Vertebrate Paleobiology and Paleoanthropology Series

Katerina Harvati
Mirjana Roksandic *Editors*

Paleoanthropology of the Balkans and Anatolia

Human Evolution and its Context

Springer

Paleoanthropology of the Balkans and Anatolia

Vertebrate Paleobiology and Paleoanthropology Series

Edited by

Eric Delson
Vertebrate Paleontology, American Museum of Natural History
New York, NY, USA
delson@amnh.org

Eric J. Sargis
Anthropology, Yale University
New Haven, CT 06520, USA
eric.sargis@yale.edu

Focal topics for volumes in the series will include systematic paleontology of all vertebrates (from agnathans to humans), phylogeny reconstruction, functional morphology, Paleolithic archaeology, taphonomy, geochronology, historical biogeography, and biostratigraphy. Other fields (e.g., paleoclimatology, paleoecology, ancient DNA, total organismal community structure) may be considered if the volume theme emphasizes paleobiology (or archaeology). Fields such as modeling of physical processes, genetic methodology, nonvertebrates or neontology are out of our scope.

Volumes in the series may either be monographic treatments (including unpublished but fully revised dissertations) or edited collections, especially those focusing on problem-oriented issues, with multidisciplinary coverage where possible.

More information about this series at http://www.springer.com/series/6978

Paleoanthropology of the Balkans and Anatolia

Human Evolution and its Context

Edited by

Katerina Harvati

Paleoanthropology, Department of Geosciences, Eberhard Karls Universität Tübingen, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany

PhD Program in Anthropology, City University of New York, Graduate Center and New York Consortium in Evolutionary Primatology, New York, NY, USA

Mirjana Roksandic

Department of Anthropology, University of Winnipeg, Winnipeg, MB, Canada

Springer

Editors
Katerina Harvati
Paleoanthropology, Department of Geosciences
Eberhard Karls Universität Tübingen
Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment
Eberhard Karls Universität Tübingen
Tübingen, Germany

PhD Program in Anthropology
City University of New York
Graduate Center and New York Consortium in Evolutionary Primatology
New York, NY, USA

Mirjana Roksandic
Department of Anthropology
University of Winnipeg
Winnipeg, MB, Canada

ISSN 1877-9077 ISSN 1877-9085 (electronic)
Vertebrate Paleobiology and Paleoanthropology
ISBN 978-94-024-0873-7 ISBN 978-94-024-0874-4 (eBook)
DOI 10.1007/978-94-024-0874-4

Library of Congress Control Number: 2016955953

Cover illustration: The cover shows the Petralona cranium on the left (Photo K. Harvati, Copyright E. Delson) and the Kokkinopilos handaxe, shown in three views (Photos and Copyright V. Tourloukis). In the background is a view of the Megalopolis basin, central Peloponnese (Photo and Copyright A. Vlachopoulos).

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer Science+Business Media B.V.
The registered company address is: Van Godewijckstraat 30, 3311 GX Dordrecht, The Netherlands

Preface

The timing, route, and origin of the earliest human dispersal into Europe, the number of Eurasian hominin taxa during the Pleistocene, the evolution and possible late survival of the Neanderthal lineage, and the Late Pleistocene arrival of modern humans in Europe continue to be central themes of discussion and research in paleoanthropology. However, in these discussions there is a glaring lack of primary data from one of the most relevant geographic regions of Europe: the Balkans. This area, together with neighboring Anatolia, is at the geographic center of the hypothesized dispersals and is often considered the most likely migration route into the continent. Furthermore, together with the Italian and Iberian peninsulae, it is one of the main refugia where fauna and flora, as well as, presumably, human populations, would have been able to survive during glacial times. This region, therefore, has been crucial in shaping the course of human evolution in Europe. Nevertheless, despite its geographic significance, it does not enjoy a strong paleoanthropological tradition, and, with a few exceptions, paleolithic research was neglected there until recent years.

This lack of past research and promise for future findings are recurring themes throughout this volume, whose goals are to present a comprehensive review of the paleoanthropological records in the Balkans and Anatolia, report recent results, provide information on the paleoenvironmental and geological background, and, where possible, attempt a regional synthesis. The volume is based on the lectures presented during the conference "*Human Evolution in the Southern Balkans*," organized by Katerina Harvati and Vangelis Tourloukis in Tübingen on December 6–8, 2012, as part of the ERC Starting Grant project "Paleoanthropology at the Gates of Europe: Human Evolution in the Southern Balkans" (PaGE). PaGE, directed by K. Harvati, is a 5-year research program aiming to increase, through systematic fieldwork, the number of paleoanthropological findings from Greece and to help reassess the human fossil record from the region. The ultimate goal of PaGE is to help shed light on open questions in European paleoanthropology by providing new primary data and to develop a research network among scholars working in these fields in South Eastern Europe. First and foremost, this network comprises the close collaborating partners of PaGE: Drs. E. Panagopoulou and A. Darlas from the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture), Profs. C. Doukas and G. Koutessi-Philippaki from the National and Kapodistrian University of Athens, Profs. G. Koufos and D. Kostopoulos from the Aristotle University of Thessaloniki, and Dr. P. Karkanas from the Wiener Laboratory, American School of Classical Studies at Athens. The PaGE 2012 conference, organized at the end of the first year of the project, brought together several research teams from across the region to present the state of the art of paleoanthropological research in their countries, showcase their most recent work, and discuss their future plans. Scholars representing various institutions from Greece, Turkey, Bulgaria, Serbia, Croatia, and Romania and their collaborating partners from Canada, the USA, UK, France, and Germany all gathered in snowy Tübingen at the imposing medieval setting of the Fürstenzimmer, Castle Hohentübingen, for 2 days of talks and lively discussion. Most of the articles presented during the conference, as well as some additions to the original program, are collected here as chapters of this volume.

The volume is organized into three parts. The first part (The Human Fossil Record: Chaps. 1–6) deals with this record from Greece, the Central Balkans, Croatia, Romania, Bulgaria, and Turkey. The second part (The Archaeological Record: Chaps. 7–14) presents the paleolithic record from the same countries, following the same order. Two chapters are devoted to new paleolithic research in Greece, while one presents a synthesis of the record of the region. Part 3 (Paleoenvironments, Biogeography, Chronology: Chaps. 15–18) provides the paleoenvironmental, geological, and biogeographic background to the regional Paleolithic.

In the first part, Chap. 1 (Harvati 2016) presents an overview of the Greek human fossil record, incorporating some recent work on material from Kalamakia and Megalopolis and placing it within the broad framework of the European record. Although Greek human paleontology is better known than that of many of the other Balkan countries, most of it samples different phases of the Neanderthal lineage. Earlier hominins, as well as Upper Paleolithic humans, are not known, with a few possible exceptions. Chapter 2 (Roksandic 2016) presents the fossil record from the Central Balkans, highlighting the recent fossil human find from Mala Balanica. Roksandic puts forth the possibility for an alternative course for human evolution in this part of Europe, different from the one proposed by the accretion hypothesis for the Western part of the continent. Chapter 3 (Janković et al. 2016) presents the Croatian hominin record. Croatia is the only country in the region with a strong paleoanthropological tradition, and Janković et al. present the material from Krapina and Vindija and outline the contributions of Croatian paleoanthropology to the development of the discipline, including the significance of the Vindija remains to the Neanderthal genome project. Chapter 4 (Harvati and Roksandic 2016) presents an overview of the fossil human record from Romania, as well as a new comparative geometric morphometric analysis of the Upper Paleolithic Romanian mandibular remains (Oase 1 and Muierii 1), in light of the new findings of recent Neanderthal ancestry for the former specimen. The results highlight the difficulties in assessing admixture from skeletal morphology. Chapter 5 (Strait et al. 2016) reviews the scant fossil human record from Bulgaria, most of which appears to have been lost. Strait et al. develop testable hypotheses for human dispersals into Eurasia, to be assessed against future discoveries. Chapter 6 (Aytek and Harvati 2016) is a review of the human fossil record from Turkey, including a preliminary comparative 3D geometric morphometric analysis of the Kocabaş *Homo erectus* specimen. Results show affinities with Eurasian *H. erectus* and *H. heidelbergensis*, but no particular similarities with early African *H. erectus*.

Part 2 starts with two chapters on the Greek paleolithic record. In Chap. 7, Darlas and Psathi (2016) present their new work at Upper Paleolithic cave sites in Mani, Southern Greece, where excavations are currently under way. These new sites are all the more important because of an extreme scarcity of evidence dating from this period in Greece. The authors present a summary of new results, including radiometric dates for two of the caves. Chapter 8 (Galanidou et al. 2016) is a report on the newly discovered Lower Paleolithic site Rodafnidia on Lesvos. Galanidou et al. present the results of their first field seasons at Rodafnidia, including a short description of the Acheulian material discovered at the site and preliminary dating results. Acheulian lithics are extremely rare in Greece and elsewhere in the region, and the authors find parallels for the Rodafnidia material in the Near East and Africa. Chapter 9 (Mihailović and Bogićević 2016) describes the paleolithic record of the Central Balkans, concentrating on the Lower to Middle Paleolithic transition in the region. The authors propose that the first appearance of the Charentian in Europe in the Middle Pleistocene could be linked to demographic factors, migrations, and cultural transmission with the Near East. Chapter 10 (Karavanić et al. 2016) discusses the evidence for the Middle to Upper Paleolithic transition from Croatia. Karavanić et al. present the evidence from Vindija in particular detail, discussing alternative hypotheses about the transition in this site. Chapter 11 (Doboş and Iovita 2016) critically addresses the evidence for Lower Paleolithic sites in Romania, most of which is deemed to be unreliable. The authors further report on the recent results of their Lower Danube Survey for Paleolithic Sites, and particularly on the Dealul Guran site, dated to OIS11. Chapter 12 (Ivanova 2016) presents evidence for the Lower Paleolithic in Bulgaria by summarizing the Lower Paleolithic assemblages from Kozarnika cave and critically evaluating their dating. Furthermore, the chapter draws attention to possible Lower

Paleolithic assemblages from open-air sites in the Rhodope Mountains. Chapter 13 (Dinçer 2016) summarizes the evidence for the Lower Paleolithic in Turkey. Dinçer insists on reconceptualizing Anatolia as a challenging environment that required substantial behavioral adaptations from the migrating hominins, and not just as a transit route, and suggests that the early human presence in Anatolia was sporadic and ephemeral, leading to continuous occupation only in later phases of the Middle Pleistocene. Chapter 14 (Sitlivy 2016) synthesizes the current debate on the Middle to Early Upper Paleolithic transition in the Balkans and the surrounding areas on the basis of technological variability, innovations, and changes in lithic technologies. These issues are examined from the point of view of understanding the reduction sequence as a key insight into technological changes that underpin this important transition.

In the third part, the authors provide a synthesis of current paleoenvironmental evidence for the Balkans. In Chap. 15, Koufos and Kostopoulos (2016) present their research on large mammal evolution in Greece. They posit a shift in environmental conditions leading to open grasslands during the late Early Pleistocene and suggest that humans may have entered Europe at this time as part of an Asian, rather than African, faunal dispersal event. Chapter 16 (Spassov 2016) continues in the same vein, also examining the evidence for the timing and the route of possible early human dispersals into Europe, focusing on recently published faunal data from Bulgaria and the Balkans. Chapter 17 (Doukas and Papayianni 2016) provides an overview of micromammalian fauna in Greece and its potential for providing relevant environmental and chronological information for hominin-bearing sites. The authors call for establishing a Balkan-specific biochronology of micro-mammals. Chapter 18 (Tourloukis 2016), the final paper in the volume, examines the spatiotemporal distribution of Lower Paleolithic sites in the Mediterranean as a function of landscape dynamics which influence both the distribution of desirable site locations and their potential for preservation and visibility in the archaeological record, in an effort to assess whether the extremely small number of known Lower Paleolithic sites in Greece might be due not only to past research priorities but also to geological factors. The geological perspective put forth by Tourloukis offers a new tool in efforts to locate such sites in the Balkans.

We are grateful to all the participants of the "*Human Evolution in the Southern Balkans*" conference and all the contributors to this volume for their outstanding presentations, critical discussions, and excellent chapters, as well as the many colleagues who carefully reviewed each chapter. We also thank Vangelis Tourloukis for co-organizing the conference and co-chairing sessions; Nicholas Conard for giving the Keynote lecture of the first evening of the conference; Monika Doll for her superb organizational skills, which made the conference possible; Thomas Rein, who volunteered his time to put together the program, abstract book, and conference poster; Laura McCarty for her help during the conference and with the copyediting of this volume; Joshua Linder for copyediting help; Sibylle Wolf for giving the tour of the Castle Museum for the conference guests; and all the University of Tübingen students and fellows who were instrumental for the smooth running of the conference: Cathi Bauer, Judith Beier, Michael Francken, Lisa Kellner, Panos Kritikakis, Marlijn Noback, Heike Scherf, and Bernd Trautmann. We thank the Editors of the Vertebrate Paleobiology and Paleoanthropology Series, Eric Delson and Eric Sargis, for agreeing to publish this volume and for their help with various issues of editorial nature, and all the colleagues who kindly gave their time and effort to provide reviews of the manuscripts. We are deeply grateful to the University of Tübingen President, Professor Dr. Bernd Engler, and Vice President for Research, Professor Dr. Peter Grathwohl, for their continuing support. Funding for the conference was provided by the European Research Council (ERC StG 283503 "PaGE"). Finally, for their unwavering patience and support throughout the years, we owe our deepest gratitude to our families and our spouses, Elias and Ivan.

