taken place at any time between the two periods.

"Salces" (ADAM-110; four skeletons) is the Cova de l'Espérit, in Roussillon, where a funerary context existed at the bottom of a chamber used for habitation in what the excavators considered the early Neolithic (Abélanet and Charles 1964). The pottery from the habitation deposits is very scarce and fragmentary, in marked contrast with the numerous bladelet and microlithic tools, including types suggestive of the late Mesolithic Tardenoisian culture; in fact, the excavators find this lithic assemblage comparable to the pre-Cardial from the classical sequence of Font-des-Pigeons (Châteauneuf-les-Martigues). In conjunction with the abundance of fish and shellfish remains and the absence of sheep, this suggests that the level represents a Mesolithic occupation in which the pottery is simply intrusive.

The use of late Early or even Middle Neolithic samples is warranted provided that it is made clear that they represent populations that were posterior to the dispersal of farming and derived from it. However, the use of samples with uncertain chronology introduces a potentially major source of noise to the analysis. Once these questionable samples are removed from the comparisons, it becomes clear that western Mediterranean early farming sites group with those from central Europe and the Balkans. That "Condeixa" and "Sicard" are outliers may simply reflect a significantly later chronology, but it is also conceivable that the discrepancy relates to analytical anomalies. For the Grotte Sicard entry ADAM cautions that Martín's variables 51, 52, 62, and 63 were obtained with an "uncertain technique," and one of these variables (M52, orbital height) is included in the principal components analysis whose results are presented in figure 9.

The notion that the Mesolithic and early Neolithic populations of Iberia were genetically distinct is supported by comparisons of ancient DNA extracted from Portuguese skeletons dating to the time period of relevance (Chandler, Sykes, and Zilhão 2004). Haplogroup frequencies in these Mesolithic and early Neolithic Portuguese samples are more closely related to present-day Iberian and Mediterranean populations than to Near Eastern ones, and haplogroup J, assumed to be the marker of a Near Eastern population input, is absent. A contribution of women of very recent Near Eastern origin to the groups involved in the emergence of farming here can therefore be excluded. However, these samples are themselves quite separate, only one haplotype being shared. These are therefore genetically distinct populations, the farmers representing a demic intrusion. These findings are fully consistent with the maritime pioneer colonization model for the spread of farming in the western Mediterranean region (Zilhão 2001).

Reply

RON PINHASI AND MARK PLUCIENNIK
London, U.K. 8 VI 04

We are grateful to all the commentators for their incisive comments and generally supportive remarks. We are indeed aware of the dangers and difficulties of covering such a wide span in time and space and the disadvantage of lacking specialist knowledge of certain sites and regions such as those referred to by Perlès and Zilhão. This makes it all the more valuable to receive the input of those familiar with both the archaeological and methodological contexts of this work. We are fully in sympathy with those who argue for additional and alternative ways of producing and addressing this kind of data, including a focus on large regional samples as suggested by Perlès for Greece, though we are constrained by the available material. Such problems of sampling and chronological and spatial resolution are widespread in many fields of archaeology (including archaeogenetics), but we hope that we have shown how biological morphometric data can contribute to the debate about some of the processes operating in this period of prehistory. We reiterate here that the comparison of groups across a variety of geographic and chronological scales was part of an attempt to discover patterns and persistent differences and see how these fitted—or contradicted—evidence from other sources.

Bentley points out that the Natufian specimens overlap with those derived from Çatal Höyük and various PPNB groups and in some ways resemble the Early Neolithic specimens from south-eastern Europe. However, our results indicate clear differentiation in terms of craniometrics between the high variability among PPNB specimens (including Çayönü) and the low variability among the south-eastern European Early Neolithic specimens and Çatal Höyük. The "remarkable homogeneity" Bentley alludes to was detected among some Early Neolithic specimens from south-eastern Europe and those from Çatal Höyük rather than for Çatal Höyük specimens as a single population. In previous work (Pinhasi 2004), necessarily condensed here, various additional statistical tests, including discriminant function analyses, comparisons of squared Mahalanobis distances between samples, and univariate non-parametric and parametric tests, were performed on the same cranial samples. One such test involved taking Çatal Höyük and Çayönü as two possible centres for the origins of the first farmers and then calculating average squared Mahalanobis distances (based on craniometric variables) and geographic distances between each of these centres and several Neolithic populations, including those of Nea Nikomedeia, Condeixa, Viesenhauser Hof, Schwetzingen, and Veszto-Mágori. The results indicated that the largest Mahalanobis distance is between Çatal Höyük and Çayönü and that in general the Early Neolithic south-eastern and central European groups are morphometrically closer to Çatal Höyük than to Çayönü (Pinhasi 2004:18–19). Examination of both median and mean boxplots for each cranial dimension for Natufian, Çayönü, Abu Hureyra, Çatal Höyük, Greek Early Neolithic, Mediterranean Early Neolithic, south-eastern European Early Neolithic, and central European Early Neolithic specimens indicated that Çayönü has the largest variance for GOL, XPB, and NPH, while Abu Hureyra has the largest variance for ZYB, NPH, NLB, and OBH. The European Early Neolithic groups and Çatal Höyük have similar means and variances for GOL, XPB, ZYB, and NPH.

