

RESEARCH ARTICLE

HUMAN GENETICS

A genetic probe into the ancient and medieval history of Southern Europe and West Asia

Iosif Lazaridis^{1,2,*}†, Songül Alpaslan-Roodenberg^{2,3,*}†, Ayşe Acar⁴, Aysen Açıkkol⁵, Anagnostis Agelarakis⁶, Levon Aghikyan⁷, Uğur Akyüz⁸, Desislava Andreeva⁹, Gojko Andrijašević¹⁰, Dragana Antonović¹¹, Ian Armit¹², Alper Atmaca¹³, Pavel Avetisyan⁷, Ahmet İhsan Aytekin¹⁴, Krum Bacvarov¹⁵, Ruben Badalyan⁷, Stefan Bakardzhiev¹⁶, Jacqueline Balen¹⁷, Lorenc Bejko¹⁸, Rebecca Bernardos², Andreas Bertsatos¹⁹, Hanifi Biber²⁰, Ahmet Bilir²¹, Mario Bodružić²², Michelle Bonogofsky²³, Clive Bonsall²⁴, Dušan Borić²⁵, Nikola Borovinić²⁶, Guillermo Bravo Morante³, Katharina Buttinger³, Kim Callan^{2,27}, Francesca Candilio²⁸, Mario Carić²⁹, Olivia Cheronet³, Stefan Chohadzhiev³⁰, Maria-Eleni Chovalopoulou¹⁹, Stella Chrysosoulaki³¹, Ion Ciobanu^{32,33}, Natalija Čondić³⁴, Mihai Constantinescu³⁵, Emanuela Cristiani³⁶, Brendan J. Culleton³⁷, Elizabeth Curtis^{2,27}, Jack Davis³⁸, Tatiana I. Demcenco³⁹, Valentin Dergachev⁴⁰, Zafer Derin⁴¹, Sylvia Deskaj⁴², Seda Devejian⁷, Vojislav Djordjević⁴³, Kellie Sara Duffett Carlson³, Laurie R. Eccles⁴⁴, Nedko Elenski⁴⁵, Atilla Engin⁴⁶, Nihat Erdoğan⁴⁷, Sabiha Erir-Pazarci⁴⁸, Daniel M. Fernandes^{3,49}, Matthew Ferry^{2,27}, Suzanne Freilich³, Alin Frinculeasa⁵⁰, Michael L. Galaty⁴², Beatriz Gamarra^{51,52,53}, Boris Gasparyan⁷, Bisserka Gaydarska⁵⁴, Elif Genç⁵⁵, Timur Gültekin⁵⁶, Serkan Gündüz⁵⁷, Tamás Hajdu⁵⁸, Volker Heyd⁵⁹, Suren Hobosyan⁷, Nelli Hovhannisyann⁶⁰, Iliya Iliev¹⁶, Lora Iliev^{2,27}, Stanislav Iliev⁶¹, İlkay İvgin⁶², Ivor Janković²⁹, Lence Jovanova⁶³, Panagiotis Karkanas⁶⁴, Berna Kavaz-Kındığıllı⁶⁵, Esra Hilal Kaya⁶⁶, Denise Keating³, Douglas J. Kennett^{37,67}, Seda Deniz Kesici⁶⁸, Anahit Khudaverdyan⁷, Krisztian Kiss^{58,69}, Sinan Kılıç²⁰, Paul Klostermann⁷⁰, Sinem Kostak Boca Negra Valdes⁶⁸, Saša Kovačević⁷¹, Marta Krenz-Niedbala⁷², Maja Krznarić Škrivanko⁷³, Rovena Kurti⁷⁴, Pasko Kuzman⁷⁵, Ann Marie Lawson^{2,27}, Catalin Lazar⁷⁶, Krassimir Leshtakov⁷⁷, Thomas E. Levy⁷⁸, Ioannis Liritzis^{79,80}, Kirsio O. Lorentz⁸¹, Sylwia Łukasik⁷², Matthew Mah^{2,27,82}, Swapan Mallick^{2,27}, Kirsten Mandi³, Kristine Martirosyan-Olshansky⁸³, Roger Matthews⁸⁴, Wendy Matthews⁸⁴, Kathleen McSweeney²⁴, Varduhi Melikyan⁷, Adam Micco², Megan Michel^{1,2,27}, Lidija Milašinović⁸⁵, Alissa Mitnick^{1,2,86}, Janet M. Monge⁸⁷, Georgi Nekhrizov¹⁵, Rebecca Nicholls⁸⁸, Alexey G. Nikitin⁸⁹, Vassil Nikolov¹⁵, Mario Novak²⁹, Iñigo Olalde^{2,90}, Jonas Oppenheimer^{2,27}, Anna Osterholtz⁹¹, Celal Özdemir¹³, Kadir Toykan Özdoğan³, Nurettin Öztürk⁶⁵, Nikos Papadimitriou⁹², Niki Papakonstantinou⁹³, Anastasia Papathanasiou⁹⁴, Lujana Paraman⁹⁵, Evgeny G. Paskary⁹⁶, Nick Patterson^{1,82}, Ilian Petrakiev⁴⁵, Levon Petrosyan⁷, Vanya Petrova⁷⁷, Anna Philippa-Touchais⁹⁷, Ashot Piliposyan⁹⁸, Nada Pocuca Kuzman⁷⁵, Hrvoje Potrebica⁹⁹, Bianca Preda-Bălănică⁵⁹, Zrinka Premuzić¹⁰⁰, T. Douglas Price¹⁰¹, Lijun Qiu^{2,27}, Siniša Radović¹⁰², Kamal Raeuf Aziz¹⁰³, Petra Rajić Šikanjić²⁹, Kamal Rasheed Raheem¹⁰³, Sergei Razumov¹⁰⁴, Amy Richardson⁸⁴, Jacob Roodenberg¹⁰⁵, Rudenc Ruka⁷⁴, Victoria Russeva¹⁰⁶, Mustafa Şahin⁵⁷, Ayşegül Şarbak¹⁰⁷, Emre Savaş⁶⁸, Constanze Schattke³, Lynne Schepartz¹⁰⁸, Tayfun Selçuk⁶⁸, Ayla Sevim-Erol¹⁰⁹, Michel Shamoon-Pour¹¹⁰, Henry M. Shephard¹¹¹, Athanasios Sideris¹¹², Angela Simalcik^{32,113}, Hakob Simonyan¹¹⁴, Vitalij Sinika¹⁰⁴, Kendra Sirak², Ghenadie Sirbu¹¹⁵, Mario Šlaus¹¹⁶, Andrei Soficaru³⁵, Bilal Söğüt¹¹⁷, Arkadiusz Softysiak¹¹⁸, Çilem Sönmez-Sözer¹⁰⁹, Maria Stathi¹¹⁹, Martin Steska¹²⁰, Kristin Stewardson^{2,27}, Sharon Stocker³⁸, Fadime Suata-Alpaslan¹²¹, Alexander Suvorov⁵⁹, Anna Szécsényi-Nagy¹²², Tamás Szeniczey⁵⁸, Nikolai Telnov¹⁰⁴, Strahil Temov¹²³, Nadezhda Todorova⁷⁷, Ulsi Tota^{74,124}, Gilles Touchais¹²⁵, Sevi Triantaphyllou⁹³, Atila Türkler¹²⁶, Marina Ugarković⁷¹, Todor Valchev¹⁶, Fanica Veljanovska¹²³, Zlatko Videvski¹²³, Cristian Virag¹²⁷, Anna Wagner³, Sam Walsh¹²⁸, Piotr Włodarczak¹²⁹, J. Noah Workman², Aram Yardumian^{130,131}, Evgenii Yarovoy¹³², Alper Yener Yavuz¹³³, Hakan Yılmaz²⁰, Fatma Zalzala^{2,27}, Anna Zetti³, Zhao Zhang², Rafet Çavuşoğlu²⁰, Nadin Rohland², Ron Pinhasi^{3,134,*}, David Reich^{1,2,27,82,*}

Literary and archaeological sources have preserved a rich history of Southern Europe and West Asia since the Bronze Age that can be complemented by genetics. Mycenaean period elites in Greece did not differ from the general population and included both people with some steppe ancestry and others, like the Griffin Warrior, without it. Similarly, people in the central area of the Urartian Kingdom around Lake Van lacked the steppe ancestry characteristic of the kingdom's northern provinces. Anatolia exhibited extraordinary continuity down to the Roman and Byzantine periods, with its people serving as the demographic core of much of the Roman Empire, including the city of Rome itself. During medieval times, migrations associated with Slavic and Turkic speakers profoundly affected the region.

The works of ancient writers provide powerful insights into the ancient world, recording information on different groups, their political organizations, customs, relations, and military conflicts. The manuscript tradition has been augmented by the archaeological record, which also includes the discovery of texts of past Mediterranean and West Asian civilizations. In this work, we leverage the power of ancient DNA to provide a third source of information about the people inhabiting the states and empires of the past. Many of these aspects have been recorded, or hinted at, in ancient texts composed close to the time of the events they describe. However, no text is fully objective, and all texts are inevitably shaped by authors' biases and world views. Ancient DNA provides independent

evidence, with its own strengths and weaknesses, and cannot paint a picture of the past on its own. Nonetheless, it complements the ancient texts and evidence from archaeology. By using genetic data, we can hope to obtain a more nuanced impression of past processes—especially with regards to movements of people and biological phenotypes—than would be possible without such data.

This study is a part of a comprehensive archaeogenetic analysis of the genetic history of the populations of the Southern Arc, spanning a trio of papers. For a description of the full dataset and analysis framework and characterization of the population history of the Chalcolithic and Bronze Age periods, see (1). For analysis of the population history of the Neolithic, see (2). The present paper focuses on

peoples for which there is also information from written texts. A main theme is to test the extent to which textual insights are supported or not supported by the genetic data and furthermore to explore what complementary information genetics can provide. When we reference ancient literature, we use standard abbreviations for locating passages in online repositories of texts, such as the Perseus Digital Library (3). Our study begins at the end of the Bronze Age and traces the region's history through the first millennium BCE, through the Roman Empire and up to the present, a time span of >3000 years.

The Bronze Age Aegean world

Previous work has demonstrated that the Bronze Age civilizations of Greece of the

periods labeled Minoan (on the island of Crete; spanning the entirety of the Bronze Age, ~3500 to 1100 BCE) and Mycenaean (on the Greek mainland and its islands; spanning the latter part of the Bronze Age since the last phase of the Middle Helladic period to the end of the Late Helladic period, ~1750 to 1050 BCE) (4) were inhabited by genetically similar populations that traced most of their ancestry to the Neolithic inhabitants of the region, who, in turn, were related to the farmers of Anatolia (4–7).