Katerina Harvati
Baden-Württemberg, Germany
Mirjana Roksandic
Winnipeg, MB, Canada
December 2015

References

Aytek, I. A., & Harvati, K. (2016). The human fossil record from Turkey. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 79–91). Dordrecht: Springer.

Darlas, A., & Psathi, E. (2016). The Middle and Upper Paleolithic on the Western coast of the Mani Peninsula (Southern Greece). In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 95–117). Dordrecht: Springer.

Dinçer, B. (2016). The Lower Paleolithic in Turkey: Anatolia and hominin dispersals out of Africa. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 213–228). Dordrecht: Springer.

Doboş, A., & Iovita, R. (2016). The Lower Paleolithic of Romania revisited: New evidence from the site of Dealul Guran. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 171–186). Dordrecht: Springer.

Doukas, C. S., & Papayianni, K. (2016). Small mammals in the Plio/Pleistocene sediments of Greece. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 291–302). Dordrecht: Springer.

Galanidou, N., Athanassas, C., Cole, J., Iliopoulos, G., Katerinopoulos, A., Magganas, A., et al. (2016). The Acheulean site at Rodafnidia, Lisvori on Lesbos, Greece: Part I. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia*: *Human evolution and its context* (pp. 119–138). Dordrecht: Springer.

Harvati, K. (2016). Paleoanthropology in Greece: Recent findings and interpretations. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia*: *Human evolution and its context* (pp. 3–14). Dordrecht: Springer.

Harvati, K., & Roksandic, M. (2016). The human fossil record from Romania: Early Upper Paleolithic Europeans and possible evidence for Neanderthal admixture. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia*: *Human evolution and its context* (pp. 51–68). Dordrecht: Springer.

Ivanova, S. (2016). A route through the Balkans and implications for the earliest settlement of Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 187–211). Dordrecht: Springer.

Janković, I., Ahern, J. C. M., Karavanić· I., & Smith, F. H. (2016). The importance of Croatian Pleistocene hominin finds in the study of human evolution. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 35–50). Dordrecht: Springer.

Karavanić, I., Šošić, R., Ahern, J. C. M., Čondić, N., Janković, I., Zubčić, K., et al. (2016). Recent research on the Middle/Upper Paleolithic interface in Croatia in the context of Central and SE Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 153–169). Dordrecht: Springer.

Koufos, G. D., & Kostopoulos, D. S. (2016). The Plio-Pleistocene large mammal record of Greece: Implications for early human dispersals into Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 269–280). Dordrecht: Springer.

Mihailović, D., & Bogićević, K. (2016). Technological changes and population movements in the late Lower and early Middle Palaeolithic of the Central Balkans. In K. Havarti & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 139–151). Dordrecht: Springer.

Roksandic, M. (2016). The role of the Central Balkans in the peopling of Europe: Paleoanthropological evidence. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 15–33). Dordrecht: Springer.

Sitlivy, V. (2016). Technological variability of the Middle-to-Upper Paleolithic transition: Examples from the Balkans and neighboring regions. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 229–265). Dordrecht: Springer.

Spassov, N. (2016). Southeastern Europe as a route for the earliest dispersal of *Homo* towards Europe: Ecological conditions and the timing of the first human occupation of Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 281–290). Dordrecht: Springer.

Strait, D. S., Orr, C. M., Hodgkins, J., Spassov, N., Gurova, M., Miller, C., et al. (2016). The human fossil record of Bulgaria, and the formulation of biogeographic hypotheses. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 69–78). Dordrecht: Springer.

Tourloukis, V. (2016). On the spatio-temporal distribution of Mediterranean Lower Paleolithic sites: A geoarchaeological perspective. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 303–323). Dordrecht: Springer.

Contents

Part I The Human Fossil Record

Part II The Archaeological Record

Part III Paleoenvironments, Biogeography and Chronology

Contributors

James C.M. Ahern Department of Anthropology, University of Wyoming, Laramie, WY, USA

Constantin Athanassas Centre de Recherche and d'Enseignement de Géosciences de l'Environnement (C.E.R.E.G.E.), Europôle Méditerranéen de l'Arbois, Aix-en-Provence, France

Ahmet İ. Aytek Department of Anthropology, Faculty of Arts and Science, Mehmet Akif Ersoy University, Istiklal Campus, Burdur, Turkey

Paleoanthropology, Department of Geosciences, Eberhard Karls, Universität Tübingen, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany

Katarina Bogićević Department of Paleontology, Faculty of Mining and Geology, University of Belgrade, Belgrade, Serbia

Natalija Čondić Archaeological Museum Zadar, Zadar, Croatia

James Cole School of Environment and Technology, University of Brighton, Brighton, UK

Andreas Darlas Ephoreia of Paleoanthropology and Speleology, Athens, Greece

Berkay Dinçer Prehistory Department, Faculty of Letters, Istanbul University, Istanbul, Turkey

Adrian Doboş Department of Palaeolithic Archaeology, Institute of Archaeology "Vasile Parvan", Bucharest, Romania

Constantin S. Doukas Department of Historical Geology and Paleontology, University of Athens, Athens, Greece

Nena Galanidou Department of History and Archaeology, University of Crete, Rethymno, Greece

Maria Gurova National Institute of Archaeology and Museum, Bulgarian Academy of Sciences, Sofia, Bulgaria

Katerina Harvati Paleoanthropology, Department of Geosciences, Eberhard Karls Universität Tübingen, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany

PhD Program in Anthropology, City University of New York Graduate Center and New York Consortium in Evolutionary Primatology, New York, NY, USA

Jamie Hodgkins Department of Anthropology, University of Colorado, Denver, CO, USA

Giorgos Iliopoulos Department of Geology, University of Patras, Rio Patras, Greece

Radu Iovita MONREPOS Archaeological Research Centre and Museum for Human Behavioural Evolution, Römisch-Germanisches Zentralmuseum, Leibniz-Forschungsinstitut für Archäologie, Neuwied, Germany

Stefanka Ivanova National Institute of Archaeology and Museum, Bulgarian Academy of Sciences, Sofia, Bulgaria

Ivor Janković Department of Anthropology, University of Wyoming, Laramie, WY, USA

Institute for Anthropological Research, Zagreb, Croatia

Ivor Karavanić Department of Archaeology, University of Zagreb, Zagreb, Croatia

Athanasios Katerinopoulos Faculty of Geology and GeoEnvironment, University of Athens, Athens, Greece

Dimitris S. Kostopoulos Department of Geology, Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Thessaloniki, Greece

George D. Koufos Department of Geology, Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Thessaloniki, Greece

Andreas Magganas Faculty of Geology and GeoEnvironment, University of Athens, Athens, Greece

John McNabb Department of Archaeology, University of Southampton, Southampton, UK

Dušan Mihailović Department of Archaeology, Faculty of Philosophy, University of Belgrade, Belgrade, Serbia

Christopher Miller Institut für Naturwissenschaftliche Archäologie, Eberhard Karls University of Tübingen, Tübingen, Germany

Caley M. Orr Department of Cell and Developmental Biology, University of Colorado School of Medicine, Aurora, CO, USA

K. Papayianni Wiener Laboratory, ASCSA, Muséum National d'Histoire Naturelle, Paris, France

Eleni Psathi Ephoreia of Antiquities of Arcadia, Tripolis, Greece

Mirjana Roksandic Department of Anthropology, University of Winnipeg, Winnipeg, MB, Canada

Valéry Sitlivy Liège, Belgium

Fred H. Smith Department of Sociology and Anthropology, Illinois State University, Bloomington-Normal, IL, USA

Rajna Šošić-Klindžić Department of Archaeology, University of Zagreb, Zagreb, Croatia

Nikolai Spassov National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria

David S. Strait Department of Anthropology, Washington University, St. Louis, MO, USA

V. Tourloukis Paleoanthropology, Department of Geosciences, Eberhard Karls Universität Tübingen, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany

Tsanko Tzankov Department of Geography, Ecology and the Preservation of the Environment, South-Western University "Neofit Rilski", Blagoevgrad, Bulgaria

Krunoslav Zubčić Croatian Conservation Institute, Zagreb, Croatia

Part I
The Human Fossil Record

Chapter 1
Paleoanthropology in Greece: Recent Findings and Interpretations

Katerina Harvati

Abstract Greece lies at the crossroads between Europe, Asia, and Africa, and represents a logical gateway through which early human populations might have repeatedly passed on the way to and from Europe. It also represents one of the three European Mediterranean peninsulas which acted as a refugium for fauna, flora and, very likely, human populations during glacial times. Evidence from this region is therefore essential in order to test hypotheses about the course of human evolution in Europe. Despite the importance of the region, paleoanthropological research has until recently been relatively neglected. In recent years, however, renewed research efforts have produced new human fossils from Greece, recovered from excavated contexts. This chapter reviews the Greek human fossil evidence in the context of broader questions in European paleoanthropology.

Keywords Neanderthals • Upper Paleolithic • Modern humans • *Homo heidelbergensis*

Introduction

The European human fossil record continues to produce unexpected discoveries even after more than a century of study. These finds are reshaping our knowledge of human evolution on the continent. Over the last 20 years, views on the short *vs.* long chronology of human presence in Europe have shifted radically toward the latter, although the identity of the earliest colonizers and their evolutionary fate remain elusive (e.g., Carbonell et al. 2008; Bermúdez de Castro et al. 2011; Toro-Moyano et al. 2013). Our understanding of the Neanderthal lineage is now clearer than ever, although paleoanthropologists still struggle with the classification and relationships of the earlier, Middle Pleistocene, European hominins (e.g., Harvati et al. 2010; Freidline et al. 2012; Arsuaga et al. 2014). Finally, the advent of modern humans, *Homo sapiens*, in Europe around 40–45 ka (Benazzi et al. 2011; Higham et al. 2011a, b, 2013), and the replacement of local populations of *H. neanderthalensis* that may have survived later in Southern European refugia, raises questions about possible interactions between the two species, about the level of cultural and/or biological exchanges that might have occurred, and about the causes for the Neanderthal extinction.

Within this research landscape, crucial primary evidence from the geographic region representing both a major dispersal corridor to and from Europe and a Mediterranean refugium for both fauna and flora (the Southern Balkans in general and Greece in particular) is missing. This unfortunate situation is likely due to the lack of a strong tradition in basic Paleolithic research in the region. Nowhere is this data gap more evident than in the human fossil record (similarly to the situation in the Central Balkans, Bulgaria, and Anatolia, see Aytek and Harvati 2016; Roksandic 2016; Strait et al. 2016). This chapter reviews the existing human fossil evidence from Greece in the framework of the research questions outlined above.

Neanderthals and Early Modern Humans

Greece lies directly on one of the proposed dispersal routes of modern humans coming into Europe from the Near East and Africa. However, Upper Paleolithic sites are rare in

K. Harvati (✉)
Paleoanthropology, Department of Geosciences,
Eberhard Karls Universität Tübingen, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment,
Eberhard Karls Universität Tübingen, Tübingen, Germany

PhD Program in Anthropology, City University of New York
Graduate Center and New York Consortium in Evolutionary
Primatology, New York, NY, USA
e-mail: katerina.harvati@ifu.uni-tuebingen.de

Katerina Harvati and Mirjana Roksandic (eds.), *Paleoanthropology of the Balkans and Anatolia*,
Vertebrate Paleobiology and Paleoanthropology, DOI 10.1007/978-94-024-0874-4_1

Greece, and to date, no definitive early Upper Paleolithic human remains are known. A skeleton from the site of Apidima (Cave Γ) in the Mani region (Fig. 1.1; see below) has been proposed to represent an early Upper Paleolithic burial (Pitsios 1985, 1995) and was reportedly found associated with lithics tentatively assigned to the Aurignacian (Darlas 1995). However, no convincing chronological assessment exists for Cave Γ, and neither the skeleton nor the lithic and faunal material from this cave have been described in detail. Therefore, the identity of the specimen and its chronology and cultural affiliation must remain uncertain until further research (Harvati et al. 2009).

