Prehistoric Migration in Europe: Strontium Isotope Analysis of Early Neolithic Skeletons

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The term Linearbandkeramik (LBK) is traditionally used to describe the first farmers of central Europe and the pottery they introduced approximately 7,500 years ago. Radiocarbon dates for the LBK suggest a rapid spread into central Europe from its origin on the Hungarian Plain. The geographic homogeneity of LBK artifacts and architecture, along with domesticated plants and animals with origins in southwestern Asia, seems to be reflective of a "wave" of colonization by migrating farmers, who may also have brought Indo-European languages and genes (Childe 1929, Quitta 1964, Ammerman and Cavalli-Sforza 1984, Bogucki 1988, Lüning, Kloos, and Albert 1989, Kreuz 1990, Price, Gebauer, and Keeley 1995, Price 2000, Troy et al. 2001).

An alternative view is that the LBK spread through the adoption of agriculture by the indigenous hunter-gatherers (Tillmann 1993, Whittle 1996) or a combination of colonization and indigenous adoption (Gronenborn 1999, Zvelebil and Lillie 2000). Indigenous people along and west of the Rhine River may have made "La Hoguette" pottery before the LBK era (Jeunesse 1987, Lüning, Kloos, and Albert 1989). In western Germany, flint tools from the earliest LBK exhibit continuity with preceding Mesolithic forms, and many are made of flint quarried from areas populated only by Mesolithic groups at that time (Mauvilly 1997, Gronenborn 1999). Mitochondrial DNA (mtDNA) studies support the case for indigenous adoption (Richards et al. 1996, 2000), although such evidence is indirect because the mtDNA has come from modern Europeans.

The two views have been difficult to resolve through architecture or artifacts because ideas or trade items can spread without people's migrating. To examine human mobility directly, we measured strontium isotopes in human skeletons from three LBK cemeteries in southwestern Germany. Strontium substitutes for calcium in the hydroxyapatite mineral of skeletal tissue, and strontium isotopes in prehistoric human teeth and bones provide a geochemical signature of the place of residence. The $^{87}Sr/^{86}Sr$ values in natural rocks vary from older granites, with $^{87}Sr/^{86}Sr$ ratios typically above 0.710 and as high as 0.740, to younger basalts, with lower $^{87}Sr/^{86}Sr$ ratios around 0.703 to 0.704. These differences, all in the third decimal place, are easily detected by thermal ionization mass spectrometry (TIMS), with which $^{87}Sr/^{86}Sr$ can be measured with a typical precision of 0.00001 or better.

Because of their large atomic mass, strontium isotopes retain the same $^{87}Sr/^{86}Sr$ ratio as they pass from weathered rocks through soils to the food chain (Hurst and Davis 1981, Beard and Johnson 2000). Even if there were some mass-dependent fractionation of strontium along biogeochemical pathways, it would be corrected for upon measurement by mass spectrometry, as strontium ratios are normalized to the constant value of $^{86}Sr/^{88}Sr$ in natural rocks (Beard and Johnson 2000). In other words, strontium isotopic signatures faithfully make their way from local geologic materials ultimately into the human skeleton.

One can identify migrant individuals who moved between geologic regions by comparing the isotope signature in adult teeth, composed between four and twelve years of age, with that in the bones, with characteristic turnover times varying between 6 and 20 years for different bones of the body (Parfitt 1983, Ericson 1985, Price et al. 1994, Grupe et al. 1997, Grupe, Price, and Söllner

1999). If the teeth and bones of an adult have different signatures, then that person spent his or her early and final years in different geochemical provinces (Ericson 1989, Sealy et al. 1991, Price et al. 1994, Price, Grupe, and Schröter 1994, Price, Burton, and Bentley 2001). Because bone phosphate is much more subject to postburial contamination than the hydroxyapatite of tooth enamel (Price, Burton, and Bentley 2001), it is often more reliable to compare each individual tooth value with a "local" $^{87}Sr/^{86}Sr$ range defined for the recovery site rather than with the different individual bone values. Here we define the local signature at a site as within two standard deviations of the average $^{87}Sr/^{86}Sr$ of the sample of human bones from the site. This conservative definition is unlikely to misidentify locals as immigrants (Grupe et al. 1997, Grupe, Price, and Söllner 1999, Price, Burton, and Bentley 2001). Local ranges in surrounding areas can be characterized by indicators such as the $^{87}Sr/^{86}Sr$ in streamwaters or (better) the skeletons or shells of local animals (Price, Burton, and Bentley 2001).

