Strontium isotopes document greater human mobility at the start of the Balkan Neolithic

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Questions about how farming and the Neolithic way of life spread across Europe have been hotly debated topics in archaeology for decades. For a very long time, two models have dominated the discussion: migrations of farming groups from southwestern Asia versus diffusion of domesticates and new ideas through the existing networks of local forager populations. New strontium isotope data from the Danube Gorges in the north-central Balkans, an area characterized by a rich burial record spanning the Mesolithic–Neolithic transition, show a significant increase in nonlocal individuals from ∼6200 calibrated B.C., with several waves of migrants into this region. These results are further enhanced by dietary evidence based on carbon and nitrogen isotopes and an increasingly high chronological resolution obtained on a large sample of directly dated individuals. This dataset provides robust evidence for a brief period of coexistence between indigenous groups and early farmers before farming communities absorbed the foragers completely in the first half of the sixth millennium B.C.

forager–farmer interaction | isotope analysis | the Balkans | Lepenski Vir | southeastern Europe

The chronological priority of southeastern Europe in the spread of the Neolithic way of life makes this region particularly important in building and evaluating models for understanding the initial spread of agriculture across Europe. At the same time, southeastern Europe is geographically adjacent to Asia, particularly the regions of central and western Anatolia, which have for a very long time been considered core areas for the Neolithic expansion into Europe. Although there are still differences among researchers as to what processes—demic diffusion, folk migration, leap-frog colonization, or acculturation of local forager populations to name the major models (1–4)—actually took place, most scholars today agree that the cultural origins of the southeast European Neolithic are in the Neolithic communities of Asia (5–10).

The traditional view of the Neolithic in the Balkan Peninsula involved the expansion of farmers out of the plains of Thessaly and northern Greece, moving up the natural corridors of the major river valleys with general northward and westward directions (11). However, more recent reevaluations of existing radiocarbon dates suggest that it is unlikely that Initial or Early Neolithic sites in Thessaly were established earlier than ∼6500/6400 calibrated (cal) B.C., many possibly later, between ∼6300 and ∼6100 cal B.C. (12, 13). Several recent accelerator mass spectrometry (AMS) radiocarbon dates for Early Neolithic communities in the central and northern Balkans suggest a rapid spread of farming communities as early as ∼6300/6200 cal B.C. (14, 15). Resolution of various competing models strongly depends on evidence regarding human mobility in this region.

Our research focuses on human mobility and migration by measuring strontium ($^{87}Sr/^{86}Sr$) isotope ratios in tooth enamel from human burial remains coming from the Danube Gorges in the north-central Balkans between present-day Serbia and Romania (Fig. 1), where a number of sites are characterized by a continuous Mesolithic and Neolithic sequence (16–19) (Table 1 and *SI Appendix*, Table S1 and Fig. S1). Strontium comes from weathering rocks, waters, and soils and through the food chain enters the body. Because tooth enamel forms around the time of birth and early childhood, it does not change through life (20) and is also the densest tissue in the body, generally resistant to decomposition and contamination after death (21–24); as a result, it is routinely analyzed to obtain an averaged geographic signature that reflects an individual's place of birth. Comparing this signature with locally bioavailable strontium, it is possible to establish nonlocal, migrant individuals in a burial sample of a particular region (25, 26).

Archaeology of the Mesolithic–Neolithic Danube Gorges

There are close to 300 radiocarbon measurements from 14 sites dating Danube Gorges Mesolithic and Neolithic contexts, of which 83 AMS dates have been made directly on human bones (17). The earliest radiocarbon dates in the Danube Gorges come from Epipaleolithic levels at the rock-shelter of Cuina Turcului (27) and Climente II Cave (28) (∼13,500–9300 cal B.C.). Possible archaeological evidence for mobility during this period primarily relates to the presence of *Cyclope neritea* and *Dentalium* marine shells (27), suggesting long-distance connections.

Early Holocene human adaptations in this particular environment can be traced back to the mid-10th millennium cal B.C. at a number of open-air sites on the Danube shores. The River Danube, which offered Danubian carp, catfish, and sturgeon, was the key to the success of these adaptations in the region where fishing was facilitated by the fast current and irregularities of the riverbed, which created numerous whirlpools and enabled specialized modes of fishing. Formal burials as well as scattered Early to Middle Mesolithic (∼9500–7400 cal B.C.) human remains have been found associated with the sites of Vlasac, Padina A, and Proto-Lepenski Vir. There are currently 14 individuals directly AMS-dated to these early Mesolithic periods. Extended supine inhumations as well as seated burials placed in lotus positions were documented. To date, there is no archaeological evidence for long-distance connections during the Early-Middle Mesolithic periods in the Danube Gorges, possibly suggesting reduced levels of human mobility among different regions of southeastern Europe.

The intensity of occupation in the Late Mesolithic (∼7400–6200 cal B.C.) might have destroyed many Early/Middle Mesolithic features in the Danube Gorges. The frequency of features, burials, and dates associated with this phase indicates successful and long-lasting Late Mesolithic communities across the region. There are currently 32 directly AMS-dated individuals falling into the time brackets of this period, with extended supine inhumations as the dominant burial form and with evidence of secondary mortuary rites, which also included cremations. Archaeological evidence for mobility during this period is based on the presence of marine gastropods *Columbella rustica* and *Cyclope neritea* (*SI Appendix*, Fig. S6), which must have come from coastal regions more than 400 km away from the Danube Gorges (29). This would suggest established interregional information and exchange networks among Late Mesolithic foragers in southeastern Europe.

