

Healthy but mortal: human biology and the first farmers of western Europe

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What do we know about the effects of the transition to agriculture on human biology? A literature has grown up that gives us the impression that we know a great deal about what happened to bones and teeth when people became sedentary farmers. A review of the sources of these ideas and the evidence supporting them, especially based on work in Portugal, reveals that a reconsideration of the biological consequences of farming in Europe is overdue.

Introduction

Ces ruraux donnent pour la plupart une impression de bonne santé, surtout si l'on prend en compte le fait qu'ils avaient bien dû mourir de quelque chose
MASSET 1993: 141

Reliance on easily stored and processed carbohydrates brought on long-term malnutrition. . . physical anthropologists often can determine exactly when a society settled into a Neolithic existence, just by noting the sudden appearance of smaller and more heavily diseased skeletal remains

TURNBAUGH *et al.* 1993: 454

The literature on the shift from foraging to farming economies often conveys the impression that we clearly know what happened to human populations as they changed from being foragers to farmers: poor nutrition; signs of stress and malnutrition; increased infection; reduced stature; reduced bone robusticity; smaller teeth with simpler morphology; reduced face and jaws; increased dental pathology; reduced sexual dimorphism; increased fertility; increased population density (e.g. Cohen 1989; 1994). It is categorically stated as fact in some undergraduate texts (e.g. Turnbaugh *et al.* 1993: 454) that malnutrition, disease, dental pathology and reduced size necessarily accompany agriculture. But these are hypotheses, said to apply to Europe, although derived primarily from research in Sudanese Nubia and the North American Midwest.

The extra-European data

There are problems with these data. Those from Nubia are incomplete. No early Neolithic skeletons are available from lower Nubia; agriculture is late and poorly recorded (Martin *et al.* 1984). The post-Neolithic A and C group populations, dated c. 5000–3500 BP, display biological continuity (Johnson & Lovell 1995; Prowse & Lovell 1995) but also show the marked dental reduction hypothesized to accompany agriculture. However, two facts are noteworthy:

- 1 both, especially the earlier A group, retained some Mesolithic subsistence patterns;
- 2 as agriculture intensifies in the C group, and dental pathology increases (Beckett & Lovell 1994), some skeletal lesions considered to mark agricultural malnutrition *decrease* very significantly. The cemeteries which have primarily contributed to the negative perception of the agricultural transformation in Nubia are medieval; some seem to provide biased samples (Jackes 1992: 216).

Data from the North American Midwest present different problems. Cassidy (1980; 1984), comparing Indian Knoll (c. 4000–5000 BP) with Hardin village (c. AD 1600), found the most sig-

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nificant indicators for health status to be the pattern of childhood deaths, frequency of periosteal reactions and mean cortical index (which refers to the thickness of the bone cortex especially in femora). However, the cortical index is age-dependent (Jackes 1992), so the differences in the estimated age distributions of adults over 17 years between the two samples is relevant. Activity is also an important factor in long bone cortical thickness, and periosteal reaction rates are activity-mediated as well as health-related (Jackes 1988a: 63). The major difference between the two sites, childhood age at death, is governed by two factors:

- 1 at Hardin village infant under-representation is evident, and
- 2 population increase at the rate of $r = .01$ is likely (see Jackes 1994 for methods used to compare palaeodemographic data).

We can assume the underlying age pyramids of the two populations were different since one was non-stationary, and we would therefore expect differences in the percentage of children among the dead. When Cassidy's (1984: 315) age distribution is tested against Indian Knoll (Howells 1960), with Hardin village adjusted for population increase, the two samples present virtually identical demographic indicators despite differences in time and subsistence.

While there may have been a dramatic change to maize agriculture around 1000 BP in eastern North America, there is evidence of seed plant cultivation c. 4000-5000 BP, and increased reliance on local seed plants by c. 2000 BP (Smith 1989; 1995). In this paper we are not just considering the effects of a revolutionary 'introduction of agriculture'. A shift in plant use or an intensified reliance on plants must also be taken into consideration.

If agricultural intensification results in a more restricted diet, might the effects be more striking than those resulting from the initial transition to agriculture? Can high levels of infection in North American skeletal samples be attributed to a diet limited to domesticated plants? Hodges (1987), showing that no deleterious consequences resulted from agricultural intensification in Oaxaca, suggested diet may be more diversified in a primary centre of agriculture than in a marginal secondary area. This interesting hypothesis needs to be tested in a wide variety of settings. Marginal agricultural Ontario Iroquoian nations, at and just before European

contact, had fairly uniform high levels of bone pathology but differing reliance on hunted and gathered food (Jackes 1988a: 109-10).

Research in the United States provides a far more consistent viewpoint (Bridges 1989), and discussions on the transition to agriculture often rest heavily on one site, Dickson Mounds (Cohen 1989; Goodman 1993; Wood *et al.* 1992), which needs to be approached carefully (Jackes 1993). Having analysed skeletons of both North American and European agriculturalists, we consider it undesirable to extrapolate from one continent to the other. Neolithic pathology is rare in Europe (e.g. Canci *et al.* 1993) by comparison with the rates in skeletal samples of North American agriculturalists (*cf.* Meiklejohn *et al.* 1984 vs North American sources in Cohen & Armelagos 1984). Maize-based agriculture, the lack of domesticated animals, together with specific patterns of housing (Jackes 1994: 173) and soil pathogens (Buikstra & Cook 1981), may have contributed to special circumstances entailing high levels of dental and skeletal pathology. For this reason, the introduction of agriculture into Europe should be examined with European evidence (e.g. Dennell 1992; Dolukhanov 1986; Donahue 1992; Keeley 1992; Kozłowski & Kozłowski 1986; Price *in press*; Price & Gebauer 1992; Price *et al.* 1995; Vencel 1986; Zvelebil 1986), without preconceptions from the Americas.

The European data

The hypothesis of the introduction of Neolithic economic practices by cultural and technological diffusion from the eastern Mediterranean, first espoused by Childe (e.g. 1958: 39ff) and now revived in various guises (e.g. Ammerman & Cavalli-Sforza 1984; Barbuiani *et al.* 1995; Cavalli-Sforza *et al.* 1993; 1994; Renfrew 1992; Sokal *et al.* 1991; Zilhão 1993; *in press*), complicates the issue. In Childe's scheme, agricultural populations from the Middle East expanded into a Europe sparsely inhabited by Palaeolithic survivors who succumbed before strong immigrant farmers. Childe was an Australian, and this view of prehistory echoes the belief which prevailed at the time of Australian Aborigines as vanishing before an expanding European frontier (see e.g. Trigger 1980: 49ff, 172; Renfrew 1994: 126 for comments on conventional aspects of Childe's thinking). This was also a time in which there was little recognition of the strength and stability of Mesolithic

adaptations. Alongside better understanding of Mesolithic intensification and variability (e.g. Brinch Petersen & Meiklejohn in press a; Byrd & Monahan 1995; Larsson 1990; Meiklejohn & Zvelebil 1991; Neeley & Clark 1990; Price 1987; 1991; Zvelebil 1986; Zvelebil & Rowley-Conwy 1986: 85–9), there is now increased discussion of variability during the period when agriculture was spreading throughout Europe (Dennell 1992; Gallay 1994; Knutsson 1995; Price 1995; van Andel & Runnels 1995; Verhart 1995; Zvelebil & Lillie 1995). With this recognition of variability, in place of a simple picture of either wholesale colonization or diffusion (e.g. Sherratt 1995), human skeletal data are all the more crucial to reconstructing how Neolithic economies came into Europe (*cf.* Constandse-Westermann & Newell 1990).

Using osteological data to resolve the problems

Analyses of human skeletal material can help determine whether biological changes resulted from population replacement or from economic change, and may also resolve a contradiction: were immigrant farmers weakened by malnutrition and infections arising from sedentary settlement and overpopulation, or were they sufficiently healthy, fertile and mobile to take over a continent rapidly? Resolution of this contradiction requires analysis of large samples that bridge the transition from within a restricted region.