Fig. 1.1 Map of Greece showing the approximate geographic location of the sites mentioned in the text. Adapted from Harvati et al. (2009)

The Klisoura site in the Northern Peloponnese has recently yielded a lithic industry closely resembling the Uluzzian (Fig. 1.1; Koumouzelis et al. 2001). This technocomplex was recently dated to *ca.* 42–45 cal kBP at the Grotta del Cavallo site in Italy, where it was associated with modern human remains (Benazzi et al. 2011). If we accept that the Uluzzian was produced by modern humans, its presence in Greece might indicate the arrival of modern humans in this region. Since the Klisoura Uluzzian layer is capped by the Campanian Ignimbrite (CI; Stiner et al. 2010; Lowe et al. 2012), it may testify to a modern human arrival predating 40 ka. Douka et al. (2014) recently obtained the radiocarbon date of 39.9–38.5 cal kBP (OxA-21068) from a shell bead from the Uluzzian layer at Klisoura, a date consistent with the presence of the CI above it. On the basis of new dates for multiple sites and their Bayesian statistical modeling, these authors concluded that the Uluzzian appeared *ca.* 45 ka in both Italy and Greece, where it persisted until *ca.* 39 ka. Unfortunately, no human remains have been found in the Uluzzian layer at Klisoura. Therefore, its attribution to early modern humans cannot be confirmed at this site (see also Sitlivy 2016). Similarly, the first Aurignacian layer at Franchthi in the Argolid, Northern Peloponnese, postdates the CI likely only by *ca.* two millennia (Fig. 1.1; Farrand 2000; Stiner and Munro 2011), again suggesting an early modern human presence, although no human remains have been recovered from this layer.

In contrast to the sparse early Upper Paleolithic fossil record, Neanderthal remains have recently been identified at Lakonis and Kalamakia, two sites in the Mani peninsula, Southern Peloponnese (Table 1.1; see also Darlas and Psathi 2016). Lakonis consists of a series of caves and collapsed

Table 1.1 Summary of the human fossil record from Greece up to the early Upper Paleolithic. Adapted from Harvati et al. 2009, 2013

Site	Hominins	Taxon	Age (ka)	Method	Assoc. Lithics
Megalopolis (Peloponnese)	Isolated LUM3	*Homo* sp.	Possibly Early/ Middle Pleistocene	Faunal, Paleomagnetism	–
Petralona Cave (Macedonia)	Petralona cranium	*H. heidelbergensis*	>240 ka	ESR/ U/Th, Faunal	–
Apidima Cave A (Mani)	LAO 1/S1 and LAO 1/S2 partial crania	*H. heidelbergensis*—*H. neanderthalensis*	Late Middle- Early Late Pleistocene	Geomorphology	–
Lakonis Site 1 (Mani)	LKH1, isolated LLM3	*H. neanderthalensis*	42–48 ka (cal)	AMS ^{14}C on charcoal	Initial Upper Paleolithic
Kalamakia Cave (Mani)	KAL1-KAL14 Isolated teeth: LUP3, LUM3, L?UP4, LLP4, RUM2, RLP4, RUI2, LUI1, LUDi2, L?Udi1; occipital fragment; right fibula shaft fragment; subadult lumbar vertebra; left navicular bone	*H. neanderthalensis*	>40–100 ka	AMS ^{14}C on charcoal, U/Th on marine shell	Mousterian
Apidima Cave Γ (Mani)	Partial skeleton LAO 1/S3	*H. sapiens*	Late Pleistocene	–	Possibly Aurignacian

Fig. 1.2 The LKH1 Neanderthal lower third molar. *Top*: Occlusal view; *Bottom Left*: Buccal view; *Bottom right*: Lingual view. Photographs copyright K. Harvati

caves along the shoreline on the Eastern coast of Mani, near the town of Gytheion (Fig. 1.1). It was excavated between 1997 and 2011 by a team from the Ephoreia of Paleoanthropology and Speleology, Greek Ministry of Culture. The site preserves a rich, although highly fragmented, fauna, and very rich Middle Paleolithic lithic assemblages throughout most of the stratigraphic sequence. Additionally, the topmost layer yielded an assemblage described as Initial Upper Paleolithic (hereafter IUP), dated to *ca*. 48–42 cal kBP by AMS ^{14}C on charcoal (Panagopoulou et al. 2002–2004; Elefanti et al. 2008). A single human specimen from this layer, LKH1, was recovered at Lakonis during excavation in 2002 (Panagopoulou et al. 2002–2004; Harvati et al. 2003).

LKH1 (Fig. 1.2) is a lower left third molar. Although an isolated specimen, it preserves morphology that strongly supports its taxonomic assignment as a Neanderthal. This includes a large anterior fovea, complex root morphology, a relatively enlarged pulp cavity, and a midtrigonid crest, a feature found at very high frequencies on Neanderthal, but almost never on modern human lower third molars (Fig. 1.2; Harvati et al. 2003). Similar to other Neanderthal samples, it exhibits relatively high enamel secretion rates and relatively thin enamel (Smith et al. 2009). LKH1 has also yielded important information about Neanderthal paleobiology. Strontium isotope analysis suggested that during the formation of the tooth crown this individual lived at least 20 km away from Lakonis, the site where it was found (Richards et al. 2008). Although the distance is limited, the evidence from this analysis is the first direct indication of Neanderthal mobility, and a first assessment of a minimum range on the seasonal or lifetime movements of Neanderthal groups. For the case of the Mani peninsula, it is an indication that the Neanderthal population living at Lakonis would likely have communicated with the one present at Kalamakia, on the other side of the peninsula and approximately 30 km away (see below). LKH1 also raises questions about the authorship of the IUP industry that it was associated with, and of possible contact with early modern humans in the region. The identification of the Uluzzian at Klisoura—and therefore the possibility of the presence of modern humans—some 200 km to the north, and dated to before 40 ka BP (Koumouzelis et al. 2001; Stiner et al. 2010; Douka et al. 2014), further highlights this possibility.

Kalamakia is the second site in the Mani peninsula to have yielded Neanderthal fossils. It is a karstic cave formed in the limestone cliff side and situated on the Western coast of the Mani peninsula (Fig. 1.1; see also Darlas and Psathi 2016). It was excavated from 1993 to 2006 by a joint team from the Ephoreia of Paleoanthropology and Speleology, Greek Ministry of Culture, and the Muséum national d'Histoire naturelle, Paris (de Lumley et al. 1994; Darlas and de Lumley 2004). The site has yielded Mousterian lithics with Levallois elements throughout the stratigraphic sequence, as well as a rich fauna comprising fallow deer, ibex, wild boar, and red deer; several species of carnivores; and numerous small vertebrates (Darlas and de Lumley 2004; Harvati et al. 2013). The deposits in the cave date to between 100,000 ka (U/Th radiometric dating of a marine shell at the Institut de Paléontologie Humaine in Paris, IPH Kal 9304: 109,000 + 14,000/−13,000; de Lumley et al. 1994) and >39,000 ^{14}C BP (^{14}C AMS dating on charcoal at Gif-sur-Yvette in France, GifA 94592; de Lumley et al. 1994).

Thirteen fragments of human remains were excavated from several layers of Unit IV, and one from the uppermost layer of Unit III. In total, ten isolated teeth, one cranial fragment, and three postcranial elements were recovered, representing at least eight individuals, two of them juveniles (Harvati et al. 2013). Although not all specimens are taxonomically informative, several elements preserve diagnostic Neanderthal morphology. Among the dental remains, the two lower premolars and the two upper incisors display combinations of crown features that are observed at very high frequencies among Neanderthals but not in Upper Paleolithic modern humans (Harvati et al. 2013). The two upper incisors (KAL10 and KAL11; Fig. 1.3) show a combination of shoveling, lingual tubercles, and labial convexity, considered unique to Neanderthals and pre-Neanderthals (e.g., Bailey 2007; Martinón-Torres et al. 2012). The two lower premolars

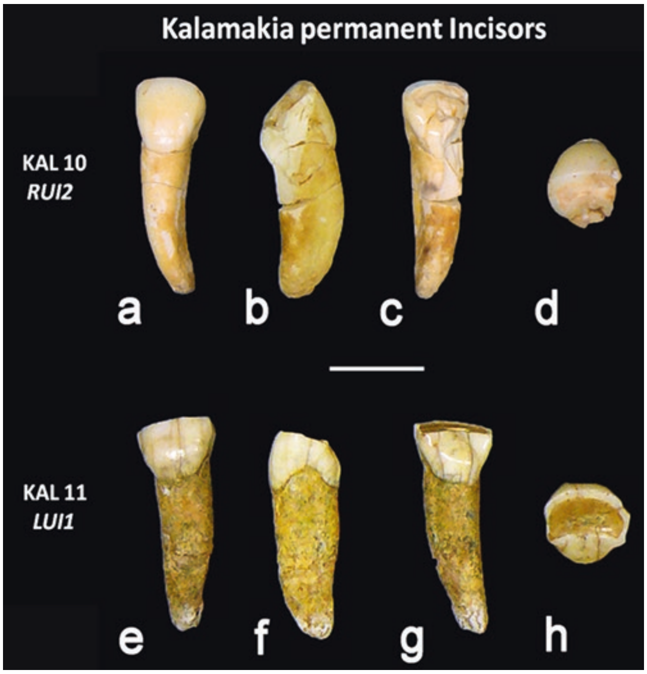

Fig. 1.3 The Kalamakia permanent incisors KAL10 (*top*) and KAL11 (*bottom*). Labial (**a**, **e**), mesial (**b**, **f**), lingual (**c**, **g**) and occlusal (**d**, **h**) views. Photographs copyright K. Harvati. Adapted from Harvati et al. (2013)

(KAL6 and KAL9) show multiple lingual cusps, a transverse crest and an asymmetric crown, again a combination thought to be unique to Neanderthals and some of their ancestors (e.g., Bailey 2007; Martinón-Torres et al. 2012). Furthermore, two additional isolated teeth, an upper third premolar (KAL2) and an upper third molar (KAL3), have crown diameters that place them closer to Neanderthals than to early modern or Upper Paleolithic modern humans (Harvati et al. 2013). Beyond the dental remains, one of the postcranial elements, the navicular bone KAL14, shows dimensions that fall within the Neanderthal, rather than the modern human range of variation (Fig. 1.4; Harvati et al. 2013; McCarty et al. 2014). This specimen also shows carnivore puncture marks, indicating that some of the human remains found at the site were scavenged, and confirming that Kalamakia was intermittently used by humans and carnivores (Harvati et al. 2013). Therefore, although the Kalamakia fossil human assemblage comprises isolated remains, it includes several dental and postcranial diagnostic elements that point to Neanderthal affinities, while none of the diagnostic elements show modern human-derived features. Their association with Mousterian lithic assemblages throughout the Kalamakia stratigraphic sequence further indicates that the Kalamakia human remains belong to a Neanderthal population.

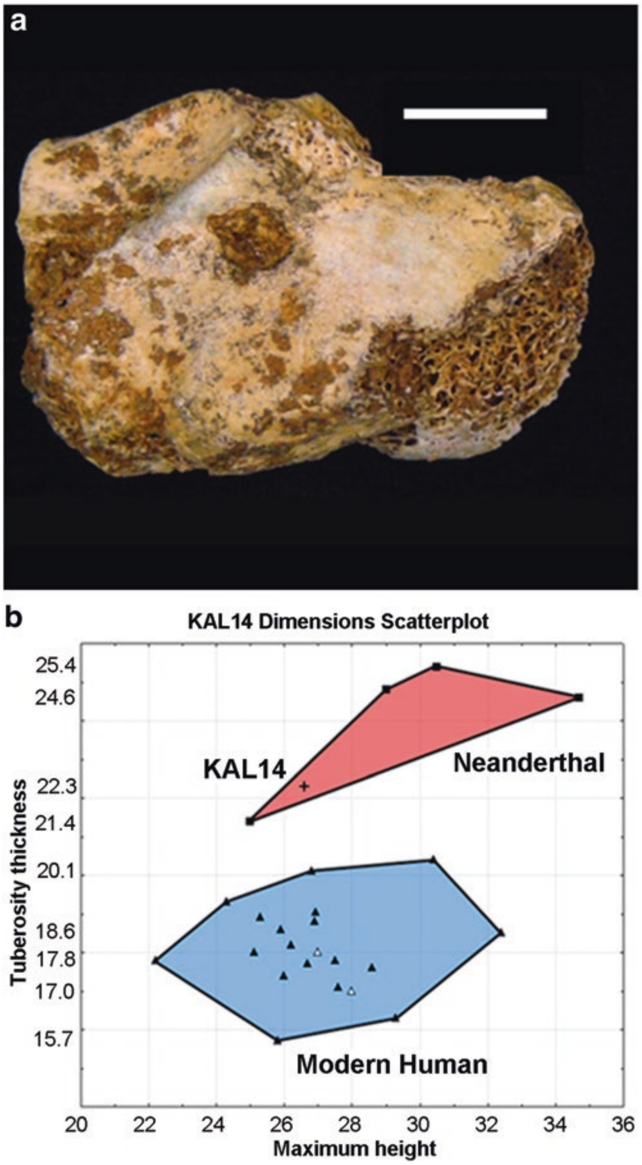

Fig. 1.4 (**a**) The Kalamakia KAL14 navicular bone. Photograph copyright K. Harvati. (**b**) Maximum thickness of navicular tuberosity plotted against minimum tuberosity thickness in Neanderthals and modern humans. Adapted from Harvati et al. (2013)

The Kalamakia and Lakonis Neanderthals might represent the same population. Although their chronology is not completely resolved, the two sites likely overlap temporally. In addition to the strontium isotope analysis of the Lakonis Neanderthal molar (see above; Richards et al. 2008), human mobility between the two sites is suggested by the use of green andesite as a lithic raw material at Kalamakia (see Harvati et al. 2013). The source of this material is near the village of Krokees, close to Lakonis, on the eastern coast of the peninsula and is the most abundant raw material used for the production of the Lakonis lithics (Panagopoulou et al. 2002–2004). Unfortunately, the Kalamakia human sample does not preserve a lower third molar; therefore, a direct comparison of the human remains from the two sites is not possible.

