

RESEARCH ARTICLE

HUMAN GENETICS

The genetic history of the Southern Arc: A bridge between West Asia and Europe

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By sequencing 727 ancient individuals from the Southern Arc (Anatolia and its neighbors in Southeastern Europe and West Asia) over 10,000 years, we contextualize its Chalcolithic period and Bronze Age (about 5000 to 1000 BCE), when extensive gene flow entangled it with the Eurasian steppe. Two streams of migration transmitted Caucasus and Anatolian/Levantine ancestry northward, and the Yamnaya pastoralists, formed on the steppe, then spread southward into the Balkans and across the Caucasus into Armenia, where they left numerous patrilineal descendants. Anatolia was transformed by intra-West Asian gene flow, with negligible impact of the later Yamnaya migrations. This contrasts with all other regions where Indo-European languages were spoken, suggesting that the homeland of the Indo-Anatolian language family was in West Asia, with only secondary dispersals of non-Anatolian Indo-Europeans from the steppe.

The Balkans and Anatolia are often portrayed as being geographically peripheral to Europe and Asia rather than as central to an interconnected region spanning both continents. Here, we take a different view by providing a systematic genetic history of what we refer to as the “Southern Arc,” a region (Fig. 1A) centered on the large Anatolian peninsula (Turkey), including in the west (in Europe) the Balkans and the Aegean, and in the south and east, Cyprus, Mesopotamia, the Levant, Armenia, Azerbaijan, and Iran. We present new genome-wide DNA data from 777 individuals from the Southern Arc: 727 previously unsampled and 50 previously published for which we report new data from 1094 newly generated ancient DNA libraries (1). As a resource to guide future sampling

efforts, we also report negative results for 476 samples that we screened using 537 libraries and that failed to yield ancient DNA data meeting the criteria for authenticity (1). Finally, we provide 239 new radiocarbon dates on the same skeletal elements analyzed for DNA (1). We studied these along with the previously published individuals for a total sample size of 1317 ancient individuals in the region (Fig. 1B) (1).

Our newly reported data fill many sampling gaps in space and time in the Southern Arc. In Turkey, our new sampling has a particular focus on the western (Aegean, Marmara), northern (Black Sea), and eastern (Eastern Anatolia, Southeastern Anatolia) regions connecting it with the rest of the Southern Arc. Another area of high-density sampling is Armenia, with sub-

stantial coverage of the Bronze and Iron Ages representing an order of magnitude more individuals than previously available. Many individuals of the Bronze-to-Iron Age time frame are also sampled from the Iranian highlands at Hasanlu, where only a single individual has previously been studied (2), and from Dinkha Tepe, neighboring Anatolia, Mesopotamia, Armenia, and the Caucasus. In the southern part of Southeastern Europe, we sample Mycenaean-era individuals from multiple regions of the Aegean. From the Southern Balkans, we present a full time transect of Albania; numerous individuals from North Macedonia, where previously data from only a single Neolithic individual had been published (3); and more than double the previously available body of ancient DNA data from Bulgaria. Farther north, at the western wing of the Southern Arc, we sample individuals from Croatia, Montenegro, and Serbia in the west and Romania and Moldova in the east, which interface with the extensively studied worlds of Central Europe and the Eurasian steppe. This dataset includes >100 Bronze Age individuals, including many from Cetina Valley and Bezdanjača Cave in Croatia, which add to only five previously published from the entire area (3, 4). Some of the Balkan individuals include culturally Yamnaya individuals from Serbia and Bulgaria,

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Connecting genes and history

Stories about the peopling—and people—of Southern Europe and West Asia have been passed down for thousands of years, and these stories have contributed to our historical understanding of populations. Genomic data provide the opportunity to truly understand these patterns independently from written history. In a trio of papers, Lazaridis *et al.* examined more than 700 ancient genomes from across this region, the Southern Arc, spanning 11,000 years, from the earliest farming cultures to post-Medieval times (see the Perspective by Arbuckle and Schwandt). On the basis of these results, the authors suggest that earlier reliance on modern phenotypes and ancient writings and artistic depictions provided an inaccurate picture of early Indo-Europeans, and they provide a revised history of the complex migrations and population integrations that shaped these cultures. —SNV

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