We refer to people associated with these archaeological contexts as Minoan and Mycenaean, recognizing that the people themselves would almost certainly not have considered themselves as belonging to two groups divided according to this framework defined by archaeology and that there was in fact extensive genetic variation in ancestry among people associated with such cultures, as we prove here. Both Mycenaeans and Minoans had extra “eastern” Caucasus-related ancestry compared

with that of the Neolithic inhabitants of Greece, but they differed from each other in that the Mycenaeans taken as a group had some steppe ancestry that Minoans lacked (4). In this work, we extend the geographical sampling to multiple sites without previously reported ancient DNA data, complementing published Mycenaean data from the Peloponnese and Salamis and Minoan data from Lasithi and Moni Odigitria (4). From Crete, we report a Middle Minoan individual from Zakros. From

¹Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA. ²Department of Genetics, Harvard Medical School, Boston, MA 02115, USA. ³Department of Evolutionary Anthropology, University of Vienna, 1030 Vienna, Austria. ⁴Department of Anthropology, Faculty of Letters, Mardin Artuklu University, 47510 Artuklu, Mardin, Turkey. ⁵Department of Anthropology, Faculty of Letters, Sivas Cumhuriyet University, 58140 Sivas, Turkey. ⁶Department of History, Adelphi University, Garden City, NY 11530, USA. ⁷Institute of Archaeology and Ethnography, NAS RA, 0025 Yerevan, Armenia. ⁸Samsun Museum of Archeology and Ethnography, Kale Mahallesi, Merkez, İlkadim, 55030 Samsun, Turkey. ⁹Iskra Museum of History, 6100 Kazanlak, Bulgaria. ¹⁰Historical Museum in Kotor, 85330 Kotor, Montenegro. ¹¹Institute of Archaeology, 11000 Belgrade, Serbia. ¹²Department of Archaeology, University of York, York YO1 7EP, UK. ¹³Amasya Archaeology Museum, Mustafa Kemal Paşa Caddesi, 05000 Amasya, Turkey. ¹⁴Department of Anthropology, Faculty of Arts and Science, Burdur Mehmet Akif University, 15100 Burdur, Turkey. ¹⁵National Institute of Archaeology and Museum, Bulgarian Academy of Sciences, 1000 Sofia, Bulgaria. ¹⁶Yambol Regional Historical Museum, 8600 Yambol, Bulgaria. ¹⁷Archaeological Museum in Zagreb, 10000 Zagreb, Croatia. ¹⁸Department of Archaeology and Heritage Studies, University of Tirana, 1010 Tirana, Albania. ¹⁹Department of Animal and Human Physiology, Faculty of Biology, School of Sciences, National and Kapodistrian University of Athens, 10679 Athens, Greece. ²⁰Department of Archaeology, Faculty of Humanities, Van Yüzüncü Yıl University, 65090 Tuşba, Van, Turkey. ²¹Department of Archaeology, Faculty of Science and Letters, Düzce University, 81620 Düzce, Turkey. ²²Stratum Ltd., 21218 Seget Donji, Croatia. ²³Independent Researcher, Berkeley, CA 94720, USA. ²⁴School of History, Classics and Archaeology, University of Edinburgh, Edinburgh EH8 9AG, UK. ²⁵The Italian Academy for Advanced Studies in America, Columbia University, New York, NY 10027, USA. ²⁶Center for Conservation and Archaeology of Montenegro, 81250 Cetinje, Montenegro. ²⁷Howard Hughes Medical Institute, Harvard Medical School, Boston, MA 02115, USA. ²⁸Servizio di Bioarcheologia, Museo delle Civiltà, 00144 Rome, Italy. ²⁹Centre for Applied Bioanthropology, Institute for Anthropological Research, 10000 Zagreb, Croatia. ³⁰Department of Archaeology, University of Veliko Tarnovo “St. Cyril and St. Methodius,” 5003 Veliko Tarnovo, Bulgaria. ³¹Hellenic Ministry of Culture and Sports, Ephorate of Antiquities of Piraeus and the Islands, 10682 Piraeus, Greece. ³²“Orheiul Vechi” Cultural-Natural Reserve, Institute of Bioarchaeological and Ethnocultural Research, 3552 Butuceni, Moldova. ³³National Archaeological Agency, 2012 Chişinău, Moldova. ³⁴Archaeological Museum in Zadar, 23000 Zadar, Croatia. ³⁵“Francisc I. Rainer” Institute of Anthropology, 050711 Bucharest, Romania. ³⁶Department of Oral and Maxillo-Facial Sciences, Sapienza University of Rome, 00161 Rome, Italy. ³⁷Institutes of Energy and the Environment, The Pennsylvania State University, University Park, PA 16802, USA. ³⁸Department of Classics, University of Cincinnati, Cincinnati, OH 45221, USA. ³⁹Independent Researcher, Aberystwyth SY23 4UH, UK. ⁴⁰Center of Archaeology, Institute of Cultural Heritage, Academy of Science of Moldova, 2001 Chişinău, Moldova. ⁴¹Department of Archaeology, Faculty of Letters, Ege University, 35100 Bornova-Izmir, Turkey. ⁴²Museum of Anthropological Archaeology, University of Michigan, Ann Arbor, MI 48109, USA. ⁴³Narodni muzej Pančevo, 26101 Pančevo, Serbia. ⁴⁴Human Paleoecology and Isotope Geochemistry Lab, Department of Anthropology, The Pennsylvania State University, University Park, PA 16802, USA. ⁴⁵Regional Museum of History – Veliko Tarnovo, 5000 Veliko Tarnovo, Bulgaria. ⁴⁶Department of Archaeology, Faculty of Science and Letters, Gaziantep University, 27310 Gaziantep, Turkey. ⁴⁷Mardin Archaeological Museum, Şar, Cumhuriyet Meydanı üstü, 47100 Artuklu, Mardin, Turkey. ⁴⁸Muğla İl Kültür ve Turizm Müdürlüğü, 48000 Muğla, Turkey. ⁴⁹Research Centre for Anthropology and Health (CIAS), Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal. ⁵⁰Prahova County Museum of History and Archaeology, 100042 Ploieşti, Romania. ⁵¹Institut Català de Paleocologia Humana i Evolució Social, 43007 Tarragona, Spain. ⁵²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, 43002 Tarragona, Spain. ⁵³School of Archaeology and Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland. ⁵⁴Department of Archaeology, Durham University, Durham DH1 3LE, UK. ⁵⁵Department of Archaeology, Faculty of Science and Letters, Çukurova University, 01330 Balçalı-Sarıçam-Adana, Turkey. ⁵⁶Department of Anthropology, Faculty of Humanities, Ankara University, 06100 Sıhhiye, Ankara, Turkey. ⁵⁷Department of Archaeology, Faculty of Science and Letters, Bursa Uludağ University, 16059 Görükle, Bursa, Turkey. ⁵⁸Department of Biological Anthropology, Institute of Biology, Eötvös Loránd University, 1053 Budapest, Hungary. ⁵⁹Department of Cultures, University of Helsinki, 00100 Helsinki, Finland. ⁶⁰Department of Ecology and Nature Protection, Yerevan State University, 0025 Yerevan, Armenia. ⁶¹Regional Museum of History, 6300 Haskovo, Bulgaria. ⁶²Ministry of Culture and Tourism, İsmet İnönü Bulvarı, 06100 Emek, Ankara, Turkey. ⁶³Museum of the City of Skopje, 1000 Skopje, North Macedonia. ⁶⁴Malcolm H. Wiener Laboratory, American School of Classical Studies at Athens, 10676 Athens, Greece. ⁶⁵Department of Archaeology, Faculty of Letters, Atatürk University, 25100 Erzurum, Turkey. ⁶⁶Muğla Archaeological Museum and Yatağan Thermal Power Generation Company, Rescue Excavations, 48000 Muğla, Turkey. ⁶⁷Department of Anthropology, University of California, Santa Barbara, Santa Barbara, CA 93106, USA. ⁶⁸Bodrum Museum of Underwater Archeology, Çarşı Neighbourhood, 48400 Bodrum, Muğla, Turkey. ⁶⁹Department of Anthropology, Hungarian Natural History Museum, 1117 Budapest, Hungary. ⁷⁰Department of Anthropology, Natural History Museum Vienna, 1010 Vienna, Austria. ⁷¹Institute of Archaeology, 10000 Zagreb, Croatia. ⁷²Faculty of Biology, Adam Mickiewicz University in Poznań, 61-614 Poznań, Poland. ⁷³Municipal Museum Vinkovci, 32100 Vinkovci, Croatia. ⁷⁴Prehistory Department, Albanian Institute of Archaeology, Academy of Albanian Studies, 1000 Tirana, Albania. ⁷⁵National Museum in Ohrid, 6000 Ohrid, North Macedonia. ⁷⁶ArchaeoSciences Division, Research Institute of the University of Bucharest, University of Bucharest, 050663 Bucharest, Romania. ⁷⁷Department of Archaeology, St. Kliment Ohridski University of Sofia, 1504 Sofia, Bulgaria. ⁷⁸Department of Anthropology, University of California, San Diego, La Jolla, CA 92093, USA. ⁷⁹Key Research Institute of Yellow River Civilization and Sustainable Development and the Collaborative Innovation Center on Yellow River Civilization of Henan Province, Laboratory of Yellow River Cultural Heritage, Henan University, 475001 Kaifeng, China. ⁸⁰European Academy of Sciences and Arts, 5020 Salzburg, Austria. ⁸¹Science and Technology in Archaeology and Culture Research Center, The Cyprus Institute, 2121 Aglantzia, Nicosia, Cyprus. ⁸²Broad Institute of Harvard and MIT, Cambridge, MA 02142, USA. ⁸³Cotsen Institute of Archaeology, University of California, Los Angeles, Los Angeles, CA 90095, USA. ⁸⁴Department of Archaeology, University of Reading, Reading RG6 6AB, UK. ⁸⁵National Museum of Kikinda, 23300 Kikinda, Serbia. ⁸⁶Department of Archaeogenetics, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany. ⁸⁷University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia, PA 19104, USA. ⁸⁸School of Archaeological and Forensic Sciences, Faculty of Life Sciences, University of Bradford, Bradford BD7 1DP, UK. ⁸⁹Department of Biology, Grand Valley State University, Allendale, MI 49401, USA. ⁹⁰BIOMICS Research Group, University of the Basque Country UPV/EHU, 01006 Vitoria-Gasteiz, Spain. ⁹¹Department of Anthropology and Middle Eastern Cultures, Mississippi State University, Mississippi State, MS 39762, USA. ⁹²Paul and Alexandra Canellopoulos Museum, 105-55 Athens, Greece. ⁹³Faculty of Philosophy, School of History and Archaeology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece. ⁹⁴Ephorate of Paleontology and Speleology, Greek Ministry of Culture, 11636 Athens, Greece. ⁹⁵Trogir Town Museum, 21220 Trogir, Croatia. ⁹⁶Moldavian Historic-Geographical Society, 2044 Chişinău, Moldova. ⁹⁷French School of Archaeology at Athens, 10680 Athens, Greece. ⁹⁸Department of Armenian History, Armenian State Pedagogical University After Khachatur Abovyan, 0010 Yerevan, Armenia. ⁹⁹Department of Archaeology, Faculty of Humanities and Social Sciences, University of Zagreb, 10000 Zagreb, Croatia. ¹⁰⁰Independent Researcher, 10000 Zagreb, Croatia. ¹⁰¹Laboratory for Archaeological Chemistry, University of Wisconsin–Madison, Madison, WI 53706, USA. ¹⁰²Institute for Quaternary Paleontology and Geology, Croatian Academy of Sciences and Arts, 10000 Zagreb, Croatia. ¹⁰³Sulaymaniyah Directorate of Antiquities and Heritage, 46010 Sulaymaniyah, Iraq. ¹⁰⁴Pridnestrovian University named after Taras Shevchenko, 3300 Tiraspol, Moldova. ¹⁰⁵The Netherlands Institute for the Near East, 2311 Leiden, Netherlands. ¹⁰⁶Institute of Experimental Morphology, Pathology and Archeology with Museum, Bulgarian Academy of Science, 1113 Sofia, Bulgaria. ¹⁰⁷Department of Anthropology, Faculty of Science and Letters, Hitit University, 19040 Çorum, Turkey. ¹⁰⁸School of Anatomical Sciences, The University of the Witwatersrand, 2193 Johannesburg, South Africa. ¹⁰⁹Department of Anthropology, Faculty of Language and History - Geography, Ankara University, 06100 Sıhhiye, Ankara, Turkey. ¹¹⁰Department of Anthropology, Binghamton University, Binghamton, NY 13902, USA. ¹¹¹Archaeological Institute of America, Boston, MA 02108, USA. ¹¹²Institute of Classical Archaeology, Charles University, 11636 Prague, Czechia. ¹¹³“Olga Necrasov” Centre of Anthropological Research, Romanian Academy Iaşi Branch, 2012 Iaşi Romania. ¹¹⁴Scientific Research Center of the Historical and Cultural Heritage, 0010 Yerevan, Armenia. ¹¹⁵Thracology Scientific Research Laboratory of the State University of Moldova, Department of Academic Management, Academy of Science of Moldova, 2009 Chişinău, Moldova. ¹¹⁶Anthropological Center of the Croatian Academy of Sciences and Arts, 10000 Zagreb, Croatia. ¹¹⁷Department of Archaeology, Faculty of Science and Arts, Pamukkale University, 20070 Denizli, Turkey. ¹¹⁸Faculty of Archaeology, University of Warsaw, 00-927 Warszawa, Poland. ¹¹⁹Ephorate of Antiquities of East Attica, Ministry of Culture and Sports, 10682 Athens, Greece. ¹²⁰Austrian Archaeological Institute at the Austrian Academy of Sciences, 1190 Vienna, Austria. ¹²¹Department of Anthropology, Faculty of Letters, Istanbul University, 34134 Istanbul, Turkey. ¹²²Institute of Archaeogenetics, Research Centre for the Humanities, Eötvös Loránd Research Network, 1097 Budapest, Hungary. ¹²³Archaeology Museum of North Macedonia, 1000 Skopje, North Macedonia. ¹²⁴Culture and Patrimony Department, University of Avignon, 84029 Avignon, France. ¹²⁵Department of the History of Art and Archaeology, Université Paris 1 Panthéon-Sorbonne, 75006 Paris, France. ¹²⁶Department of Archaeology, Faculty of Science and Letters, Ondokuz Mayıs University, 55139 Atakum-Samsun, Turkey. ¹²⁷Satu Mare County Museum, 440031 Satu Mare, Romania. ¹²⁸School of Natural Sciences, University of Central Lancashire, Preston PR1 2HE, UK. ¹²⁹Institute of Archaeology and Ethnology, Polish Academy of Sciences, 31-016 Kraków, Poland. ¹³⁰Department of History and Social Sciences, Bryn Athyn College, Bryn Athyn, PA 19009, USA. ¹³¹Penn Museum, University of Pennsylvania, Philadelphia, PA 19104, USA. ¹³²History of the Ancient World and Middle Ages Department, Moscow Region State University, Moscow Region, 141014 Mytishi, Russia. ¹³³Department of Anthropology, Burdur Mehmet Akif Ersoy University, Istiklal Campus, 15100 Burdur, Turkey. ¹³⁴Human Evolution and Archaeological Sciences, University of Vienna, 1030 Vienna, Austria.