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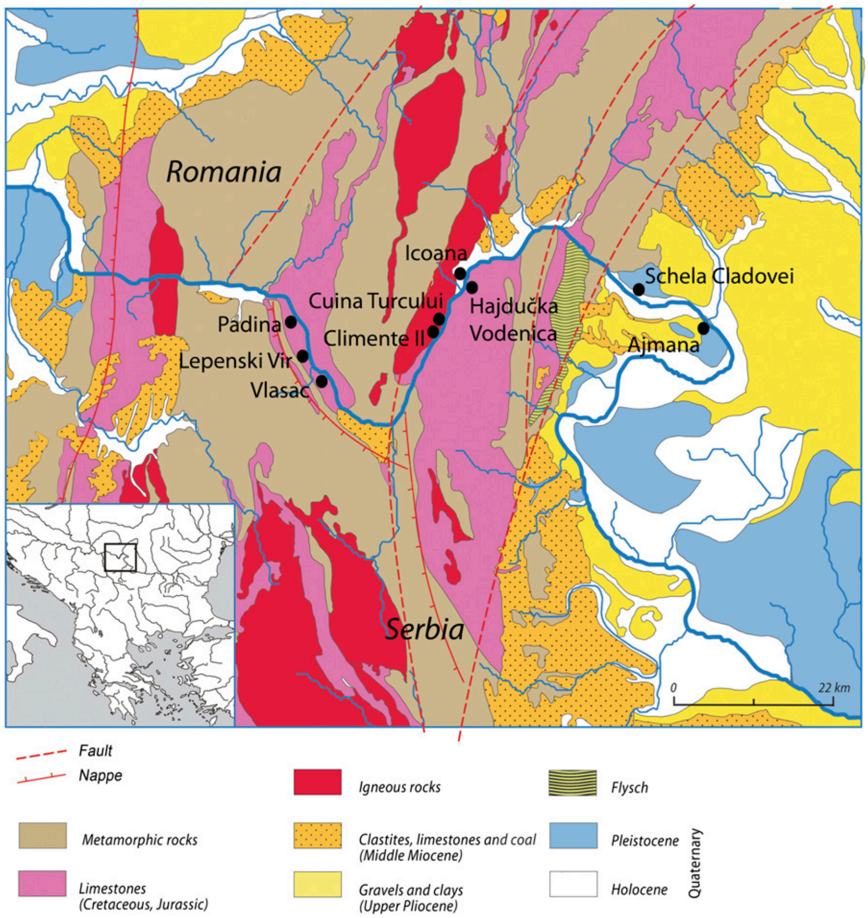

Fig. 1. Simplified geology of the Danube Gorges with the position of sampled sites.

The ensuing period has been referred to as the Final Mesolithic (16) or Mesolithic–Neolithic transformation phase (17, 30) and is currently dated to ~6200–6000/5950 cal B.C., making this phase in the Danube Gorges entirely contemporary with early Neolithic sites in the Morava, middle Danube, and Tisza valleys (14). Remarkable art in the form of sculpted boulders and innovative architectural features such as red limestone trapezoidal-shaped building floors found at the key site of Lepenski Vir (*SI Appendix*, section I and Fig. S2) are attributed to this phase (ref. 31 and *SI Appendix*). This is the phase of cultural hybridity in the Danube Gorges. Early Neolithic pottery (32, 33), polished stone axes (34), nonlocal good quality yellow white-spotted "Balkan" flint from areas 200 km away from the Danube Gorges in northern Bulgaria (35) as well as novel, typical Neolithic morphologies in osseous tools were found associated with trapezoidal buildings at the sites of Lepenski Vir and Padina. At the same time, these buildings harnessed many indigenous architectural and material culture elements, whereas the lack of domesticates (except for dogs) during this phase suggests an unaltered subsistence pattern (30). Mortuary practices were still characterized by extended supine burials during this period (*SI Appendix*, Figs. S3 and S4), yet there is unequivocal evidence from new excavations at Vlasac about the adoption of ornaments from *Spondylus* and stone characterized by typical Neolithic morphologies (ref. 17 and *SI Appendix*, Figs. S4–S6). There are 25 AMS dates for 21 individuals attributed to this phase from the region, mostly from the site of Lepenski Vir (18 dates for 14 individuals). There are also two AMS-dated burials from the Early Neolithic site of Ajmana that seem to suggest the existence of a newly founded fully Neolithic settlement in the downstream area of the gorges and its contemporaneity with forager sites farther upstream. Further changes in the patterns of habitation in the Danube Gorges can be seen in the period after ~6000/5950 cal B.C. when the first crouched/flexed inhumations appear at several sites, indicating the spread of typical Neolithic mortuary rites, which, at Lepenski Vir, might have coexisted with the dominant form of Mesolithic burial position—extended supine inhumations placed parallel to the Danube (*SI Appendix*, section II). There are currently 12 directly AMS-dated burials falling into this period. During this last Neolithic phase, trapezoidal buildings were abandoned at the site of Lepenski Vir, which became dominated by typical Early/Middle Neolithic pattern of habitation, and the current evidence suggests an increase in the number/visibility of settlements across the region as a whole (17).