Our study area in southwestern Germany is geochemically appropriate for this investigation. Higher $^{87}Sr/^{86}Sr$ values (> 0.715) are found in area uplands underlain by granites, including (fig. 1) the Odenwald (near Flomborn and Schwetzingen), the Bavarian Forest (near Dillingen), and the Vosges and Black Forest mountains (Grupe et al. 1997, Tricca et al. 1999, Probst et al. 2000, Price et al. 2001). These uplands are isotopically distinct from most of the regional lowlands ($^{87}Sr/^{86}Sr < 0.710$). Elsewhere, loess sediment can have higher $^{87}Sr/^{86}Sr$ values, ranging from 0.713 to 0.716 in Brittany and Normandy, for example (Gallet et al. 1998). Within the study region, however, loess patches appear to be unlikely sources for the higher $^{87}Sr/^{86}Sr$ values because (1) loess in southern Germany is rich in carbonates derived from the Alps (Mahaney and Andres 1991, Schnetger 1992, Hatté et al. 1998), for which the expected $^{87}Sr/^{86}Sr$ is about 0.7080–0.7095 and (2) snail and human bone samples so far analyzed from Dillingen and Flomborn, both on loess, exhibit $^{87}Sr/^{86}Sr$ below 0.710 (Bentley 2001: table 5.1).

We sampled human skeletal remains from LBK cemeteries and found a high incidence of migration at the LBK cemeteries of Flomborn and Schwetzingen, near Heidelberg, and at Dillingen, near Ulm (fig. 1, table 1) [The data are presented in the electronic edition of this issue on the journal's web page]. We identified 7 nonlocals out of the 11 individuals (64%) sampled from Flomborn, 9 out of 36 (25%) from Schwetzingen, and 11 out of 17 (65%) from Dillingen. Four patterns have emerged from the data (fig. 2, table 2) which, taken together, suggest that nonlocals in these LBK cemeteries had social identities different from the locals. These patterns are as follows:

1. Nonlocal females are common. Of the individuals

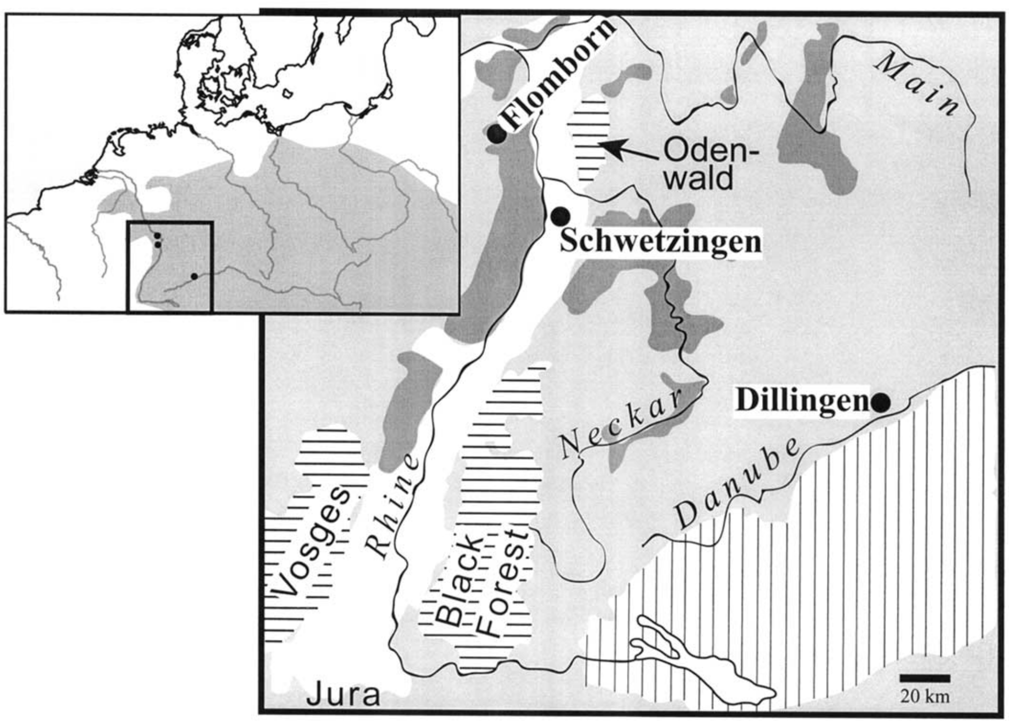

FIG. 1. *Simplified geologic map of southwestern Germany, showing sample sites.* Vertical stripes, *Palaeozoic granite and gneiss* ($^{87}Sr/^{86}Sr > 0.715$); light gray, *Triassic and Jurassic sedimentary* ($^{87}Sr/^{86}Sr \sim 0.708-0.709$); dark gray, *loess* ($^{87}Sr/^{86}Sr \sim 0.708-0.7095$); white, *Pliocene and Quaternary alluvium* ($^{87}Sr/^{86}Sr \sim 0.708-0.709$); horizontal stripes, *Tertiary molasse and glacial moraine.* Inset*: the distribution of LBK settlement ca. 5300 B.C.*

TABLE 1
Immigration at Three LBK Cemeteries as Determined by $^{87}Sr/^{86}Sr$ in Tooth Enamel

Site	Era	Excavated Burials	*n*	Male	Female	?	Total Immigrants
Flomborn	Early LBK	85	11	2/3 (67%)	3/4 (75%)	1/4	64%
Schwetzingen	Late LBK	202	36	3/16 (19%)	5/16 (31%)	1/4	25%
Dillingen	Middle-Late LBK	27	17	6/12 (50%)	5/5 (100%)	–	65%

NOTE: "Immigrant" is defined as beyond two standard deviations of the average bone value at the site.

at Flomborn that have been identified by sex, all 4 (100%) of the females are nonlocals (fig. 2, *a*). At Schwetzingen, 5 of 16 females (31%) are nonlocals, all with tooth-enamel values above the local range (fig. 2, *b*). Three of the 16 males (19%) are nonlocals, but 2 of those have tooth values below the local range, that is, characteristic of a different geochemical zone from that of individuals above the range. Thus five of the six tooth values above the local range at Schwetzingen are from females. At Dillingen (fig. 2, *c*), all 5 (100%) of the females are nonlocals (all above the local range) compared with 6 out of 12 nonlocal males (5 above the local range, 1 below).

2. $^{87}Sr/^{86}Sr$ may correlate with burial orientation. At Schwetzingen, 7 (30%) of the 23 burials with head directions ranging from north to east are nonlocals, compared with two nonlocals (15%) among the 13 burials facing in other directions (fig. 2). At Flomborn, 4 (80%) of the 5 sampled west-facing burials are immigrants.