Unfortunately, delimited regions with sufficiently large and reliable samples of Mesolithic skeletons are uncommon; those where good Neolithic samples immediately follow the Mesolithic are even rarer (Meiklejohn *et al.* 1997).

The Baltic is one possible region. The surviving sample from Mesolithic Olenii Ostrov in Karelia, where up to 500 people were buried around 8000 BP, has been studied by Jacobs (1992; 1995) who emphasizes the dental heterogeneity between Skateholm and Olenii Ostrov, contemporaneous populations from a single environmental context using similar technologies and foraging strategies. Meiklejohn *et al.* (n.d.) have shown a similar separation using craniometric data. Another potentially valuable sample is Zvejnieki in northern Latvia (Zagorska & Larsson 1994), for which the osteological data are not yet available to us.

Southeastern Europe is another possibility. Meiklejohn *et al.* (1997) touch upon the sam-

ple from Vlasac on the Danube as an example of Mesolithic population stability — low mortality and low fertility, with a balance between them; it has enough skeletons for a satisfactory palaeodemographic study — 117 at c. 8700 BP. Skeletons from Neolithic phase III at Lepenski Vir, c. 8000 BP, have been compared with the Mesolithic by y'Edynak (1989; y'Edynak & Fleisch 1983). The teeth become a little smaller; they become more complex rather than simpler; and dental pathology does not increase into the Neolithic. y'Ednyak proposes that the changes in the dentition were already established prior to the Neolithic. Work at other sites in the region with both Mesolithic and Neolithic occupations continues (Boroneanț *et al.* 1995; Radovanovic 1995).

A third region with sequential Mesolithic and Neolithic samples is around the Dnieper Rapids in Ukraine where the Neolithic dates are early, c. 8450 BP. Jacobs (1994: 57–8) reports stable isotope evidence showing that millet formed an important subsistence component before the introduction of pottery. Whether or not this is confirmed (*cf.* Lillie 1996; Potekhina & Telegin 1995), it is evident that the Neolithic does not arrive suddenly and as a complete package in the Dnieper Rapids area, and that there are increases in both dental size and general skeletal robusticity.

The Mesolithic–Neolithic transition in Portugal: a case study

There are large samples of Mesolithic and Neolithic skeletal material from central and southern Portugal (FIGURE 1) available for analysis (TABLE 1).

Archaeological evidence for the Mesolithic–Neolithic transition in Iberia, and the various schemes proposed to explain it, are reviewed in detail by Zilhão (1993; in press) who argues in favour of a 'maritime pioneer colonization' of Portugal, as originally proposed by Arnaud (1982; 1989; see also González Morales & Arnaud 1990). This model may not apply to all Iberia; Zilhão accepts the view of Arias-Cabal (1991) and others (see Straus 1992; chapters 8 & 9) 'that the neolithization of the Cantabrian coastal strip is best interpreted as the local acquisition of novel resources by local hunter-gatherers' (Zilhão in press). In fact, Arias-Cabal (1995) suggests that the coastal sites represent only one part of the Mesolithic settlement of

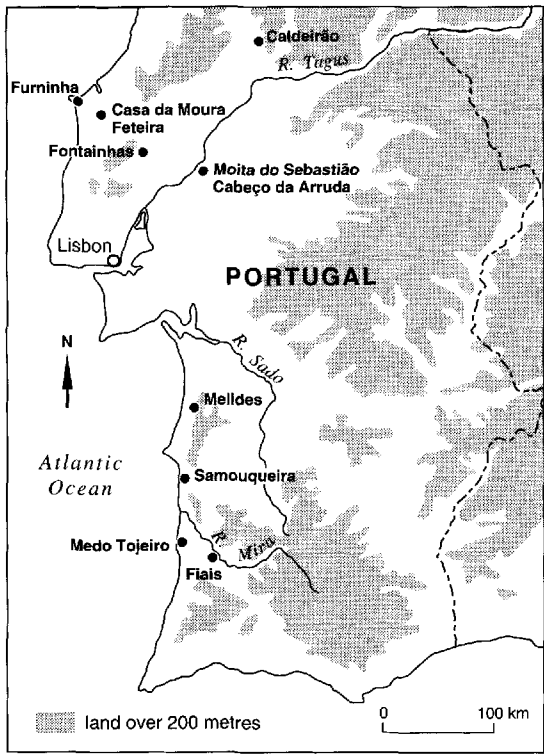


FIGURE 1. Map of Portugal showing major sites discussed.

Cantabria. Zilhão sees in Portugal complete geographical and technological discontinuity (see also Vierra 1992) between an indigenous Mesolithic (e.g. estuarine shell middens at Muge and along the Sado) and an intrusive Neolithic (e.g. Caldeirão (Zilhão 1992) and other sites). Emphasizing site distributions, stratigraphy and

radiocarbon chronology, and using aspects of the population genetics model for Iberia proposed by Calafell & Bertranpetit (1993), Zilhão (in press) believes that colonization along the Atlantic coast by seafaring Neolithic peoples provides the best explanation.

The probability distribution (at 1σ) for the calibrated ranges of charcoal and bone collagen radiocarbon samples shows considerable overlap for Portuguese Mesolithic and Neolithic sites (FIGURE 2). The contemporaneity of the Mesolithic and Neolithic in central and southern Portugal poses a problem (cf. Bicho 1994; Lubell *et al.* 1994; Straus 1991). It is not simply a matter of the presence of Cardial ceramics or apparently domestic ovicaprids, for there is a complete disparity in burial pattern (Zilhão in press). The hundreds of Mesolithic skeletons from the Muge (Moita do Sebastião, Cabeço da Arruda and Cabeço da Amoreira) and Sado shell middens (no osteological data yet available) are found within deposits containing occupation debris, almost always as primary individual interments lacking artefactual evidence for status differentiation. The hundreds of Neolithic skeletons from sites such as Casa da Moura, Feteira, Furninha and Fontainhas in the Portuguese Estremadura appear almost always to have been secondary, collective burials (as for many French Neolithic skeletons) in caves used specifically as ossuaries, accompanied by artefacts which may in some way have indicated social ranking (cf. Knutsson 1995).

The Neolithic burial pattern was not uniform. The recently discovered Neolithic collective burial site of Algar do Bom Santo, dating

		site	range in years BP	no. of ¹⁴ C samples	mean date used (BP)	skeletal MNI
		Mesolithic				
TABLE 1. Chronology and skeletal MNI of Portuguese sites discussed. All samples except two each from Caldeirão NA1 (Bos) & NA2 (Ovis) were human bone collagen.		Moita do Sebastião	7597–8037	5	7900	79
		Cabeço da Arruda	7224–7783	5	7600	97
		Samouqueira	7224	1	7200	2
		Neolithic				
		Caldeirão NA1	6668–6810	3	6700	13
		Caldeirão NA2	6965–7225	3	7100	6
		Furninha	est. 5500–6900	0	6000	43
		Casa da Moura	5595–6869	4	5700	214
		Melides (Lagares Cave)	6144	1	6100	29
		Melides (Zambujal Cave)	4989	1	5000	51
		Feteira (partial excavation)	4660–5297	2	5300 & 4660	30
		Fontainhas	4724	1	4700	17

around 5500 BP (Zilhão in press: figure 7), shows that bodies were sometimes deposited intact in burial caves with artefacts, perhaps indicating status (Zilhão pers. comm.). Some of these caves were artificially excavated cavities. Other Neolithic burial types are the *mamoas* (tumuli with varying details of construction) of northern Portugal and the megaliths of the Alentejo for which there is some evidence of contemporaneity with the latest shell-midden sites (Gilman 1992; Kalb 1989; Straus 1991; Straus *et al.* 1990).