Although it indicates a strong Neanderthal presence, the current evidence does not point to a late survival of this taxon in the Mani region, as might be predicted for a refugium area. If modern humans were already in the Northern Peloponnese before 40 ka, as suggested by the evidence from Klisoura (Douka et al. 2014), their presence might account for an early Neanderthal demise in the region. The current state of research, however, does not allow for any conclusions on this topic. Ongoing work in the Mani and elsewhere (see Darlas and Psathi 2008, 2016) will help test this hypothesis.

Middle-Late Pleistocene and the Origins of the Neanderthals

The Greek human fossil record presents two possible cases of early Neanderthal or pre-Neanderthal hominins that can add to the discussion of Neanderthal evolution (Table 1.1). One of these also comes from the Mani region, from the Apidima cave site.

Apidima is another karstic cave complex on the Western coast of the Mani peninsula (Fig. 1.1) in the vicinity of Kalamakia. It was investigated between 1978 and 1985 by a team from the University of Athens Medical School (Pitsios 1995; Harvati and Delson 1999; Harvati et al. 2009). As mentioned above, Cave Γ has yielded a modern human skeleton of uncertain chronology and cultural affiliation, which may represent an Upper Paleolithic burial (Pitsios 1985). One of the other caves in the complex, Cave A, has produced two human fossil crania, found encased in a block of matrix attached to the cave walls and close to the ceiling (Pitsios 1985, 1995, 1999; Harvati and Delson 1999; Harvati et al. 2009, 2011). Apidima 1 (LAO 1/S1) was partially eroded before discovery and preserves the posterior part of the neurocranium and cranial base. Apidima 2 (LAO 1/S2) is in better condition and is a relatively complete cranium (Fig. 1.5; Harvati et al. 2009). Excavation of Cave A yielded lithic artifacts likely of Middle Paleolithic character (see Harvati and Delson 1999) and a mixed fauna (Tsoukala 1999). However, these finds are not associated with the human specimens, and neither are the ESR dates produced on travertine samples from the entrances of Cave B and of the cave complex (Liritzis and Maniatis 1989; see Harvati et al. 2009, 2011). The chronological framework of these specimens is therefore uncertain.

In terms of its morphology, Apidima 2 shows a low neurocranium, a strong supra-orbital torus, a wide interorbital breadth, no canine fossa, large orbits and nasal aperture, and a prognathic face, suggesting Neanderthal or pre-Neanderthal affinities (Harvati and Delson 1999; Pitsios 2002; Harvati et al. 2009, 2011). Because of its relative gracility it has been considered to be a female, perhaps representing a female *H. heidelbergensis* comparable to Petralona in its chronology (Harvati and Delson 1999; Pitsios 2002; Harvati et al. 2009, 2011). However, the lack of detailed description or extensive metric data for either of the Apidima specimens precluded their more precise identification.

Fig. 1.5 The Apidima 2 cranium. Photo courtesy and copyright E. Delson

A recent study sought to elucidate the affiliations and temporal placement of these specimens by reanalyzing published original measurements for Apidima 2 and by reexamining the site's geological context (Harvati et al. 2011). This analysis pointed to strong Neanderthal affinities for Apidima 2 and found little resemblance to Petralona or *Homo heidelbergensis* in general (Fig. 1.6). It suggested a late Middle–early Late Pleistocene timeframe as most consistent with the geological setting of the site as well as with the specimen's morphology (Harvati et al. 2011). If these results are correct, the Apidima specimens do not belong to a Petralona-like population of *Homo heidelbergensis*. Instead they are early Neanderthals and likely represent the ancestors of the populations found at Kalamakia and Lakonis, pointing to a long history of Neanderthal presence in the Mani. Nonetheless, it must be kept in mind that

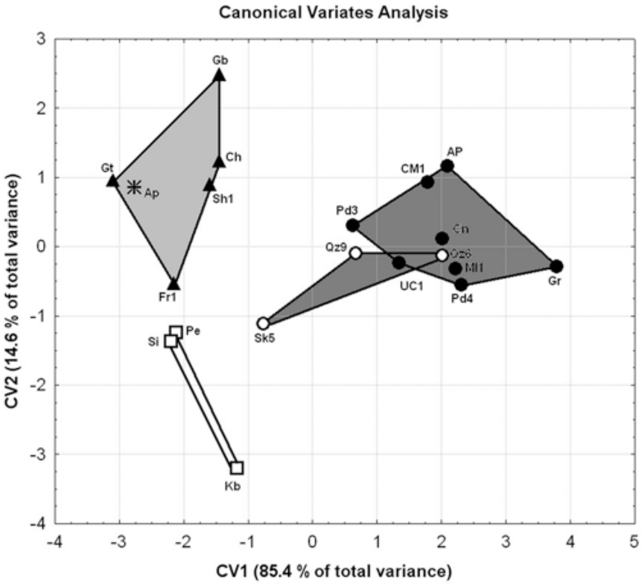

Fig. 1.6 Canonical variates analysis. *Black triangles*: Neanderthals; *open squares*: Middle Pleistocene hominins; *open circles*: Skuhl-Qafzeh; *Black circles*: Upper Paleolithic Europeans; star: Apidima 2. Adapted from Harvati et al. (2011)

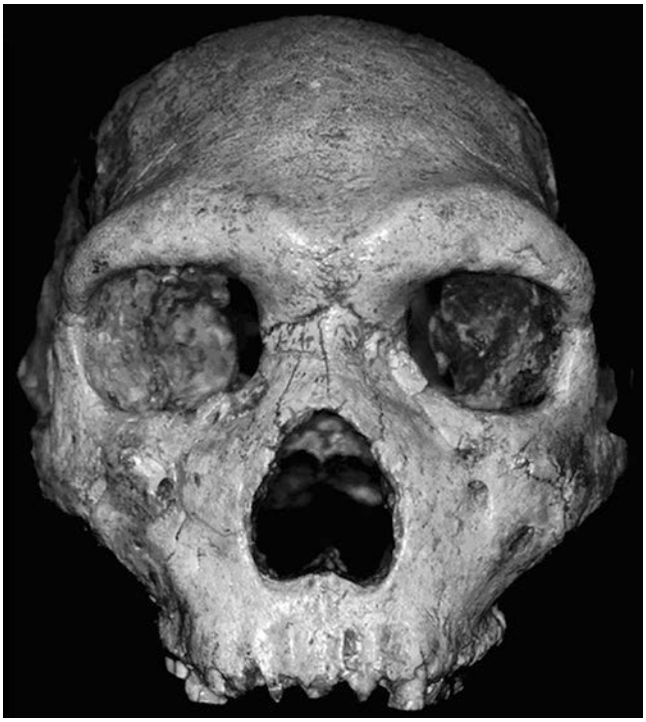

Fig. 1.7 The Petralona cranium. Photo courtesy and copyright E. Delson

these findings were obtained on the basis of a handful of published measurements. A thorough description and metric comparative study of the Apidima crania is still required to confirm our preliminary results and to assess the relationships between Apidima and Neanderthal populations from Europe and the Near East.

Undoubtedly the best known individual human fossil from Greece is the Petralona cranium (Fig. 1.7). It was discovered in 1960 in the Petralona Cave, Northern Greece (Fig. 1.1) by a group of villagers. Petralona cave was, until recently, the only excavated Middle Pleistocene site in Greece. It was joined in 2013–2015 by the Marathousa 1 site in Megalopolis, a site identified and excavated by a team from the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture) and the University of Tübingen, within the framework of the PaGE research (Panagopoulou et al. 2015; see also below); and by Rodafnidia (see Galanidou et al. 2016). The Petralona cranium is in excellent state of preservation and perhaps one of the most complete cranial specimens in the fossil human record of Europe. It is commonly thought to be of Middle Pleistocene age with a proposed date of *ca*. 250 ka, although there is a high degree of uncertainty about its chronological placement (see Harvati et al. 2009). Current consensus assigns Petralona to *H. heidelbergensis*, generally believed to be ancestral to Neanderthals in Europe. Along with other early European *H. heidelbergensis*, it has been described as showing incipient Neanderthal facial characteristics (e.g., Dean et al. 1998). However, it also shows strong overall similarities with African representatives of this taxon, and particularly with the Kabwe cranium (e.g., Stringer 1974; Stringer et al. 1979). Recent reappraisal of the Petralona facial morphology using landmark- and semilandmark-based geometric morphometrics to quantify the subtle morphology of such 'incipient' features could not confirm a more Neanderthal-like morphology in Petralona than in African *H. heidelbergensis* in all instances (Harvati 2009; Harvati et al. 2010; but see Freidline et al. 2012). These analyses, however, confirmed the strong similarity of this specimen with its African counterparts. For the Greek fossil record, these findings suggest contact with Africa at the time of Petralona in the Middle Pleistocene.

Early Colonization of Europe

Recent paleoanthropological discoveries have pushed back the date of the human settlement of Europe to more than a million years before present. The most important securely dated such discoveries come from two Iberian sites, Sima del Elefante and Gran Dolina, both in the Sierra de Atapuerca, Spain, and both yielding excavated human remains and artifacts dated to as early as *ca*. 1.2 Ma (Carbonell et al. 2008) and *ca*. 800 ka respectively (Bermúdez de Castro et al. 1997).

To these early sites can be added lithic assemblages and human footprints dating to *ca*. 700–900 ka, recovered in the United Kingdom at Pakefield and Happisburg (Parfitt et al. 2005, 2010; Ashton et al. 2014). Additional sites, including Pirro Nord in Italy, and Lézignan-la-Cèbe and Pont-de-Lavaud in France, are purported to have produced lithic remains of an even earlier chronology (Arzarello et al. 2009; Crochet et al. 2009; Despriée et al. 2010; Spassov 2016). A recently published isolated human deciduous tooth from Barranco-León associated with lithic assemblages and faunal remains could be as old as 1.2–1.4 Ma (Toro-Moyano et al. 2013; but see Muttoni et al. 2013).

On the basis of this evidence it has been hypothesized that Southern Europe may have been colonized earlier than the Northern or Central parts of the continent (Roebroeks 2001). Once more, South-East Europe is a logical dispersal corridor for early hominins spreading into Europe from either the Near East or the Caucasus region. With the exception of Kozarnika cave, which has yielded Lower Paleolithic artifacts suggested to be as old as 1.5 Ma (Sirakov et al. 2010; but see Kahlke et al. 2011; Spassov 2016; Ivanova 2016), evidence for early hominin presence in the region is conspicuously absent.

The existing human fossil record from Greece offers a glimpse of human presence possibly as early as the late Lower–early Middle Pleistocene at Megalopolis (Table 1.1). The Megalopolis Basin is an intramontane lacustrine basin located in central Peloponnese, in the vicinity of the town of Megalopolis (Fig. 1.1). The area has been known since the late nineteenth century for the fossiliferous deposits of its Marathousa beds, and several paleontological localities were excavated in the 1960s by the University of Athens. Stratified lithic artifacts were observed in the region by Darlas (2003), and more recently by a team from the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture) and the University of Tübingen working in the region within the framework of the PaGE project, most importantly at the Middle Pleistocene site of Marathousa 1 (Panagopoulou et al. 2015). A geological survey of the Megalopolis lignite beds, conducted in 1962–1965 by the Geological Society of Hannover, also collected a large fossil mammal assemblage from the Marathousa beds, which comprised a human upper third molar. Sickenberg (1975) assigned this assemblage to the early Middle Pleistocene. Due to the significant financial interest of the Megalopolis lignite beds, the geology of the region has been well studied, with a solid faunal and paleomagnetic framework (van Vugt 2000). The Sickenberg fauna can therefore be assigned to one of the fossil bearing horizons, ranging in time from *ca*. 870 ka and 850 ka (CHO 1 and 2, respectively), to 730 ka (CHO 3) and 600 ka (CHO 4; van Vugt 2000). The exact provenance of the Megalopolis tooth, however, is currently not known, and concerns have been raised that the specimen might be an intrusive *H. sapiens* (see Sickenberg 1975).