*Corresponding author. Email: lazaris@genetics.med.harvard.edu (I.La.); msglalpaslan@gmail.com (S.A.-R.); ron.pinhasi@univie.ac.at (R.P.); reich@genetics.med.harvard.edu (D.R.)

†These authors contributed equally to this work.

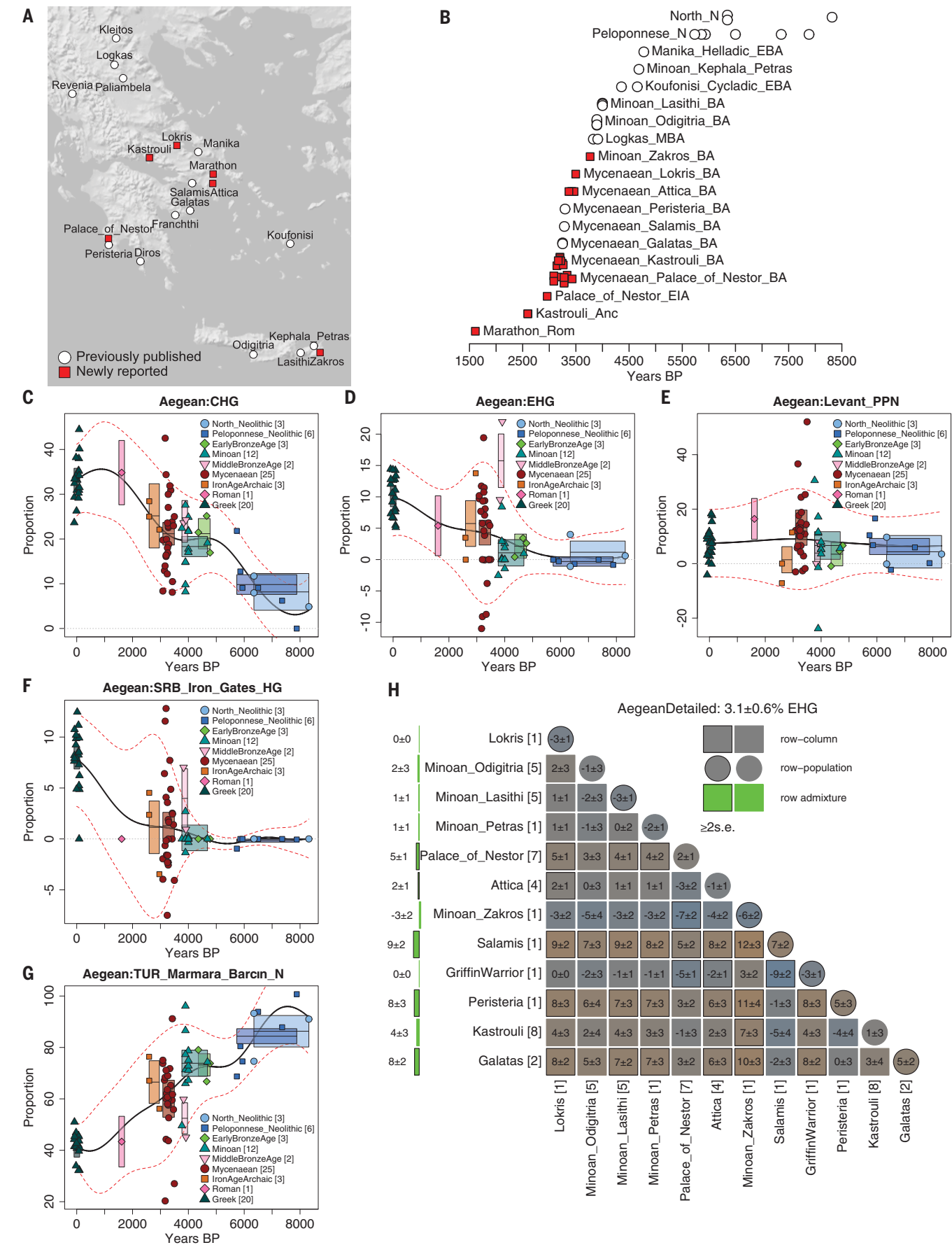


Fig. 1. Genetic heterogeneity in the Aegean. (A) A map of Aegean sites. (B) Timeline of Aegean individuals, with vertical jitter added to distinguish contemporaneous individuals. BP, before the present. (C to G) Ancestry changes of five components show an increase of Caucasus hunter-gatherer (CHG) and Eastern European hunter-gatherer (EHG) ancestry over time and a dilution of Anatolian Neolithic ancestry. (H) During the Minoan and Mycenaean periods of the Bronze Age, Eastern European hunter-gatherer ancestry was variable, absent in Minoan individuals of Crete, and present in most but not all Mycenaean individuals of the mainland. s.e., standard error.

mainland contexts, we report the first Mycenaean data from Central Greece—that is, the previously unsampled region north of the Isthmus of Corinth—including Attica, Kastrouli near Delphi in Phokis, and Lokris in Phthiotis. South of the Isthmus in the Peloponnese, we report data from many individuals from the “Palace of Nestor” at Pylos and its environs, including the elite “Griffin Warrior,” a young (30 to 35 years old) male buried in a large stone-built tomb with hundreds of precious artifacts, many of them made in Minoan Crete (8).

To contextualize the transformations in the Bronze Age Aegean, it is critical to characterize the pre-Bronze Age genetic landscape (Fig. 1). We begin with the Neolithic inhabitants (4, 6, 7), estimating proportions of ancestry using a five-source model that we developed for Southern Arc Holocene populations (1), which includes as proxies for the sources Caucasus hunter-gatherers (9), Eastern European hunter-gatherers (5, 10), Levantine Pre-Pottery Neolithic (11), Balkan hunter-gatherers from the Iron Gates in Serbia (7), and Northwestern Anatolian Neolithic from Barcin (5). We infer that not only Neolithic Greeks from the Peloponnese (7) but also those from Northern Greece (6) had ~8 to 10% Caucasus hunter-gatherer-related ancestry (Fig. 1C). We find small amounts of Caucasus hunter-gatherer-related ancestry in Southeastern Europe and Neolithic populations in general, which is different from the pattern in Central/Western Europe where there is none (1). This provides proof of multiple streams of migration from different Anatolian Neolithic populations into Europe.

Both Caucasus and Eastern European hunter-gatherer-related ancestry increased in the Bronze Age in the Aegean just as the Anatolian-related ancestry decreased (Fig. 1), with Mycenaean Greeks having $21.2 \pm 1.3\%$ Caucasus hunter-gatherer ancestry and $4.3 \pm 1.0\%$ Eastern European hunter-gatherer ancestry. Given the evenly balanced proportions of these components in the Yamnaya and the “high steppe” cluster from the Balkans (1), it can be assumed that the Eastern European hunter-gatherer component in the Aegean was not introduced there on its own but rather was accompanied by an approximately matching amount of Caucasus hunter-gatherer ancestry, thus leaving a remainder of $\sim 21.2 - 4.3 = 16.9\%$ Caucasus hunter-gatherer. This allows us to infer that steppe migrants admixed with a population whose composition must have

included $\frac{16.9}{100-2 \times 4.3}$ or ~18.5% Caucasus hunter-gatherer-related ancestry. Notably, the estimated proportion of Caucasus hunter-gatherer ancestry in Minoans is virtually identical at $18.3 \pm 1.2\%$. Thus, our analyses resolve the question of the origins of the Late Bronze Age population by strongly supporting one of two previously proposed hypotheses (4)—that Mycenaeans were the outcome of admixture of descendants of Yamnaya-like steppe migrants with a Minoan-like substratum, rather than the hitherto plausible alternative scenario of an Anatolian Neolithic-like substratum admixing with an Armenian-like population from the east. This alternative scenario is further contradicted by the fact that pre-Mycenaean period individuals belonging to the Early Bronze Age from the islands of the Cyclades and Euboea in Southern Greece in ~2500 BCE (12) had $21.2 \pm 1.7\%$ Caucasus hunter-gatherer-related ancestry (12), consistent with our inferred proportion and providing direct evidence for the predicted Minoan-like substratum (4).