3. Many nonlocals are buried without a shoe-last adze (a characteristic artifact of the LBK). At both Flomborn and Dillingen, burials with shoe-last adzes are significantly more likely to be locals than those without (table 2). Four of the 6 (67%) Flomborn burials without a shoe-last adze have tooth values above the local range. Of the

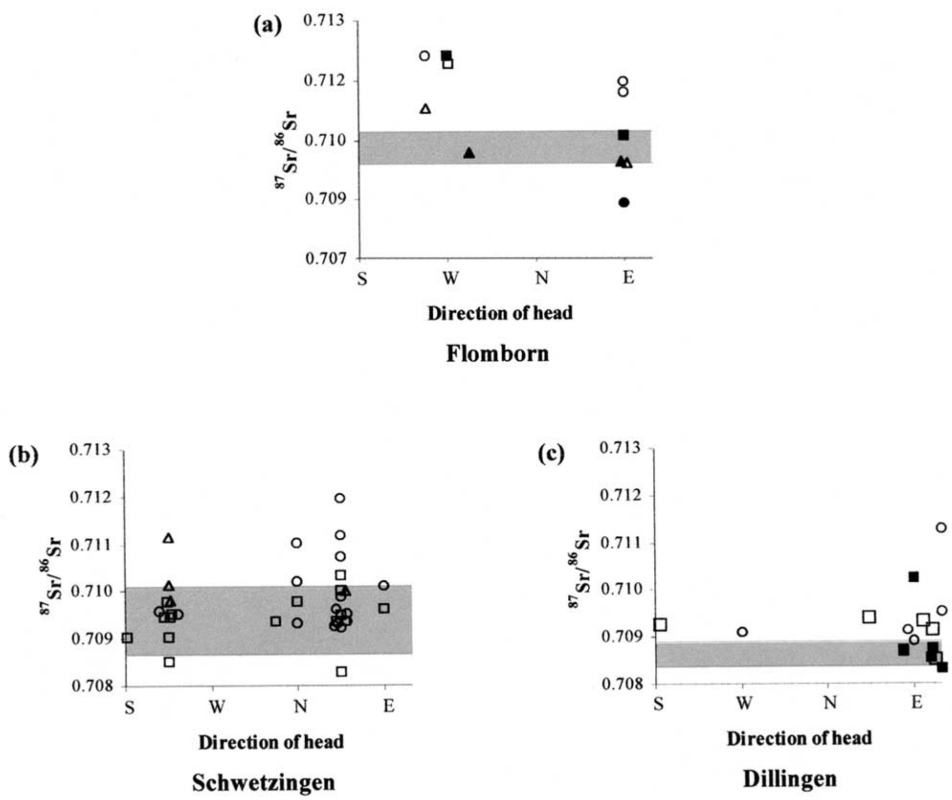

FIG. 2. *Strontium isotopes in tooth enamel from three LBK cemeteries:* a, *Flomborn,* b, *Schwetzingen, and* c, *Dillingen. Each symbol represents a different individual:* circles, *female;* squares, *male;* triangles, *unknown sex (due to young age at death).* Filled symbols, *burials with shoe-last adze;* empty symbols, *burials without adze. (There were no adzes in the sampled Schwetzingen burials.) The "local" $^{87}Sr/^{86}Sr$ range has been defined as two standard deviations from the average human bone value at each site (individual bone values not shown). The local range for each site is indicated by a gray bar.*

TABLE 2
T-*test Results Comparing the Distribution of* $^{87}Sr/^{86}Sr$ *Values in Teeth from Individuals of Different Categories with All the Bone Values at the Site*

Hypothesis	Flomborn	Schwetzingen	Dillingen
Females local	0.314	*0.031*	0.097
Males local	0.134	0.993	0.065
Without shoe-last adze local	*0.021*	n.d.	*0.013*
With shoe-last adze local	0.822	n.d.	0.461
Westerly burials local	*0.036*	0.482	0.118
Easterly burials local	0.693	*0.048*	*0.026*

NOTE: Low *p*-values (< 5% in italics) indicate that the hypothesis is probably *not* true, that is, that there is a significant difference between the mean tooth value of the category and the mean bone value at the site. Since there are many *p*-values, some "significant" values could have occurred by chance. The most convincing patterns are those that are repeated.