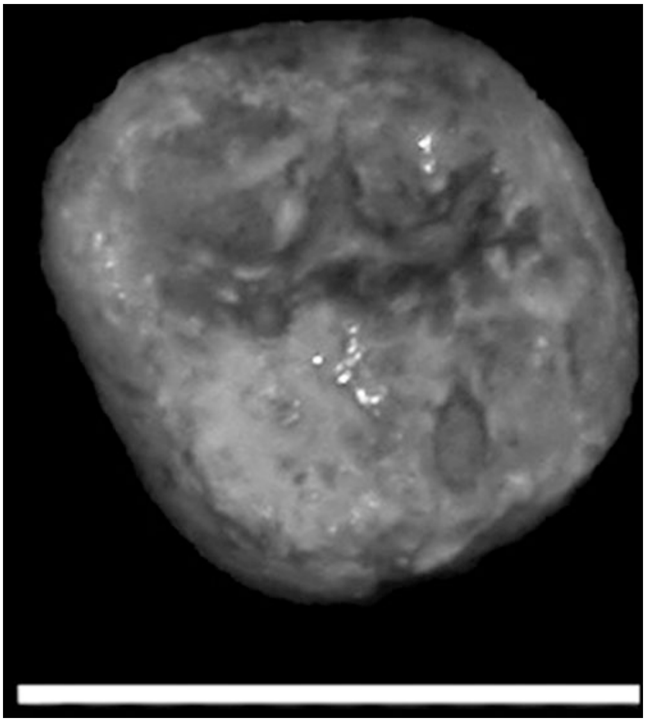

Fig. 1.8 The Megalopolis upper third molar. Photograph copyright K. Harvati

The Megalopolis human specimen is an isolated upper third molar (Fig. 1.8). With the exception of a short article on its enamel prism morphology (Xirotiris et al. 1979), there has been no study or publication of this specimen to date. Its crown appears eroded, perhaps due to acid etching, with the result that the details of the crown morphology cannot be observed, making its analysis difficult. Nonetheless, the Megalopolis M^3 is notable for its very small size. Bucco-lingual and mesio-distal crown dimensions were recorded and compared with a large comparative sample of hominin upper M^3s from the literature (Table 1.2; Fig. 1.9). Megalopolis is among the smallest ones, overlapping in its crown dimensions with modern humans, but also with the low end of the Neanderthal, *H. heidelbergensis* and *H. erectus* ranges of variation. However, when crown shape is assessed using the Crown Shape Index (BL/MD*100), Megalopolis is more similar to earlier taxa, particularly African early *Homo*, than to the later *Homo* specimens included in our comparative samples (Fig. 1.10). This analysis is intriguing and tentatively supports an early geological age for the Megalopolis tooth. However, it is very preliminary, and further work is planned to help elucidate the specimen's affinities, including the potentially taxonomically informative analysis of the crown outline and of the enamel thickness.

Table 1.2 Comparative samples used in the Megalopolis dental analysis: Measurements reported in mm

Specimen	Taxon	M-D	B-L	CBA	CSI (BL/MD*100)	Source
Megalopolis	**Megalopolis**	**9.10**	**10.30**	**93.73**	**113.19**	This study
KNM-ER 1813 right	*H. habilis*	11.70	13.50	157.95	115.38	Walker and Leakey (1993)
KNM-ER 1813 left	*H. habilis*	11.50	13.00	149.50	113.04	
Olduvai 13	*H. habilis*	12.00	13.00	156.00	108.33	Day (1986)
Dmanisi 2700 left	*H. erectus* - Dmanisi	10.00	11.90	119.00	119.00	Rightmire et al. (2006)
Dmanisi 2711 right	*H. erectus* - Dmanisi	9.80	11.90	114.60	121.43	Martinón-Torres et al. (2008)
Konso	*H. ergaster*	12.00	12.80	153.60	106.67	Suwa et al. (2007)
KNM 807	*H. ergaster*	11.00	13.00	143.00	118.18	Walker and Leakey (1993)
Sangiran S7-3d	*H. erectus*	9.50	12.00	114.00	126.32	Grine and Franzen (1994)
Sangiran S7-6	*H. erectus*	9.90	11.80	116.82	119.19	
Sangiran S7-17	*H. erectus*	9.70	11.50	111.55	118.56	
Sangiran S7-73	*H. erectus*	12.40	15.30	189.72	123.39	
Zkd46 R	*H. erectus*	9.10	10.90	99.19	119.78	Walker and Leakey (1993)
Zkd 47 L	*H. erectus*	9.40	11.30	106.22	120.21	
Zkd 48	*H. erectus*	9.90	12.00	118.80	121.21	
Zkd49 R	*H. erectus*	8.70	10.40	90.48	119.54	
Zkd112 R	*H. erectus*	10.10	12.50	126.25	123.76	
Zkd113 L	*H. erectus*	10.40	12.10	125.84	116.35	
Zkd146′	*H. erectus*	9.80	12.50	122.50	127.55	
Z.M	*H. erectus*	9.80	12.00	117.60	122.45	
ATA (SM) 171 (L)	*H. heidelbergensis*	8.80	11.80	103.80	134.09	Bermúdez de Castro (1986, 1993)
ATA (SM) 194 (R)	*H. heidelbergensis*	8.70	12.10	105.30	139.08	
ATA (SM) 274 (L)	*H. heidelbergensis*	8.00	10.10	80.80	126.25	
ATA (SM) 140 (L)	*H. heidelbergensis*	9.30	13.00	120.90	139.78	
ATA (SM) 10 (R)	*H. heidelbergensis*	8.60	11.50	98.90	133.72	
Arago XXI (R)	*H. heidelbergensis*	9.50	12.60	119.70	132.63	Condemi (1992)
Petralona (R)	*H. heidelbergensis*	10.00	12.50	125.00	125.00	Koufos (pers. comm.)
Petralona (L)	*H. heidelbergensis*	10.10	12.20	123.22	120.79	Koufos (pers. comm.)
Kabwe (L)	*H. heidelbergensis*	9.00	12.00	108.00	133.33	Day (1986)
Amud 1	*H. neanderthalensis*	8.20	11.10	91.02	135.37	Coppa et al. (2005)
Kebara 2	*H. neanderthalensis*	9.30	13.00	120.90	139.78	
Tabun C1	*H. neanderthalensis*	8.50	10.40			
Shanidar 1R	*H. neanderthalensis*	9.70	11.60	112.52	119.59	Condemi (1992)
Shanidar 2R	*H. neanderthalensis*	10.00	12.90	129.00	129.00	
Shanidar 3R	*H. neanderthalensis*	9.60	12.80	122.88	133.33	
Shanidar 5 L	*H. neanderthalensis*	9.60	13.00	124.80	135.42	
Shanidar 6R	*H. neanderthalensis*	10.60	12.20	129.32	115.09	
Tabun BC7	*H. neanderthalensis*	9.10	11.50	104.65	126.37	Coppa et al. (2005)
Hortus XI	*H. neanderthalensis*	8.7	11.60	100.92	133.33	de Lumley (1973)
Saccopastore 2 (R)	*H. neanderthalensis*	9.00	11.50	103.50	127.78	Condemi (1992)
Spy1	*H. neanderthalensis*	9.50	11.60	110.20	122.11	de Lumley (1973)
Spy 2	*H. neanderthalensis*	10.10	12.80	129.28	126.73	
La Quina 5	*H. neanderthalensis*	11.50	13.00	149.50	113.04	
Krapina	*H. neanderthalensis*	12.20	12.00	146.40	98.36	
Krapina	*H. neanderthalensis*	10.00	12.50	125.00	125.00	
Krapina	*H. neanderthalensis*	10.20	12.50	127.50	122.55	
Le Moustier	*H. neanderthalensis*	11.00	12.00	132.00	109.09	
Klasies River (L)	Early *H. sapiens*	7.60	10.50	79.80	138.16	Rightmire and Deacon (2001)
Skhul VII	Early *H. sapiens*	8.60	11.00	94.60	127.91	de Lumley (1973)
Skhul IV	Early *H. sapiens*	9.40	11.10	104.34	118.09	
Skhul 5	Early *H. sapiens*	9.10	11.80	107.38	129.67	

(continued)

Table 1.2 (continued)

Specimen	Taxon	M-D	B-L	CBA	CSI (BL/MD*100)	Source
Qafzeh 7 (R)	Early *H. sapiens*	9.40	12.10	113.74	128.72	Vandermeersch (1981)
Qafzeh 9 (R)	Early *H. sapiens*	10.90	12.10	131.89	111.01	
Qafzeh 9 (L)	Early *H. sapiens*	9.50	13.50	128.25	142.11	
Early UP France (*n*=4)	*H. sapiens*	8.80	10.80	95.04	122.73	Coppa et al. (2005)
Early UP Italy (*n*=5, BL 6)	*H. sapiens*	8.60	11.00	95.00	127.91	
Early UP Central Europe (*n*=10)	*H. sapiens*	8.90	11.70	104.13	131.46	
Late UP France (*n*=10, BL 11)	*H. sapiens*	8.80	11.60	102.90	131.82	
Late UP Italy (*n*=9, BL 12)	*H. sapiens*	8.60	11.70	101.10	136.05	
Late UP Central Europe (*n*=1)	*H. sapiens*	7.90	10.60	83.74	134.18	
European Mesolithic (*n*=9)	*H. sapiens*	8.50	10.70	90.95	125.88	

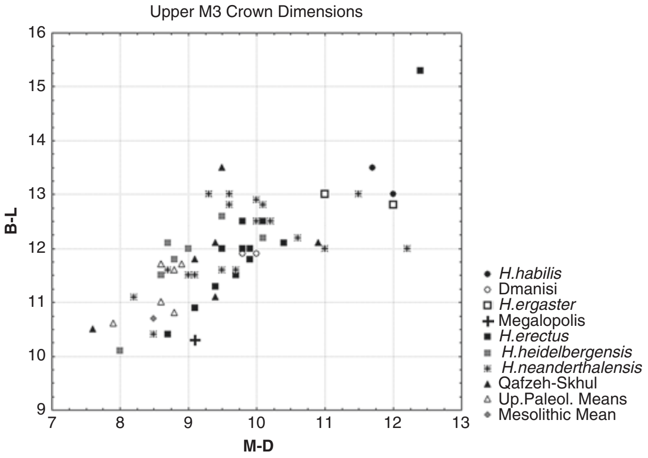

Fig. 1.9 Scatterplot of crown dimensions of fossil and recent human upper third molars. Comparative samples listed in Table 1.2. Crown dimensions from: de Lumley 1973; Vandermeersch 1981; Bermúdez de Castro 1986, 1993; Day 1986; Condemi 1992; Walker and Leakey 1993; Grine and Franzen 1994; Rightmire and Deacon 2001; Coppa et al. 2005; Rightmire et al. 2006; Suwa et al. 2007; Martinón-Torres et al. 2008

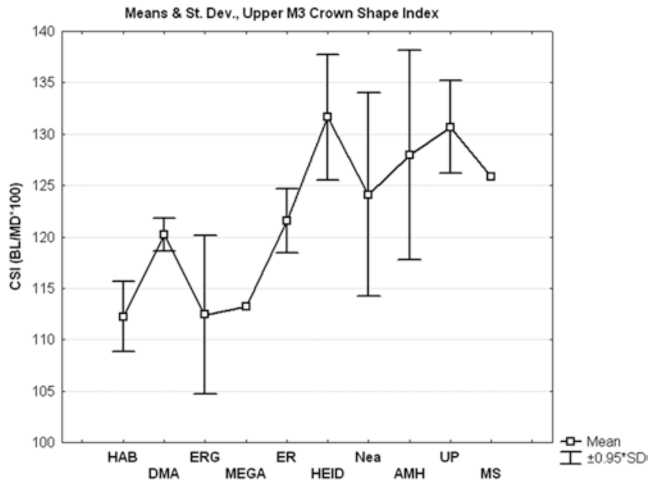

Fig. 1.10 Box plot of the Crown Shape Index (mean and standard deviation) of upper third molars among hominin samples (Table 1.2)

Conclusions

Despite many decades of relatively little research, the fossil human record of Greece is relatively rich, albeit sporadic in both time and space. Neanderthals are best represented in this record, with remains of both early and relatively late Neanderthals recovered from the Mani peninsula in Southern Greece. Most of these are isolated skeletal elements, although well-preserved cranial remains have also been recovered (Apidima). This part of the record closely mirrors that of Croatia, where both early and late Neanderthals are known from different sites (e.g., Janković et al. 2016). Comparisons with the Croatian and Near Eastern record in the context of Western European Neanderthal variation would therefore be of great interest for future study of this material.