The fact that Mycenaeans can be modeled as a mixture in an ~1:10 ratio of a Yamnaya-like steppe-derived population and a Minoan- or Early Bronze Age-like Aegean population suggests that any contribution of geographically intermediate populations (between the steppe and the Aegean) to the formation of Mycenaeans was minor. This conclusion is further supported by the following: (i) the lower (~5%) Caucasus hunter-gatherer ancestry in the Neolithic of the Balkans compared with the ~20% inferred for the Aegean substratum (1), (ii) the near absence of Balkan hunter-gatherer (fig. S1) ancestry in the Aegean in contrast to other Southeastern European populations (~10%) (1), and (iii) the presence of Yamnaya-like individuals with minimal local ancestry—immediately to the north of the Aegean—in Albania and Bulgaria during the Early Bronze Age (1). Whatever the genetic makeup of people mediating the spread of steppe ancestry into the ancestors of Mycenaeans, the genetic impact of steppe on Aegean populations was quantitatively minor. We estimate the Yamnaya-related steppe ancestry proportion in Mycenaeans to be ~ $\frac{1}{3}$ of the level of that in the Balkans to the north, ~ $\frac{1}{2}$ of that in Armenia in the east, and ~ $\frac{1}{3}$ to $\frac{1}{2}$ of that of populations of Central/Northern Europe associated with the Bell Beaker and Corded Ware cultures (1).

Eastern European hunter-gatherer ancestry as a marker for Yamnaya steppe pastoralist

ancestry is absent in a newly reported Middle Minoan period individual from Zakros on the eastern edge of Crete. This individual's ancestry is generally similar to those previously published (13), but with significant Levantine admixture ($30.5 \pm 9.1\%$), which is consistent with her either being a migrant to the island from the east or part of a structured Cretan population whose past ethnic diversity was noted as early as the *Odyssey* of Homer (Hom. Od. 19.172-177).

We show that Eastern European hunter-gatherer ancestry was also absent in some Mycenaean individuals, which suggests that although the contrast between the mainland and Crete was significant (fig. S1), the penetration of Eastern European hunter-gatherer ancestry did not reach the totality of the mainland population during the Late Bronze Age and was even significantly variable within Mycenaean sites. The Griffin Warrior (8), the earliest individual (~1450 BCE) from the Palace of Nestor in Pylos, is genetically right in the middle of the general population of the Aegean and was thus plausibly of entirely local Aegean origin. He had no detectable Eastern European hunter-gatherer ancestry (compared with the average of $4.8 \pm 1.1\%$ for the rest of the Mycenaean-era individuals sampled at the Palace; Fig. 1H). This finding could be consistent with a Cretan origin of this individual or his ancestors; alternatively, he could be drawn from a mainland population that had not experienced Eastern European hunter-gatherer admixture, as could two later individuals from Pylos—one buried near the Palace in a chamber tomb and another in a cist grave. Variation in Eastern European hunter-gatherer ancestry is observed at short geographical distance scales and within the same time periods: We observe that four individuals (~1450 BCE) of the sample from Attica buried at Kolikrepi-Spata had only $2 \pm 1\%$ Eastern European hunter-gatherer ancestry that was significantly less (by more than two standard errors) than that of individuals from the neighboring island of Salamis and all sampling locations in the Peloponnese. This suggests that the classical Athenian claim (e.g., Plat. Menex. 237b) of having received fewer migrants than other Greek poleis in the remote past may have had an element of truth, although larger sample sizes will be necessary to definitively establish such geographic patterns.

Northern migrants made an impact throughout mainland Greece, even if it was a modest one. This is also attested in the male line, for

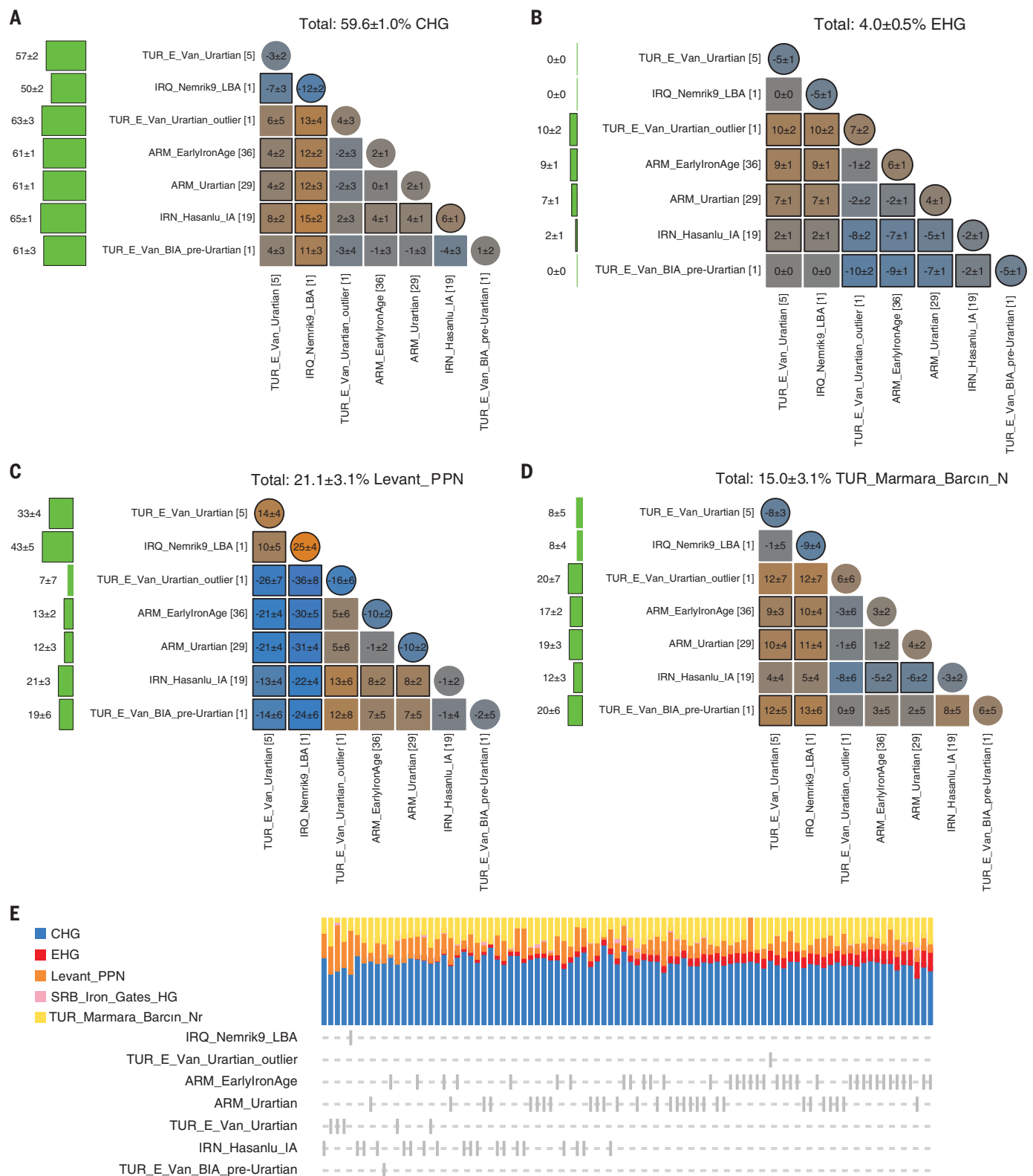


Fig. 2. The Kingdom of Urartu and its neighbors. (A to D) Comparisons of ancestry in four ancestral components [SRB_Iron_Gates_HG, the fifth component of the model of (1) is negligible]. This analysis shows a stark contrast between Armenia and the other populations in terms of Eastern European hunter-gatherer ancestry (B) and between Van and Assyrian Mesopotamia (represented by the site of Nemrik 9 in Iraq) in terms of Levantine ancestry (C). When unlabeled individuals are ordered in increasing Eastern European hunter-gatherer ancestry (E), Assyrian Mesopotamia and Van lack this ancestry (except for an outlier individual from Van), whereas individuals from Armenia mostly have it, and those from Hasanlu have a limited range from zero Eastern European hunter-gatherer ancestry to a maximum level that is less than that seen in Armenia.

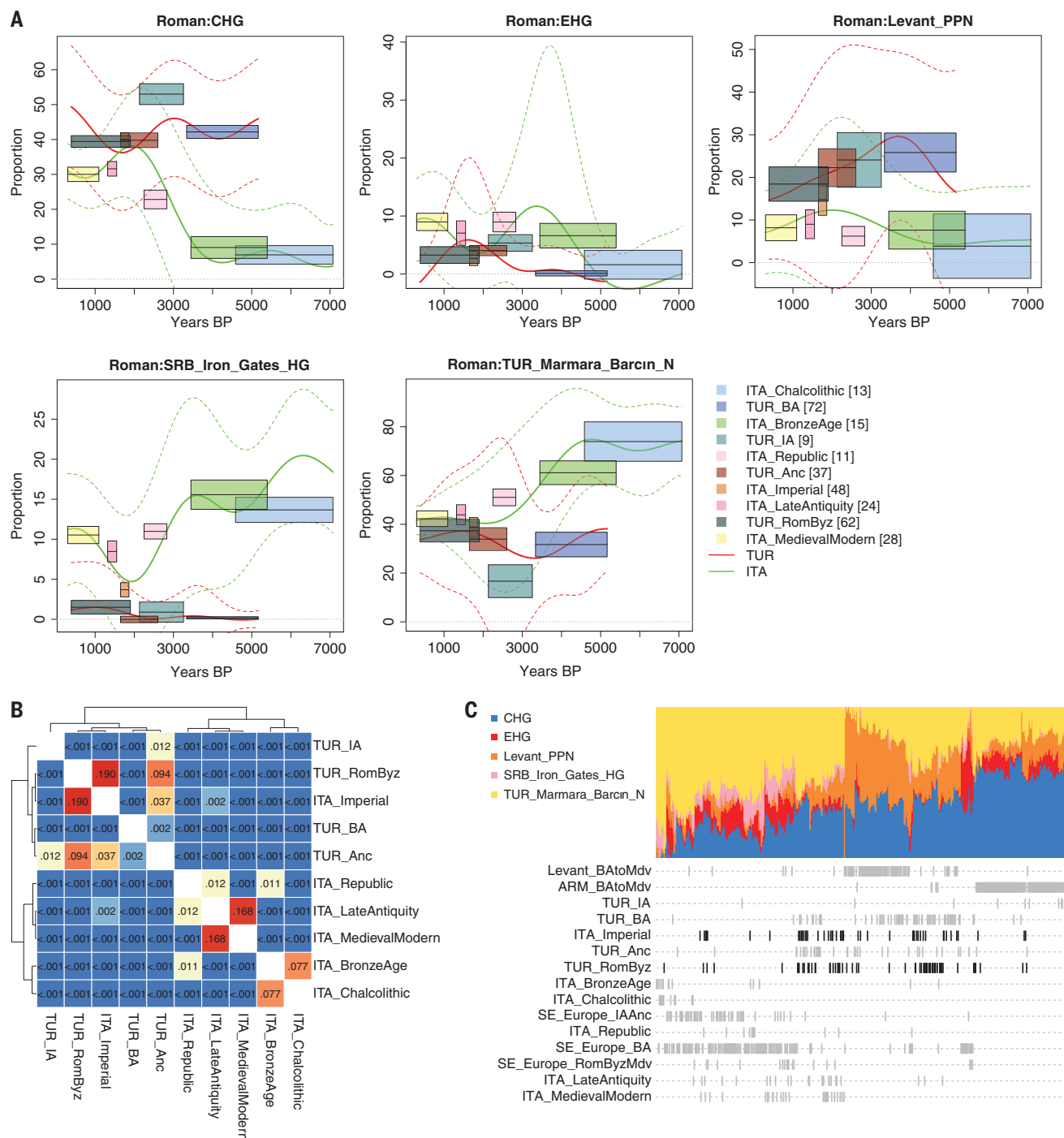


Fig. 3. The Roman Empire, east and west. (A) The Imperial period Romans from the vicinity of the city of Rome in Central Italy resembled Roman-Byzantine Anatolians in their average admixture proportions [95% confidence interval (CI) of ± 1.96 standard errors shown as boxes, and a heteroskedastic Gaussian process is fitted to unlabeled Italian and Anatolian individuals; dashed lines indicate 5% and 95% quantiles]. **(B)** P values of the Baringhaus-Franz multivariate two-sample test (45) for pairs of populations indicate that Imperial