Variations in burial patterns were clearly contemporaneous. Caldeirão NA2, in which six individuals were buried (Jacks & Lubell 1992), is not significantly different in its radiocarbon determinations from Mesolithic sites south of the Tagus (FIGURE 2). Dates equivalent to TO-953 (Casa da Moura, 6877 BP) are derived from sites that can only be considered Mesolithic, involving midden burials, and others that have cave burial. At least 13 individuals were identified in Caldeirão NA1, and Casa da Moura was first used as an ossuary cave at the same date. The pattern of long-term (or at least earlier and later) use of burial places documented for Casa da Moura is known at other sites, e.g. Escoural G (Araújo *et al.* 1993). Thus we have widespread and diverse burial practices all within one time-period, precluding argument for clear separation based on the radiocarbon record.

It cannot be assumed that variable Neolithic burial patterns necessarily indicate that different peoples were establishing themselves in Portugal. Evidence from elsewhere in Europe, from Asia and from North America are pertinent here. At the Danish Mesolithic (Kongemose) site of Gøngehusvej 7, there are burials varying from single extended inhumation to multiple cremation (Brinch Petersen *et al.* 1993; Brinch Petersen & Meiklejohn in press b). At Jiangzhai, a large Neolithic village in north China, burial patterns changed dramatically from individual to collective burial (Jacks & Gao in press). Neither case shows evidence for population change. Burial practices may change

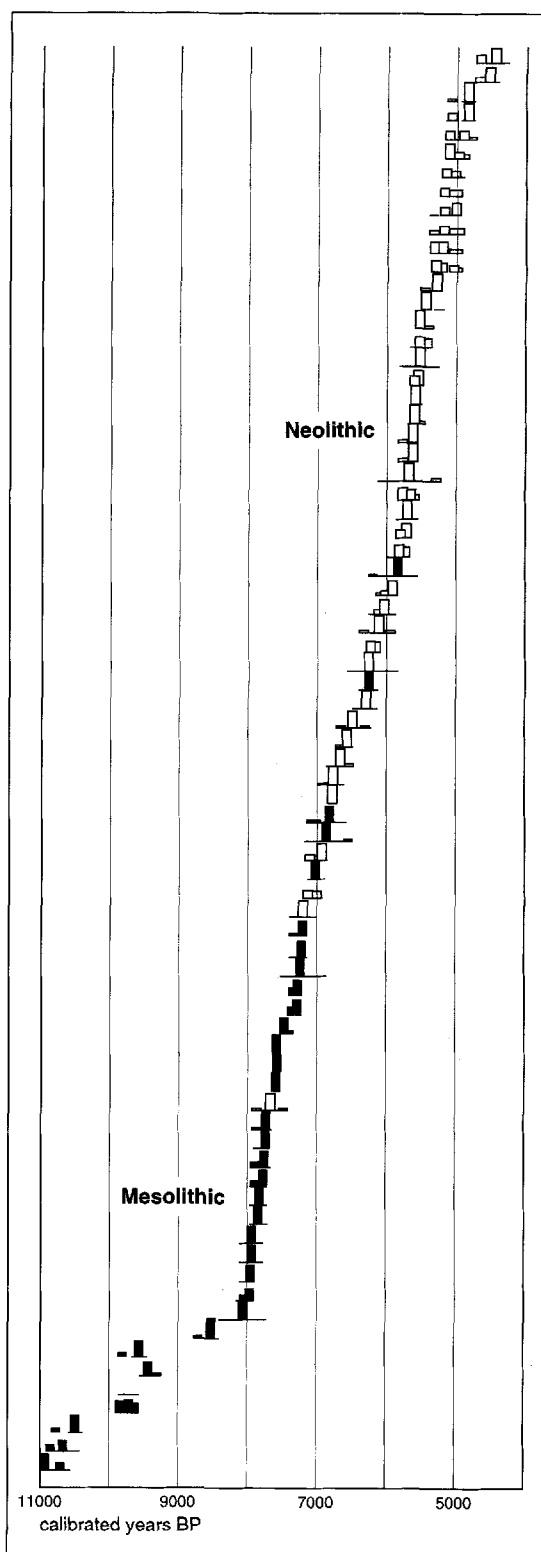


FIGURE 2. Probability range (calculated using CALIB 3.0.3c, Stuiver & Reimer 1993) of selected published radiocarbon dates (charcoal and bone collagen only) for Mesolithic and Neolithic sites in Portugal. For original dates and sources, see <http://intarch.ac.uk/antiquity/jacks/dates.html>

or diversify so rapidly that they are not a good marker of cultural affiliation. The neighbouring Iroquoian Huron and Neutral nations of Ontario, for which there are unusually detailed ethnohistorical sources, were described by early 17th-century French missionaries as having identical 'manners and customs'. Except for a few specific individuals, the Huron practised ossuary burial (collective burial with disarticulation), accompanied by a 'Feast of the Dead' occurring when a village moved every 10 to 15 years. In contrast, the Neutral had diverse burial types, from single graves to elaborate collective burials in which individuals were maintained to such an extent that differentiation by sex, age, status, family association and physical condition can often be discerned (Jackes 1996).

If burial patterns can be considered a defining characteristic of the Neolithic, then it was well established in Portugal, with at least some types of Neolithic burial, by 6800 BP. The Portuguese dates are at least as early as the earliest dates for French collective burials: Bougon (Deux-Sèvres) is dated about 6700 BP (Masset 1993: 45, see also Giot *et al.* 1994); in the eastern Pyrenees, the oldest collective grave in Mediterranean western Europe appears to be La Caune at Bélesta-la-Frontière where about 30 partially articulated skeletons are dated to c. 6500 BP (Zammit 1991: 241).

If domesticated animals, other than dog, are to be the defining characteristic of the Neolithic, then Caldeirão shows that sheep/goat were present by c. 7300 BP (Rowley-Conwy 1992), about the same time that full-scale agriculture was apparently well established just north of the Pyrenees. Our stable isotope studies (Lubell *et al.* 1994) show that, in at least some places in Iberia, a Neolithic diet was well established by 6800 BP.

While interpretations may differ regarding the presence of legumes (peas, lentils, chick peas), nuts, grapes and stone fruits at Mesolithic sites such as Balma de l'Abeurador in southern France (e.g. Binder 1995 citing Watez 1992), it is unarguable that such resources were available. We believe that foods of this sort were gathered and stored by Portuguese Mesolithic groups (Lubell *et al.* 1994), and that domestication of plants would not have been such a huge step for the late Mesolithic inhabitants of the Iberian Peninsula (*cf.* Hopf 1987; 1991; Holden *et al.* 1995; Zvelebil 1994). It is clear

that some elements of the Neolithic diet (wheat, barley, sheep and goat) originated to the east, but not at all clear that their introduction into Portugal necessarily involved human migrations (e.g. Lewthwaite 1986; 1988).

Many elements of the Neolithic in Portugal may be dated earlier than 7000 BP. It seems to us likely that the introduction of the Neolithic involved a slow and piecemeal intensification of many factors already present, as appears to have been the case elsewhere in western Europe except for the sudden, and as yet poorly understood, appearance of the LBK (e.g. Thorpe 1996).

Population replacement at the Mesolithic–Neolithic transition? The problem of genetic change

The coastal distribution of Cardial impressed pottery across the Maghreb (Gilman 1992; Lubell *et al.* 1992) is evidence of circum-Mediterranean contacts by sea. The diffusion of ideas and technologies, and thus new economic elements, is hardly to be questioned. The discussion here, however, is on 'demic diffusion', and the possibility of a Neolithic replacement population must be appraised before we can go further. Two lines of relevant evidence are:

- 1 direct evidence from bones, and
- 2 evidence provided by research into population genetics.