The Mesolithic and Early Neolithic sites of the Danube Gorges contain one of the most important samples of human skeletal remains from the time of the transition to agriculture (36, 37). There are more than 500 primary and secondary graves with even larger number of individuals identified. Of this number, around 250 are adults. Examination of the physical remains themselves has been revealing (36). Both individuals with robust and gracile features have been noted in the human skeletal material, and recent reexamination indicates these could relate to differences between populations. Light isotope ratio data from bone collagen have provided essential information on diet, which suggests that there was a substantial contribution of protein derived from freshwater as well as migratory fish throughout the Mesolithic (38–41). This pattern begins to alter ~6200 cal B.C. For most of the earlier, Mesolithic burials in the Danube Gorges, a reservoir effect has been reported due to significant intake of protein coming from aquatic resources that exhibit lower ^{14}C values than terrestrial organisms. This in turn affects

Table 1. Summary of isotopic ($\delta^{15}N$ and $^{87}Sr/^{86}Sr$) results from the Danube Gorges for each site/phase and with separate columns for males and females

Site	Phase	*n* (all, F, M, unknown)	Mean $\delta^{15}N$ (‰)	SD	Site/phase median $^{87}Sr/^{86}Sr$	Females mean $^{87}Sr/^{86}Sr$	Females SD $^{87}Sr/^{86}Sr$	Males mean $^{87}Sr/^{86}Sr$	Males SD $^{87}Sr/^{86}Sr$
Padina (29)	Early Mesolithic	23, 11, 5, 7	14.3	1.40	0.709017	0.709132	0.00035	0.709038	0.000088
	Late Mesolithic	3, 0, 1, 2	15.4		0.709095				
	Mesolithic–Neolithic	3, 1, 1, 1	16.3	0.49	0.709244				
Lepenski Vir (38)	Early Mesolithic	5, 1, 4, 0	14.6	0.59	0.709476			0.709336	0.00018
	Mesolithic–Neolithic	19, 10, 7, 2	14.0	2.19	0.70946	0.709688	0.00062	0.709607	0.00068
	Early Neolithic	14, 7, 3, 4	12.1	1.74	0.709472	0.709463	0.00141	0.709326	0.00063
Vlasac (48)	Early Mesolithic	2, 1, 1, 0	14.8	0.49	0.709152				
	Late Mesolithic	46, 19, 23, 4	14.8	0.89	0.709133	0.709307	0.00037	0.709226	0.00026
Hajdučka Vodenica (12)	Late Mesolithic	9, 1, 4, 6	15.5	0.83	0.709515			0.709893	0.00135
	Mesolithic–Neolithic	3, 0, 1, 2			0.709157				
Ajmana	Early Neolithic	12, 0, 3, 9	10.3	0.35	0.709330			0.708795	0.00079
Icoana	Late Mesolithic	1, 1, 0, 0							
Schela Cladovei	Late Mesolithic	9, 0, 1, 8			0.709276				
Cuina Turcului	Epipaleolithic	2, 2, 0, 0			0.709508				
Climente II	Epipaleolithic	1, 0, 0, 1							

F, female; M, male. See detailed list in *SI Appendix*, Table S1.

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radiocarbon measurements on fish, and further affects humans and some other animal species (e.g., otter, domesticated dogs) who consume fish. This intake of "old carbon" in organisms associated with the aquatic food chain makes radiocarbon measurements older by around 200–400 y. The correction factor for the affected radiocarbon values made on human bones has been devised for the Danube Gorges on the basis of age offsets between measured human burials and associated artifacts made on the bones of ungulate taxa (41), and has successfully been applied (*SI Appendix*, Table S1).

Geology and Strontium Isotopes in the Danube Gorges

The geology of the region is remarkably complex (Fig. 1). The route of the Danube, connecting the Carpathian and the Dacian Basins through the Danube Gorges, is composed of three smaller valleys and four gorges (42, 43). The rock formations of the Danube Gorges themselves are dominated by limestone massifs with typical karst topography in the form of cliffs, sinkholes, and the like. The siliceous bedrock in the more open parts of the Gorges includes metamorphic formations such as granites, green shists, micashists, amphibolites, sandstones, conglomerates, and gabbro. On top of these rocks are often found sand, clays, and pebble formations in addition to scree deposits from formations at higher elevations. It is also important to note that the archaeological sites are almost always at the river's edge and located on rock shelves or sedimentary deltas from side valleys. This geological diversity ensures that there will be substantial variation in strontium isotope ratios in the region and that migrant individuals should be identifiable. We can estimate strontium isotope ratios for some of these formations, based in part on measurements of similar formations elsewhere in Europe (44, 45). The limestones, composed of marine sediments, will be similar to values for seawater, depending on the age of deposition, measuring between 0.7075 and 0.709 radiogenic points. Metamorphic rocks, again depending on age, should exhibit higher strontium isotope ratios. The conglomerates are more difficult to estimate but are likely terrestrial. To the east of the outlet of the Danube Gorges, the Romanian plain is dominated by the alluvium of the Danube, measured further west at 0.7088–0.7092 (46). However, measurements of various human and animal samples from this area suggest that higher values may be more accurate. In addition to the geological information from the Gorges, we have measured strontium isotopes in modern and archaeological fauna from several sites in the area (*SI Appendix*, Table S2). This dataset provides some baseline information for variation, but of course reflects only terrestrial values. There is some variation in these values within the sites, especially with regard to pigs (*Sus scrofa*) from Schela Cladovei because this site is located in an area of open landscape different from other sites upstream the Danube (Fig. 1).

Results

For the sample of analyzed burials (Table 1 and *SI Appendix*, Table S1), the relationships among isotope measurements ($\delta^{13}C$, $\delta^{15}N$, and $^{87}Sr/^{86}Sr$) and age are examined through correlation coefficients (*SI Appendix*, Table S3). We can establish a very distinctive relationship in $\delta^{15}N$ and $^{87}Sr/^{86}Sr$ with the chronological age of samples, where a major change is seen after ∼6200 cal B.C. (i.e., during the Mesolithic–Neolithic transition and in the Early Neolithic) (Fig. 2). Nitrogen isotopes show significant patterning with all other isotopes, most strongly with radiocarbon. The most significant correlation is the negative relationship between radiocarbon and strontium isotope ratios as noted previously. Most of the younger points have greater variation, with higher occurrence of radiogenic points, ranging up to almost 0.711. There is also one exceptionally low value among the younger samples (Early/Middle Neolithic crouched burial 66 from Lepenski Vir measured at 0.706772, which corresponds to young volcanic rocks). These data clearly suggest that there is a major change in the variability of places of origin among the inhabitants of the Gorges after the Neolithic spread in the Balkans. This pattern can also be seen by plotting $\delta^{15}N$ against $^{87}Sr/^{86}Sr$, where there is greater variation in strontium isotope values in the lower values for nitrogen. It relates to individuals with lower trophic levels, as is characteristic of more terrestrial diets in the period after ∼6200 cal B.C., which is in stark contrast with the preceding Mesolithic dietary pattern of heavy reliance on aquatic sources (38–41). However, we suggest that lighter trophic levels cannot straightforwardly be connected with nonlocal individuals because we find both individuals with lower $\delta^{15}N$ values (<13.0‰) and local strontium signatures (e.g., 7/I from Lepenski Vir) as well as those with $\delta^{15}N$ values >13.0‰ with distinctly nonlocal signatures (e.g., 7/II, *SI Appendix*, Fig. S3).