Romans can be drawn from the same distribution as Roman-Byzantine ones ($P = 0.19$) but are significantly different ($P \leq 2.16 \times 10^{-3}$) from all other periods of Italy. **(C)** Hierarchical clustering of raw ancestry estimates of diverse individuals shows overlapping distributions of Imperial Roman and Anatolian Roman-Byzantine individuals (black) without knowledge of their ancestry labels and differentiated from the distributions of Southeastern Europe, Armenia, and the Levant.

example, by a Y chromosome match of the rare R-PF7562 haplogroup between a pair of patrilineal relatives from the Palace of Nestor, which links Late Bronze Age Mycenaean Greece with an Early Bronze Age individual of the

North Caucasus at Lysogorskyja that is genetically similar to the Yamnaya (14). This patrilineal connection to the Yamnaya should not be interpreted as a general association of steppe ancestry with elite burial status, as

the common people, making up most of our Mycenaean-era individuals, also had steppe ancestry, whereas some members of the elite (such as the Griffin Warrior) did not have significant evidence of it. A parallel example of an

elite individual with less steppe ancestry than others from the same cultural context during a period of steppe ancestry spread is given by the “Amesbury Archer,” the most well-furnished grave in the Stonehenge mortuary landscape of Great Britain (15). These two examples highlight the pitfalls of conflating genetic ancestry with narratives of social dominance. Whatever the social role of early steppe migrants into the Aegean, they did not establish a system that precluded admixture with locals or prevented them from rising to positions of power. This inclusiveness may explain the substantial dilution of steppe ancestry in the Aegean, as migrants and locals blended to form the ancestors of the Mycenaean-era population, and may shed light on the genesis of the Greek language linked, on one hand, with the rest of Indo-Europeans through steppe ancestry (1) and, on the other, with the people of the Aegean who preceded the Proto-Greek speakers (16).

One of the two patrilineal relatives at Pylos (I13518) was almost certainly the offspring of first cousins; we document such close-kin unions not only in elite Mycenaean society but also in different localities of the Bronze Age Southern Arc (fig. S2) (17), including an individual from Bezdanjača in Croatia (I18717) who was likely the offspring of an uncle-niece pairing. This documents the later persistence of the practice of close-kin matings that had started with the Neolithic (18, 19), although whether this is the result of the burials we analyzed being a biased subset of a population or reflects society-wide cultural preferences cannot be resolved with our available sample. Did descriptions of such unions in classical mythological accounts of the “Heroic Age” reflect practices that persisted to the authors’ own time? Ancient DNA studies from more locations would allow these patterns of mating preferences inferred from a handful of sites to be characterized at higher resolution.

The era of Greek colonization

We report a preliminary look at demographic patterns associated with the Greek colonial period (eighth to sixth centuries BCE) by identifying individuals from both the Southern Arc and outside of it who were genetically similar to Bronze Age individuals of the Mycenaean period (supplementary text S1 and fig. S3) (17). This identifies an Archaic period individual from Kastrouli near Delphi in Phokis on the Greek mainland and individuals at Empúries in Northeastern Spain who are genetically very similar to Mycenaean-era individuals from the Greek mainland (20). Empúries was an outpost colonized by Phocaeans from Western Anatolia, who were themselves said to be colonists from Phokis (Paus. 7.3.10). Thus, we capture the end points of a long chain of transmission, with little admixture, across the Mediterranean. Could the ancestry of the

Empúries individuals be traced back to the beginning of this chain, or was it drawn from another genetically similar source? Although we do not yet have rich sampling of the peoples of the Greek colonial world, systematic sampling of diverse Greek colonies spread over the Mediterranean and Black Sea coasts would make it possible to systematically test for evidence of specific metropolis-colony connections and document the extent to which migration, admixture with local populations, and genetic heterogeneity played a role in Greek colonization.

Ancestry typical of the Mycenaean period also spread to the Eastern Mediterranean, as in the case of an individual from Ashkelon associated with a Philistine archaeological context (21). We also show the similarity of some individuals from inland Thrace (at Kapitan Andreevo) with the Mycenaean genetic profile, which suggests that Mycenaeans were genetically similar to some Thracians from the East Balkans, outside the sphere of the Late Bronze Age Aegean. This provides a cautionary tale highlighting the dangers of conflating genetic and cultural similarity.

The coastal regions of Anatolia formed another area of Greek settlement, and much of the Anatolian peninsula was incorporated into the Hellenistic kingdoms established by the successors of Alexander the Great, providing opportunity for population transfer from Southeastern Europe to Anatolia. Yet, we do not find Mycenaean-like individuals either at first millennium BCE Greek colony sites, such as Halicarnassus (modern Bodrum), or Amisos (modern Samsun) in the Aegean and Black Sea regions, respectively. This pattern is qualitatively different from that at Empúries in Iberia and is consistent with the account of Herodotus that early Greek colonists of Anatolia married indigenous Carian women of Anatolia when they first settled there (Hdt. 1.146). It is also reminiscent of the marriages of Alexander himself and his companions with local women of the conquered Persian Empire (Arr. An. 7.4.4ff). Clearly, Greeks segregated themselves socially and reproductively from non-Greeks in some parts of the Greek world and not in others; an important topic for future research is to identify the factors that correlated with Greeks mixing with peoples from local communities.

The Urartian Kingdom and its neighbors in Iran and Mesopotamia

We have already seen how the Aegean was an area of limited Eastern European hunter-gatherer penetrance that nonetheless differentiates it from neighboring Anatolia, where Eastern European hunter-gatherer ancestry was negligible (1). An even more notable case is that of the Iron Age Kingdom of Urartu, situated in the mountainous and geographically fragmented regions of eastern Turkey

and Armenia, where the linguistic landscape must have been complex in the Bronze and Iron Ages. The people at the center of this kingdom in the Lake Van region of Turkey (Çavuştepe) and its northern extension in Armenia were strongly connected by material culture and were buried only ~200 km apart, yet they formed distinct genetic clusters with little overlap during the kingdom’s early (ninth to eighth centuries BCE) period (Fig. 2). The Van cluster is in continuity with the pre-Urartian population (~1300 BCE) at neighboring Muradiye also in the Van region and is characterized by more Levantine ancestry and the absence of steppe ancestry. It contrasts with the cluster of Urartian period individuals from Armenia, who have less Levantine and some steppe ancestry, like the pre-Urartian individuals of the Early Iron Age (1). Our genetic results help to explain the formation of linguistic relationships in the region. Population continuity of the Lake Van core population with greater Levantine ancestry may well correspond to the Hurro-Urartian language family (22) that linked the non-Indo-European Urartian language of the kingdom with the earlier Bronze Age Hurrian language, whose more-southern distribution encompassed parts of Syria and Northern Mesopotamia. Into the periphery of this Hurro-Urartian linguistic sphere came a steppe-admixed population from the north, whose presence marks the southern edge of steppe expansion that we discussed above and whose proximity to the Urartian speakers would provide a mechanism for the incorporation of Urartian words into the Armenian lexicon.

When we compare (Fig. 2E) the Urartian individuals with their neighbors at Iron Age Hasanlu in Northwestern Iran (~1000 BCE), we observe that the Hasanlu population had some Eastern European hunter-gatherer ancestry but to a lesser degree than their contemporaries in Armenia. The population was also linked to Armenia by the presence of the same R-M12149 Y chromosomes (within haplogroup R1b), linking it to the Yamnaya population of the Bronze Age steppe (1). Which language was spoken in this case is not clear, but the population shows no connection with the high-Eastern European hunter-gatherer R-Z93 (within haplogroup R1a) haplogroup-bearing groups from Central and South Asia belonging to steppe populations ancestral to Indo-Aryan speakers (23)—the closest linguistic relatives of Iranian speakers (24). Present-day Iranians do have R-Z93 Y chromosomes (25) or the more general upstream R1a-M17 ones [observed in every one of 19 diverse populations from Iran (26), as well as in present-day Indians (27), and modern Iranians almost completely lack R1b Y chromosomes (<1% frequency)]. Thus, it appears that R1a haplogroup Y chromosomes represent a

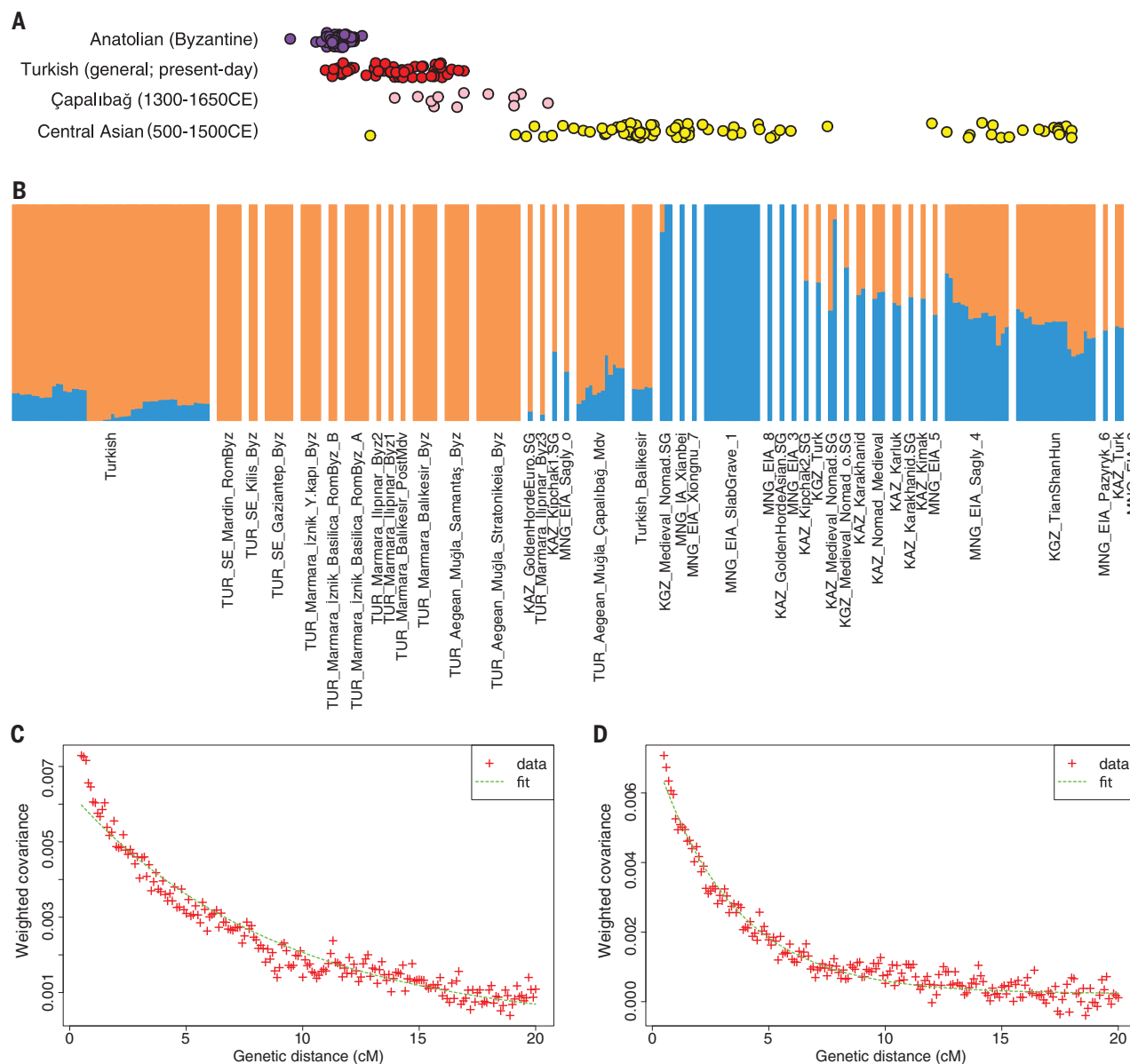


Fig. 4. Central Asian Turkic admixture in Anatolia. (A) Individuals from Çapalıbağ (1300 to 1650 CE) and present-day Turkish individuals are intermediate between Byzantine Anatolia and 500 to 1500 CE Central Asians along a global principal components analysis distinguishing West from East Eurasians (left-to-right on the horizontal dimension; noise added on the vertical dimension to distinguish points). (B) Two-way unsupervised ADMIXTURE analysis of eastern ancestry: Byzantine (0%); present-day Turkish (9%); Çapalıbağ (18%); and

