



DEPARTMENT OF GEOSCIENCES AND GEOGRAPHY A6

**THE MIOCENE OF WESTERN ASIA;
FOSSIL MAMMALS
AT THE CROSSROADS OF
FAUNAL PROVINCES AND
CLIMATE REGIMES**

MAJID MIRZAIE ATAABADI



UNIVERSITY OF HELSINKI
FACULTY OF SCIENCE

The Miocene of Western Asia; fossil mammals at the crossroads of faunal provinces and climate regimes

MAJID MIRZAIE ATAABADI

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Sciences of the University of Helsinki, for public examination in the auditorium D101, The Physicum building, on 5 November 2010, at 12 noon.

© Majid Mirzaie Ataabdi (synopsis and Papers III, IV, V, VI)

© J. T. Eronen, M. Mirzaie Ataabadi, A. Micheels, A. Karme, R. L. Bernor & M. Fortelius (Paper II)

© Reprinted with kind permission of Vertebrata PalAsiatica (Paper I)

Cover photo: Late Miocene outcrops, Ivand district, northwestern Iran, September 2007

Author's address: Majid Mirzaie Ataabadi
 Department of Geosciences and Geography
 P. O. Box 64
 00014 University of Helsinki
 Finland
 majid.mirzaie@helsinki.fi

Supervised by: Professor Mikael Fortelius
 Department of Geosciences and Geography
 University of Helsinki
 Finland

Reviewed by: Professor Sevket Sen
 Departement Histoire De La Terre
 Muséum National d'Histoire Naturelle, Paris
 France

 Professor Jordi Agustí
 Institute of Human Paleoecology and s. Evolution
 University Rovira Virgili, Tarragona
 Spain

Opponent: Professor George D. Koufos
 Department of Geology
 Aristotle University of Thessaloniki
 Greece

ISSN 1798-7911

ISBN 978-952-10-6307-7 (paperback)

ISBN 978-952-10-6308-4 (PDF)

<http://ethesis.helsinki.fi>

Helsinki University Print

Helsinki 2010



صبر آرد آرزو را نی شتاب

Patience brings what you desire, not haste

Mawlana Rumi

تقدیم به خانواده ام

تقدیم به مردم ایران

To my Family

To the people of IRAN

چکیده

آسیای باختری با قرار داشتن در گذرگاه قاره های دنیای قدیم (اروپا، آسیا و آفریقا) دارای جایگاه ممتازی است که از راه آن کوچ و پراکنش پستانداران و اقلیم های جانوری صورت گرفته است. با وجود این جایگاه ویژه، آثار پستانداران فسیل میوسن در باختر آسیا اندک بوده، نبوده های بزرگ مکانی و زمانی در بین آنها مشاهده می شود. در این پژوهش تلاش شده است تا با انجام کاوش های صحرایی و بررسی آثار فسیلی پستانداران از قبیل رد پاها و بقایای اسکلتی تا حد ممکن این نبوده های فسیلی کاهش یابد. بررسی های یاد شده نشان داده است که رد پای پستانداران میوسن در چندین نقطه از شمال و شمال باختری ایران وجود دارد. علاوه بر این، بقایای اسکلتی پستانداران موجود در نواحی فسیلی تازه یافت شده در شمال باختر ایران بیانگر نزدیکی آنها با مجموعه های جانوری تورولین میانی (۷-۸ میلیون سال پیش) می باشد.

بررسی اقلیم های جانوری مجموعه های فسیلی در این پژوهش به بهبود دانسته های پیشین در این زمینه منجر شده است و نشان میدهد در باختر آسیا چهار اقلیم جانوری فسیلی با یکدیگر برخورد داشته اند که شامل اقلیم های بالکان-آنتولی-ایران، آفریقا-عربستان، سیوالیک-جنوب شرق آسیا، و چین-آسیای مرکزی می باشند. گسترش این اقلیم ها در نتیجه وجود رشته کوه های بلندی است که بر پراکنش پستانداران فسیل و الگوهای آب و هوایی اثر داشته است.

دمای بالاتر و سطوح بالاتر دی اکسید کربن موجود در جو زمین در میوسن میانی (۱۵-۱۷ میلیون سال پیش) آشکارا برای گسترش جنگل ها و برتری پستانداران همخوانی یافته با بوم های بسته جنگلی مفید بوده است. افزونی آب و هوای فصلی، و خنکی و خشکی پیشرونده هوا در عرض های جغرافیایی میانی به سمت میوسن بالایی باعث برتری جانوران همخوانی یافته با بوم های باز نیمه جنگلی و صحرایی شده است. این جابجایی بومی به احتمال ۱۰-۱۲ میلیون سال پیش اتفاق افتاده است.

تاریخچه پراکنش مجموعه های جانوری همخوان با بوم های بسته و باز نشان میدهد که در باختر آسیا مجموعه های دارای پراکنش جهانی و محلی هر دو وجود داشته است. مجموعه های همخوان با بوم های بسته جنگلی مانند زیای عربی در میوسن زیرین و میانی دارای پراکنش و همه گیری شتاب داری می باشند در حالیکه زیای همخوان با بوم های باز مانند زیای مراغه در میوسن بالایی به آهستگی گسترش یافته، با پر کردن بوم های باز حاصل از نابودی جنگل ها و با واکنش به دگرگونی الگوهای نمناکی، جابجایی مکانی داده است. زیای سیوالیک (پاکستان- هند) در ابتدای میوسن بالایی دارای گسترش محلی و محدود بوده است.

این پژوهش بیانگر نیاز به کاوش های صحرایی بوده، نشان میدهد که پی جویی در نواحی گسترده آسیای باختری که آثار فسیلی اندکی در آنها یافت شده است هنوز می تواند نتیجه بخش باشد. بررسی اقلیم های جانوری با استفاده از روش های آماری خوشه ای با کمک ثابت های مشابهت بیانگر پایداری الگوهای دانسته از دیر باز می باشد که این الگوها در این پژوهش به روز شده است. همچنین روشهای کمی به کار گرفته شده در بررسی فراوانی نسبی موجودات همخوان با بوم های بسته جنگلی و باز صحرایی رویکردی نوین است که برآمدهای قابل قبولی ارائه داده است. بررسی تاریخچه گسترش مجموعه های جانوری در زمان و مکان نیز با کاربرد روشهای نوین محاسباتی و نماسازی رویکرد تازه ای است که میتوان آنرا به عرصه های تازه گسترش داد.

Abstract

Being at the crossroads of the Old World continents, Western Asia has a unique position through which the dispersal and migration of mammals and the interaction of faunal bioprovinces occurred. Despite its critical position, the record of Miocene mammals in Western Asia is sporadic and there are large spatial and temporal gaps between the known fossil localities.

Although the development of the mammalian faunas in the Miocene of the Old World is well known and there is ample evidence for environmental shifts in this epoch, efforts toward quantification of habitat changes and development of chronofaunas based on faunal compositions were mostly neglected. Advancement of chronological, paleoclimatological, and paleogeographical reconstruction tools and techniques and increased numbers of new discoveries in recent decades have brought the need for updating and modification of our level of understanding.

We undertook fieldwork and systematic study of mammalian trace and body fossils from the northwestern parts of Iran along with analysis of large mammal data from the NOW database. The data analysis was used to study the provinciality, relative abundance, and distribution history of the closed- and open-adapted taxa and chronofaunas in the Miocene of the Old World and Western Asia.

The provinciality analysis was carried out, using locality clustering, and the relative abundance of the closed- and open-adapted taxa was surveyed at the family level. The distribution history of the chronofaunas was studied, using faunal resemblance indices and new mapping techniques, together with humidity analysis based on mean ordinated hypsodonty.

Paleoichnological studies revealed the abundance of mammalian footprints in several parts of the basins studied, which are normally not fossiliferous in terms of body fossils. The systematic study and biochronology of the newly discovered mammalian fossils in northwestern Iran indicates their close affinities with middle Turolian faunas. Large cranial remains of hipparionine horses, previously unknown in Iran and Western Asia, are among the material studied. The initiation of a new field project in the famous Maragheh locality also brings new opportunities to address questions regarding the chronology and paleoenvironment of this classical site.

Provinciality analysis modified our previous level of understandings, indicating the interaction of four provinces in Western Asia. The development of these provinces was apparently due to the presence of high mountain ranges in the area, which affected the dispersal of mammals and also climatic patterns.