5 Flomborn burials with a shoe-last adze, only 1 (20%) has a tooth value above the local range (fig. 2). Among the 11 burials without a shoe-last adze at Dillingen, 9 (82%) are nonlocals, all with tooth values above the local range. Of the 6 Dillingen burials with a shoe-last adze, 2 (33%) are nonlocals, and only 1 of those is above the local range. The presence of nonlocal males without adzes confirms that the correlation is not merely between shoe-last adzes and males who happen to be locals.

4. Nonlocal $^{87}Sr/^{86}Sr$ values are mostly above the local range for their place of burial. Of the 27 immigrants from the three sites, 23 tooth values are above the local range for the site and only 4 below it.

The last pattern is suggestive of where the nonlocals obtained their diet in the younger part of their lives. The $^{87}Sr/^{86}Sr$ values for the nonlocals are not high enough, however, to be "from" the granitic uplands, where water samples are generally above 0.720 (Tricca et al. 1999, Probst et al. 2000). The best interpretation at this point may be that the higher $^{87}Sr/^{86}Sr$ values reflect a significant *proportion* of the diet from the regional uplands. If so, the higher $^{87}Sr/^{86}Sr$ values may reflect a larger diet catchment rather than a fixed "origin" for the nonlocals. Optimal foraging theory predicts that a six-household LBK village in southwestern Germany would require 6 km^2 of agricultural land, supplemented by about 14% wild foods (Gregg 1988). At the same time, Gregg (1988) estimates the optimal diet for Mesolithic foragers as 80% wild game, 20% wild plants. A simple calculation based on these figures and the local geology shows that if one-quarter of the wild foods came from the granitic uplands and all the agricultural foods were locally grown, the predicted $^{87}Sr/^{86}Sr$ would be 0.71036 for Flomborn farmers and 0.71113 for foragers (Bentley 2001:247–51).

The enamel $^{87}Sr/^{86}Sr$ values for many of the nonlocals at Flomborn and Schwetzingen are close to the value predicted for foragers. Because Early LBK sites are numerous in the Rhine Valley lowlands but scarce in the uplands, a viable hypothesis is that some of the nonlocals were the foragers who may have frequented the area uplands during the early LBK (Cziesla 1994). The frequent absence of a shoe-last adze with these nonlocals also suggests that they may have been foragers. Indigenous foragers were significant agents in the spread of farming into southwestern Germany, influenced by small groups of immigrant farmers (Gronenborn 1999, Price et al. 2001). Near the western limit of the LBK at the time, nonlocals of both sexes at Flomborn may represent its initial residents, whose diet catchment had been larger before they settled. Later on in the same region, at Schwetzingen, there is less immigration overall, mostly involving females with similar "upland" strontium isotope signatures. The nonlocal females invite a comparison with models and ethnographic cases of forager women who marry into farmer or pastoral communities (Zvelebil and Rowley-Conwy 1984, Cronk 1989, Zvelebil and Lillie 2000, Thorp 2000).

An alternative interpretation for the data we have presented here is that the migration did not involve foragers at all. There are few archaeological traces of Mesolithic occupation in the uplands around Bavaria or the Upper Rhine Valley at the time of the transition to the Neolithic (Nielsen 1997, Taute 1988, Jochim 1998). However, the reason so few Terminal Mesolithic sites have been discovered is at least partly their ephemeral nature. Late dates from Late/Terminal Mesolithic sites in southern Germany and eastern France overlap with the early LBK period, indicating that foragers persisted into the LBK (Brunnacker et al. 1967, Kind 1997, Gronenborn 1999, Jochim 2000).

In any case, strontium isotope analysis of LBK skeletons suggests that many people made residential changes during the LBK of the Rhine Valley. Whether it involved foragers or farmers, the observed pattern of female migration is consistent with genetic evidence for patrilocality in European prehistory (Seielstad, Minch, and Cavalli-Sforza 1998). Although our evidence is not conclusive, it can be seen to support the interpretation (e.g., Gronenborn 1999, Zvelebil 2000, Price 2000) that Neolithic colonization of southeastern Europe was followed by some degree of indigenous adoption in central and northern Europe.

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