The evidence is sparser in both earlier and younger periods of the Paleolithic. The Petralona cranium is commonly accepted as an early member of the Neanderthal lineage, belonging to *Homo heidelbergensis*. This specimen, however, is not well dated and shows strong affinities with the African Middle Pleistocene record. The affinities of the Megalopolis tooth, as well as its chronology, are also not well understood. On the opposite end of the temporal spectrum, very few Upper Paleolithic remains are currently known in Greece. This situation contrasts with other regions of the Balkans, which have yielded numerous Upper Paleolithic human fossils, such as Romania (e.g., Harvati and Roksandic 2016), highlighting the critical role of the Danube river in the dispersal of modern humans into Europe. An earlier modern human dispersal along the Mediterranean coast has been suggested on the basis of the Uluzzian sites in Italy and Greece (Mellars 2011), since the Uluzzian technocomplex was recently found to be associated with modern human remains (Benazzi et al. 2011). Nevertheless, until the discovery of taxonomically identifiable human remains from Greek Uluzzian sites, this scenario must remain hypothetical.

Perhaps the greatest shortcoming of the human fossil record from Greece is that the most complete and most important specimens were not recovered from excavations (Petralona, Apidima, Megalopolis). With the systematic excavation of Paleolithic sites in the last decades this situation has begun to change, and human fossil remains are now known also from excavated contexts. While the potential for paleoanthropological research in the country is far from having been fulfilled, we are now in a position to formulate hypotheses about the course of human evolution in the region and to target areas for future research. High research priorities include the Middle–Upper Paleolithic transition, as well as the Lower Paleolithic. Both periods are currently not well understood but are of great potential interest. An important goal of PaGE ('Paleoanthropology in the Southern Balkans')—a 5-year research program led by the author in collaboration with the Ephoreia of Paleoanthropology and Speleology of Southern Greece (Ministry of Culture), the University of Athens, and the University of Thessaloniki and funded by the European Research Council—is to help fill this research gap by conducting systematic fieldwork in areas selected for their strong research potential. These areas include, among others, the North-Western Mani peninsula, where new Paleolithic cave sites have been identified (Tourloukis et al. 2016); the Megalopolis basin, where stratified lithic artifacts have now been documented in Middle Pleistocene deposits (Panagopoulou et al. 2015); and the Mygdonia basin, Northern Greece, where new Early Pleistocene paleontological localities were identified and excavated (Konidaris et al. 2015). PaGE is one of several Paleolithic and Paleoanthropological projects currently active in the country (see e.g., Darlas and Psathi 2016; Galanidou et al. 2016). Together, their results promise to build an increasingly detailed and informative picture of human evolution in this crucial, but currently little known, region.

Acknowledgements I am deeply grateful to all my collaborators who have enabled the research summarized here: Eleni Panagopoulou, Andreas Darlas, Constantin Doukas, George Koufos, Dimitris Kostopoulos, Panagiotis Karkanas, Georgia Kourtessi-Philippaki and many others too numerous to list. I also thank the members of Tübingen Paleoanthropology and of the PaGE team, and particularly Monika Doll and Vagelis Tourloukis, for their contribution to the organization of the PaGE conference 'Human Evolution in the Southern Balkans,' where this paper was presented. K. Harvati is the PI of the European Research Council Starting Grant 'Paleoanthropology at the Gates of Europe' (PaGE; ERC-2011-StG-283503). This manuscript was greatly improved by the comments and suggestions of three anonymous reviewers and M. Roksandic.

References

Arsuaga, J. L., Martínez, I., Arnold, L. J., Aranburu, A., Gracia-Téllez, A., Sharp, W. D., et al. (2014). Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science, 344*, 1358–1363.

Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., et al. (2009). L'industrie lithique du site Pléistocène inférieur de Pirro Nord (Apricena, Italie du sud): une occupation humaine entre 1.3 et 1.7 Ma. *L'Anthropologie, 113*, 47–58.

Ashton, N., Lewis, S. G., De Groote, I., Duffy, S. M., Bates, M., Bates, R., et al. (2014). Hominin footprints from early Pleistocene deposits at Happisburgh, UK. *PLoS One, 9*, e88329.

Aytek, I. A., & Harvati, K. (2016). The human fossil record from Turkey. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Bailey, S. (2007). The evolution of non-metric dental variation in Europe. *Mitteilungen der Gesellschaft für Urgeschichte, 15*, 9–30.

Benazzi, S., Douka, K., Fornai, C., Bauer, C. C., Kullmer, O., Svoboda, J., et al. (2011). Early dispersal of modern humans in Europe and implications for Neanderthal behavior. *Nature, 479*, 525–528.

Bermúdez de Castro, J. M. (1986). Dental remains from Atapuerca (Spain) I. Metrics. *Journal of Human Evolution, 15*, 265–287.

Bermúdez de Castro, J. M. (1993). The Atapuerca dental remains. New evidence (1987–1991 excavations) and interpretations. *Journal of Human Evolution, 24*, 339–371.

Bermúdez de Castro, J. M., Arsuaga, J. L., Carbonell, E., Rosas, A., Martinez, I., & Mosquera, M. (1997). A hominid from the lower Pleistocene of Atapuerca, Spain: Possible ancestors to Neandertals and modern humans. *Science, 276*, 1392–1395.

Bermúdez de Castro, J. M., Martinón-Torres, M., Gómez-Róblez, A., Prado-Simón, L., Martín-Francés, L., Lapresa, M., et al. (2011). Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): A comparative morphological study. *Journal of Human Evolution, 61*, 12–25.

Carbonell, E., Bermúdez de Castro, J. M., Parés, J. M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., et al. (2008). The first hominin of Europe. *Nature, 452*, 465–469.

Condemi, S. (1992). Les Hommes Fossiles de Saccopastore et Leurs Relations Phylogénétiques. In *Cahiers de Paléoanthropologie*. Paris: CNRS Éditions.

Coppa, A., Grün, R., Stringer, C., Eggins, S., & Vargiu, R. (2005). Newly recognized Pleistocene human teeth from Tabun Cave, Israel. *Journal of Human Evolution, 49*, 301–315.

Crochet, J.-Y., Welcomme, J.-L., Ivorra, J., Ruffet, G., Boulbes, N., Capdevila, R., et al. (2009). Une nouvelle faune de vertébrés continentaux, associée à des artefacts dans le Pléistocène inférieur del'Hérault (Sud de la France), vers 1.57 Ma. *Comptes Rendus Palevol, 8*, 725–736.

Darlas, A. (1995). Τα λίθινα εργαλεία του σκελετού ΛΑΟ 1/Σ 3 (Απήδημα—Μάνη). *Acta Anthropologica, 1*, 59–62.

Darlas, A. (2003). Palaeolithic finds from the Megalopolis basin: Their relation to the fossils of the same area. In A. Vlachopoulos & K. Birtaha (Eds.), *Αργοναύτης: Τιμιτικός Τόμος για τον Καθηγητή Χρήστο Γ. Ντούμα από τους Μαθητές του στο Πανεπιστήμιο Αθηνών (1980–2000)* (pp. 27–37). Athens: Kathimerini.

Darlas, A., & de Lumley, H. (2004). La grotte de Kalamakia (Aréopolis, Grèce). Sa contribution à la connaissance du Paléolithique moyen de Grèce. *BAR, 1239*, 225–233.

Darlas, A., & Psathi, E. (2008). Le Paléolithique supérieur dans la péninsule du Mani (Péloponnèse, Grèce). In A. Darlas & D. Mihailovic (Eds.), *The Paleolithic of the Balkans* (pp. 51–59). Oxford: Archaeopress.

Darlas, A., & Psathi, E. (2016). The Middle and Upper Paleolithic on the Western coast of the Mani Peninsula (Southern Greece). In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Day, M. H. (1986). *Guide to fossil man*. Chicago: University of Chicago Press.

de Lumley, M. A. (1973). *Anténéandertaliens et Néandertaliens du bassin méditerraneen occidental européen. Études Quaternaires 2*. Marseille: Université de Provence.

de Lumley, H., Darlas, A., Anglada, R., Cataliotti-Valdina, J., Desclaux, E., Dubar, M., et al. (1994). Grotte de Kalamakia (Aréopolis, Péloponnèse). *Bulletin de Correspondance Hellenique, 118*, 535–559.

Dean, D., Hublin, J.-J., Holloway, R., & Ziegler, R. (1998). On the phylogenetic position of the pre-Neanderthal specimen from Reilingen, Germany. *Journal of Human Evolution, 34*, 485–508.

Despriée, J., Voinchet, P., Tissoux, H., Moncel, M.-H., Arzarello, M., Robin, S., et al. (2010). Lower and middle Pleistocene human settlements in the Middle Loire River Basin, Centre Region, France. *Quaternary International, 223*, 345–359.

Douka, K., Higham, T., Wood, R., Boscato, P., Gambassini, P., Karkanas, P., et al. (2014). On the chronology of the Uluzzian. *Journal of Human Evolution, 68*, 1–13.

Elefanti, P., Panagopoulou, E., & Karkanas, P. (2008). The transition from the Middle to the Upper Palaeolithic in the Southern Balkans: The evidence from the Lakonis I cave, Greece. *Eurasian Prehistory, 5*, 85–96.

Farrand, W. R. (2000). Depositional history of Franchthi Cave: Stratigraphy, sedimentology, and chronology. In *Excavations at Franchthi Cave, Greece, Fascicle 12*. Indiana: Indiana University Press.

Freidline, S. E., Gunz, P., Harvati, K., & Hublin, J.-J. (2012). Middle Pleistocene human facial morphology in an evolutionary and developmental context. *Journal of Human Evolution, 63*, 723–740.

Galanidou, N., Athanassas, C., Cole, J., Iliopoulos, G., Katerinopoulos, A., Magganas, A., & McNabb, J. (2016). The Acheulean site at Rodafnidia, Lisvori on Lesbos, Greece: Part I. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Grine, F. E., & Franzen, J. L. (1994). Fossil hominid teeth from the Sangiran dome (Java, Indonesia). *Courier Forschungsinstitut Senckenberg, 171*, 5–103.

Harvati, K. (2009). Petralona: Link between Africa and Europe? In L. Schepartz, C. Bourbou, & S. Fox (Eds.), *New directions in the skeletal biology of Greece* (pp. 31–49). Athens: Wiener Laboratory Series.

Harvati, K., Darlas, A., Bailey, S. E., Rein, T. R., El Zaatari, S., Fiorenza, L., et al. (2013). New Neanderthal remains from Mani peninsula, Southern Greece: The Kalamakia Middle Paleolithic cave site. *Journal of Human Evolution, 64*, 486–499.

Harvati, K., & Delson, E. (1999). Conference report: Paleoanthropology of the Mani Peninsula (Greece). *Journal of Human Evolution, 36*, 343–348.

Harvati, K., Hublin, J.-J., & Gunz, P. (2010). Evolution of Middle-Late Pleistocene human cranio-facial form: A 3-D approach. *Journal of Human Evolution, 59*, 445–464.

Harvati, K., Panagopoulou, E., & Karkanas, P. (2003). First Neanderthal remains from Greece: The evidence from Lakonis. *Journal of Human Evolution, 45*, 465–473.

Harvati, K., Panagopoulou, E., & Runnels, C. (2009). The paleoanthropology of Greece. *Evolutionary Anthropology, 18*, 131–143.

Harvati, K., & Roksandic, M. (2016). The human fossil record from Romania: Early Upper Paleolithic Europeans and possible evidence for Neanderthal admixture. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Harvati, K., Stringer, C., & Karkanas, P. (2011). Multivariate analysis and classification of the Apidima 2 cranium from Mani, Southern Greece. *Journal of Human Evolution, 60*, 246–250.

Higham, T., Basell, L., Jacobi, R., Wood, R., Bronk Ramsey, C., & Conard, N. J. (2011a). Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radiocarbon chronology of Geißenklösterle. *Journal of Human Evolution, 62*, 664–676.

Higham, T., Compton, T., Stringer, C., Jacobi, R., Shapiro, B., Trinkaus, E., et al. (2011b). The earliest evidence foranatomically modern humans in northwestern Europe. *Nature, 479*, 521–524.

Higham, T., Wood, R., Moreau, L., Conard, N. J., & Bronk Ramsey, C. (2013). Comments on 'Human-climate interaction during the early Upper Palaeolithic: Testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignaican' by Banks et al. *Journal of Human Evolution, 65*, 806–809.

Ivanova, S. (2016). A route through the Balkans and implications for the earliest settlement of Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Janković, I., Ahern, J. C. M., Karavanić, I., & Smith, F. H. (2016). The importance of Croatian Pleistocene hominin finds in the study of human evolution. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Kahlke, R.-D., García, N., Kostopoulos, D., Lacombat, F., Lister, A., Mazza, P., et al. (2011). Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. In J. Carrión, J. Rose & C. Stringer (Eds.), *Ecological scenarios for human evolution during the Early and early Middle Pleistocene in the western Palaearctic. Quaternary Science Reviews* (Vol. 30, pp. 1368–1395).