Higher temperatures and possibly higher CO₂ levels in the Middle Miocene Climatic Optimum apparently favored the development of the closed forested environments that supported the dominance of the closed-adapted taxa. The increased seasonality and the progressive cooling and drying of the midlatitudes toward the Late Miocene maintained the dominance of open-adapted faunas. It appears that the late Middle Miocene was the time of transition from a more forested to a less forested world.

The distribution history of the closed- and open-adapted chronofaunas shows the presence of cosmopolitan and endemic faunas in Western Asia. The closed-adapted faunas, such as the Arabian chronofauna of the late Early–early Middle Miocene, demonstrated a rapid buildup and gradual decline. The open-adapted chronofaunas, such as the Late Miocene Maragheh fauna, climaxed gradually by filling the opening environments and

moving in response to changes in humidity patterns. They abruptly declined due to demise of their favored environments. The Siwalikan chronofauna of the early Late Miocene remained endemic and restricted through all its history.

This study highlights the importance of field investigations and indicates that new surveys in the vast areas of Western Asia, which are poorly sampled in terms of fossil mammal localities, can still be promising. Clustering of the localities supports the consistency of formerly known patterns and augments them. Although the quantitative approach to relative abundance history of the closed- and open-adapted mammals harks back to more than half a century ago, it is a novel technique providing robust results. Tracking the history of the chronofaunas in space and time by means of new computational and illustration methods is also a new practice that can be expanded to new areas and time spans.

Acknowledgements

I thank the almighty God for giving me the opportunity and assistance to complete my PhD studies. My sincere gratitude goes to my teachers in Iran who educated and inspired me to follow their path in science. I thank Prof. Djafarian (University of Esfahan) and Prof. Fakhr (University of Tehran) for mentoring and Prof. Hamedani (University of Esfahan) for involving me in his field campaign with Finnish scientists in 2001, which eventually resulted in my PhD studies at the University of Helsinki.

I am grateful and deeply indebted to Prof. Mikael Fortelius for facilitating my endeavor in science outside Iran and also for his guidance and supervision of my doctoral studies. I also wish to thank my reviewers, Prof. Sevet Sen and Prof. Jordi Agustí, for their encouraging comments and nice reports, and Dr. James Thompson for language revision of my synopsis.

I appreciate the generous financial support from various Finnish organizations, including the Academy of Finland, Center for International Mobility (CIMO), University of Helsinki Funds, and Finnish graduate school in Geology, as well as grants from the RHOI project and the Japan-Scandinavia Sasakawa Foundation which enabled me to live and study for the past 6 years in Finland and travel about 200.000 km around the northern hemisphere in order to take part in the field surveys, excavations, scientific meetings, excursions, and courses in addition to visiting fossil collections.

I acknowledge the collaboration of my co-authors. I am especially grateful to Dr. Mahito Watabe (Hayashibara Center for Paleobiological Research, Okayama) and Dr. Ray Bernor (Howard University, Washington DC) for their hospitality and assistance during my trips to Japan and USA, and sharing years of their experience in studying fossil horses.

I appreciate the curators in the Natural History Museum, London (Dr. P. Brewer, Dr. A. Current, and Dr. J. Hooker), Muséum National d'Histoire Naturelle, Paris (Dr. P. Tassy, Dr. C. Sagne, and Dr. C. Argot), Naturhistorisches Museum, Vienna (Dr. U. Göhlich), Bayerische Staatssammlung für Paläontologie/Geologie, Munich (Dr. G. Rössner), and Senckenberg Museum, Frankfurt (Dr. R. Brocke and J. Oelkers-Schaefer) for facilitating the study of Miocene fossil mammals hosted in their institutes.

I also thank Dr. M. Armour-Chelu and D. Wolf (Howard University, Washington DC), USA, Dr. Z. Zhang (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing), China, Dr. M. Nakatsukasa and Dr. H. Matsuoka (Kyoto University) and Dr. H. Nakaya (Kagoshima University), Japan, Dr. A. Van der Meulen and Dr. W. Wessels (Utrecht University), the Netherlands, Dr. N. Abbassi (Zanjan University) and J. Mohammadizadeh (Hamedan University), Iran, for assisting me at their institutes.

Many thanks to my fellow colleagues and students at the Department of Geosciences and Geography, University of Helsinki for their help: Prof. Juha Karhu, Prof. Velli-Pekka Salonen, Dr. Anu Kaakinen, Dr. Jussi Eronen, Dr. Liu Liping, Dr. Diana Pushkina, Dr. Seija Kultti, Dr. Laura Arppe, Dr. Mia Kotilainen, Kirsi-Marja Äyräs, Helena Korkka, Leena Selänne, Susanna Sova, Mikko Haaramo, Aleksis Karme, Pierre Mauriès, Kari Lintulaakso, and Hui Tang. I would also like to thank my Iranian friends in Helsinki who were helpful on many occasions and with whom I shared my good times.

Last, but not least, I would like to express my thankfulness to my family, my wife Zohreh, and her family for all of their support and love. I dedicate this thesis to them and to the people of Iran.

Contents

Abstract	5
Acknowledgements	7
List of original publications	9
Authors' contribution to the publications	10
Abbreviations/ List of Figures	11
1. Introduction	12
1.1 Aims of the study	14
2. Material and methods	15
3. New evidence of Miocene mammals in Iran (I, III, V, VI)	16
3.1 Trace fossils (I)	18
3.2 Body fossils (III, V, VI)	20
4. Faunal provinciality in the Miocene of Western Asia	25
4.1 Results	26
4.2 Discussion	28
4.2.1 Balkan-Anatolia-Iran province	28
4.2.2 Afro-Arabia province	29
4.2.3 China-central Asia province	29
4.2.4 Siwalik-Southeast Asia province	30
4.3 Conclusions	30
5. The relative abundance history of the closed- and open-adapted taxa	31
5.1 Results	35
5.1.1 The Miocene relative abundance history	35
5.1.1.1 Western and central Europe	35
5.1.1.2 Balkan-Anatolia-Iran province	35
5.1.1.3 China-central Asia province.....	36
5.1.1.4 Africa-Arabia province	36
5.1.1.5 Siwalik-Southeast Asia province	36
5.2 Discussion	36
5.3 Conclusions	40
6. Distribution history of the Western Asian Miocene chronofaunas	40
6.1 Results	43
6.1.1 Arabian chronofauna	43
6.1.2 Siwalikan chronofauna	45
6.1.3 Maraghean chronofauna	47
6.2 Discussion	49
6.2.1 Arabian chronofauna	49
6.2.2 Siwalikan chronofauna	50
6.2.3 Maraghean chronofauna	51
6.3 Conclusions	52
7. Concluding remarks	53
References	55
Appendices	68
Publications I-VI	88

List of original publications

This thesis is based on the following articles referred to in the text by their bold Roman numerals.

- I. **Mirzaie Ataabadi, M.** and Abbassi, N. 2007. Affinities and implications of new Miocene mammal footprints from Iran. *Vertebrata Palasiatica* 45:128-136.
- II. Eronen, J. T., **Mirzaie Ataabadi, M.**, Micheels, A, Karme, A., Bernor, R. L., and Fortelius, M. 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. *Proceedings of the National Academy of Sciences* 106:11867-11871.
- III. **Mirzaie Ataabadi, M.**, Zaree, G., and Orak, Z. Large mammals from the new Late Miocene fossil localities in Varzeghan area, northwest Iran. *Vertebrata Palasiatica*, (accepted).
- IV. **Mirzaie Ataabadi, M.**, Liu, L., Eronen, J. T., Bernor, R. L., and Fortelius, M. Continental Scale Patterns in Neogene Mammal Community Evolution and Biogeography: A Europe-Asia Perspective. In: *Asian Neogene Mammal Biostratigraphy and Chronology* (eds. Xiaoming, W., Fortelius, M. and Flynn, L.), Columbia University Press, (accepted).
- V. **Mirzaie Ataabadi, M.**, Bernor, R. L., Kostopolus, D., Wolf, D., Orak, Z., Zaree, G., Nakaya, H., Watabe, M. and Fortelius, M. Recent Advances in the Paleobiological Research of the Late Miocene Maragheh Fauna, Northwest Iran. In: *Asian Neogene Mammal Biostratigraphy and Chronology* (eds. Xiaoming, W., Fortelius, M. and Flynn, L.), Columbia University Press, (submitted).
- VI. **Mirzaie Ataabadi, M.**, Mohammadalizadeh, J., Zhang, Z., Watabe, M., Kaakinen, A. and Fortelius, M. Late Miocene Large mammals from Ivand (northwestern Iran). *Geodiversitas*, (submitted).

In addition, unpublished analyses and results have been presented.