The mean ratio in the Danube Gorges is 0.7095 ± 0.0007 (1 SD) excluding extreme outliers. Sources of $^{87}Sr/^{86}Sr$ are constants and variation is largely due to (*i*) the locally bioavailable $^{87}Sr/^{86}Sr$ values and (*ii*) the mix of dietary inputs from different $^{87}Sr/^{86}Sr$ sources. Because there are several isotope ratio sources in this region, there is no objective way to define a specific threshold for identifying foreign individuals. A reasonable means to identify foreign individuals in this series of samples would be to combine previously mentioned inferences and designate the individuals below 0.7085 and above 0.7100 as nonlocal (Fig. 2).

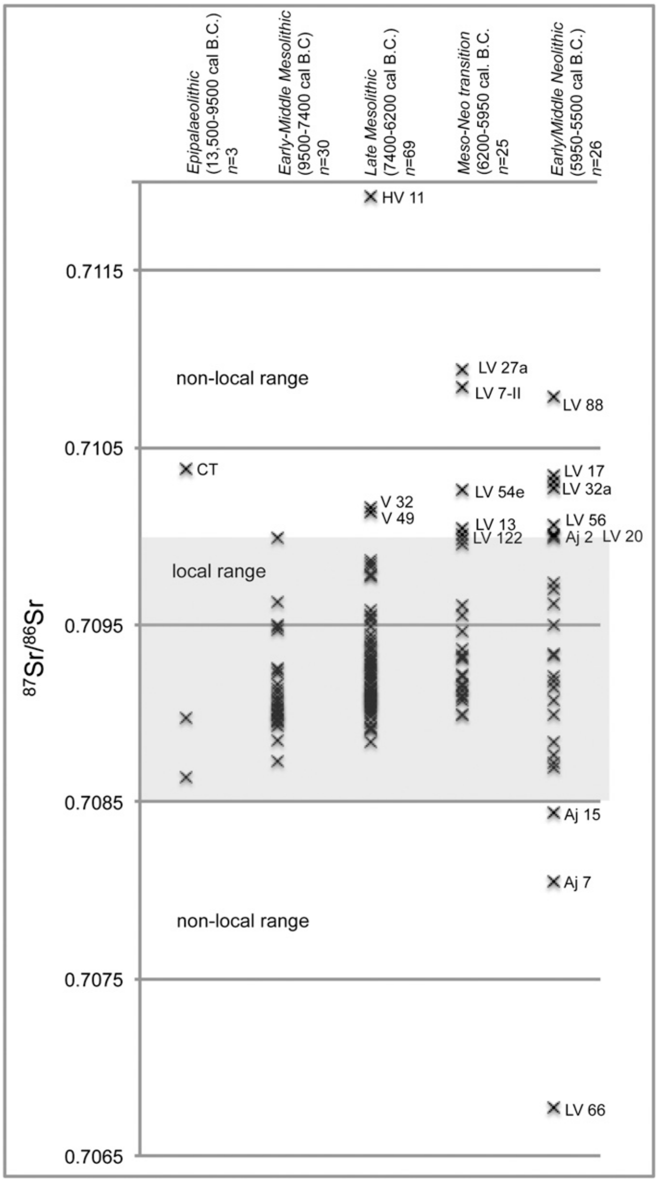

Fig. 2. Summary plot of $^{87}Sr/^{86}Sr$ ratios for 153 individuals in the Danube Gorges ordered by main chronological periods. Shaded area shows the assumed range of the local strontium signature in the Danube Gorges. All individuals outside the local range are marked by site initial(s) and burial number. Aj, Ajmana; CT, Cuina Turcului; HV, Hajdučka Vodenica; LV, Lepenski Vir; V, Vlasac.

Sites in the Gorges (Padina, Lepenski Vir, Vlasac, Hajdučka Vodenica, and Icoana) have average values between 0.7091 and 0.7096. Taking individuals below 0.7085 and above 0.7100 as nonlocal for the region of the Danube Gorges as a whole, one is struck by the very few nonlocal individuals for all sites but Lepenski Vir. Fig. 3 plots strontium values against available AMS dates for 37 directly dated individuals from five sites. This sample is representative and illustrative of the underlying pattern, which suggests a limited level of regional mobility characterizing the population in the Danube Gorges throughout the Early, Middle, and Late Mesolithic periods (i.e., from ~9500 to ~6200 cal B.C.). One outlier from the site of Cuina Turcului is found in a small sample of three Epipaleolithic burials and may correspond well with expectations for human mobility during this period based on archaeological evidence alone (see *Introduction*). There are no nonlocal individuals in the sample of 30 securely dated Early/Middle Mesolithic burials from three sites; this pattern corresponds with archaeological evidence for human mobility during the period. In the large and representative sample of 69 securely dated Late Mesolithic burials from five sites with obtained strontium ratios, there are only three individuals from two sites with nonlocal values. Two of these are extended supine inhumation burials found at the site of Vlasac (nos. 32 and 49, the latter is the only burial at Vlasac with *Columbella rustica* marine ornaments suggesting possible long distance movement), whereas one outlier is an isolated skull from the site of Hajdučka Vodenica (no. 11).