The bones

Our analyses are based on skeletons representing a minimum of 581 individuals from three Mesolithic and six Neolithic sites in the Estremadura and Alentejo regions of Portugal (TABLE 1). The chronology is based on AMS radiocarbon dates on human bone collagen (Lubell *et al.* 1994: table 1 with additional information on Caldeirão from Zilhão 1992). The weighted mean of Casa da Moura 2, 3, 4 is 5006 ± 45 b.p. (5734 BP); the date for Casa da Moura used in Lubell *et al.* (1994) is based on the weighted mean of all four available dates, including Casa da Moura 1 (6869 BP, see also Straus *et al.* 1988). Our choice of date for Casa da Moura here is founded on direct dating of three skeletons which we assume represent the majority of individuals we analysed, all excavated by Delgado (1867); it takes into account Zilhão's opinion (*in litt.* 20 January 1996; 18 August 1996) that Casa da Moura was used most intensively during the late Neolithic and thus

the skeletal sample should, in large part, be given a younger, rather than an older, date.

As discussed in Jackes & Lubell (in press), we give Furninha an estimated date slightly older than Casa da Moura: no collagen remained in the Furninha sample submitted for dating, therefore no radiocarbon date is available; on the basis of molar breadths a predicted date older than Casa da Moura is reasonable. Data on percent of tooth surfaces with caries and the occlusal/approximal caries ratio place the Furninha dental sample with Casa da Moura, and distinguish it from later material at Feteira and Fontainhas (see Lubell *et al.* 1994: figure 9a).

Craniometry

Few studies in physical anthropology consider changes in western European skeletal biology at the Mesolithic–Neolithic transition. Harding *et al.* (1990) found evidence in the means of 10 Martin measurements (Martin 1957–66) from European skulls, of a cline which did not reflect a pattern of demic expansion at the introduction of agriculture. Ahlström (1995) used six Martin measurements on seven small samples of Mesolithic and Neolithic skulls from Karelia, Latvia, Sweden, Gotland and Denmark, to propose that marginal areas of Europe would be most likely to demonstrate physical changes due to demic expansion. But the samples are so widely spread in space and time that his study is unsatisfactory.

Lalueza Fox (1996) states that craniometric data, alone among data from other areas of osteological research, support the hypothesis of Neolithic population replacement in the Iberian peninsula. He argues that the influx of Neolithic genes was sufficient to homogenize the Iberian population as represented by samples of crania from the Neolithic to modern times. Analysis of a wider range of samples, with more complete Mesolithic data, demonstrates that Neolithic to modern cranial material does not support his view (Jackes *et al.* 1997).¹

Non-metrical traits

Jackes & Lubell (in press) suggest that analyses of dental and postcranial non-metrical traits demonstrate the relationships among Portuguese

Mesolithic and Neolithic skeletal samples more convincingly than do analyses of metrical variables. Cluster analysis of eight dental and postcranial traits from five Neolithic and two Mesolithic samples showed the Mesolithic samples, as expected, to be closely related genetically. Clear separation of Mesolithic and Neolithic samples was not demonstrated.² This preliminary study, however, required the addition of some controls before the degree of separation or isolation among the sites could be interpreted correctly. We therefore include a control here; data from southern Ontario, an area exceptionally well documented in terms of ethnohistory, archaeology and human skeletal biology, will provide the means of validating our interpretation.

For this type of analysis, widely used by zoologists when studying intra-specific relationships, proportions of samples exhibiting a trait are given as theta (θ) values symmetrical around 0, such that an incidence of 50% equals a theta of zero. Sjøvold (1977) has determined that the Anscombe formula is the best modification for calculation of theta, most accurately transforming the incidences of traits, except perhaps when incidences are extremely high or low, and stabilizing the variance well. The Freeman-Tukey transformation is judged to provide slightly better variance stabilization than the Anscombe formula when sample sizes are small and incidences are correspondingly low.³

The Mean Measure of Divergence (MMD) is the summed divergences between two samples, divided by the number of traits. Jackes & Gao (in press) show that it is essential to assess the significance of the MMD value, and we have chosen Z as the most appropriate statistic. In order to confirm the Z value, we also calculate the Degree of Isolation (DI). FIGURE 3 shows the results of two different analyses of dental morphological traits comparing Portuguese Mesolithic and Neolithic samples with several Iroquois samples from southern Ontario dating from c. AD 1450–1650. These Iroquoian peoples belonged to the Huron and Neutral nations living in a marginal area to which agriculture had spread less than a thousand years before (Chapdelaine 1993) — an area of rich

1 For additional data and diagrams see <http://intarch.ac.uk/antiquity/jackes/craniometry.html>

2 For data see <http://intarch.ac.uk/antiquity/jackes/non-metric.html>

3 For formulae used to calculate genetic distances see <http://intarch.ac.uk/antiquity/jackes/non-metric.html>

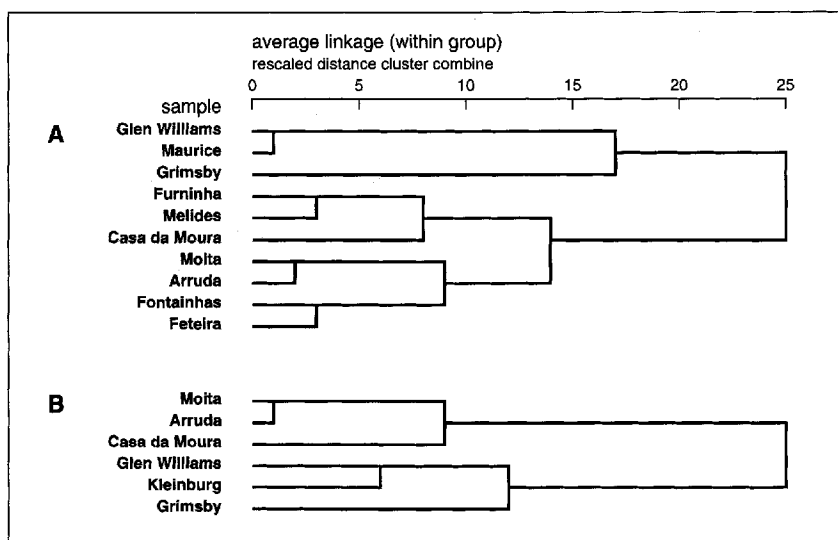


FIGURE 3A. Average linkage (within group) dendrogram derived from hierarchical cluster analysis of the Z values matrix⁴ using eight morphological features of the mandibular and maxillary molars (Freeman-Tukey transformation).

3B. Average linkage (within group) dendrogram derived from hierarchical cluster analysis of the Z values matrix⁵ using seven morphological features of the first and second mandibular and maxillary molars (Anscombe transformation).

soils and abundant game, a climate moderated by the surrounding Great Lakes, and gene flow maintained by constant trading (see Jackes 1988a: 31 regarding sexual relations between trading partners).

FIGURE 3a is based on analysis of eight dental traits from ten samples using the Freeman-Tukey transformation, required here because of small sample sizes. Moita and Arruda cannot be regarded as different from the other Portuguese samples. However, the lack of significant differences might be due to inadequate sample sizes, rather than to genetic relationships, a possibility confirmed by examination of some of the non-significant values.⁶

FIGURE 3b is based on only seven traits from seven samples — due to the exigencies of finding suitable comparative material. We have chosen standard traits for which inter- and intra-observer error should be minimal (e.g. only positive expressions of the Carabelli trait) and for which different attrition rates should make little difference in observations (e.g. avoiding the observation of cusps 5, 6 and 7). We have

used only dentitions still in bone, so that there will be no circularity in the identification of loose teeth by morphology, the morphology then being analysed by tooth. We have used only those samples large enough to give reliable results (between 45 and 265 average number of observable teeth in any pairs of comparisons here — compared with 12 to 60 in FIGURE 3a) and we have avoided, so far as is possible, traits such as the protostylid which are commonly close to 0% in expression. We have used one side only to avoid any bias caused by taphonomic differences between the Mesolithic and Neolithic sites which might have resulted in increased numbers of right/left pairs of teeth in Mesolithic samples.