The authors' contribution to the publications

- I.** **M. Mirzaie Ataabadi** interpreted the data and wrote the article. The field work was done by N. A.
- II.** **M. Mirzaie Ataabadi**, J. T. E., R. L. B., and M. F. designed the research; J. T. E., **M. M. A.**, A. M., and M. F. performed the research; J. T. E., **M. M. A.**, and A. K. contributed new reagents/analytic tools; J. T. E., **M. M. A.**, A. M., A. K., and M. F. analyzed data; and J. T. E., **M. M. A.**, A. M., R. L. B., and M. F. wrote the paper.
- III.** **M. Mirzaie Ataabadi** studied the fossil material and wrote the paper. G. Z. and Z. O. did the field and office work.
- IV.** **M. Mirzaie Ataabadi**, L. L., and M. F. planned the research; **M. M. A.**, J. T. E., L. L. and M. F analyzed the data and performed the research. All the authors contributed to the writing.
- V.** **M. Mirzaie Ataabadi**, R. L. B., and M. F. designed the research; **M. M. A.**, Z. O., G. Z., H. N., M. W. and M. F. did the field work; **M. M. A.**, R. L. B., D. K., and D. W. studied fossil collections and **M. M. A.**, R. L. B., D. K., and M. F. wrote the paper.
- VI.** **M. Mirzaie Ataabadi** and J. M. planned the research and the field work, **M. M. A.** and M. W. studied the hipparionine horses, Z. Z. studied the bovids, and A. K. interpreted sedimentology. **M. M. A.**, Z. Z., and A. K. wrote the paper. M. F. commented the text.

Abbreviations

AFRARB: Africa-Arabia

BAANIR: Balkan-Anatolia-Iran

CHNCAS: China-central Asia

DOE: Department of Environment (Environment Protection Organization), Iran

EMED: Eastern Mediterranean

GFRI: Genus level Faunal Resemblance Index

HMNH: Hamedan Museum of Natural History, Hamedan

HYP: Hypsodonty

INSPE: International Sahand Paleobiology Expedition

LRE: Lake Rezaieh Expedition

MMTT: Muze Meli Tarikh Tabiei (National Museum of Natural History), Tehran

MNEQ: European Mammal Neogene Faunal Zone Equivalents

MNHN: Muséum National d'Histoire Naturelle, Paris

NBS: North Black Sea

NOW: Neogene of the Old World database

O/C: Open-adapted/Closed-adapted

SIWSEAS: Siwalik-Southeast Asia

WAS: Western Asia

WEUCEU: Western Europe-central Europe

List of Figures, Tables, and Appendices

Fig. 1. Geographic position of fossil localities and faunal provinces

Fig. 2. Clusters showing the relationships of faunal provinces

Fig. 3. Mean hypsodonty and diversity patterns of open- and closed-adapted taxa

Fig. 4. Relative abundance of the closed- and open-adapted taxa and sampling data

Fig. 5. Relative abundance of open- and closed-adapted taxa, evolution of atmospheric CO₂, and global climate in the Miocene

Fig. 6. Mean ordinated hypsodonty values mapped for each MNEQ unit

Fig. 7. Maps of faunal similarity to the Arabian MNEQ 4-5

Fig. 8. Maps of faunal similarity to the Siwalik MNEQ 9-10

Fig. 9. Maps of faunal similarity to the Maragheh MNEQ 11-12

Fig. 10. Trend lines of the average similarity to the studied chronofaunas

TABLE 1. History of studies on the Maragheh fauna

TABLE 2. List of Maragheh taxa updated in this research

TABLE 3. Faunal provinces and regional names, and their geographic extensions by different authors

APPENDIX 1. Additional locality clusters from Dice, Jaccard, and Simpson indices

APPENDIX 2. List of localities with GFRI, O/C, and HYP values

1. Introduction

The Miocene Epoch, 23–5.3 million years (Ma) ago, in the Neogene Period is a time when the world assumed its modern configuration. Major orogenic/tectonic events such as intensification of the uplift of the Alpine-Himalayan Belt in Eurasia and development of the Rift Valley system in East Africa occurred at this time and new mountain ranges were formed. The Tethyan Ocean was also gradually dismembered and diminished, and the landbridges between Africa and Eurasia were formed, facilitating the interchange of faunas between these continents. Thus, the continental environments changed significantly.

During the Miocene, life also attained many of its modern aspects. Miocene mammals were very similar to modern mammals and most of today's mammalian families were already present at that time. Modern climatic and circulation patterns also have their roots in the Miocene. Although the Miocene belongs to the late phase of the Cenozoic climate cooling, it was warmer and more humid than the Pliocene and today (Zachos *et al.* 2001).

Due to the Late Oligocene and Early Miocene global expansion of the tropical belts, the Early Miocene experienced warm tropical and subtropical climates with evergreen plants. During this time (ca. 20–19 Ma ago), the Tethyan Seaway continued to shrink and the African and Eurasian tectonic plates (Arabian, Iranian and Anatolian plates) collided, generating the rise of the Iranian and the Turkish Plateau. The formation of a consequent landbridge (*Gomphotherium* landbridge) facilitated the continental mammal exchange between Eurasia and Africa across Western Asia during MNEQ4 and MNEQ5 (Koufos *et al.* 2005, Rögl 1999, 1998, Bernor 1983). During the Middle Miocene, the Tethyan Seaway reopened, due to the Langhian Transgression. This was a short

event and the intercontinental landbridges soon appeared again (Popov *et al.* 2006, 2004, Rögl 1999, 1998).

One of the prominent episodes of the Miocene was the warm period known as the “Climatic Optimum” between 17–15 Ma ago (Middle Miocene). During this time subtropical, warm-temperate evergreen forests with low seasonality prevailed in most of the areas (Mosbrugger *et al.* 2005, Kovar-Eder 2003, Agustí and Antón 2002, Bernor 1983). This climax in Neogene warming was followed by a major cooling event that occurred between 14.8–14.1 Ma ago, as a result of the Antarctic Ice Sheet expansion (Böhme 2003, Zachos *et al.* 2001, Flower and Kennett 1994). The continued expansion of this ice sheet and the interruption of the circum-Equatorial Current system, due to closure of the Tethyan Seaway, caused persistence in the Neogene cooling and the ultimate passage of the earth into the icehouse state later in the Pliocene-Pleistocene (Agustí and Antón 2002, Zachos *et al.* 2001).

During the Late Miocene a climatic deterioration occurred, characterized by greater seasonality and a significant expansion of the more open-country floras that replaced the closed, forested environments (Mosbrugger *et al.* 2005, Kovar-Eder 2003, Agustí and Antón 2002, Bernor 1983). The continued uplift of the Tibetan Plateau and the regression of the Paratethys were important for the climatic changes at this time. These events caused large-scale changes in the continental/marine distribution and global climatic circulation patterns, which resulted in monsoon-dominated environments in East Asia and indirectly (through long-range connections or teleconnections) influenced the humidity and aridity pattern in other regions (Zhang *et al.* 2006, Liu and Yin 2002, Fluteau *et al.* 1999, Ramstein *et al.* 1997). At the end of the

Miocene, the continued expansion of the Antarctic Ice Sheet and the consequent drop in global sea levels, together with tectonic events (Krijgsman *et al.* 1999), led to desiccation and isolation of the Mediterranean Basin (Messinian Salinity Crisis). Uplift of the Zagros mountain chain and the activity around the Turkish tectonic plate at this time (Alavi 2004, 1994) established a permanent land connection between Eurasia and Africa.

The Miocene Epoch also records substantial changes in mammalian communities. Osborn (1910) divided the Miocene into old and new parts, and considered the new part to be the time of change in mammalian communities from forest to savanna forms. Crusafont and Golpe (1971) erected the Vallesian stage to indicate the local transition between the Astaracian forest fauna and Turolian savanna forms. Van Couvering and Van Couvering (1976) and Van Couvering (1980) demonstrated a close correlation of shift in environments and mammalian community succession. They suggested that the Miocene mammal faunas showed a succession from less seasonal forests and wooded communities to more seasonal savanna-mosaic communities.

Nevertheless, the replacement of the early Neogene forest communities with the Late Miocene savannalike faunas was not a synchronous event. The evolution of this community type commenced during the Middle Miocene in central Asia, Western Asia, and East Africa and spread in a time-transgressive manner to other areas and dominated the Late Miocene. This was hypothesized, based on the Middle Miocene evolutionary radiation of felid, hyaenid, giraffid, and bovid taxa (Bernor 1983, 1978). However, they displaced the subtropical forest communities of Western Europe and Southwest Asia (Indian subcontinent) significantly later (Agustí *et al.* 1999).