Strontium isotope ratios indicate a dramatic increase in the numbers of nonlocal, first-generation migrants buried in this region at two sites—Lepenski Vir and Ajmana—during the course of Mesolithic–Neolithic transformations in the Danube Gorges (~6200–6000/5950 cal B.C.) in the sample of 25 securely dated individuals from three sites. This trend continues into the period of the Early/Middle Neolithic after ~6000/5950 cal B.C. in the sample of 26 securely dated individuals from two sites. Strontium isotope ratios associated with individuals dated to these periods occur outside both the upper and lower boundaries of the defined local strontium range (Figs. 2 and 3), suggesting at least two or more geologically distinct regions of origin for these incomers.

The site of Ajmana is a newly founded site dated to the Early Neolithic, situated in a landscape more suitable for agricultural practices downstream from the main forager sites in this region (Fig. 1). The site is characterized by a group burial with individuals placed in several levels one on top of the other (47). Of 12 individuals with dental evidence (48) and strontium values, three burials (nos. 2/81, 7, and 15) have nonlocal values. Typically for the Neolithic period across the Balkans, all individuals were placed in crouched/flexed positions (17).

At Lepenski Vir, of the sample of 45 individuals with available dental evidence, there are five nonlocal individuals associated with Mesolithic–Neolithic transition phase I-II (~6200–6000/5950 cal B.C.)—three primary extended inhumations (nos. 13, 54e, and 27a) and two isolated skulls (nos. 122 and 7-II)—and seven individuals (nos. 8, 17, 20, 32a, 56, 66 and 88) associated with Early/Middle Neolithic phase III (~6000/5950–5500 cal B.C.), all primary crouched/flexed inhumations (of the total number of 20 primary crouched/flexed burials associated with phase III at this site).

There are three possibly significant patterns observable here. First, there might have been several waves in the arrival of nonlocal individuals into the Danube Gorges who were buried at Lepenski Vir after ~6200 cal B.C. using the dominant Mesolithic burial rite of extended supine inhumations during the early phase (~6200–

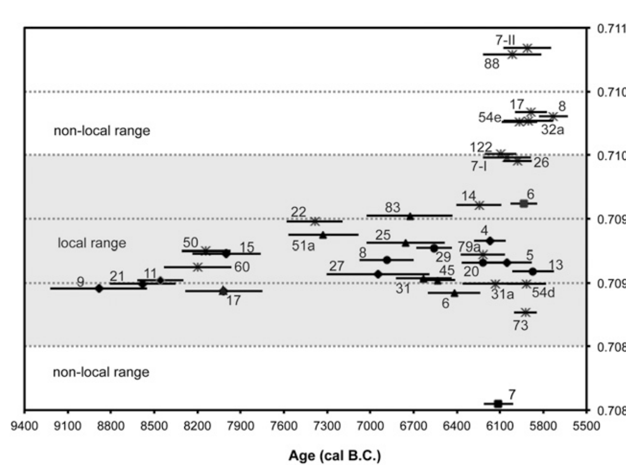

Fig. 3. Scatterplot between $^{87}Sr/^{86}Sr$ and radiometric dates for directly AMS-dated individuals (n = 37) with obtained strontium values. Lines correspond to calibrated ^{14}C ranges B.C. at 95% confidence, and each line represents directly dated burials, which are marked by burial numbers that are site-specific. Each symbol associated with the middle point of the line/calibrated range corresponds to a particular site: Ajmana (square); Hajdučka Vodenica (circle); Lepenski Vir (star); Padina (diamond); Vlasac (triangle).

6000/5950 cal B.C.) and with the absolute dominance of crouched inhumations in the later phase (after ∼6000/5950 cal B.C.). Second, two disarticulated nonlocal skulls associated with the Mesolithic–Neolithic transformation phase perhaps may relate to enemy trophy heads. Finally, the wide spectrum of nonlocal values suggests that migrants are coming from more than one place of origin.

Average isotope values for individual sex are presented in Table 1. Of 10 nonlocal individuals associated with the Mesolithic–Neolithic transition phase I-II and Early/Middle Neolithic phase III at Lepenski Vir, all but one burial (no. 20) are females or possible females. This pattern could be interpreted as suggesting a reciprocal mating network between the Danube Gorges foragers and the earliest farming communities in the surrounding areas, with largely nonlocal women being buried at the central forager site of Lepenski Vir during these phases. Average isotope values for age classes (child, teen, adult, and older adult) and burial positions (extended supine, seated, flexed legs, crouched/flexed, and disarticulated) are provided in the *SI Appendix*, Table S4 and S5. Of 17 individuals that have $^{87}Sr/^{86}Sr$ ratios measured and that were also found in crouched/flexed positions at the sites of Lepenski Vir and Ajmana, 7 from Lepenski Vir and 3 from Ajmana are nonlocal individuals, indicating a clear correlation between the novel burial position and nonlocal strontium ratio. In addition, two nonlocal individuals from Lepenski Vir, burials 32a (*SI Appendix*, Fig. S7) and 88 (Fig. 4), both buried in crouched positions and characterized by largely terrestrial dietary intake, are the only individuals among all Mesolithic and Neolithic burials in the Danube Gorges with traces of caries on their teeth (49), suggesting significantly different dietary habits, which were likely based on foods rich in starch as is typical of the Neolithic cereal-based diet.