Central Asian individuals, who differ between 100% (in Mongolia) and 43% (some ancient populations of Kazakhstan and Kyrgyzstan). **(C)** Individuals from Çapalıbağ in Turkey admixed 12.2 ± 1.4 generations (342 ± 39 years) before their time using Byzantine Anatolians and Central Asians (from 500 to 1500 CE) as sources. cM, centimorgan. **(D)** Present-day Turkish people genotyped on the Human Origins array (34) admixed 30.6 ± 1.9 generations ago (857 ± 53 years ago) using the same sources as in (D).

common link between ancient and modern Indo-Iranians, whereas R1b haplogroup Y chromosomes (to which many of the Hasanlu males belonged) do not. The absence of any R1a examples among 16 males at Hasanlu, who are instead patrilineally related to individuals from Armenia, suggests that a non-Indo-Iranian (either related to Armenian or belonging to the non-Indo-European local population) language may have been spoken there and that Iranian languages may have been introduced to the Iranian plateau from

Central Asia only in the first millennium. Finally, a single individual from the Late Bronze Age of Assyrian Northern Mesopotamia (~1250 BCE) resembled the Urtartian Van individuals in lacking Eastern European hunter-gatherer ancestry, had the highest amount of Levantine autosomal ancestry ($42.8 \pm 5.3\%$), and had a J-P58-derived Y chromosome with strong Levantine geographical associations (1) and may have plausibly been a speaker of a Semitic language, such as those that have been spoken and recorded in the region for

most of its history. Archaeology and historical texts have furnished a wealth of information about the political geography of the ancient Near East, and future genetic studies will elucidate changes of population that occurred either due to voluntary migration or forced movements of peoples implemented by state policies.

The Anatolian origins of the population of the Roman-Byzantine Empire

A paleogenomic time transect of the city of Rome in Central Italy (28) identified an ancestry

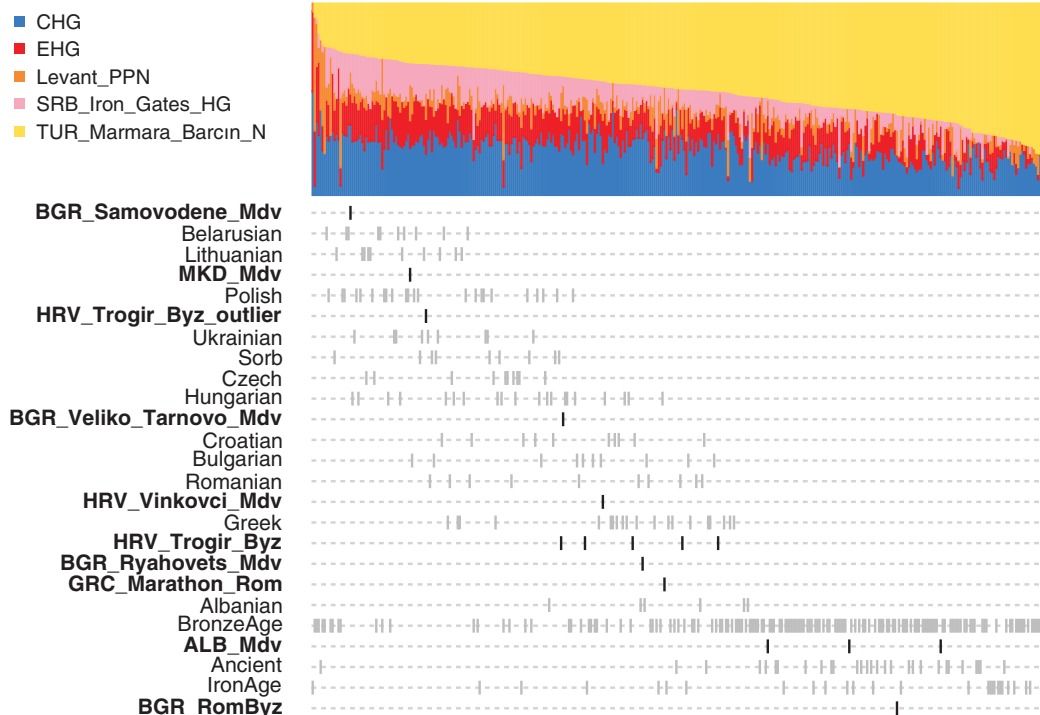


Fig. 5. Byzantine and medieval Southeastern Europe. We sorted admixture proportions of Anatolian Neolithic ancestry to investigate the dilution of this ancestry in present-day populations from South-eastern Europe. Roman-, medieval-, and Byzantine-era individuals are all indicated in bold. During the Bronze Age, the range of this ancestry was immense, as observed in (1), but present-day people from the Balkans have less of this ancestry than was the case in individuals from the Bronze Age through the Iron Age and down to classical antiquity (Ancient). Medieval and Byzantine people from the Balkans were diverse, with some (right) continuing the ancient pattern of high Anatolian Neolithic ancestry, several (middle) overlapping with the range of present-day people, and some (left) having as little of such ancestry as present-day Balto-Slavic people from Eastern Europe.

shift toward the Near East during the Imperial period (27 BCE to 300 CE) but was unable to localize the origin of the migrants driving this phenomenon. We sought to identify the geographic sources of these Imperial-era Romans by coanalyzing the data from Italy with data from the Southern Arc. Unexpectedly, the ancestry of the sample of people whose genomes were analyzed who lived around Rome in the Imperial period was almost identical to that of Roman and Byzantine individuals from Anatolia in both their mean (Fig. 3A) and pattern of variation (Fig. 3B), whereas Italians before the Imperial period had a very different distribution (28, 29). We clustered diverse Roman, Byzantine, and medieval individuals and their immediate predecessors without any knowledge of their population labels and found that the Italian and Anatolian individuals clustered together with those of pre-Roman Anatolia, whereas pre-Imperial people around the city of Rome were systematically different (Fig. 3C). This suggests that the Roman Empire in both its shorter-lived western part and the longer-lasting eastern centered on Anatolia had a diverse but similar population plausibly drawn, to a substantial extent, from Anatolian pre-Imperial sources. In an irony of history, although the Roman Republic prevailed in its existential military struggle against the Anatolians rallied by Mithridates VI of Pontus during the first century BCE, the final incorporation of Anatolia into the Roman Empire and the increased connectivity that ensued may have set the stage

for the very same Anatolians to become the demographic engine of Imperial Rome itself. This recreated, in historical time, the mythical journey of Aeneas and his Trojan exiles from Anatolia to the shores of Italy.

The Southern Arc was also a recipient of many immigrants from outside the region in the Historical period, such as two individuals sampled in Samsun in the Black Sea region from the Roman era in the second to third centuries CE (17). These individuals have both Eastern European hunter-gatherer and some East Eurasian ancestry that contrasts them with the local population of the Black Sea region that had been stable since the Chalcolithic (30), across the Early Bronze Age transition at Amasya, and down to the time of the Kingdom of Pontus (first century BCE). Broad genetic stability in Anatolia during the Roman-Byzantine period did not mean isolation, as outliers of likely Levantine, Northern European or Germanic, and Iberian origin are detected in the Marmara region (in the Basilica of Nicaea or present-day Iznik and the Virgin Mary Monastery at Zeytinliada, Erdek) close to the Imperial capital of Constantinople (present-day Istanbul), which may have attracted a more diverse set of foreigners. Other outliers are found at the periphery of the Southern Arc in the Iron Age, in Moldova and Romania, long after the early steppe migrants previously discussed. These are distinctive because of the East Eurasian admixture of Central Asian Scythian individuals (31–33).

Medieval migrations into Anatolia and the Balkans

East Eurasian ancestry also helps identify a noteworthy set of outliers at Çapalıbağ in the Aegean coast of Turkey dating from the 14th to 17th centuries (Fig. 4) (17). These have ~18% such ancestry, unlike Byzantine-era individuals from Turkey (Fig. 4B), which suggests a Central Asian influence. An admixture date estimate of 12.2 ± 1.4 generations before their time using Roman-Byzantine and Central Asian sources (Fig. 4C) suggests that the admixture occurred in the period surrounding the 11th century arrival and expansion of Seljuq Turks to Anatolia. Present-day Turkish individuals have an admixture date estimate of 30.6 ± 1.9 generations (Fig. 4D) and thus from the same early centuries of the 1000s CE, which coincided with the transfer of control of Anatolia from the Romans to the Seljuqs and eventually the Ottomans. The genetic contribution of Central Asian Turkic speakers to present-day people can be provisionally estimated by comparison of Central Asian ancestry in present-day Turkish people (~9%) and sampled ancient Central Asians (range of ~41 to 100%) to be between $\frac{9}{100}$ and $\frac{9}{41}$, or ~9 to 22%. Our sample of present-day Turkish people is broadly representative of the general population, as it derives from eight localities across the country ($n = 58$) (34). The genetic data point to Turkish people carrying the legacy of both ancient people who lived in Anatolia for thousands of years covered by our study and people coming from Central Asia bearing Turkic languages.