Later studies concluded that development of the Late Miocene open-country chronofauna

was not related to a savanna environment but closely tied to the development of sclerophyllous evergreen woodland vegetation that later shifted to more seasonal patterns. In such a biome hyaenids, felids, equids, **rhinocerotids**, giraffids, and bovids reached their greatest diversity (Solounias *et al.* 2010, 1999, Bernor 1984, 1983, Bernor *et al.* 1979).

Although the Miocene development of the mammalian communities in the Old World is well known (e.g. Bernor 1984, 1983, Van Couvering 1980), the main patterns of the faunal provinces have been established (e.g. Fortelius *et al.* 1996, Bernor 1983, Bernor *et al.* 1979) and the main temporal and spatial developments of chronofaunas and the eco-morphological features of their mammalian taxa are recognized (Eronen 2006, Fortelius *et al.* 2006, 2003, 2002, 1996, Bernor 1983), less effort has been taken toward the quantification of mammalian faunal developments.

Since the early 1980s, discovery of new fossil assemblages, especially in less-known areas, and detailed studies of some important faunas have enhanced our understanding of the Miocene faunas of the Old World. Advances in bio- and geo-chronological methods have provided better age estimates for the localities and hence more precise dating of major events. Substantial progress has been made in the field of paleoclimatology and paleogeography that helps to evaluate the influence of past climatic patterns and geographic configurations on the distribution of mammalian communities. Finally, establishment and development of paleontological databases such as the Neogene of the Old World (NOW) database (Fortelius 2010, see www.helsinki.fi/science/NOW) have made large amounts of data available, and new study methods and techniques have been developed for their analysis. Therefore, we have better tools, information, and opportunity to more precisely understand, quantify, and illustrate patterns known to us for a long time.

1.1 Aims of the study

Being at the heart of Western Asia and at the crossroads of the Old World continents, Iran and Western Asia have been poorly sampled in terms of mammalian faunas. Any new information from this area is crucial to increasing the temporal and spatial resolution of our data. Therefore, this dissertation has two aims:

The first aim was the acquisition of new evidence of fossil mammals in Western Asia and Iran in particular, the systematic study of such new trace and body fossil material, and the biochronological correlation of the new and old localities (**I, III, V, VI**).

The second aim was to investigate the Miocene development of mammalian faunas and communities in the Old World, with special focus on Western Asia as a hub for the open-country chronofaunas and interprovincial exchanges.

Based on previous findings and new analysis, the provinciality of the Miocene faunas was examined and modified. In addition, the provincial relationships and delineations, and their paleogeographic, paleoecologic, and paleoclimatic contexts are discussed.

The relative abundance history of the forest and nonforest or closed-adapted and open-adapted taxa was also examined, using quantitative methods, and the influence of climate on their abundance was assessed.

Lastly, using new illustration methods and recently developed paleogeographical reconstructions to assist our interpretations, the distribution in space and time of the main Western Asian Miocene chronofaunas was surveyed and its relationship with humidity and climatic patterns discussed (**II, IV**, and the synopsis).

2. Material and methods

Body and trace fossils

The body fossil material studied here (**III**, **VI**) was deposited in the Hamedan Museum of Natural History (HMNH), Hamedan and the Department of the Environment (DOE), Maragheh branch, Iran. All the measurements on the hipparionine material were carried out, using digital calipers and following the instructions of Eisenmann *et al.* (1988). Logarithmic ratio diagrams and other plots were prepared in Excel 2007 (Microsoft Corp. Redmond, WA, USA). The trace fossil material (**I**) was investigated *in situ* and the outlines of footprints were duplicated on transparent sheets for further study and analysis in the laboratory. Some of the trace fossil material was deposited in the Department of Geology, University of Zanjan, Iran.

Data and chronology

The NOW database (Fortelius 2010, see www.helsinki.fi/science/NOW) is the source of the Miocene fossil mammal data for this work (**II**, **IV**, **V**, and the synopsis). Data for the synopsis were downloaded from the NOW on November 25, 2009. All small mammals (orders Lagomorpha, Chiroptera, Rodentia, and Insectivora) and singletons, i.e. sites containing only one taxon occurrence, were excluded from the dataset. Thus, only large mammal data between 23 Ma and 4 Ma in age (MNEQ 2 – MNEQ 14) were used. As provisional common coinage for Eurasian mammal biostratigraphy, the *ad hoc* MN-equivalents (MNEQ) were applied here. The MNEQ is defined and computed from minimum and maximum age estimates for the locality as given; according to where the computed range midpoint fell in the MN correlation scheme of the NOW database (Steininger *et al.* 1996).

Relative abundance analysis

To quantify the relative abundance history of the closed- and open-adapted mammalian taxa, the closed-adapted group was defined as members of Anthracotheridae, Cervidae, Hippopotamidae, Moschidae, Suoidea, Tapiridae, Tragulidae, and Proboscidea. The open-adapted group consists of Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae**. The percentages of these groups in the faunas (557 localities with at least seven taxa identified at the family level) during each MNEQ unit were calculated and plotted, and the trend lines of their average points were drawn, using Excel 2007. Only localities with age spans of less than or equal to two MN units (i.e. ≤ 4.80 Ma) were used. In this context, the localities with long age spans (i.e. more than 3 Ma) comprised about 10% of all the localities in the dataset (see Appendix 2).

Clustering and similarity analysis

The following criteria were applied for undertaking these analyses: localities were excluded from the analysis when they (1) had fewer than seven taxa identified at the genus level, (2) lacked geographic positional data (coordinates), and (3) were not assigned to a single MNEQ unit. Our studies (**II**, **IV**) suggested that the number of taxa used did not affect the spatial patterns, since the east-west and north-south dispersions of localities were essentially the same and the patterns were robust. However, when we used fewer than seven taxa the analytical noise increased, and when we limited the analysis to localities with 10 or more taxa, the number of available localities was too low.

I prepared the binary (0/1) dataset (409 localities and 674 species) with Excel 2007 and used PAST (PAleontological STatistics; see <http://folk.uio.no/ohammer/past/>) for the

paired-group clustering and similarity analysis (Hammer and Harper 2006, Hammer *et al.* 2001). Dice (1945), Jaccard (1912), Simpson (1960), and Raup-Crick (1979) similarity measures were used to obtain the clusters and genus-level faunal resemblance index (GFRI) values. The results were compared to determine the disparities in overall trends and between indices. Only the results for Dice GFRI are shown on the maps and the clusters by Raup-Crick are presented. Other GFRI values and clusters, which gave similar results, are presented in Appendices 1 and 2.