Discussion and Conclusions

The most recent genetics research on mtDNA in Europe (50, 51) suggests that local foragers contributed significantly to the mitochondrial genome along with the genetic contribution of Neolithic migrants. This evidence sits well with the isotopic evidence we have outlined for the Danube Gorges. On the basis of the strontium isotopic evidence from Mesolithic and Neolithic sites in this region, identified migrants, primarily found buried at the central site of Lepenski Vir, originated in several geologically distinct areas. There were also probably several chronologically separate events during which individuals from likely Neolithic communities interacted with and became incorporated into forager communities in the Danube Gorges in the centuries after ∼6200 cal B.C. Our study unequivocally proves that in the earliest phases of the Neolithic in southeastern Europe, perhaps paradoxically, farming communities were much more mobile than local foraging populations, which in the case of the Danube Gorges remained tied to the exploitation of particular ecological niches since the beginning of the Holocene up until ∼6200 cal B.C. Conclusions reached by the strontium isotope evidence for the Danube Gorges region are corroborated by other archaeological indicators. After almost a century of debates about the actual degree of movement of individuals and groups with the start of the Neolithic in Europe, we are able to demonstrate a significant level of human mobility in the last centuries of the seventh and the first centuries of the sixth millennium B.C., judging by the number of selected migrants buried at the central forager site of Lepenski Vir in the Danube Gorges. There is greater variance of strontium ratios at this time among females in comparison with males, suggesting that women came to these sites from Neolithic communities as part of an ongoing social exchange. New aspects of body decoration, such as the first appearance of *Spondylus* and stone Neolithic-looking beads in burials placed in typical Mesolithic posture of extended supine inhumation at both Lepenski Vir and Vlasac (refs. 17 and 52 and *SI Appendix*, section II and Figs. S4–S6), along with the appearance of other items of material culture (e.g., pottery, flint, polished stone axes, a new tradition of bone artifacts), confirm important changes were taking place in these forager societies that came under pressure from the growing Neolithic presence in the adjacent areas after ∼6200 cal B.C. (14, 16, 17). This process of asymmetrical acculturation ended up in a complete absorption of forager specificity in the first several centuries of the sixth millennium B.C.

Our findings prefer the model of intense and prolonged, over at least two centuries, interaction between certain indigenous forager communities, such as those found in the Danube Gorges, and the earliest farming and stock-breeding communities in the Balkans. Moreover, the Danube River Basin might have been of considerable importance in the spread of Neolithic communities through southeastern Europe with the general direction from the south and southeast to the north and northwest. A route from western Anatolia, Bosphorus, Thrace and along the Black Sea coast into the Danube, and farther through the Danube Gorges might have been a very important dispersal axis for the earliest Neolithic groups. This assumed route for the spread of the Neolithic communities is important in the context of a recent suggestion that the western and northwestern parts of present-day Turkey "became the core or the primary zone of the European Neolithic" in the last centuries of the seventh millennium B.C. (7). The Danube Gorges region with its strong forager presence must have been of considerable importance as a zone of special interest for these highly mobile and expanding Neolithic communities. The social ethos of these Neolithic communities might have been in large part aiming at incorporation of foreign groups encountered in parts of southeastern Europe, as a way of "domesticating the other" (53). As for the Danube Gorges foragers, judging by, at first, a rather organic appropriation and incorporation of new elements of social and material existence as well as biologically "new blood" into the existing modes of being, and, consequently, the abandonment of forager cultural specificity, the mentioned process might have had a predominantly positive connotation or at least represented the only viable solution in the face of the emerging demographics.

The current dating evidence suggests a rather rapid spread of Neolithic groups establishing new settlements across the Balkans in the last two centuries of the seventh millennium B.C. and onwards. We suggest that the evidence from the Danube Gorges and surrounding areas is representative of the type of transfor-

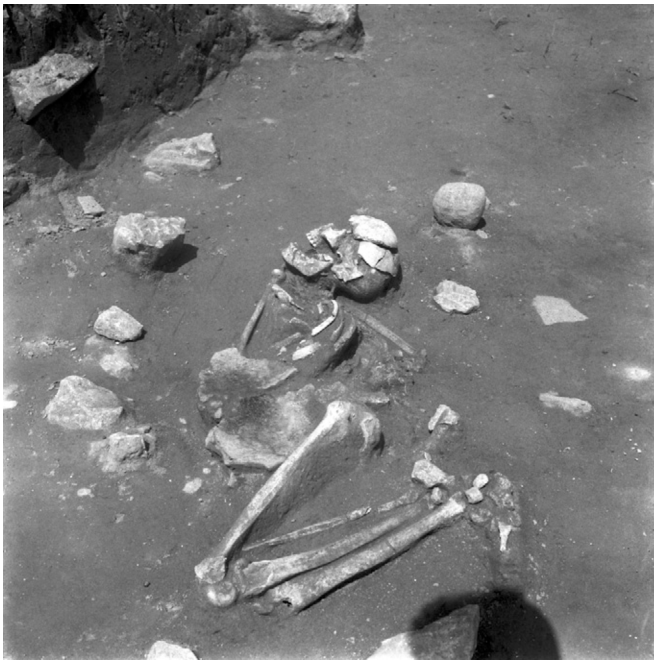

Fig. 4. Neolithic Burial 88 (possible female) from Lepenski Vir (phase III), dated in the range 5984–5644 cal B.C. at 95% confidence (AMS date lab ID OxA-5831), is one of seven primary inhumations from this site placed in a flexed position and with a nonlocal strontium isotope value.

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mation processes that took place in those areas of southeastern Europe and Europe as a whole where one finds strong forager presence at the time of contact.