Konidaris, G., Tourloukis, V., Kostopoulos, D. S., Thompson, N., Giusti, D., Mihailidis, D., Koufos, G. D., & Harvati, K. (2015). Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): Preliminary results. *Comptes Rendus Palevol, 14*, 353–362.

Koumouzelis, M., Boleslawm, G., Kozlowski, J. K., Pawlikowski, M., Bar-Yosef, O., Albert, R. M., et al. (2001). The early Upper Paleolithic in Greece: The excavations at Klisoura cave. *Journal of Archaeological Science, 28*, 515–539.

Liritzis, Y., & Maniatis, Y. (1989). ESR experiments on Quaternary calcites and bones for dating purposes. *Journal of Radioanalytical and Nuclear Chemistry, 129*, 3–21.

Lowe, J., Barton, N., Blockley, S., Ramsey, C. B., Cullen, V. L., Davies, W., et al. (2012). Volcanic ash layers illuminate the resilience of Neanderthals and early modern humans to natural hazards. *Proceedings of the National Academy of Sciences of the United States of America, 109*, 13532–13537.

Martinón-Torres, M., Bermúdez de Castro, J. M., Gómez-Robles, A., Margvelashvili, A., Prado, L., Lordkipanidze, D., et al. (2008). Dental remains from Dmanisi (Republic of Georgia): Morphological analysis and comparative study. *Journal of Human Evolution, 55*, 249–273.

Martinón-Torres, M., Bermúdez de Castro, J. M., Gómez-Robles, A., Prado-Símon, L., & Arsuaga, J. L. (2012). Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution, 62*, 7–58.

McCarty, L., Rein, T. R., Scherf, H., Darlas, A., & Harvati, K. (2014). Geometric morphometric and trabecular bone analysis of the Kalamakia Neanderthal navicular bone: A comparative study. *American Journal of Physical Anthropology, 153*(S58), 180.

Mellars, P. (2011). The earliest modern humans in Europe. *Nature, 479*, 483–485.

Muttoni, G., Scardia, G., & Kent, D. V. (2013). A critique of evidence for human occupation of Europe older than the Jaramillo subchron (~1 Ma): Comment on 'The oldest human fossil in Europe from Orce (Spain)' by Toyo-Moyano et al. (2013). *Journal of Human Evolution, 65*, 746–749.

Panagopoulou, E., Karkanas, P., Tsartsidou, G., Kotjabopoulou, E., Harvati, K., & Ntinou, M. (2002–2004). Late Pleistocene archaeological and fossil human evidence from Laconis Cave, Southern Greece. *Journal of Field Archaeology, 29*, 323–349.

Panagopoulou, E., Tourloukis, V., Thompson, N., Athanassiou, A., Tsartsidou, G., Konidaris, G. E., Giusti, D., Karkanas, P., & Harvati, K. (2015). Marathousa 1: A new Middle Pleistocene archaeological site from Greece. *Antiquity Project Gallery, 89*(343).

Parfitt, S. A., Ashton, N. M., Lewis, S. G., Abel, R. L., Coope, G. R., Field, M. H., et al. (2010). Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature, 466*, 229–233.

Parfitt, S. A., Barendregt, R. W., Breda, M., Candy, I., Collins, M., Coope, G. R., et al. (2005). The earliest record of human activity in northern Europe. *Nature, 438*, 1008–1012.

Pitsios, T. K. (1985). Παλαιοανθρωπολογικές έρευνες στη θέση «Απήδημα» της Μέσα Μάνης. *Αρχαιολογία, 15*, 26–33.

Pitsios, T. K. (1995). Paleoanthropological Research at the cave site of Apidima, Laconia, Greece. *Acta Anthropologica, 1*, 1–180.

Pitsios, T. (1999). Paleoanthropological research at the cave site of Apidima and the surrounding region (South Peloponnese, Greece). *Anthropologischer Anzeiger, 57*, 1–11.

Pitsios, T. (2002). The fossil hominid findings from the Cave site of Apidima, South Peloponnese Greece. *Collegium Anthropologicum, 26*(Suppl.), 158.

Richards, M., Harvati, K., Grimes, V., Smith, C., Smith, T., Hublin, J.-J., et al. (2008). Isotope evidence of Neanderthal mobility. *Journal of Archaeological Science, 35*, 1251–1256.

Rightmire, P. G., & Deacon, H. J. (2001). New human teeth from Middle Stone Age deposits at Klasies River, South Africa. *Journal of Human Evolution, 41*, 535–544.

Rightmire, P. G., Lordkipanidze, D., & Vekua, A. (2006). Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republik of Georgia. *Journal of Human Evolution, 50*, 115–141.

Roebroeks, W. (2001). Hominid behaviour and the earliest occupation of Europe: An exploration. *Journal of Human Evolution, 41*, 437–461.

Roksandic, M. (2016). The role of the Central Balkans in the peopling of Europe: Paleoanthropological evidence. In K. Harvati, & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 15–33). Dordrecht: Springer.

Sickenberg, O. (1975). Eine Säugertierfauna des tieferen Bihariums aus den Becken von Megalopolis (Peloponnes, Griechenland). *Annales Géologiques des Pays Helléniques, 27*, 26–71.

Sirakov, N., Guadelli, J.-L., Ivanova, S., Sirakova, S., Boudadi-Maligne, M., Dimitrova, I., et al. (2010). An ancient continuous human presence in the Balkans and the beginnings of human settlement in western Eurasia: A Lower Pleistocene example of the Lower Palaeolithic levels in Kozarnika cave (North-western Bulgaria). *Quaternary International, 223–224*, 94–106.

Sitlivy, V. (2016). Technological variability of the Middle-to-Upper Paleolithic transition: Examples from the Balkans and neighboring regions. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Smith, T. M., Harvati, K., Olejniczak, A. J., Reid, D. J., Hublin, J. J., & Panagopoulou, E. (2009). Dental development and enamel thickness in the Lakonis Neanderthal molar. *American Journal of Physical Anthropology, 138*, 112–118.

Spassov, N. (2016). Southeastern Europe as a route for the earliest dispersal of *homo* towards Europe: Ecological conditions and the timing of the first human occupation of Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Stiner, M. C., Kozlowski, J. K., Kuhn, S. L., Karkanas, P., & Koumouzelis, M. (2010). Klissoura Cave 1 and the Upper Paleolithic of Southern Greece in cultural and ecological context. *Eurasian Prehistory, 7*, 309–321.

Stiner, M. C., & Munro, N. D. (2011). On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchthi Cave (Peloponnese, Greece). *Journal of Human Evolution, 60*, 618–636.

Strait, D. S., Orr, C. M., Hodgkins, J., Spassov, N., Gurova, M., Miller, C., & Tzankov, T. (2016). The human fossil record of Bulgaria, and the formulation of biogeographic hypotheses. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.

Stringer, C. B. (1974). A multivariate study of the Petralona skull. *Journal of Human Evolution, 3*, 397–404.

Stringer, C. B., Howell, F. C., & Melentis, J. (1979). The significance of the fossil hominid skull from Petralona, Greece. *Journal of Archaeological Science, 6*, 235–253.

Suwa, G., Berhane, A., Haile-Selassie, Y., White, T., Katoh, S., Wolde Gabriel, G., et al. (2007). Early Pleistocene Homo erectus fossils from Konso, southern Ethiopia. *Anthropological Science, 115*, 113–151.

Toro-Moyano, I., Bienvenido Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J. M., Martinón-Torres, M., et al. (2013). The oldest human fossil in Europe dated to ca. 1.4 Ma at Orce (Spain). *Journal of Human Evolution, 65*, 1–9.

Tourloukis, V., Thompson, N., Garefalakis, C., Konidaris, G., Karkanas, P., Panagopoulou, E., & Harvati, K. (2016). New Middle Paleolithic sites from the Mani peninsula, Southern Greece. *Journal of Field Archaeology, 41*(1), 68–83.

Tsoukala, E. (1999). Quaternary large mammals from the Apidima caves (Lakonia, S Peloponnese, Greece). *Beiträge zur Paläontologie, 24*, 207–229.

van Vugt, N. (2000). Orbital forcing in late Neogene lacustrine basins from the Mediterranean; A magnetostratigraphic and cyclostratigraphic study (Ph.D. Dissertation, University of Utrecht, 2000).

Vandermeersch, B. (1981). Les Hommes Fossiles de Qafzeh (Israel). In *Cahiers de Paléontologie*. Paris: CNRS Éditions.

Walker, A., & Leakey, R. (1993). *The Nariokotome Homo erectus Skeleton*. Cambridge: Harvard University Press.

Xirotiris, N., Henke, W., & Symeonidis, N. (1979). Der M^3 von Megalopolis—ein Betrag zu seiner morphologischen Kennzeichnung. *Zeitschrift für Morphologie und Anthropologie, 70*, 117–122.

Chapter 2
The Role of the Central Balkans in the Peopling of Europe: Paleoanthropological Evidence

Mirjana Roksandic

Abstract The paucity of fossil human remains from the Central Balkans represents a very serious lacuna in our understanding of human evolution in the Pleistocene of Europe, which is—as a result—strongly influenced by the material from the better researched parts of the continent further to the west of the Balkans. The scant fossil record from the Central Balkans suffers from a lack of archaeological/geological context, and with the exception of the Balanica hominin (BH-1) has no associated chronological data. In this chapter, I present all of the *purported* Pleistocene specimens currently known from the area and discuss their possible affinities.

Keywords Human evolution • *Homo* • Pleistocene • Balkan Peninsula

Introduction

The last three decades have brought about important insights into human evolution in Europe. Dominated over the past 160 years by relatively abundant Upper Pleistocene fossil remains from more westerly parts of Europe and the explanatory models they engendered, the field is rapidly changing with the opening of new geographic areas to intensive research. The discovery of Dmanisi (Gabunia and Vekua 1995) demonstrated a human population outside of Africa by 1.8 Ma, and a recent publication on the Dmanisi cranium D4500 (Lordkipanidze et al. 2013) indicated greater variation among early hominins from a single locality than previously suspected. At the other end of the continent, well-dated Early Pleistocene sites and contexts emerged in Spain with the oldest hominin find in Europe dated to *ca.* 1.4 Ma at Orce (Toro-Moyano et al. 2013; but see Muttoni et al. 2013; also Spassov 2016 and references therein). Well-documented Early Pleistocene archaeological sites are also known from Italy, although no human remains have been recovered there so far (Manzi et al. 2011). Further to the east, a proposed, though contentious, date of 1.4 Ma at Kozarnika cave in Bulgaria (Ivanova 2016; Spassov 2016) would be contemporaneous with Ubeidiya in Israel (Belmaker et al. 2002). The opening of these new geographic foci to systematic survey and excavation resulted in possibly the greatest advances in human evolutionary studies in Europe over the last two decades. However, we are still far from fully understanding who the first inhabitants of the continent were; what was their relationship to fossil hominins in Asia, Africa, and later European fossil populations; how many migrations into and out of Europe occurred in the Pleistocene; where the migrants came from; and what route they took. The paleoanthropological record of the Central Balkans—currently consisting for the most part of fortuitous finds, or finds gathered from excavations that leave much to be desired—could represent a crucial piece in this puzzle.

The Central Balkans area is at the crossroads of the south-to-north and east-to-west migratory routes that run through the Balkan Peninsula (see also, e.g., Aytek and Harvati 2016; Doboş and Iovita 2016; Harvati 2016; Spassov 2016; Strait et al. 2016). At the gates to the continent, the Balkan Peninsula is the most logical route of migration from the Levant into Europe—already identified as the confirmed route of animal migrations during the colder phases of the Early Pleistocene (Belmaker et al. 2002). The Central Balkans, defined by the Morava and Vardar rivers and their tributaries, covers most of what is today Serbia (without Vojvodina, which belongs to the Pannonian basin and therefore Central Europe), Eastern Bosnia and Northern Macedonia. More than just a migratory route, this region was also an integral part of the Balkan refugium (Hewitt 2011; Griffiths et al. 2004) for temperate decid-

M. Roksandic (✉)
Department of Anthropology, University of Winnipeg,
515 Portage Avenue, Winnipeg, MB, Canada R3B 2E9
e-mail: m.roksandic@uwinnipeg.ca

Katerina Harvati and Mirjana Roksandic (eds.), *Paleoanthropology of the Balkans and Anatolia*,
Vertebrate Paleobiology and Paleoanthropology, DOI 10.1007/978-94-024-0874-4_2

uous forests and associated biota (Eastwood 2004; Tzedakis 2004). The potential benefits of a more vigorous research program into the Pleistocene of the Central Balkan Peninsula cannot be overstated: the area could have played an important role in the initial peopling of the continent, in the repopulation of more northerly areas during interglacials, as well as in the demise of the Neanderthals and the advancement of modern humans. Whatever speculative role we can ascribe to the Central Balkans, the region is conspicuous by its absence in most discussions of migration(s) into and out of Europe (see, for example, a recent review by Bar-Yosef and Belfer-Cohen 2013).