Hypsodonty analysis

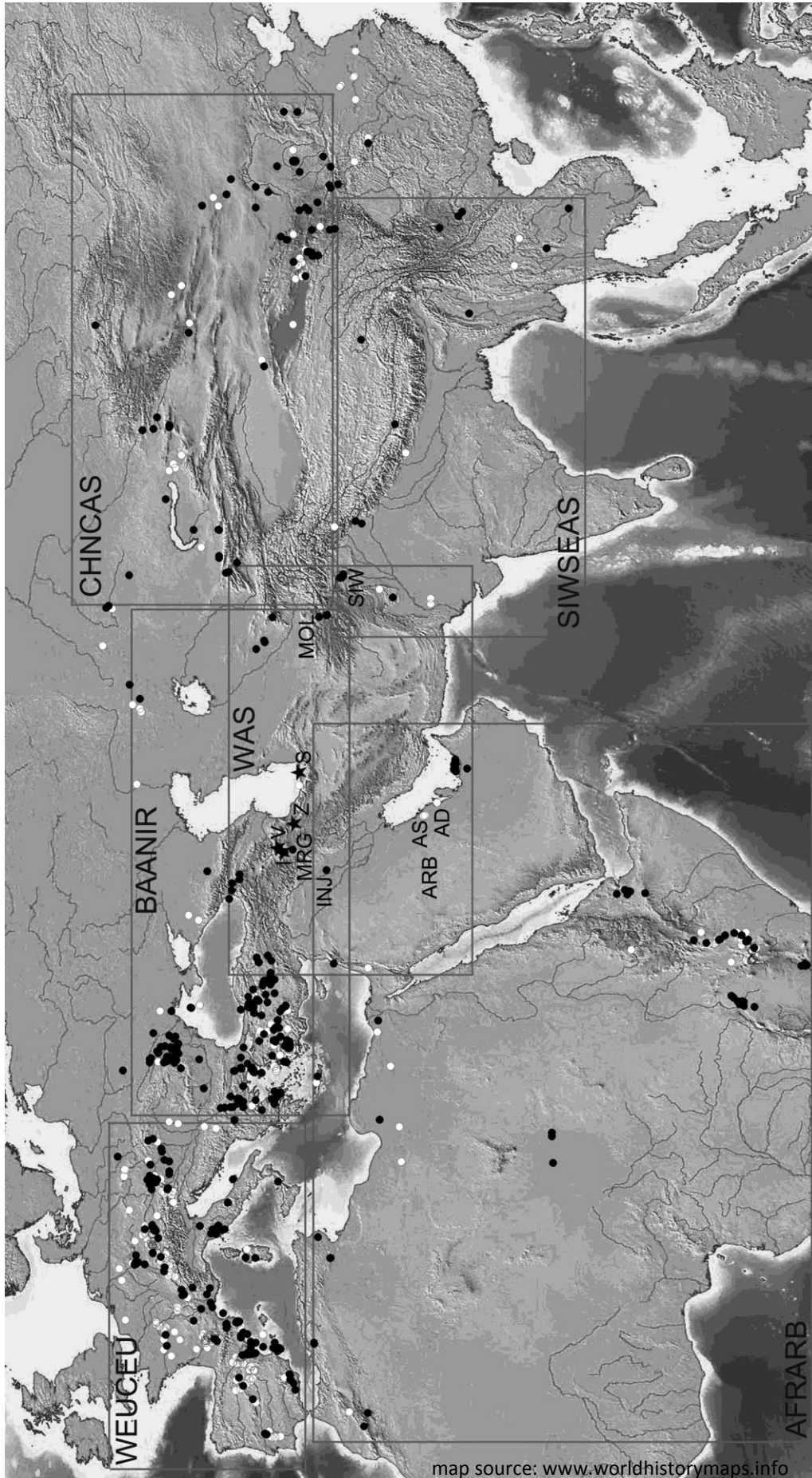
Herbivore molar tooth crown height or hypsodonty (HYP) is used as a rough proxy for humidity (Eronen *et al.* 2010 a,b, Liu *et al.* 2009, Eronen 2006, Eronen and Rook 2004, Fortelius *et al.* 2006, 2003, 2002). Three classes of hypsodonty are recorded in the NOW database: brachydont, mesodont, and hypsodont. The criteria for assigning species to these classes are based on the ratio of height to length of the second molar (upper or lower). Brachydont teeth have a ratio of less than 0.8, mesodont a ratio in the range of 0.8–1.2, and hypsodont over 1.2. For the present study, the hypsodonty classes were assigned the values 1, 2, and 3. This is a relatively conservative method, since the difference in crown height between a hypsodont and a brachydont species is usually more than 3:1. The mean hypsodonty value is calculated for each locality by averaging these ordinated scores. For this purpose, carnivores (orders Carnivora and Creodonta) and localities with only one herbivore species were also deleted from the dataset. Localities with an age span of more than one MNEQ unit were also used. Therefore, compared with other analyses, the number of localities (1092) is doubled in the hypsodonty analysis.

Mapping

All maps depicting GFRI and HYP values were made in MapInfo Professional 8.5 (Pitney Bowes Business Insight, Troy, NY, USA) using color grid interpolation and the inverse distance-weighted (IDW) algorithm with the following settings: cell size 20 km, search radius 500 km, grid border 500 km, 10 inflections, values rounded to 0.01 (0.1 for HYP). The inflection values were manually set to range from 1 to 3 for HYP and from 0 to 1 for the GFRI maps. I used opacity of 20% for the color interpolation to show the base map below the interpolated values. The Miocene paleogeographic maps of the circum-Mediterranean region (after Popov *et al.* 2004) were overlaid on present-day maps to show the paleogeographic setting.

3. New evidence for Miocene mammals in Iran (I, III, VI)

There is a huge gap of about 3000 km between the Late Miocene body fossil localities of Maragheh in northwestern Iran and the Molayan and Taghar localities (Sen *et al.* 1997) of Afghanistan (Fig. 1). It is evident that any discovery of new fossil localities in this area is crucial to our understanding of mammalian faunas in this gap area. Although vast outcrops of terrestrial Neogene sediment are present in Western Asia, our knowledge of Miocene mammals is mostly limited to a few localities, due to lack of a sufficient number of investigations. Recent discovery of several Miocene trace and body fossil localities in northern and northwestern Iran indicates the favorable potential for discovery of new sites in these areas. The record of mammal trace fossil sites in Asia generally and in Western Asia in particular is scarce. The only records of Neogene mammal tracks outside of Iran are the newly discovered proboscidean tracks in the Late Miocene Baynunah Formation of Abu Dhabi, United Arab Emirates (Higgs *et al.* 2005).



map source: www.worldhistorymaps.info

FIGURE 1. Geographic positions and spatial relationships of the Miocene Old World fossil localities and faunal provinces investigated in this study. **WEUCEU:** Western Europe-central Europe province, **BAANIR:** Balkan-Anatolia-Iran province, **CHNCAS:** northern China-central Asia province, **SIWSEAS:** Siwalik-Southeast Asia province, **AFRARB:** Africa-Arabia province, **WAS:** Western Asia, **Z:** Zanjan, **S:** Sati, **MRG:** Maragheh, **I:** Ivand, **V:** Varzeghan, **ARB:** Arabia, **AS:** As Sarrar, **AD:** Ad Dabtyah, **INJ:** Injana, **MOL:** Molayan, **SIW:** Siwaliks. ○ Early–Middle Miocene localities ● Late Miocene localities ★ Localities studied in this work

3.1 Trace fossils (I)

North Central Basin

Mammalian footprints from this basin (Z in Fig. 1) are associated with deposits of the Upper Red Formation. The Upper Red Formation consists of terrestrial and lagoonal deposits that were formed under molasselike conditions, in which fault-controlled subsidence of the basin and gradual uplift of adjacent mountain belts caused an enormous amount of sedimentation. This formation consists mainly of red to brownish sandstone and mudstone, but conglomerates, evaporites, and local marls have also been observed (Amini 1997). A post-Burdigalian (Middle – Late Miocene) age of the Upper Red Formation has been specified, based on its position above the marine Qom Formation and below the thick Pliocene conglomerates (Stöcklin and Setudehnia 1970). However, the track-bearing layers most probably belong to the Late Miocene, due to their stratigraphic position in the upper levels of the Upper Red Formation (Abbassi and Shakeri 2005).

Ichnofauna

Mammal tracks have been identified in the red sandstones and marls of Shokorchi village in the Zanzan district, northwest of central Iran (I: Fig.1). These tracks (I: Fig. 3) belong to gazelle-sized bovids (*Gazella* and a variety of spiral-horned antelopes) that were among the most common Late Miocene bovids (Agustí and Antón 2002). Considering the Maragheh fauna as the closest Late Miocene body fossil locality to this tracksite, the likely trackmakers resembled bovids such as *Gazella*, *Prostrepsiceros*, *Oioceros*, or similarly sized taxa that were quite common in this fauna (V: Table 3).

Other mammalian tracks at this locality belong to a plantigrade to semiplantigrade carnivorous mammal (I: Fig. 3). The most common representatives of such carnivores in the Middle – Late Miocene were amphicyonids

and ursids. Miocene ursids were larger than these trackmakers and amphicyonids were less common in the Late Miocene. Moreover, the latter are generally considered as forest dwellers (Viranta 1996) not suited to the paleoenvironment of the Upper Red Formation (see below under Paleoenvironment). Therefore, a large mustelid may be a likely trackmaker.

Mammal footprints have also been identified in the Upper Red Formation of the Mushampa district of Zanzan province (Abbassi and Shakeri 2005) and Evanekey (Evan-e-key) district of Semnan province (Abbassi and Amini 2008) (I: Fig. 1). Footprints from the latter locality (Evanekey) belong to two types of carnivores related to felids. In the Mushampa area, the mammalian tracks belong to a large felid similar in size to extant large felids (Mirzaie Ataabadi 2007) and Late Miocene (Turolian) machairodontine cats (I: Fig. 2). Smaller tracks from this locality belong to small carnivores, such as mustelids, that were fairly common in the Late Miocene throughout the Old World (Fortelius 2009, Agustí and Antón 2002).