Only two comparisons are not significantly different: Moita and Arruda, to be expected since we believe them to have represented one breeding group; Glen Williams (Hartney 1978; Grey 1982) and Kleinburg (Jackes 1977; Wright 1977) — ossuary sites to the north and east of Toronto, separated by around 30 km and probably less than 200 years, the former being late

4 See TABLES 2 & 3 at <http://intarch.ac.uk/antiquity/jackes/non-metric.html>

5 See TABLES 4 & 5 at <http://intarch.ac.uk/antiquity/jackes/non-metric.html>

6 Data available at <http://intarch.ac.uk/antiquity/jackes/non-metric.html>

prehistoric and the latter protohistoric. What is relevant to our argument is that the significant difference between Moita and Casa da Moura ($Z = 2.86$, $DI = .069$), separated by c. 100 km across the Tagus River and as much as 2000 years, is considerably less significant than the difference between Kleinburg and Grimsby ($Z = 5.53$, $DI = .131$) (Jackes 1988a; Tait 1988), on a documented trade route, separated by less than 100 km without a significant geographic barrier and considerably less than 100 years. In a comparison of five Ontario Iroquoian samples using 20 dental traits (Jackes 1988a), Kleinburg and Grimsby were found to be the most significantly different. The same study, using 16 cranial traits and nine samples, found Glen Williams and Kleinburg to be among the three samples most different from Grimsby.

The Portuguese samples are as close genetically as those within southern Ontario (representing people regarded as culturally homogeneous by Europeans who lived with them in the early 17th century). The degree of this cultural homogeneity may be subject to debate (Jackes 1996), but there is no doubt that they were biologically homogeneous. Analysis based on dental morphology therefore indicates genetic continuity between the Portuguese Mesolithic and Neolithic.

Can we be confident in using Casa da Moura as representative of the Portuguese Neolithic? The limited range of Mesolithic samples gives the impression that the Portuguese Neolithic population was more heterogeneous (for example, in non-metrical trait frequencies, cranial size and shape and dental pathology) than the Mesolithic, an impression deepened by the timespan represented by the Neolithic sites. Neolithic heterogeneity might indicate sporadic settlement by immigrants: Zilhão, however, has 'never argued for *separate* colonizations of the Portuguese coast' (*in litt.* 18 August 1996, emphasis original). From this standpoint, Casa da Moura can be taken as an exemplar of post-Mesolithic Portugal. But caution is necessary; studies of additional Mesolithic and Neolithic skeletal samples are essential.

The Mesolithic and Neolithic sites analysed here were all utilized over long time periods, perhaps as long as 2000 years in some cases, possibly masking biological variations resulting from trends through time. As pointed out in Jackes & Lubell (*in press*), while we see and

expect to see a degree of Neolithic heterogeneity, based on the geographical and chronological spread of the sites analysed, our Mesolithic samples come from sites that represent an extremely restricted area. We have no basis for knowing the extent of Mesolithic heterogeneity. We can only assume that it must have been as great as, or greater than the evident Neolithic heterogeneity, since it has been possible to demonstrate that the samples from Moita and Arruda are not identical and to show chronological trends between these two Mesolithic sites (e.g. Meiklejohn & Schentag 1988; Lubell *et al.* 1994).

Population genetics

Jackes *et al.* (1997) have shown that there is good cause to question the demic diffusion model as proposed by Cavalli-Sforza and colleagues (e.g. Ammerman & Cavalli-Sforza 1984; Bertranpetit & Cavalli-Sforza 1991; Calafell & Bertranpetit 1993; Cavalli-Sforza *et al.* 1994), and used by others (e.g. Lalueza Fox 1996) to argue for Neolithic population replacement in Iberia. Recent work on mtDNA variation and HLA haplotypes (Arnaiz-Villena *et al.* 1995; Côté-Real *et al.* 1996; Martínez-Laso *et al.* 1995; Richards *et al.* 1996 and Semino *et al.* 1996 among others) shows that genetic data which appeared to support the model of demic diffusion for Neolithic origins in the Iberian Peninsula were incomplete and interpreted in such a way as to exclude alternative models (Jackes *et al.* 1997; see also Fix 1996). The recent paper by Moral *et al.* (1997) confirms the conclusions we reached based on blood group, red cell enzyme and serum protein data. While Iberian archaeological data can be interpreted as evidence for discontinuity at the Mesolithic–Neolithic transition (Zilhão 1993; *in press*), both human osteological data and research in population genetics suggest otherwise (Lubell *et al.* 1994; Jackes *et al.* 1997). Neolithic immigrants are unlikely to have contributed significantly to the later Iberian gene pool.

In summary, while we would not deny the possibility of sporadic transcoastal incursions from any direction around the Iberian Peninsula, we see no evidence for immigration at the levels required to alter the gene pool. This being so, we will now examine human skeletal evidence for changes across the Mesolithic–Neolithic transition, to try to understand why and how human biology may alter during times of transition.

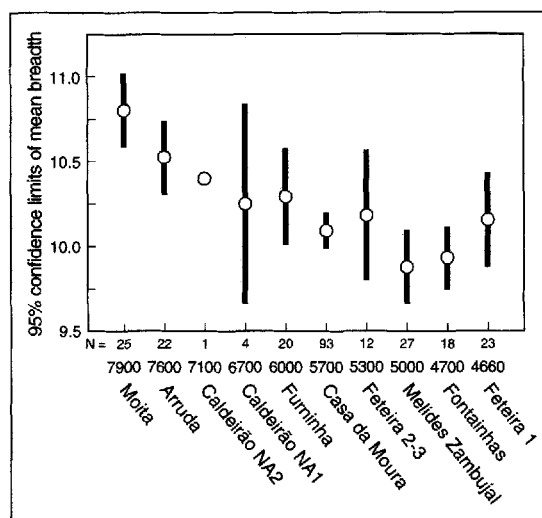


FIGURE 4. 95% confidence limits of mean breadth measurements in mm for lower second molars. Sample size, age in years BP, and site are shown along the horizontal axis.⁷

Evidence for changes at the Mesolithic–Neolithic transition attributable to factors other than population replacement

Beginning in the Mesolithic and intensifying into the Neolithic, the Portuguese diet changed towards one that was more terrestrial-based, less abrasive and less cariogenic (Lubell *et al.* 1994). A basic assumption on the effect of the introduction of agriculture to dietary change is contradicted by our data. While a maize-based diet may have been inimical to teeth in the Americas, in southern Europe the Mesolithic diet entailed more, not less, dental pathology than the Neolithic diet (*contra* Lalueza Fox 1996). We have discussed this in a number of papers — considering also the sampling and methodological problems which complicate caries frequency comparisons (e.g. Jackes & Lubell 1995; Meiklejohn *et al.* 1992; Schentag & Meiklejohn n.d.). Despite any sample bias, dental pathology decreases during the late Mesolithic and into the early Neolithic; it becomes variable in the later Neolithic.

Lower second molars

But it is true, as predicted by the hypothesis outlined at the beginning of this paper, that Portuguese teeth became smaller, and continued

to become smaller (FIGURE 4), right up to modern times (Galera & Cunha 1993). We restrict our analysis to lower second molars; for taphonomic reasons they provide the largest sample (Jackes & Lubell 1995; Linaza Peña & Basabe 1987), and they appear to provide the clearest evidence for change (Galera 1989; Meiklejohn & Schentag 1988). The sample consists of 245 lower second molars without extreme wear; FIGURE 4 shows that lower molars decrease in breadth down to around 5000 BP.

Testing the relative variance of each set of tooth breadths, as we have done for all the data discussed (using the Levene test for variance homogeneity available in SPSS), gives a fair degree of certainty that sexual dimorphism did not suddenly shift during the period from 8000 to 4500 BP.

Is dental size reduction due to simplification of tooth morphology as a response to increased pathology? Of the Mesolithic right second mandibular molars, 98% (52/53) are four-cusped, compared with 58.5% (24/41) from Casa da Moura and 70.6% (12/17) from Melides. Neolithic teeth are therefore more likely to be complex five-cusped structures than are Mesolithic teeth, and, as stated above, dental pathology is reduced into the Neolithic.