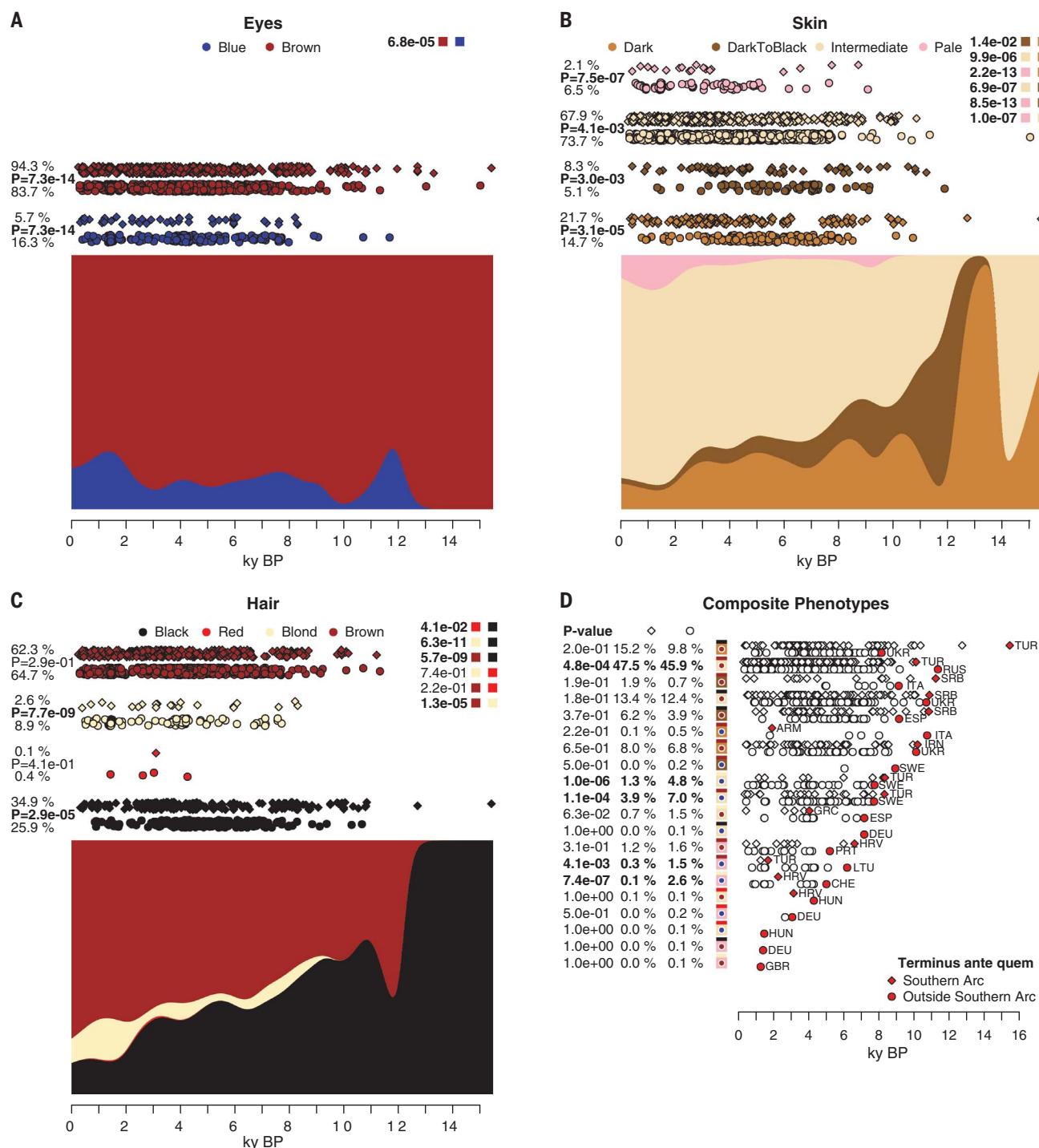


Fig. 6. Pigmentation in West Eurasia. (A to C) We show the temporal distribution of genetically predicted eye (A), skin (B), and hair (C) color in West Eurasians of the last 16,000 years; each point represents an individual, with the top row for each subphenotype corresponding to the Southern Arc and the bottom row corresponding to Northern, Central, and Western Europeans and people of the Eurasian steppe. ky BP, thousand years before the present. (D) Composite

phenotypes of all three aspects of pigmentation using the same color scheme as (A) to (C) and denoted as eye color (circle), hair color (top), and skin color (bottom) in the composite phenotype symbols. The modal phenotype of West Eurasians had brown eyes, intermediate skin pigmentation, and brown hair, with the highest prevalence (Fisher's exact test) of low pigmentation outside the Southern Arc (in the rest of Europe and the Eurasian steppe).

The medieval period was marked by Slavic migrations into the Balkans on the basis of the genetic analysis of present-day populations (35, 36). It is also recorded in historical sources, such as those of Procopius (37) in

the sixth century BCE, when Slavic groups came into contact with the Roman Empire (38). The South Slavs of today in the Balkans are one of the major groups of Slavic speakers, and the question of which migrations played

a role in their origin is of interest for understanding how this group of languages, little-attested until medieval times, came to be so widespread across the greater part of Eastern Europe. We highlight Roman, Byzantine, and

medieval individuals from Albania, Bulgaria, Croatia, Greece, North Macedonia, and Serbia, which we studied in conjunction with those that preceded them in the Balkans and with published data from present-day people genotyped on the Human Origins array (34, 39) (Fig. 5). The reduction of Anatolian Neolithic ancestry was a long-term process in Southeastern Europe (2), which allows us to differentiate present-day populations from those preceding the Slavic migrations. When we order individuals along this component of ancestry (Fig. 5), we observe that present-day Slavs outside the Balkans have the least, whereas pre-Slavic inhabitants from the Balkans have the most of this type of ancestry, with present-day people from Southeastern Europe intermediate between the two extremes. Three individuals from Bulgaria (Samovodene), North Macedonia (Bitola), and an outlier individual from Trogir in Croatia (700 to 1100 CE) have the lowest levels of this ancestry. Most individuals from Trogir (a port city of the Adriatic in Croatia that was founded by Ancient Greek colonists and was part of the Byzantine Empire) overlapped with present-day people from ~700 to 900 CE, as did 12th century CE individuals from Veliko Tarnovo and Ryahovets in Bulgaria and a mid-fourth century CE Roman-era individual from Marathon in Greece, who, however, lacked the Balkan hunter-gatherer ancestry found consistently in the present-day population (Fig. 1). Finally, three medieval individuals from Albania (500 to 1100 CE) and a Late Antique (~500 CE) individual from Boyanovo in Bulgaria preceding the Slavic migrations, overlapped with the more ancient population, having high levels of Anatolian Neolithic ancestry. Among present-day people, Greeks and Albanians have more Anatolian Neolithic ancestry than their South Slavic neighbors. Slavic migrations have some echoes, ~3000 years later, to the spread of the descendants of Yamnaya steppe pastoralists into Southeastern Europe (1, 7). Although both events were transformative, any analogy should not be pushed too far. The medieval movements were carried out by large, organized communities engaging with complex states, such as the Avar Khaganate and Byzantine Empire, and no comparable polities existed in Yamnaya times. Collectively, our data suggest that although Balkan groups experienced a shift of ancestry in the medieval period, the fusion of locals and migrants was variable with individuals of diverse ancestry being present in medieval times and persisting up to the present.

Phenotypes of the Southern Arc in their West Eurasian context

Our survey of populations of the Southern Arc focuses on ancestry, but it also illuminates other aspects of biology. Superficial phenotypes, such as pigmentation, were remarked

upon by ancient writers. We carried out a survey of predicted pigmentation and other phenotypes of West Eurasian populations across time (supplementary text S3 and Fig. 6) (17) to discover the extent to which ancient authors' perceptions (based on direct observation or through accounts of faraway peoples) might correspond to the genetic inference of their appearances (40). We find that the modal phenotype of eye, skin, and hair pigmentation in ancient West Eurasians was brown-eyed, of intermediate complexion, and brown-haired—even among Yamnaya steppe pastoralists—contradicting stereotypical characterizations of Steppe peoples as being blue-eyed, pale-skinned, and light-haired (41, 42). Note that when we use categorizations—such as intermediate—of the continuous skin tone phenotype, we refer to the scheme adopted by HirisPlex-S (40); in that scheme, intermediate skin tones are commonly found in present-day Mediterranean populations and pale ones in present-day Northern European ones. A general depigmentation trend can be seen across time (Fig. 6), with a reduction of black hair and darker skin tones accompanying the increase of brown hair and intermediate skin tones. However, inhabitants of the Southern Arc had significantly darker pigmentation on average than those of the north (defined as Europe outside the Southern Arc and the Eurasian steppe) over all periods (Fig. 6), which provides support for the identification by ancient writers of light-pigmentation phenotypes as being more common in some groups of the north, such as the Celts and Scythians. Another contrast made by ancient writers was with people of Africa, such as Egyptians and Ethiopians, who were said to be of darker pigmentation (e.g., Hdt. 2.104); a comparison of people of the Southern Arc with their southern neighbors will become possible when genomic data from people living south of the Mediterranean become available. When examining composite pigmentation phenotypes (Fig. 6D), we observe that although average pigmentation did differentiate between populations of the Southern Arc and the north, light phenotypes were found in both areas at similar early dates, growing in parallel in the more recent millennia of history. Light pigmentation in West Eurasia was the result of selection across time, which continued into the Historical period (43, 44), and not of the survival of supposed ancient Indo-European phenotypes as some 19th and 20th century writers supposed (41, 42) or the product of the direct influence of climate that some Greco-Roman writers hypothesized to explain patterns they observed during their own time (17). The malleability of human phenotypes across time and the presence of diverse ones—whether dark, light, or intermediate—across space undermine prejudiced views of history

that overemphasize superficial traits at the expense of the more meaningful aspects of human culture and biology.

This study illustrates the potential of archaeogenetic studies of people of the civilizations of the ancient world in conjunction with archaeological and textual evidence. Ancient writings are replete with the descriptions of little-known groups, such as the numerous tribes encountered by Xenophon the Athenian at the end of the fifth century BCE and recorded in his *Anabasis*, as he and his fellow mercenaries escaped from Mesopotamia northward to the Black Sea. To what extent did these and other named entities of antiquity correspond to ancestral groups that may one day be placed on the genetic landscape of the ancient world? Ancient DNA is bringing some of the stories of these forgotten peoples back to life and paying homage to their legacies.

REFERENCES AND NOTES

1. I. Lazaridis et al., *Science* **377**, eabm4247 (2022).
2. I. Lazaridis et al., *Science* **377**, 982–987 (2022).
3. G. R. Crane, Ed., *Perseus Digital Library* (Tufts University); <http://www.perseus.tufts.edu>.
4. I. Lazaridis et al., *Nature* **548**, 214–218 (2017).
5. I. Mathieson et al., *Nature* **528**, 499–503 (2015).
6. Z. Hofmanová et al., *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6886–6891 (2016).
7. I. Mathieson et al., *Nature* **555**, 197–203 (2018).
8. J. L. Davis, S. R. Stocker, *Hesperia* **85**, 627–655 (2016).
9. E. R. Jones et al., *Nat. Commun.* **6**, 8912 (2015).
10. W. Haak et al., *Nature* **522**, 207–211 (2015).
11. I. Lazaridis et al., *Nature* **536**, 419–424 (2016).
12. F. Clemente et al., *Cell* **184**, 2565–2586.e21 (2021).
13. D. Adamov, V. M. Gurianov, S. Karzhavin, V. Tagankin, V. Urasin, *Russ. J. Genet. Geneal.* **7**, 1920–1997 (2015).
14. C.-C. Wang et al., *Nat. Commun.* **10**, 590 (2019).
15. N. Patterson et al., *Nature* **601**, 588–594 (2022).
16. M. B. Sakellariou, *Les Proto-grecs* (Ekdotikē Athenon, 1980).
17. Detailed information is provided in the supplementary materials.
18. R. Yaka et al., *Curr. Biol.* **31**, 2455–2468.e18 (2021).
19. H. Ringbauer, J. Novembre, M. Steinrücken, *Nat. Commun.* **12**, 5425 (2021).
20. I. Olalde et al., *Science* **363**, 1230–1234 (2019).
21. M. Feldman et al., *Sci. Adv.* **5**, eaax0061 (2019).
22. I. M. D'jakonov, S. A. Starostin, *Hurro-Urartian as an Eastern Caucasian Language* (R. Kitzinger, 1986).
23. V. M. Narasimhan et al., *Science* **365**, eaat7487 (2019).
24. A. S. Kassian et al., *Linguistics* **59**, 949–979 (2021).
25. P. A. Underhill et al., *Eur. J. Hum. Genet.* **23**, 124–131 (2015).
26. V. Grugni et al., *PLOS ONE* **7**, e41252 (2012).
27. S. Sengupta et al., *Am. J. Hum. Genet.* **78**, 202–221 (2006).
28. M. L. Antonio et al., *Science* **366**, 708–714 (2019).
29. T. Sauepe et al., *Curr. Biol.* **31**, 2576–2591.e12 (2021).
30. E. Skourtanioti et al., *Cell* **181**, 1158–1175.e28 (2020).
31. M. Unterländer et al., *Nat. Commun.* **8**, 14615 (2017).
32. P. B. Damgaard et al., *Nature* **557**, 369–374 (2018).
33. M. Krzewirska et al., *Sci. Adv.* **4**, eaat4457 (2018).
34. I. Lazaridis et al., *Nature* **513**, 409–413 (2014).
35. P. Ralph, G. Coop, *PLOS Biol.* **11**, e1001555 (2013).
36. G. B. J. Busby et al., *Curr. Biol.* **25**, 2518–2526 (2015).
37. E. James, *Europe's Barbarians: AD 200–600* (Pearson Longman, 2009).
38. I. Olalde et al., *bioRxiv* 2021.08.30.458211 [Preprint] (2021). <https://doi.org/10.1101/2021.08.30.458211>.
39. N. Patterson et al., *Genetics* **192**, 1065–1093 (2012).
40. L. Chaitanya et al., *Forensic Sci. Int. Genet.* **35**, 123–135 (2018).
41. L. Poliakoff, *Le Mythe Aryen: Essai sur les Sources du Racisme et du Nationalisme* (Calmann-Lévy, 1971).
42. J. V. Day, *Indo-European Origins: The Anthropological Evidence* (Institute for the Study of Man, 2001).
43. D. Ju, I. Mathieson, *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2009227118 (2021).
44. S. Wilde et al., *Proc. Natl. Acad. Sci. U.S.A.* **111**, 4832–4837 (2014).