We agree with Bentley that data are always subject to interpretation and that our data as presented do not support any unequivocal conclusion. We did attempt to recognize this and indeed—echoing Bentley's own observation—pointed out, for example, that the centroids for the Danube Gorge Mesolithic and Neolithic groups were close together in the discriminant analysis for region 5. Elsewhere we mentioned "significant exceptions" to our general statements. The results certainly do suggest possible Mesolithic-to-Neolithic regional continuity in the case of the Danube Gorge as in figure 7 and are supported by analysis of squared Mahalanobis distances in Pinhasi (2003). We would also note, however, that the archaeological and dating contexts for these particular specimens are continually changing, which itself suggests a fluid situation regarding the meaning of these data.

We welcome Bocquet-Appel's remarks about principal components analysis and sexual dimorphism. A previous study (Pinhasi 2003) examined sexual dimorphism using principal component analysis in combination with univariate analysis of variance on males and females from various sites and comparing period-specific (i.e., Mesolithic, Early Neolithic, and Middle/Late Neolithic) trends in the data set. The results indicated that differences in size (shown by the first principal component) between sexes were significant in all three periods. However, the distribution of the factor scores showed a different pattern of dimorphism in each of these periods. Sexual differences in shape (as seen in the second and third principal components) were pronounced for the Middle/Late Neolithic and for the third principal component within the Mesolithic but insignificant during the Early Neolithic. This perhaps suggests that the degree of intrapopulation variability was reduced during the Early Neolithic and subsequently increased again during the Middle/Late Neolithic. These results support the idea that sexual dimorphism plays a role in the analysis and interpretation of craniometric affinities and distances but that some sexual dimorphism is shape-related. Thus Bulbeck's prediction that "if the sex of each specimen in figures 4–6, 8, and 9 were disclosed, there would be a clear predominance of females to the left side of the graphs and males to the right" is erroneous. He apparently misunderstands the complexity of the analysis of sexual dimorphism from craniometric data (see Van Vark and Schaafsma 1992 for a discussion of some remedies). Many years ago Howells (1973), in his analysis of cranial variation among various world populations, pointed out that the degree of sexual dimorphism varies not only between populations but also in relation to particular morphological features. By removing the first principal component, which contains information on several morphometric features, one eliminates from the data set not sexual dimorphic variability but most of the total variability that can be attributed to size. The decision to analyse pooled samples was justified on the basis of the above analyses and others (unpublished) of sexed groups that yielded similar relationships between the samples. We used a specific set of measurements reflecting the main dimensions of the face and vault first because it is the set that is most often utilized in craniometric studies (the ADAMS database mainly contains data on these variables), second because the use of other, more extensive variable sets yielded similar results (Pinhasi 2003), and third because the use of subtenses is problematic in that angular data cannot be analysed in the same manner as linear data.

Both Perlès and Zilhão point out some of the errors and ambiguities in the inclusion of specimens from questionable contexts (e.g., "Cardial") and question the grouping of specimens from Greek and non-Greek sites as a single group. We accept that our collation of such extensive craniometric data for specimens from Epipaleolithic, Mesolithic, and Neolithic sites in Europe, the Levant, and Anatolia has its faults, such as the inclusion of specimens from sometimes dubious contexts and occasional misattributions. We also agree that pooling of samples inevitably proceeds on the basis of prior assumptions. However, we hope that we have made the basis of our own choices clear, and we are certainly open to discussing whether other methods might be more instructive. We believe that our main conclusions remain reasonable in the current state of knowledge. We have tried to be cautious about the overinterpretation of certain "affinities" and rather focused on patterns that appear to be robust across several tests (for example, through both principal components and discriminant function analysis). In part, the problems posed by skewed samples could not be overcome because of the uneven distribution of skeletal finds across Europe, Anatolia, and the Levant, differential bone preservation, different retrieval and conservation methods, excavation bias, lack or uncertainty of dating, and other factors. Nevertheless, we hope that making some of this material more widely available will result in further consideration of how best to incorporate these data into the continuing debates.

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