Armélagos *et al.* (1989), summarizing hypotheses on the reasons for dental reduction, have shown that, for Nubia, mandibular body length decreases as tooth dimensions decrease. The Portuguese Neolithic collections do not provide us with unbroken mandibles; data from Meiklejohn & Schentag (n.d.) indicate that palatal length seems to decrease from the Mesolithic into the Neolithic. Despite small sample sizes for all but Moita, there is a trend for decreased palatal length (Martin measurement 62) from nearly 47 mm at Moita, to 45 mm at Arruda, to 42 mm at Casa da Moura, to just over 41 mm at Melides Zambujal — an overall decrease of 12.8%. There is a clear correlation between reductions in tooth size and jaw dimensions.

Postcranial measurements: body size

Is the reduction in lower molar size a simple reflection of reduced body size? To answer this question we must take burial patterns into account. Mesolithic burials were in shell-midden deposits as more-or-less complete individuals.

⁷ For data see TABLE 1 at <http://intarch.ac.uk/antiquity/jackes/zmetric.html>

But almost all the Neolithic material we have analysed comes from ossuaries; the one exception is Caldeirão where, as Zilhão (1992) emphasizes, bioturbation is an important factor. This has necessitated analysis by skeletal elements rather than whole skeletons when comparing Mesolithic and Neolithic Portuguese.

Metatarsals

A neutral bone with constant weight bearing may provide a control relative to overall body size. Since people must continue walking, the robusticity of feet might serve in this capacity. Using a sample of 302 third metatarsals, we have shown that from the Mesolithic to the Neolithic, the Portuguese were neither getting smaller, nor significantly larger (Jackes & Lubell in press: figure 5).

Femora

To test this stability further, we used a sample of 521 femora, first ensuring as far as possible that no broken juvenile shafts were included and that sex ratios were not biased. Far from Neolithic people getting smaller, it appears that the proximal femoral shaft increased in size, fairly consistently in the transverse dimension, less consistently in the anterior-posterior diameter. An increase in proximal transverse dimension of the femur is most likely to reflect changes in activity. In two North American samples, from Pecos Pueblo and the Georgia coast, Ruff *et al.* (1984) show that femoral mid-shaft and subtrochanteric dimensions altered with the transition to agriculture; genetic change was not adduced as the cause; rather, they propose reduced mechanical stress and — especially for males — altered mechanical stresses, as the major factor. Bridges (1989), on the other hand, finding that agriculturalist long bone diaphyses in Alabama are more robust than those of their Archaic predecessors, especially in males, proposed that activities for males were more strenuous after the introduction of agriculture (could the work of clearing the forest cover explain this?). The mid-shaft circumference of femora is particularly important to Bridges' argument. In the same way, the increase in femoral circumference for left femora from Arruda to Casa da Moura is significant (means of 79.6 mm, $n = 41$ and 82.7 mm, n

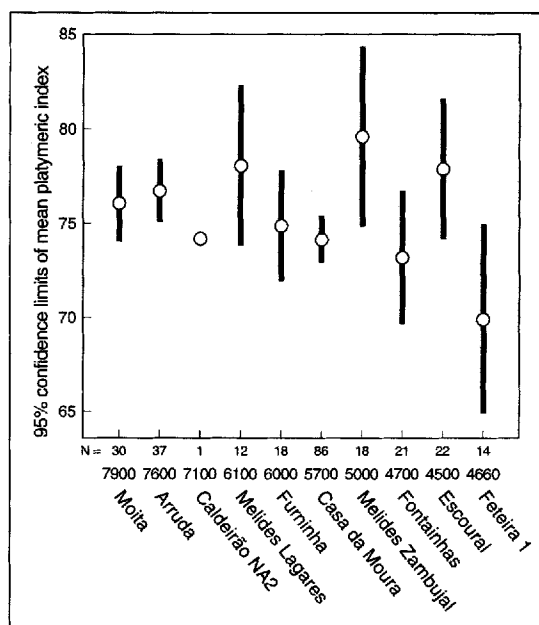


FIGURE 5. 95% confidence limits of the mean platymetric index of the proximal shaft of adult left femora. Sample size, age in years BP, and site are shown along the horizontal axis. Feteira sample includes Level 1 together with those from unknown level assumed to be mostly from Level 1.⁸

= 86, a significant difference for t , separate variances estimate, $p = .010$).

The apparent trend towards increased robusticity in Portuguese femora may therefore result from changes in shaft shape, since long bones are so clearly plastic they may alter in shape without genetic change. Activity patterns may mediate femoral shape.

We can discern no significant gender-based difference in the proximal femoral index in the Mesolithic material. Side differences are evident: the left proximal femur of Portuguese Mesolithic and Neolithic adults has a significantly lower platymetric index than the right (left, $n = 246$, mean = 75.1; right, $n = 240$, mean = 77.3; equal variances, $p = .000$).

The finding of side differences suggests that biomechanical factors, activity and terrain, but not genetics, must be considered important to platymeria. The low sandy coast around Melides seems to lead to higher proximal indices than the rocky coast and limestone country of the Estremadura: for this sample of left femora from

8 For data see TABLE 2 at <http://intarch.ac.uk/antiquity/jackes/metric.html>

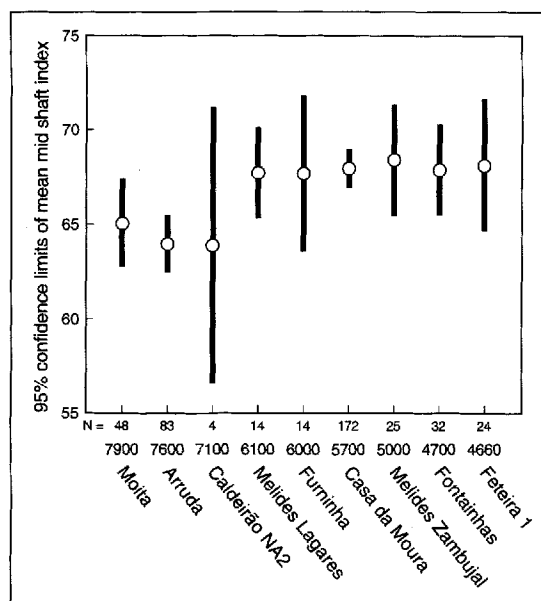


FIGURE 6. 95% confidence limits of the mean adult tibial mid-shaft index (transverse*100/sagittal diameter). Sample size, age in years BP, and site are shown along the horizontal axis. Feteira sample includes Level 1 together with those from unknown level assumed to be mostly from Level 1.⁹

Portugal, it appears that the less rugged the terrain, the higher the index, just as one might predict from the hypothesis that lower mechanical stresses lead to a rounder proximal femoral shaft cross-section. As a possible check on this interpretation, we include in FIGURE 5 data on Escoural (Isidoro 1981), a Neolithic ossuary to the north and inland of Melides and dated to a mean of c. 4500 BP. The data appear comparable with our measurements of the proximal femoral shaft, suggesting that geography or topography, rather than chronology, mediates femoral shape.

In FIGURE 5 we use only the left femur since there is inequality of variances across sites for pooled sides, but not for the left side alone. We include the one femur (P12-133/O12-35, ♂, from NA2) from Caldeirão for which data are available (Jackes & Lubell 1992). The mid-shaft index displays less of a trend than the proximal, no doubt related to the fact that the mid-shaft index has a stronger correlation (negative) with the sex-dependent maximum shaft diam-

eter, than does the proximal index (mid-shaft $r = -.414$, df 326; cf. proximal $r = -.270$, df 262). All femoral proximal index means are within the limits of platymeria, that is, all sites analysed have proximal femoral shaft indices below 85, indicating marked flattening. More recent Portuguese femora are slightly rounder: in the Eira Pedrinha sample, which is probably post-Neolithic (Arnaud 1982; Garralda & Mesa 1984), the left platymeric index is about 74.4; Visigothic period platymeria values are about 78 (Cunha & Neto 1955); those for 19th-century Portuguese from the Coimbra collection are 84 for males and 80 for females (Tamagnini & Vieira de Campos 1949).