Despite its likely importance and the strong tradition of archaeological research in the region, the Central Balkans Paleolithic record is scant (similar to the situation in many neighboring countries; see e.g., Aytek and Harvati 2016; Harvati 2016; Strait et al. 2016). A strong initial interest in Pleistocene-fauna and tool-bearing caves in the late 1800s–early 1900s (Cvijić 1903, 1918; Žujović 1893; Jovanović 1892) coincided with the discovery of Krapina in adjoining Croatia (Gorjanović-Kramberrger 1906; Janković et al. 2016). However, with the exception of some sporadic forays in the 1950s (Gavela 1951), this particular area of archaeology was all but forgotten until the very end of the twentieth century (Mihailović 2008; Mihailović and Bogićević 2016). Against this background, it is not surprising that the hominin fossil record is limited. Most of the purported Pleistocene specimens were uncovered in the late nineteenth and early twentieth century and subsequently lost during the First and the Second World Wars. In a recent AMS ^{14}C dating of six purported Pleistocene specimens from the Natural History Museum in Belgrade and the National Museum in Kraljevo, all were demonstrated to be of Holocene age (Roksandic et al. 2014), stressing the need for great caution in interpreting finds from old excavations.

The total tally of putative fossil hominins currently known from the Central Balkans (Fig. 2.1) includes: (1) a calotte from Bajloni's building discovered and described in 1892 (Jovanović 1892); (2) a mandible from the "loess in the vicinity of Belgrade" found in 1920 and published in 2001 (Roksandic and Dimitrijević 2001); (3) a tooth from Jerinina cave found in 1951, not described (Gavela 1951); (4) a skull fragment from the Kolubara gravel pit found in 1952, not described (Roksandic and Dimitrijević 2001); (5) a mandible found in Mala Balanica cave in 2006 (Roksandic et al. 2011). I will include in this review two additional cranial fragments: (6) a calotte from Bački Petrovac found in 1952 and published in 1966; and (7) a frontal from Žitište found in 1960 and described in 1966 (Živanović 1966; Radović et al. 2014). Both of these were found just north of the Central Balkans in the Pannonian plain of Central Europe. Popular lore mentions several more finds of which there is no mention in the published record. In addition to the specimen from "Bajloni's building" (Jovanović 1892) discussed later, there is mention of an "antediluvian man" uncovered from unspecified excavations in Cetinjska street. Since "Bajloni's building" refers to the brewery between Skadarska and Cetinjska streets in downtown Belgrade, this "antediluvian man" could potentially refer to the same specimen as the one from the Bajloni's building. A "Neanderthal" from Banovo brdo could be the one described as a "brachycephalic skull" (Žujović 1893, p. 21) uncovered from a loess deposit while excavating pylons for the bridge over the Sava river in Belgrade. Another "Neanderthal skull" from "Palata Albanija" was presumably found together with mammoth bones in 1938. The latter two specimens were recently located in the Natural History Museum in Belgrade. With the generous help of Sanja Paunović and Dr. Zoran Marković, I obtained permission to examine them and take samples for dating. Both skulls are clearly brachycephalic and therefore of post-Pleistocene age and will not be discussed in this chapter.

With the exception of the mandible from Mala Balanica, none of these specimens is associated with an archaeological context. Although unspecified stone tools were reportedly found with the Bački Petrovac specimen (Živanović 1966), given the accidental nature of the discovery, as well as the fact that the tools were neither described nor preserved, such an association cannot be confirmed. A very vague geological context reported as "*with bones of Elephas antiquus*" (Jovanović 1892, p. 30) in "*quaternary layers*" (Jovanović 1892, p. 31) has been reported for "Bajloni's building"; the Belgrade mandible was designated on its museum label as "*from the upper loess*" by its discoverer Professor Laskarev (Roksandic and Dimitrijević 2001, p. 28). The "*brachycephalic skull*" uncovered during the excavations for the Sava bridge—even according to the author—is not of Pleistocene age, although it was found in the loess deposit (Žujović 1893, p. 21): "*Under the third pylon, closer to the Austrian bank, plain river shells were unearthed as low as 12 m below the river bottom, while at the 14th meter, there was a human skull of a brachycephalous man.*" Noting other non-Pleistocene fauna in the river deposits in the area, Žujović (1893, p. 21) quite convincingly describes the taphonomic process that he considered responsible for the mixing: "*The river Sava still, within our memory, raises the plane; it still brings us deposits in which, mixed with river shells and snails, one finds fragments of horse, cattle, pig and sometimes mammoth skeletons that it unearthed from its original layers.*"

In this chapter, I will review what we know about each of the finds recorded in the scientific literature, and what we can learn about them by reexamining the very scant published measurements and descriptions. I will then offer some preliminary suggestions about the place of the Central Balkans in human evolution based on this rather limited evidence.

Fig. 2.1 Map of sites discussed in the chapter: Beograd (Belgrade) stands for both Bajloni's building calotte (BAJ in further text) and the "mandible from the loess in the vicinity of Belgrade" (RGF94/1) specimens. Inset shows the Balkan Peninsula and its relationship with the Black sea and adjoining regions; location of Belgrade and Balanica anchors the larger map in relation to well-known sites of Krapina (in Croatia) and Dmanisi (Georgia)

Materials and Methods

Before proceeding to describe the specimens in question, a note on the choice of measurements and morphological traits, as well as specimens and taxonomic groups included in the comparative sample, should be made. All the measurements were gathered from the reported original descriptions (for the more recently published material) and from large sets of data on originals by Rightmire (2008) for earlier discoveries (see Table 2.1 for the list of sources). Morphological traits of the mandible were taken from Mounier et al.'s (2009) comprehensive scoring of mandibular specimens. The choice of measurements and morphological traits was guided by the preserved morphology that could be measured or scored, or by the information available in the literature. This has of course resulted in limited comparative samples, which comprise only specimens that preserve the same measurements. In order to maximize the comparative sample, in some cases it was necessary to reduce the number of measurements used (notably for Bački Petrovac), as the alternative—i.e., to compute missing values—could introduce unknown biases.

When discussing hominin populations in the Pleistocene, the notion of "Paleo-deme" or "p-deme" (Howell 1996, 1999), which allows us to distinguish between geographically and chronologically restricted populations and discuss their possible phyletic relationships without implying or rejecting species status is the most appropriate. *Homo heidelbergensis* is a case in point, as it is differently interpreted to include European Middle Pleistocene specimens (*Homo heidelbergensis sensu stricto*), or European and African Middle Pleistocene specimens, (*Homo heidelbergensis sensu lato*), or even to extend to Asian samples (Rightmire 1998; Mounier et al. 2009; Harvati et al. 2010; Stringer 2012; Manzi 2012), or dismissed altogether (Mounier and Caparros 2015). The term Middle Pleistocene European *Homo* (MPEH) will be used here to denote European Middle Pleistocene humans with affinities to Neanderthals. Whenever possible, the comparative sample is grouped into the following categories: (1) *Homo habilis*/*rudolfensis*, (2) African *Homo erectus* /*ergaster*, (3) Early Pleistocene Eurasian *Homo*, (4) Asian *Homo erectus*, (5) Middle Pleistocene Asian *Homo*, (6) Middle Pleistocene African *Homo* (MPAfH), (7) Middle Pleistocene

Table 2.1 Linear measurements and angles used in the analysis[a]

Group/Specimen		Measurements used (Martin's number)[b]							References
	Abbrev.	M1	M8	M29	M26	M32(5)	M10	M9	
Early Pleistocene Euroasian *Homo*									
Dmanisi 2700	Dm2700	155	126	89	95	150	85	67	Lordkipanidze et al. (2006)
Dmanisi 2280	Dm2280	177	136	101	108	149	105	65	Lordkipanidze et al. (2006)
Dmanisi 3444	Dm3444	163	132	80	90	148	91	67.5	Lordkipanidze et al. (2006)
African *Homo erectus/ergaster*									
Daka	Dk	180	133	101	116	141	105	89	Asfaw et al. (2008)
KNM-ER3733	ER3733	182	142	104	119	139	110	83	Lordkipanidze et al. (2006) and Rightmire (1990)
KNM-ER3883	ER3883	182	140	101	118	140	105	80	Lordkipanidze et al. (2006) and Rightmire (1990)
Asian *Homo erectus*									
Sangiran 17	San17	207	161	118	–	–	–	–	Lordkipanidze et al. (2006)
Bukuran	Bk	194	149	110	–	–	–	–	Grimaud-Herve et al. (2012)
Sinanthropus III	Sin3	188	144	102	–	–	–	–	Weidenreich (1943)
Sinanthropus X	Sin10	190	150	115	–	–	–	–	Weidenreich (1943)
Sinanthropus XI	Sin11	192	145	106	–	–	–	–	Weidenreich (1943)
Sinanthropus XII	Sin12	195.5	147	113	–	–	–	–	Weidenreich (1943)
Ngandong 1	Ng1	198	153	114	128	141	120	106	Kaifu et al. (2008) and Rightmire (1990)
Ngandong 7	Ng2	192	147	116	125	140	116	103	Kaifu et al. (2008) and Rightmire (1990)
Ngandong 11	Ng11	203	160	120	130	138	122	112	Kaifu et al. (2008) and Rightmire (1990)
Ngandong 12	Ng12	201	151	113	121	146	114	103	Kaifu et al. (2008) and Rightmire (1990)
Middle Pleistocene African *Homo*									
Kabwe	Kb	209	149	120	139	140	118	98	Rightmire (2008) and Murrill (1981)
Elandsfontein	El	202	138	116	–	–	–	–	Rightmire (2008)
Bodo	Bd	–	–	125	144	139	119	105	Rightmire (1996, 2008)
Middle Pleistocene Asian *Homo*									
Dali	Dl	206.5	149.5	114	135	128	119	104	Wu and Athreya (2013)
Jinniushan	Jn	199	140	113	–	–	–	–	Coppens et al. (2008)
Middle Pleistocene European *Homo*									
Sima de los Huesos 4	SH4	201	164	115	126	140	126	117	Rightmire (2008)
Sima de los Huesos 5	SH5	185	146	106	114	145	118	105.7	Rightmire (2008)
Petralona	Pt	208	165	109	128	140	120	110	Rightmire (2008)
Ceprano	Cep	198	151	106	118	138	118	106	Ascenzi et al. (2000)
Upper Pleistocene *Homo sapiens*									
Skhul IV	Sk4	206	148	118	132	129.7	121	106	Vandermeersch (1981), Murrill (1981) and Cartmill and Smith (2009)
Skhul V	Sk5	193	146	106	118	130.7	114	99	Murrill (1981), Howells (1989) and Cartmill and Smith (2009)
Skhul IX	Sk9	213	145	114	130	131.6	120	96	Cartmill and Smith (2009)
Djebel Qafzeh 6	Q6	195	144	114	133	126.6	125	109.5	Vandermeersch (1981) and Howells (1989)
Djebel Qafzeh 9	Q9	–	–	115	130	133.8	117	103	Vandermeersch (1981) and Simmons et al. (1991)
Jebel Irhoud 1	JIr1	198	152	108	–	–	–	–	Howells (1989)
Upper Paleolithic *Homo sapiens*									
Predmosti 3	Pr3	202	143.4	120	137	135	128	104	Lubsen and Corruccini (2011) and Howells (1989)
Predmosti 4	Pr4	192	144	114	133	130	122	98	Lubsen and Corruccini (2011) and Howells 1989
Chancelade	Chan	–	–	111	130	128	127	101	Vandermeersch (1981) and Howells (1989)
Cro-Magnon 1	CrM1	206	153	125	147	125	126	102.5	Howells (1989) and Lubsen and Corruccini 2011
Mladeč 5	Ml5	205.6	156	116	–	–	–	–	Frayer et al. (2006)
Mladeč 6	Ml6	200.5	166.5	120.5	–	–	–	–	Frayer et al. (2006)
Mladeč 1	Ml1	198.5	141.5	114	133	123	126.5	103.5	Wolpoff et al. (2006)
Obercassel 1	Ob1	195	144	118.9	–	–	–	–	Vandermeersch (1981)
Obercassel 2	Ob2	183	134	106.4	–	–	–	–	Vandermeersch (1981)
Khvalynsk	Khv	–	–	115.9	130	136.1	115	94.2	Stansfield and Gunz (2011)
Podkumok	Pod	–	–	108.6	125.4	129.8	115	94.1	Stansfield and Gunz (2011)
Satanay	Sat	–	–	111.4	123	141.9	105	91.5	Stansfield and Gunz (2011)
Skhodnya	Skho	–	–	122.5	140.7	134.9	114	98.9	Stansfield and Gunz (2011)

(continued)