Materials and Methods

Adult burials were chosen for the most part, with a roughly equal number of female and male burials. Strontium isotopes were measured successfully on 153 Epipaleolithic, Mesolithic, and Neolithic individuals from the Danube Gorges (Table 1 and *SI Appendix*, Table S1). Depending on preservation and availability, mostly molars (preferably M1) were selected but premolars, canines, and incisors were also used. There are fewer measurements of carbon and nitrogen isotope ratios for the same sample (17, 38, 39). Teeth were cleaned with a dental drill to remove any visible dirt or contamination from the tooth crown and a sample was taken from the tooth crown. Approximately one quarter to one half of the tooth crown is removed with a subsequent removal of dentin from enamel, sometimes using light microscope. Enamel powder was measured at the Geochronology and Isotope Geochemistry Lab University of North Carolina-Chapel Hill by Paul Fullagar. Milligram to submilligram quantities of sample are dissolved in 15 mL Savillex PFA vials using 250 μL of 2× distilled 5N HNO_3 in a class 100 filtered air environmental hood. Sr is separated from matrix using EiChrom SrSpec resin, a crown-ether Sr-selective resin (50–100 μm diameter) loaded into either the tip of a 10 mL BioRad polypropylene column, or into a Teflon column (10 mm × 4 mm) with reservoir. The SrSpec resin is presoaked and flushed with H_2O to remove Sr present from the resin manufacturing process. The resin is further cleaned in the column with repeated washes of deionized H_2O and conditioned with 5N HNO_3. Total procedural blanks for Sr are typically 100–200 picograms. Isotopic ratios were measured on a VG Sector 54 thermal ionization mass spectrometer at the University of North Carolina-Chapel Hill in quintuple-collector dynamic mode, using the internal ratio $^{86}Sr/^{88}Sr = 0.1194$ to correct for mass fractionation. Internal precision for Sr carbonate runs is typically 0.0006–0.0009% SE, based on 100 dynamic cycles of data collection.