Paleoenvironment

Generally, the Upper Red Formation has been deposited in two major environments: a clastic facies in the margins of basins and a lagoonal facies with fine clastic and evaporites in the central playas (Amini 1997). The cyclic occurrence of evaporites, such as gypsum layers in some areas (Rahimzadeh 1994), is evidence for cyclic oversupply of water to the playas (Yechieli and Wood 2002). These conditions disappear toward the top, where normally less evaporite is observed. This tendency may indicate aridification in the upper parts, which resulted in decline of the water supply to the basin and stoppage of gypsum accumulation (Dupont-Nivet *et al.* 2007). The abundance of calcrete layers and nodules also led Amini (1997) to postulate arid and semiarid conditions during deposition of the Upper Red Formation. The abundance of

artiodactyl tracks in the Upper Red Formation and the absence of groups other than carnivores indicate that like their modern counterparts, these artiodactyls have been open-adapted and less dependent on permanent bodies of water to survive the arid conditions (Stuart and Stuart 2006).

The increasing seasonal aridity and midlatitude drying patterns during the Middle Miocene – Pliocene in Western Eurasia was previously proposed (Kutzbach *et al.* 1993) and has recently been demonstrated by mammal data (Eronen *et al.* 2010 b, Liu *et al.* 2009, Fortelius *et al.* 2006, 2003, 2002). As mentioned above, sedimentological and ichnological evidence from the Upper Red Formation also supports similar conditions for the north Central Iran Basin.

South Caspian Basin

The southern parts of the Caspian Sea (north of Iran) were under the influence of the Eastern Paratethys (the northern extension of the Tethys stretched to central Asia and the Aral Sea) and its fluctuations. The Neogene sequence in these areas was transgressive and covered pre-Oligocene deposits (Aghanabati 2004). This transgressive sequence was later succeeded by fine sandstones, siltstones, claystones and intercalations of thin carbonates. These deposits contain abundant molluscs that have been used for assignment of these beds to the Karaganian and Konikian ages or mid-Middle Miocene (Rahimzadeh 1994). This sequence was covered by Sarmatian deposits, which have more carbonates than the previous units but still have clastic components. By the Late Miocene the Caspian-Euxinian Basin had shrunk, many parts formerly covered by this basin had emerged, and clastic sedimentation had been initiated (Rahimzadeh 1994). These clastic deposits unconformably covered the mainly lacustrine lower beds and are known as the “Continental Series”, which is a thick sequence of conglomerates interbedded with sandstones

and mudstones. A Late Miocene – Pliocene age was considered for this in general poorly fossiliferous series, based on some freshwater molluscs (Stöcklin and Setudehnia 1970) and a few mammalian bones (Papp and Thenius 1959).

Ichnofauna

Several tracks of mostly large mammals (I: Fig. 4) have been discovered in these continental deposits in the Sari district, north of Iran (S in Fig. 1). The robust large tracks belong to a proboscidean with a 2.5-m height at the shoulders (Mirzaie Ataabadi 2007) and the oval-shaped perissodactyl tracks with three toes are similar in form and size to the tracks of rhinos (Stuart and Stuart 2006). The small artiodactyl tracks belong to gazelle-sized bovids.

The mammal body fossils are known from a nearby locality (Takam or Tokoum), but they only represent a single giraffid mandible (Papp and Thenius 1959). Due to geographical proximity, trackmakers of the Sari district are likely to have affinities with the mammalian fauna of Maragheh (V). Two proboscideans are known from Maragheh: *Deinotherium* and *Choerolophodon*. Based on the size of the proboscidean tracks, *Choerolophodon* is more likely to be related to these tracks, since the larger size of *Deinotherium* implies larger footprints. There are four genera of rhinocerotids at Maragheh: *Diceros*, *Chilotherium*, *Iranotherium* and *Rhinocerotidae* gen. and sp. nov. (V). *Chilotherium* is the smallest of these taxa, therefore rhino tracks of the Sari district were likely made by individuals showing affinities with the larger rhinocerotids of Maragheh.

Biochronology and paleoenvironment

With no diagnostic fossils in the Miocene Continental Series of northern Iran, these tracks are important for constraining the age of this sequence. With the dispersal of proboscideans from Africa to Eurasia through the “*Gomphotherium* landbridge” at about 18

Ma ago (Koufos *et al.* 2005, Rögl 1999, 1998) or 23 Ma ago, based on “proboscidean datum” in Western Asia (Bugti and Zinda Pir faunas of Pakistan, Lindsay *et al.* 2005), the maximum age of the track-bearing strata in the South Caspian Basin of northern Iran could be as early as the Early Miocene. However, due to fluctuations of the Eastern Paratethys and higher water levels before the Sarmatian, which is evident in the lower lacustrine beds of the Paratethyan deposits in northern Iran, these mammalian tracks most likely belong to the post-Sarmatian (Late Miocene) age.

The occurrence of proboscidean and rhinocerotid tracks and lesser abundance of bovid and other tracks may indicate a more closed environment near a body of water. Lack of sedimentological evidence for arid conditions (unlike the Upper Red Formation) also supports this interpretation. Thus, during the Late Miocene more humid and closed environments prevailed in the north of the Alborz Range (South Caspian Basin), while more arid and open areas were found in the south of these mountains (Upper Red Formation). This likely points to a possible Late Miocene influence of the Alborz Mountains on the development of environmental contrast on its opposite sides, similar to that of present conditions.

Zagros Basin

In the Zagros Basin, southwestern Iran, Early Miocene – Pliocene deposits are regressive cycles incorporating the evaporites of the Gachsaran Formation, marly deposits of the Mishan Formation, and terrigenous deposits of the Aghajari Formation. The Aghajari Formation, formed largely from sandstones, siltstones, and marls, consists of fining-upward cycles that were deposited in braided and meandering river systems and floodplains. The Lahbari Member, the upper fine-grained member of this formation, with a coarsening-upward trend, is equivalent to the Lower Bakhtiari Formation (Motiei 1993). The Lower

Bakhtiari beds in northern Iraq (INJ in Fig. 1) have produced significant numbers of Late Miocene fossil mammals (Thomas *et al.* 1980). In Iran, only fragmentary fossil mammals were recovered from the Aghajari Formation and Lahbari Member (Stöcklin and Setudehnia 1970). However, available evidence including the field reports in the archives of the DOE and unpublished personal data obtained from National Iranian Oil Company geologists imply the occurrence of mammal and bird footprints in the Miocene deposits (Aghajari Formation) of the Zagros Basin.

Conclusions

The above-mentioned basins (central Iran, South Caspian, and Zagros) are structurally depressed, accumulating sediments under terrestrial conditions in response to the orogenies. Such basins (especially in the marginal parts) are high-energy environments and typically poor in terms of vertebrate body fossils (Remeika 2001). Nonetheless, they show favorable potential for preserving vertebrate trace fossils which, to some extent, can fill the gaps in the body fossil record.

3.2 Body fossils (III, V, VI)

New localities (III, VI)

For more than 150 years, the famous Late Miocene vertebrate localities in Maragheh were the focus of attention (Table 1) and the exclusive sources of information for the Neogene mammalian faunas of Iran. However, recent discovery of new localities in the northwestern parts of Iran has demonstrated a wider distribution of mammal-bearing deposits in this area of Western Asia. These new fossiliferous areas are situated north and northeast of Tabriz, the capital city of East Azarbaijan province of Iran, app. 110–150 km away from Maragheh (I and V in Fig. 1).

During the Late Miocene and Pliocene, tectonic activities established new erosional cycles in northwestern Iran that filled the locally closed basins with fluvial and lacustrine

deposits (Aghanabati 2004). While pyroclastic sediments accumulated and preserved abundant mammalian fossils in the Maragheh area, these basins were filled in the Tabriz area by lacustrine deposits with abundant

freshwater fish and rare mammalian remains. The new fossil localities in the Ivand and Varzeghan districts were formed in similar local basin troughs, but under different sedimentary environments.

Table 1. History of the excavations and studies in the Maragheh fossil localities, northwestern Iran (after Bernor 1986 and personal data).