Tibiae

The tibia may be especially relevant in a consideration of long bone plasticity. While Portuguese Mesolithic and Neolithic tibiae remain relatively stable in size as measured by the shaft dimensions, there is a clear distinction between Mesolithic and Neolithic people, based on our sample of 423 adult tibia (FIGURE 6).

The index expressing the shape of the mid-shaft of the tibia is lower in Mesolithic than in Neolithic samples, that is, the shin bone is narrow relative to ventro-dorsal depth, a condition referred to as 'sabre-shinned'. The four tibial shafts from Caldeirão NA2 are included in FIGURE 6, although with such a small sample size it is impossible to note more than an apparent trend. Testing the equality of the means and variances for Arruda and Caldeirão shows no significant difference. Less obvious — and unsurprising in view of the unsatisfactory sample sizes for both sites — is that there is no statistically significant difference between Melides (Lagares) and Caldeirão NA2. Arruda and Casa da Moura are significantly different ($p = .004$, variances homogeneous). The Samouqueira 1 tibia, dated at 7224 BP, has a mid-shaft index of 64.5 (Lubell & Jackes 1985). As this is a single specimen, no comparison is possible.

The index more commonly recorded in the literature for the tibial shaft is the platycnemic index (correlated in this data set with the mid-shaft index at $r = .646$, $n = 294$, $p = .000$). Anderman (1976) has questioned the value of this index because it is measured at the nutrient foramen, rather than a fixed point. The values

9 For data see TABLE 3 at <http://intarch.ac.uk/antiquity/jackes/metric.html>

for Escoural certainly suggest variation in measurement techniques (Isidoro 1981), and mid-shaft indices are provided in the Portuguese literature (e.g. Sueiro & Fernandes 1933a; 1938; Mendes Corrêa & Teixeira 1949), so we choose to illustrate the mid-shaft index here.

The trend is for a change to rounder tibial shafts between 6000 and 7000 years ago, the same trend recorded in Greece from the Palaeolithic on, which Angel (1971: 85–6) explained as due to a change in activity. In Portugal the trend began in the Neolithic (e.g. Eira Pedrinha at c. 69·4) and continued through the Roman period (mean index of c. 76·6 (Sueiro & Fernandes 1933b)) and into the Visigothic (at about AD 600, c. 77·2). However, urban 19th-century Portuguese (70·96; Serra *et al.* 1952) have flatter tibiae again. This is unusual: steep cobblestone streets may explain this reversal of the trend, since the explanation for platycnemia that has been best tested (Lovejoy *et al.* 1976) is that a flat bone has greater strength in torsion.

Are there other possible explanations? Does protein deficiency cause flat bones (cf. Renfrew & Bahn 1991: 398, based on the tragically uncompleted work of Sarah Biesel at Herculaneum)? According to the early-farmer hypothesis outlined above, it should be Neolithic people who have flat bones. But to argue that the flat tibiae of the Mesolithic population results from protein deficiency ignores the faunal evidence: the Mesolithic Portuguese diet was protein-rich — shellfish (oysters, mussels and clams), venison, wild boar and rabbits (Lentacker 1991).

Humeri

The evidence, then, is that the lower limbs may change somewhat in *shape*, but not in *size*. However, Formicola (1986) has claimed that, even if the lower limbs do not get smaller in the Neolithic, the upper limbs do (see also Bridges 1989). Once again, none of the tests on means or variances indicate differences in that direction for Portuguese samples. Whether in minimum or maximum shaft diameters, only Moita is different from the others. Moita has quite small humerus dimensions, but Arruda has less differentiation from the Neolithic. A trend, established soon after 8000 BP, continued on into the Neolithic, with the largest humeri found just before 6000 BP at Casa da Moura and Melides Lagares (Jackes & Lubell in press).

We have seen that tooth size might decrease, but that body size does not. Can we determine whether stature changes?

Stature and body proportions

Mesolithic people were short. Mesolithic males, with an average height of about 160 cm (Lubell & Jackes 1985: table 6), were nearly 10 cm shorter than 19th-century Portuguese males in the Coimbra collections (Queiros Lopes & Serra 1944). But Sobral (1990), reporting on the stature of rural and urban conscripts for four administrative areas in central and southern Portugal from 1930 to 1980, shows a range of means going from 162 to 171 cm (rural males were shorter). We have no idea of Neolithic stature. Not only are sample sizes too small and unrepresentative, but in the absence of complete individuals we cannot be certain of the proportions of bones relative to each other. In proportions of limb segments, medieval and 19th-century Portuguese are similar — Mesolithic Portuguese were quite different; they had short humeri in proportion to femora, longer radii in proportion to humeri, and longer tibiae in proportion to femora. So the arms were short and the distal portions of the limbs were longer than in modern western Europeans. While the Melides sample appears to have body proportions resembling the Mesolithic population, rather than more recent Portuguese, it is impossible to confirm this for any of the other Neolithic sites because of the lack of identifiable individuals in ossuaries.

Population structure and health

The Mesolithic population was relatively sedentary — base camps are a definite possibility as determined from the age and sex breakdown of the human burials as well as faunal analyses (e.g. Lentacker 1991). The Neolithic population still relied on hunting and gathering to some extent, so a certain amount of seasonal movement among some sectors of the population continued into the Neolithic. Medo Tojeiro is a coastal shell midden with a Neolithic component probably dated to c. 6200 BP, while the upper levels of Arruda have been dated to c. 5900 BP. We certainly have an individual from 'Neolithic' Gruta do Lagar (Melides), dated at 6100 BP, who maintained a 'Mesolithic' style of diet as determined by stable isotope analyses.

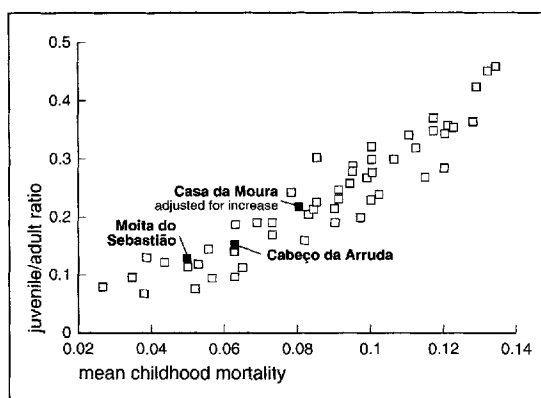


FIGURE 7. *Demographic change, showing demographic estimators for Moita do Sebastião and Cabeço da Arruda, with Casa da Moura adjusted for non-stationary demographic status, plotted against 51 archaeological samples sufficiently large for reliable statistical analysis.*

As there is some evidence of relatively high continuity in the degree of sedentary settlement between the Mesolithic and the Neolithic, lack of an increase in rates of skeletal infection does not surprise us. Apart from one individual at Casa da Moura with cavitation and collapse of vertebrae at the thoraco-lumbar junction, there is nothing like the extreme skeletal pathology known from North American or Near Eastern agricultural sites. There is perhaps an increase in cribra orbitalia, which might indicate iron deficiency in children. Pitting of the orbit is likely to appear in young children and to heal in adulthood. Since the average age at death is higher in the Mesolithic than the Neolithic samples, it is meaningless to postulate poor nutrition in the Neolithic population based on age-related condition such as cribra orbitalia. Furthermore, the skulls of adults seem to be very under-represented in the Neolithic sites. There were at least 214 individuals buried at Casa da Moura (Jackes 1992), but less than a third are represented by orbits, and most of the orbits are of children or young females — precisely those in whom we would expect lesions of cribra orbitalia to occur.