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1. Bogucki P (1996) The spread of early farming in Europe. *Am Sci* 84:242–253.
2. Chapman JC (1994) The origins of farming in southeast Europe. *Préhistoire Européenne* 6:133–156.
3. Rowley-Conwy P (2011) Westward ho! The spread of agriculture from Central Europe to the Atlantic. *Curr Anthropol* 52:S431–S451.
4. Whittle A (1996) *Europe in the Neolithic. The Creation of New Worlds* (Cambridge Univ Press, Cambridge).
5. Bar-Yosef O (2004) Guest editorial: East to west – agricultural origins and dispersal into Europe. *Curr Anthropol* 45(S4):S1–S3.
6. Bocquet-Appel J-P, Naji S, Vander-Linden M, Kozłowski JK (2009) Detection of diffusion and contact zones of early farming in Europe from the space-time distribution of 14C dates. *J Archaeol Sci* 36:807–820.
7. Özdoğan M (2011) Archaeological evidence on the westward expansion of farming communities from eastern Anatolia to the Aegean and the Balkans. *Curr Anthropol* 52(S4):S415–S430.
8. Pinhasi R, Fort J, Ammerman AJ (2005) Tracing the origin and spread of agriculture in Europe. *PLoS Biol* 3(12):e410.
9. Krauß R, ed (2011) *Beginnings – New Research in the Appearance of the Neolithic Between Northwest Anatolia and the Carpathian Basin* (Verlag Marie Leidorf GmbH, Rahden/Westfalen, Germany).
10. Perlès C (2005) From the Near East to Greece: Let's Reverse the Focus. Cultural Elements That Didn't Transfer. *How did Farming Reach Europe?* ed Lichter C (BYZAZ 2, Ege Yayinlari, Istanbul), pp 275–290.
11. van Andel T, Runnels C (1995) The earliest farmers in Europe. *Antiquity* 69:481–500.
12. Reingruber A (2011) Early Neolithic settlement patterns and exchange networks in the Aegean. *Documenta Prehistorica* 38:291–305.
13. Reingruber A, Thissen L (2009) Depending on ^{14}C data: Chronological framework in the Neolithic and Chalcolithic of southeast Europe. *Radiocarbon* 51(2):751–770.
14. Whittle A, Bartosiewicz L, Borić D, Pettitt P, Richards M (2002) In the beginning: New radiocarbon dates for the Early Neolithic in northern Serbia and south-east Hungary. *Antaeus* 25:63–117.
15. Biagi P, Shannon S, Spataro M (2005) Rapid Rivers and Slow Seas? New Data for the Radiocarbon Chronology of the Balkan Peninsula. *Prehistoric Archaeology and Anthropological Theory and Education* (Reports of Prehistoric Research Projects 6-7), eds Nikolova L, Fritz J, Higgings J (Karlovo, Salt Lake City, UT), pp 41–50.
16. Bonsall C (2008) *Mesolithic Europe*, eds Bailey GN, Spikins P (Cambridge Univ Press, Cambridge), pp 238–279.
17. Borić D (2011) Adaptations and Transformations of the Danube Gorges Foragers (c. 13,000–5500 Cal. BC): An Overview. *Beginnings – New Research in the Appearance of the Neolithic Between Northwest Anatolia and the Carpathian Basin*, ed Krauß R (Verlag Marie Leidorf GmbH, Rahden/Westfalen, Germany), pp 157–203.
18. Radovanović I (1996) *The Iron Gates Mesolithic*, *Archaeological Series 11*. (International Monographs in Prehistory, Ann Arbor, MI).
19. Tringham R (2000) *Europe's First Farmers*, ed Price TD (Cambridge Univ Press, Cambridge), pp 19–56.
20. Hillson S (1996) *Dental Anthropology* (Cambridge Univ Press, Cambridge).
21. Budd P, Montgomery J, Barreiro B, Thomas RG (2000) Differential diagenesis of strontium in archaeological human tissues. *Appl Geochem* 15:687–694.
22. Hoppe KA, Koch PL, Furutanic TT (2003) Assessing the preservation of biogenic strontium in fossil bones and tooth enamel. *Int J Osteoarchaeol* 13:20–28.
23. Price TD, Burton JH, Bentley RA (2002) Characterization of biologically available strontium isotope ratios for the study of prehistoric migration. *Archaeometry* 44:117–135.
24. Faure G (1986) *Principles of Isotope Geology* (Wiley, New York).
25. Price TD, Gestsdóttir H (2006) The first settlers of Iceland: An isotopic approach to colonisation. *Antiquity* 80:130–144.
26. Price TD, Bentley RA, Lüning J, Gronenborn D, Wahl J (2001) Prehistoric human migration in the Linearbandkeramik of central Europe. *Antiquity* 75:593–603.
27. Paunescu A (1970) Epipaleoliticul de la Cuina Turcului-Dubova. *Studii si Cercetari de Istorie Veche si Arheologie* 21:3–47.
28. Bonsall C, et al. (2012) Interrelationship of age and diet in Romania's oldest human burial. *Naturwissenschaften* 99(4):321–325.
29. Cristiani E, Borić D (2012) 8500-year-old garment embroidery from the Late Mesolithic site of Vlasac (Serbia): Technological, use-wear and residue analyses. *J Archaeol Sci* 39:3450–3469.
30. Borić D, Dimitrijević V (2007) When did the 'Neolithic package' reach Lepenski Vir? Radiometric and faunal evidence. *Documenta Praehistorica* 35:53–72.
31. Borić D (2005) Body metamorphosis and animality: Volatile bodies and boulder artworks from Lepenski Vir. *Camb Archaeol J* 15(1):35–69.
32. Garašanin M, Radovanović I (2001) A pot in House 54 at Lepenski Vir I. *Antiquity* 75:118–125.
33. Jovanović B (1987) Die Architektur und Keramik der Siedlung Padina B am Eisernen Tor, Jugoslawien. *Germania* 65(1):1–16.
34. Antonović D (2006) *Stone Tools From Lepenski Vir* (Arheološki Institut, Beograd).
35. Biagi P, Starnini E (2010) A source in Bulgaria for Early Neolithic 'Balkan flint'. Antiquity 84(325):Project Gallery.
36. Roksandić M (2000) Between foragers and farmers in the Iron Gates gorge: Physical anthropology perspective. Djerdap population in transition from Mesolithic to Neolithic. *Documenta Praehistorica* 27:1–100.
37. Borić D, Stefanović S (2004) Birth and death: Infant burials from Vlasac and Lepenski Vir. *Antiquity* 78(301):526–547.
38. Bonsall C, et al. (1997) Mesolithic and Early Neolithic in the Iron Gates: A palaeodietary perspective. *J Eur Archaeol* 5:50–92.
39. Borić D, Grupe G, Peters J, Mikić Ž (2004) Is the Mesolithic-Neolithic subsistence dichotomy real? New stable isotope evidence from the Danube Gorges. *Eur J Archaeol* 7(3):221–248.
40. Cook G, et al. (2009) *Chronology and Evolution Within the Mesolithic of North-west Europe*, eds Crombé Ph, Van Strydonck M, Sergant J, Boudin M, Bats M (Cambridge Scholars Publishing, Newcastle upon Tyne, UK), pp 497–515.
41. Cook G, et al. (2002) Problems of dating human bones from the Iron Gates. *Antiquity* 76:77–85.
42. Vulcanescu R, ed (1972) *The Iron Gate Complex Atlas* (The Academy of the Socialist Republic of Romania, Bucharest).
43. Marković-Marjanović J (1978) *Vlasac – Mezolitsko Naselje u Djerdapu* [*Vlasac – Mesolithic Settlement in the Danube Gorges*] (Vol. II), ed Garašanin M (Srpska akademija nauka i umetnosti, Beograd), pp 11–27. Serbian.
44. Knipper C (2011) *Die räumliche Organisation der linearbandkeramischen Rinderhaltung: naturwissenschaftliche und archäologische Untersuchungen* [*Spatial organization of the Linear Pottery cattle husbandry: Natural sciences and archaeological investigations*]. (BAR Int Ser 2305, Oxford). German.
45. Tricca A, et al. (1999) Rare earth elements and Sr and Nd isotopic compositions of dissolved and suspended loads from small river systems in the Vosges Mountains (France), the River Rhine and groundwater. *Chem Geol* 160:139–158.
46. Price TD, Knipper C, Grupe G, Smrcka V (2004) Strontium isotopes and prehistoric human migration: The Bell Beaker period. *Eur J Archaeol* 7:9–40.
47. Stalio B (1992) Grupno sahranjivanje na Ajmani – Mala Vrbica [The group burial at Ajmana – Mala Vrbica]. *Zbornik Narodnog muzeja* 14-1 (arheologija):65–76. Serbian.
48. Radosavljević-Krunić S (1986) Resultats de l'étude anthroplogique des squélettes provenant du site Ajmana. *Cahiers des Portes de Fer* 3:51–58.
49. Grga Đ (1996) Karijes u humanoj populaciji kulture Lepenskog Vira. *Starinar* 47:177–185.
50. Soares P, et al. (2010) The archaeogenetics of Europe. *Curr Biol* 20(4):R174–R183.
51. Soares P, et al. (2009) Correcting for purifying selection: An improved human mitochondrial molecular clock. *Am J Hum Genet* 84(6):740–759.
52. Borić D (2007) *Mesolithic-Neolithic Interactions in the Danube Basin*, eds Kozłowski JK, Nowak M (Archaeopress, Oxford), pp 31–45.
53. Borić D (2008) *Prehistoric Europe*, ed Jones A (Blackwell Publishing, Malden, MA), pp 109–142.