Year	Excavators	Nationality	Fossil Depository	Publications
1840	Khanikoff <i>et al.</i>	Russian	?	Abich 1858 Brandt 1870 Grewingk 1881
1884	Pohlig <i>et al.</i>	Austrian	Naturhistorisches Museum, Vienna?	Pohlig 1886
1885?	Damon?	British?	Natural History Museum, London	Lydekker 1886 Forsyth Major 1893
1885	Rodler and Kittl <i>et al.</i>	Austrian	Naturhistorisches Museum, Vienna	Kittl 1885, 1887 Rodler 1887, 1890, Rodler and Weithofer 1890
1904	de Mecquenem <i>et al.</i>	French	Muséum National d'Histoire Naturelle, Paris	Mecquenem 1905, 1906, 1908, 1911, 1924-1925
1956	Takai <i>et al.</i>	Japanese	?	Takai 1958
1958	Savage <i>et al.</i>	British	Natural History Museum, London	
1967	Tobien <i>et al.</i>	German	Bayerische Staatssammlung für Paläontologie/Geologie, Munich	Tobien 1968
1973	Erdbrink <i>et al.</i>	Dutch/German	Department of Earth Sciences, Utrecht University, Utrecht Bayerische Staatssammlung für Paläontologie/Geologie, Munich	Erdbrink <i>et al.</i> 1976 Erdbrink 1976 (a,b), 1977, 1978, 1982, 1988
1973	Kamei <i>et al.</i>	Japanese	Department of Geology, Kyoto University, Kyoto	Kamei <i>et al.</i> 1977 Watabe 1990, Watabe and Nakaya 1991a,b
1974 1975 1976	Campbell <i>et al.</i> (LRE project)	American	Laboratory of Evolutionary Biology, Department of Anatomy, College of Medicine, Howard University, Washington DC	Campbell <i>et al.</i> 1980, Bernor <i>et al.</i> 1980, 1996 Bernor 1978, 1985, 1986 Morris 1997
1987	Partoazar <i>et al.</i>	Iranian	Geological Survey of Iran	
2005	Pourabrishemi <i>et al.</i> (DOE project)	Iranian	Department of the Environment, (DOE) Maragheh	
2008 2009	Fortelius <i>et al.</i> (INSPE project)	International- Iranian	Department of the Environment, (DOE) Maragheh	Mirzaie Ataabadi <i>et al.</i> Submitted (V)

Varzeghan locality (III)

The occurrence of fossils near the surface and lack of sediment exposures in this locality obscure the nature of the fossil-bearing sequence and its sedimentology and depositional environment. However, based on observations from a small trench near the fossil locality in Abkhare village, fine-grained sediments and coarser channel deposits are clearly present at the fossiliferous sites, indicating fluvial environments.

The fossils in this locality are very well preserved and show no signs of weathering or abrasion. The prospect of finding (partially) articulated fossil animals at this locality is probably higher than at other localities in northwestern Iran. The fossil material collected from this locality includes several cranial and postcranial elements of a large deinothere and a large number of isolated maxillary and mandibular cheek teeth, several mandibular fragments, part of a juvenile skull, and a few distal metapodial fragments of hipparionine horses. This material is stored in the DOE branch in Maragheh.

Two species of hipparionine horses are distinguished in the Varzeghan district, based principally on the size and dental morphology of mandibular fragments. *Hipparion* sp.1 is represented by a single mandibular fragment (III: Fig. 2) and belongs to a small-to medium-sized species. Based on the comparisons, *Hipparion* sp. 1 is in the size range of *H. moldavicum*, which is abundant in the Maragheh fauna and may belong to it. Deeper ectoflexids and V-shaped linguaflexids in the molars of *Hipparion* sp.1 support this assignment. Other mandibular fragments (III: Fig. 2) belong to a larger species. The ectoflexid in the larger species is deeper and the linguaflexid is more open and shallow and the plicabalinid is weak. *Hipparion* sp. 2 is similar in size to *H. prostylum*-*H. dietrichi* and may belong to either of these species, based on size and cheek teeth morphology.

The *Deinotherium* material from the Varzeghan district belongs to a very large individual. The molars (III: Fig. 3) are comparable in size to *Deinotherium giganteum* from Obuhovka (MN 12) of southern Russia (Bajgusheva and Titov 2006), but are smaller than the teeth of *D. gigantissimum* (III: Fig. 4).

Ivand locality (VI)

In the locality of Ivand, the lithology of the sequence consists mainly of thick layers of conglomerates interbedded with finer clastic sediments. The characteristics of the conglomerates suggest that they are deposits of gravity flows, sheet flows, and to a lesser extent, channelized flows on an alluvial fan. A vertical trend of upward coarsening and thickening of the beds suggests an overall progradational pattern of the alluvial fan.

A substantial amount of fossil material has been collected from this locality, among which hipparionine horses are predominant. Several cranial and postcranial elements of these animals have been recovered. Among this fossil material, a large hipparion represented by an almost complete skull and mandibles is noteworthy (VI: Fig. 2). The skull in general is similar to that of *Hippotherium brachypus* and *H. giganteum* (*H. giganteum*-*H. brachypus* lineage *sensu* Vlachou and Koufos 2009). A logarithmic ratio diagram (VI: Fig. 4) shows similarities of the large skull from Ivand with *H. brachypus* from several Turolian localities of the Eastern Mediterranean (EMED) region, such as Pikermi (Koufos 1987), Hadjidomovo (Hristova *et al.* 2003), and Akkaşdağı (Koufos and Vlachou 2005). However, due to some differences in facial morphology, such as the shape of the preorbital fossa (POF) and its lack of posterior pocketing, I refrain from assigning the hipparion skull from Ivand to *H. brachypus* and refer to it as *Hipparion* sp. large.

The large-sized skull from Ivand is not proportionally similar to any of the hipparionine horses from Maragheh (VI: Fig. 4). This skull apparently belongs to a large-

sized species previously unknown from the cranial material in northwestern Iran (i.e. the Maragheh area). The presence of large hipparions in Maragheh was previously evinced by the presence of medium to large, robust third metapodials. These robust metapodials from Maragheh were assigned to *Hipparion prostylum*, even though they showed greater similarity to the metapodials of *H. brachypus* from Pikermi (Watabe and Nakaya 1991a: Fig. 15). Bernor (V) is of the opinion that *H. prostylum*, originally defined based on skull morphology alone, did not occur at Maragheh and that *Hippotherium brachypus* is a more likely referral for the Maragheh hipparion samples (both cranial and postcranial) housed by the MNHN, Paris, formerly assigned to *H. prostylum* (Bernor 1985).

A small number of bovid horn cores attributed to *Oioceros* and *Gazella* are also recorded from Ivand (VI: Fig. 7). The *Oioceros* specimen is smaller and less laterally compressed than *Oioceros rothii* from Pikermi and its size and morphology falls into the variation in *Oioceros atropatenes* which is the most abundant bovid specimen present in the Maragheh fossil localities.

Postcranial evidence (VI: Fig. 5) also points to the presence of *Deinotherium giganteum* (proportionally close to both *Deinotherium giganteum* from Pikermi and an undetermined specimen from Maragheh) and **Rhinocerotinae indet. The rhino is clearly distinct from *Chilotherium* and is more similar to *Ceratotherium neumayri* and *Stephanorhinus pikermiensis* from Eastern Mediterranean localities such as Pikermi, Akkaşdağı, and Maragheh (VI: Fig. 6).**

Carnivores are rare in the Ivand locality and the only known specimen is a medium-sized machairodontine cat, smaller than *Machairodus aphanistus* and *M. giganteus*, which were quite common in the Turolian localities of the Eastern Mediterranean region. Other fossil material identified (in collections

other than in the HMNH) from Ivand includes postcranials of a giraffe, larger than *Palaeotragus* and in the size range of *Samotherium* and *Helladotherium*, and a partial skull with preserved basal parts of the horn cores resembling *Urmiatherium* (unpublished personal data and observations).

More recently, the first fossil porcupine remains from Iran were described from this locality. This material consists of upper cheek teeth and lower incisors identified as *Hystrix aryanensis*, previously recorded from the Late Miocene locality of Molayan in Afghanistan (Sen and Purabrishemi 2010).

Maragheh locality (V)

The fossil localities of Maragheh are located in the province of eastern Azarbaijan, northwestern Iran and have long been considered as one of the classical Western Eurasian Late Miocene “Pikermian” chronofaunas (Bernor *et al.* 1996, Bernor 1986). In recent years, Iran’s DOE and National Museum of Natural History, Tehran (MMTT) started a new initiative and sponsored new excavations in the Maragheh fossil sites.

The MMTT-University of Helsinki initiative, known as the International Sahand Paleobiology Expedition (INSPE), was also recently started (Table 1). These programs have further reinitiated study of the mammalian fauna with the intention of bringing them into a contemporary taxonomic context for comparative paleoecological and paleobiogeographic studies. Bernor (1986) and Bernor *et al.* (1996) provided an account of the mammalian species reported from Maragheh. Since 1996, there have been a number of taxonomic revisions that affected the documentation of fossils at Maragheh. Taxonomic changes and updates of the Maragheh fauna are summarized in Table 2.

Table 2. List of Maragheh taxa updated in this research (after Bernor 1986).