45. L. Baringhaus, C. Franz, *J. Multivariate Anal.* **88**, 190–206 (2004).
46. S. Alpaslan-Roodenberg *et al.*, *Nature* **599**, 41–46 (2021).

ACKNOWLEDGMENTS

This study was carried out following the principles for ethical DNA research on human remains laid out in (46). We are grateful to the authorities and sample stewards, including museums, museum curators, and archaeologists, for providing written permission to sample each set of human remains. We acknowledge the ancient individuals whose genetic data we analyzed and whose permission we could not directly ask. We aimed to write a manuscript that was respectful of the ancient individuals, treating samples from them as derived from real people, whose memories must be respected. We sought to reflect the perspectives of people from the diverse geographic regions and cultural contexts from which the sampled individuals came by having each sample be represented by at least one coauthor who was a sample steward and was part of a network engaged with local communities. We thank J. Bennett, V. Narasimhan, H. Ringbauer, J. Sedig, A. Shaus, L. Vokotopoulos, M. Wiener, and several anonymous reviewers for critical comments. **Funding:** The newly reported dataset is described in detail in an accompanying manuscript, where we also acknowledge the funders who supported dataset generation (1). Analysis of data was supported by the National Institutes of Health (GM100233 and HG012287), the John Templeton Foundation (grant 61220), a private gift from Jean-Francois Clin, the Allen Discovery Center program, a Paul G. Allen Frontiers Group advised

program of the Paul G. Allen Family Foundation, and the Howard Hughes Medical Institute (to D.R.). **Author contributions:** Conceived of the study: I.La., S.A.-R., R.P., and D.R. Supervised the study: S.A.-R., D.J.K., N.Pat., N.R., R.P., and D.R. Assembled archaeological material and prepared the site descriptions: S.A.-R., A.Aca., A.Aci., A.Ag., L.A., U.A., D.And., G.A., D.Ant., I.A., A.At., P.A., A.I.A., K.Ba., R.Ba., J.B., L.B., A.Be., H.B., A.Bi., M.Bod., M.Bon., C.B., D.B., N.B., M.Ca., S.Cho., M.-E.C., S.Chr., I.C., N.C., M.Co., E.Cr., J.D., T.I.D., V.De., Z.D., S.Des., S.Dev., V.Dj., N.El., A.E., N.Er., S.E.-P., A.F., M.L.G., B.Gas., B.Gay., E.G., T.G., S.G., T.H., V.H., S.H., N.H., I.I., S.I., I.I., I.J., L.J., P.Ka., B.K.-K., E.H.K., S.D.K., A.K., K.K., S.Ki., P.Kl., S.K.B.N.V., S.Ko., M.K.-N., M.K.S., R.K., P.Ku., C.L., K.L., T.E.L., I.Li., K.O.L., S.L., K.M.-O., R.M., W.M., K.Mc., V.M., L.M., J.M.M., G.N., R.N., A.G.N., V.N., M.N., A.O., C.O., N.O., N.Papad., N.Papak., A.Pa., L.Pa., E.G.P., I.P., L.Pe., V.P., A.P.-T., A.Pi., N.P.K., H.P., B.P.-B., Z.P., T.D.P., S.Rad., K.R.A., P.R.S., K.R.R., S.Raz., A.R., J.R., R.R., V.R., M.S., A.S., E.S., A.Su., L.S., T.Se., A.S.-E., M.S.-P., H.M.S., A.Sid., A.Sim., H.S., V.S., G.S., M.S., A.Sof., B.S., A.Sof., Ç.S.-S., M.Sta., M.Ste., S.S., F.S.-A., A.S.-N., T.Sz., N.Te., S.Te., N.To., U.T., G.T., S.Tr., A.T., M.U., F.V., Z.V., C.V., S.W., P.W., A.Y., E.Y., A.Y.Y., H.Y., R.Ç., and R.P. Performed laboratory work: S.A.-R., G.B.M., K.Bu., K.C., F.C., B.J.C., E.Cu., K.S.D.C., L.R.E., D.M.F., M.F., S.F., B.Gam., L.I., D.K., A.M.L., K.Ma., M.Mi., J.O., K.T.Ö., L.Q., C.S., K.Si., K.St., A.W., J.N.W., F.Z., A.Z., and N.R. Performed population genetic analyses: I.La. and D.R. Analyzed data: I.La., S.A.-R., R.Be., O.C., M.Ma., S.M., A.Mic., A.Mit., I.O., Z.Z., N.R., and D.R. Wrote the manuscript and compiled the supplementary sections with the input of all other coauthors: I.La.,

S.A.-R., and D.R. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** Genotype data for individuals included in this study can be obtained from the Harvard Dataverse repository (<https://doi.org/10.7910/DVN/3AR0CD>). BAM files of aligned reads can be obtained from the European Nucleotide Archive (accession number PRJEB54831). All (other) data needed to evaluate the conclusions in the paper are present in the paper or the supplementary materials. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abq0755
Materials and Methods
Supplementary Text
Figs. S1 to S5
Tables S1 to S5
References (47–75)

[View/request a protocol for this paper from Bio-protocol.](#)

Submitted 16 September 2022; resubmitted 17 March 2022
Accepted 21 July 2022
[10.1126/science.abq0755](https://doi.org/10.1126/science.abq0755)

A genetic probe into the ancient and medieval history of Southern Europe and West Asia

Iosif LazaridisSongül Alpaslan-RoodenbergAyşe AcarAyşen AçkkolAnagnostis AgelarakisLevon AghikyanUğur AkyüzDesislava AndreevaGojko AndrijaševićDragana AntonovićIlan ArmitAlper AtmacaPavel AvetisyanAhmet Hsani AytekKrum BacvarovRuben BadalyanStefan BakardzhievJacqueline BalenLorenc BejkoRebecca BernardosAndreas BertsatosHanifi BiberAhmet BilirMario BodružićMichelle BonogofskyClive BonsallDušan BorićNikola BoroviniGuillermo Bravo MoranteKatharina ButtingerKim CallanFrancesca CandilioMario CarićOlivia CheronetStefan ChohadzhievMaria-Eleni ChovalopoulouStella Chrysoulakilon CiobanuNatalija ĆonđićMihai ConstantinescuEmanuela CristianiBrendan J. CulletonElizabeth CurtisJack DavisTatiana I. DemcencoValentin DergachevZafer DerinSylvia DeskajSeda DevejyanVojislav DjordjevićKellie Sara Duffett CarlsonLaurie R. EcclesNedko ElenskiAtilla EnginNihat ErdoğanSabiha Erir-PazarcıDaniel M. FernandesMatthew FerrySuzanne FreilichAlin FrînculeasaMichael L. GalatyBeatriz GamarraBoris GasparyanBisserka GaydarskaElif GençTimur GültekinSerkan GündüzTamás HajduVolker HeydSuren HobosyanNelli HovhannisyaniLiya IlievLora IlievStanislav IlievIşık İyigünLence JovanovaPanagiotis KarkanisBernadette Kavaz-KandemirEsra Hilal KayaDenise KeatingDouglas J. KennettSeda Deniz KesiciAnahit KhudaverdyanKrisztián KissSinan KöksalPaul KlostermannSinem Kostak Boca Negra ValdesSaša KovačevićMarta Krenz-NiedbalaMaja KrznarićŠkrivankoRovena KurtiPasko KuzmanAnn Marie LawsonCatalin LazarKrassimir LeshtakovThomas E. LevyIoannis LiritzisKirsi O. LorentzSylwia ŁukasikMatthew MahSwapan MallickKirsten MandlKristine MartirosyanOlshanskyRoger MatthewsWendy MatthewsKathleen McSweeneyVarduhi MelikyanAdam MiccoMegan MichellLidija MilašinovićAlissa MittnikJanet M. MongeGeorgi NekhrizovRebecca NichollsAlexey G. NikitinVassil NikolovMario NovaklićIñigo OlaldeJonas OppenheimerAnna OsterholtzCelal ÖzdemirKadir Toykan ÖzdoğanNurettin ÖztürkNikos PapadimitriouNiki PapakonstantinouAnastasia PapatheanasiouLujana ParamanEvgeny G. PaskaryNick PattersonLilian PetrakievLevon PetrosyanVanya PetrovaAnna Philippa-TouchaisAshot PiliposyanNada Pocuca KuzmanHrvoje PotrebicaBianca Preda-BalnicZrinka PremužićT. Douglas PriceLijun QiuSiniša RadovićKamal Raeuf AzizPetra RajićŠikanjićKamal Rasheed RaheemSergei RazumovAmy RichardsonJacob RoodenbergRudenc RukaVictoria RussevaMustafa ŞahinAyşegül ŞarbakEmre SavaConstanze SchattkeLynne SchepartzTayfun SelçukAyla Sevim-ErolMichel Shamon-PourHenry M. ShephardAthanasios SiderisAngela SimalcikHakob SimonyanVitalij SinikaKendra SirakGhenadie SirbuMario ŠlausAndrei SoficaruBilal SöütArkadiusz SołtysiakÇilem Sönmez-SözerMaria StathiMartin SteskalKristin StewardsonSharon StockerFadime Suata-AlpaslanAlexander SuvorovAnna Szécsényi-NagyTamás SzeniczeyNikolai TelnovStrahil TemovNadezhda TodorovaUlsi TotaGilles TouchaisSevi TriantaphyllouAtila TürkerMarina UgarkovićTodor ValchevFanica VeljanovskaZlatko VidevskiCristian ViragAnna WagnerSam WalshPiotr WłodarczakJ. Noah WorkmanAram YardumianEvgenii YarovoyAlper Yener YavuzHakan YılmazFatma ZalzalaAnna ZettlZhao ZhangRafet ÇavuşoğluNadin RohlandRon PinhasiDavid Reich

Science, 377 (6609), • DOI: 10.1126/science.abq0755

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

View the article online

Use of this article is subject to the [Terms of service](#)

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title Science is a registered trademark of AAAS.

Copyright © 2022 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works

<https://www.science.org/doi/10.1126/science.abq0755>

Permissions

<https://www.science.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of service](#)

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.
Copyright © 2022 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works