Fertility

Do we have evidence of increasing fertility? The answer is yes, despite Pennington's (1996) contention that the indication is for greater childhood survival, rather than higher birth rates. The two possibilities cannot be distinguished

from age at death distributions as employed here. However, low infant and early childhood mortality is not followed by higher middle childhood and adolescent mortality; the juvenile/adult ratio (deaths at ages 5 to 14-99/deaths after age 25) used in FIGURE 7 remains a good estimator of the shape of the population pyramid (*cf.* Bocquet-Appel & Masset 1996: 580 *ff.*) which is determined most importantly by fertility rates. We continue to emphasize fertility, and note that the earlier weaning and appropriate supplements to breast milk provided by domesticates may or may not increase childhood survival, depending on a number of factors, but are very likely to increase fertility (Jackes 1994).

Increased fertility might elicit non-genetic change, in that increased fertility rates could reduce the birth weight and nutrition level of children if the mother has more than one live born child each two or three years. We believe we *can* demonstrate increased fertility in the Neolithic, using the estimators derived from the proportions of juveniles aged between 5 and 14-99 in a skeletal sample (mean childhood mortality or MCM, see Jackes 1992: 215 *ff.*). There is a mathematical relationship between an increased MCM and an increased level of fertility; it is probable that while Mesolithic women had four children on the average, Neolithic women had about six. The logic behind this (Jackes 1988b; 1992; 1994) allows us to show that the population at Casa da Moura was probably increasing by close to 1% (FIGURE 7), despite the large numbers of very young infants, even pre-term neonates, buried at Arruda, and the relative absence of young infants among the dead at Casa da Moura (infant under-representation is a common feature of ossuaries).

Population density

The Mesolithic family groups living along the Muge must have been small. We calculate that only about three women of child-bearing age in each generation lived in the area of Arruda and Moita (together with Cabeço da Amoreira, a smaller site, adjacent to Moita and perhaps slightly later in date, from which the skeletal sample remains unstudied). Only a small group is necessary to account for all the dead.

The ossuaries or collective burials of the Neolithic make one think that the population had increased enormously, and that there were

large settlements. However, one small group could contribute all the dead, just as with the Mesolithic midden burials. At Casa da Moura there may have been only one woman of child-bearing age in each generation.

We suggest that the population as a whole was increasing at about 1%, an increase which can be accommodated by the wider range of geography covered by the Neolithic sites. The distribution map of Portuguese Neolithic megalithic monuments or burial caves is formidably dense (Kalb 1991), and dramatically different from the distribution map of known Mesolithic sites. Yet the density of population did not result in high rates of infection. In the confines of the Nile Valley, perhaps, but not in Portugal.

An increase in fertility could alter some population characteristics, simply because of the added stress placed on the mother's system by more closely spaced pregnancies. Macchiarelli & Bondioli (1986) recall the demonstration by Garn *et al.* (1979) that the health of pregnant women can influence crown size in the baby's teeth. y'Edynak (1989) has summarized evidence that prenatal and lactational maternal deficiencies in vitamin A and protein may cause reduction in tooth size.

There is decrease in Mesolithic dental size (Meiklejohn & Schentag 1988), but we cannot ascribe this to a diet poor in vitamin A and protein when fish oils, liver and meat were so abundantly available. We have unpublished data on the localized circular enamel defects in deciduous canine teeth which have been attributed to either calcium (Skinner & Hung 1989; Lukacs 1991) or vitamin A deficiencies (Skinner *et al.* 1994). The rate and distribution of this defect remains about the same — 40% — in the children from Moita, Arruda and Casa da Moura. Whatever interpretation is put on this defect, whether in terms of genetics or diet or stress, it can only be seen as a sign of population stability and/or continuity. Whatever the aetiology, Casa da Moura deciduous canines with defects are not smaller than those without.

There is fairly clear evidence that adolescent Nubians in Wadi Halfa in the 1960s showed extraordinary sexual dimorphism in tooth size (Smith & Shegev 1988). This dimorphism could be ascribed to postnatal and childhood deprivation of females in times of great stress (see also Keene 1991: table 4). FIGURE 8 (based on the work of Mizoguchi 1993) may best be in-

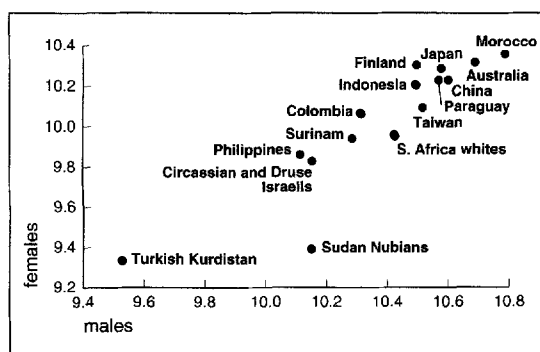


FIGURE 8. Mean bucco-lingual diameters in mm for lower second molars in modern populations, males vs females (data from Mizoguchi 1993).

terpreted as showing that the diet of children may well affect tooth size. Deprivation may affect tooth size more than skeletal size because there can be catch-up growth for skeletons, but not for teeth.

While Mizoguchi (1993) has shown that a wheat-based diet correlates to some extent with decreased dental size, the trend was not necessarily directly related to the introduction of agriculture. In Europe and elsewhere, the trend seems to have been established thousands of years before, and we clearly cannot attribute such a trend to progressively poorer nutrition — based on cereals — from the late Palaeolithic and throughout the entire Mesolithic.

Thus a reduction in molar breadths during the Mesolithic–Neolithic transition cannot be ascribed either to population replacement or to a revolutionary change in diet. Since the 32 adult teeth change in breadth at various rates and at different times and places during the Holocene, it is obvious that no single explanation can be advanced. As El-Nofely & Tawfik (1995: 59) say, 'determination of crown size is not totally genetic and the responsible factors are not identically acting on all teeth'.

Adult second molars, the teeth we have discussed in this paper, begin to develop around 36 months — after the age of weaning in most populations. Our reconstruction of the Casa da Moura population might entail breastfeeding for slightly over 24 months, and birth intervals of close to 36 months. Children of three years might therefore be vulnerable to dietary deprivation because of the presence of a newborn sibling. There may have been short-term periods of poor nutrition, affecting the second

molars, but we cannot posit general dietary deprivation.

Conclusion

Dental reduction is often said to be one of the effects of the shift to agriculture. And, for Portugal at the period of the Mesolithic-Neolithic transition, this is almost the only skeletal characteristic confirmed as altering. Yet the change was *not* caused by the subsistence shift; it was the continuation of a trend which began much earlier and which was not the result of decreased body size (though there was probably a concomitant shortening of the dental arcade). Nor was dental reduction associated with increased dental pathology or of changes in dental morphology. While increased fertility might be a factor in Neolithic Portuguese dental reduction, we certainly cannot invoke impoverished diets during the whole period of childhood when tooth crowns form.

An increase in fertility has long been proposed as either accompanying or initiating the transition to agriculture. On the evidence of skeletal biology, we are able to:

- 1 postulate an increase in fertility during the period of the adoption of domesticates by the Mesolithic population of Portugal, and
- 2 conclude that the diet was not greatly impoverished by the introduction of agriculture.

We find no evidence that the comfortable way of life of the Portuguese Mesolithic was replaced by a wretched and unhealthy Neolithic existence.

Future studies may discern changes in skeletal biology towards the end of the Neolithic which might in part be responses to agricul-

tural intensification, but we suggest that biological changes which could result from a subsistence shift at the beginning of the Neolithic will not be shown to be significant or to have had a negative effect on the population.

We find no evidence for biological discontinuity amongst human groups in Portugal across the Mesolithic-Neolithic transition; all our biological data argue against the model of demic diffusion and corroborate more recent interpretations based on mtDNA and HLA.

We recognize that there are archaeological distinctions between Mesolithic and Neolithic artefact assemblages, burial customs and settlement patterns. But we point out that our studies have found trends already under way towards the end of the Mesolithic in Portugal, trends suggesting slow change in dietary regimes, fertility levels and activities.

Note. Additional supplementary material relating to this article is available on the ANTIQUITY web page, currently at <http://intarch.ac.uk/antiquity>

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