Order/Family	Bernor 1986	This research (V)
Hyaenidae	<i>Percrocuta eximia</i>	<i>Adcrocuta eximia</i>
Felidae	<i>Machairodus aphanistus</i>	<i>Amphimachairodus aphanistus</i>
Proboscidea	<i>Deinotherium</i> sp. indet.	<i>Deinotherium gigantissimum</i>
Rhinocerotidae	-	Rhinocerotidae gen. and sp. nov.
Equidae	<i>Hipparion prostylum</i>	<i>Hippotherium brachypus</i>
Suidae	<i>Microstonyx erymanthius</i>	<i>Microstonyx major</i>
Giraffidae	<i>Helladotherium</i> cf. <i>duvernoyi</i>	<i>Helladotherium duvernoyi</i>
Giraffidae	-	<i>Bohlinia attica</i>
Bovidae	<i>Gazella deperdita</i>	<i>Gazella capricornis</i>
Bovidae	<i>Gazella rodleri</i>	" <i>Gazella</i> " <i>rodleri</i>
Bovidae	-	<i>Gazella</i> cf. <i>ancyrensis</i>
Bovidae	-	<i>Prostrepsiceros</i> cf. <i>vinayaki</i>
Bovidae	" <i>Prostrepsiceros</i> " <i>rotundicornis</i>	<i>Prostrepsiceros</i> cf. <i>rotundicornis</i>
Bovidae	-	<i>Prostrepsiceros fraasi</i>
Bovidae	-	? <i>Palaeoreas</i> sp.
Bovidae		<i>Skoufotragus laticeps</i>
Bovidae	<i>Palaeoryx laticeps</i>	<i>Palaeoryx</i> sp.
Bovidae		<i>Mirabilocerus</i> cf. <i>maius</i>
Bovidae	<i>Miotragocerus amalthea</i>	<i>Miotragocerus</i> cf. <i>vallenciennesi</i>
Bovidae	-	? <i>Criotherium</i> sp.
Bovidae	-	<i>Tragoportax</i> cf. <i>amalthea</i>
Bovidae	-	<i>Samokeros minotaurus</i>
Bovidae	<i>Palaeoryx crassicornis</i>	? <i>Skoufotragus schlosseri</i>
Rodentia	-	<i>Hystrix</i> sp.

Biochronology and relationships of the fossil mammal localities in NW Iran

Based on the geographical proximity of the fossil localities in northwestern Iran (MRG, I, V in Fig. 1), their comparison is of interest. Although *Deinotherium* has a broad stratigraphical distribution from the Middle Miocene to the Pliocene (18–2 Ma ago), the deinotheriid trend toward increasing size during the Miocene (Huttunen 2002) and large size of deinotherium material from Ivand and Varzeghan suggest a Late Miocene age for

these localities.

The chronology of *Hippotherium brachypus* and *Cremohipparion moldavicum* in Eastern Mediterranean faunas (e.g. Pikermi, Samos, and Akkaşdağı) also indicates a Middle Turolian age (MNEQ 12) for the new localities in northwestern Iran. The presence of *Hystrix aryanensis*, a species previously known from the locality of Molayan in Afghanistan (Sen 1998) ca. 8–7 Ma ago (Sen and Purabrishemi 2010), support this age assignment for the Ivand locality.

The known *Deinotherium* remains from Maragheh are recorded from the upper biostratigraphical interval of this formation (the K1 locality of Erdbrink *et al.* 1976; identical to MMTT locality 31 of Bernor 1986). The absolute ages obtained from the zircon fission track and the potassium/argon (K/Ar) dating of pumicites from higher levels of the Maragheh Fm. imply an age of 7.4 Ma for these levels (Bernor 1986). In addition, the presence of *Hippotherium brachypus* in Maragheh is now expected. This taxon occurs with *Cremohipparion aff. moldavicum* in the Middle Maragheh interval dated 8.1–7.6 Ma ago (V). Therefore, based on the fossil material from these new localities and their correlation with the Middle and Upper biostratigraphic intervals of the Maragheh Fm., a MNEQ 12 age (ca. 8–7 Ma ago) is plausible for them.

The lophodont and brachydont cheek teeth of the deinotheriids indicate a folivorous diet, implying a forested environment. The very large size of the animal, however, suggests a more open landscape than that of a forest (Poulakakis *et al.* 2005). The paleoecological profile of the Maragheh fauna indicates a mixture of open and closed characters, paleoenvironmentally between the Greek localities of Pikermi and Samos (Koufos *et al.* 2009, Fig. 7). The brachydont, mesodont, and hypsodont taxa in Maragheh are almost evenly distributed, and each group comprises at least 30% of the community (V: Fig. 8). Primates as well as diversified felids, mustelids, and hipparionine horses exist together with browsing and grazing proboscideans, rhinos, giraffes, and bovids in Maragheh. Therefore, the Late Miocene environment of northwestern Iran had considerable amounts of wooded settings in its predominantly grassy/bushy vegetation.

4. Faunal provinciality in the Miocene of Western Asia

There have been a number of previous studies on the faunal provinciality of the Old World land mammals in the Neogene. Using cluster analysis of 38 Late Miocene localities with Simpson's faunal similarity index, Bernor (1978) and Bernor and Pavlakis (1987) investigated the faunal provinciality of the Miocene mammals of Eurasia and Africa. Bernor (1984, 1983) proposed several Eurasian and African paleobiogeographic provinces (bioprovinces) that were distinct in their faunal characteristics and ecology (Table 3). These zoogeographic provinces include: 1) the Western and Southern European province, 2) Eastern and central European province, 3) Romanian and western Russian province, 4) Sub-Paratethyan province (Turkey, Greece, and Iran), 5) North African province, and 6) Siwalik province. The possible presence of a Chinese and East African province was also put forward by Bernor (1984), based on the works of other scholars.

Fortelius *et al.* (1996) also studied provinciality in the Eurasian land mammals of the Miocene. They (*a priori*) divided Eurasia into Western and Eastern blocks and further divided these into six geographical regions including: Western Europe, West central Europe, Austria, Black Sea region, Balkans, and Anatolia and Iran (see Table 3 for the geographical extent of these regions). They measured faunal similarity between these blocks and regions, using Dice, Pielou, and Simpson similarity indices. These studies found a correlation between the geographic proximity and degree of similarity between regions and locality clustering. Due to problems with identification and temporal range of the paleospecies, these authors found that analyses at the genus level are more logical and useful for studies of faunal similarity, correlation, and interprovincial zoogeography. This is supported by the analysis of North American mammal data by Alroy (1996), who concluded that genus-level data are taxonomically robust and show much

of the same signals seen in the species-level data.

More recently, Casanovas-Vilar *et al.* (2005) studied provinciality in the Miocene of Europe based on cluster analysis with the unweighted pair-group method with arithmetic mean (UPGMA) algorithm and Raup-Crick index. They distinguished three main bioprovinces (Iberian (including southern France), central European, and Greek-Iranian) for most of this time span. Nargolwalla (2009) also conducted provinciality analysis, using raw presence/absence data in addition to similarity indices and identical cluster analyses, using the Jaccard, Dice, and Raup-Crick similarity indices. She used both genus- and species-level analyses to define Spanish, central European, Italian, and Eastern European/Western Asian provinces as four distinct paleobioprovinces. These studies used the NOW database and both large and small mammal data in their analyses.

In this research, I analyzed the provinciality of 407 localities in the Miocene of the Old World, using pair-group clustering based on presence/absence data and similarity indices. These indices work, based on the pair-wise comparisons of these presence and absence data. I used Dice (1945), Jaccard (1912), Simpson (1960), and Raup-Crick (1979) similarity measures. I present here the results for the Raup-Crick index and demonstrate the results of other indices, which show similar clusters, in Appendix 1. Raup-Crick similarity index (Raup and Crick 1979) is useful for locality clustering studies (Werdelin 2008, Casanovas-Vilar *et al.* 2005). This index weights data on the basis of frequency and uses Monte Carlo randomization to compare the observed number of co-occurrences in a pair of localities with the distribution of co-occurrences in 200 random iterations (Hammer and Harper 2006). Therefore both the widespread (common) and unique (rare) taxa proportionately affect the results, and the main clusters are strongly asserted.

4.1 Results

As shown by the previous studies and also supported here, geographic proximity plays a major role in the clustering of localities. Therefore, I named each group of clustered localities, based on their regional (and temporal) characteristics and presented the results here in a concise way (Fig. 2, see also Appendix 1). Nevertheless, occurrence of spatially or temporally exotic localities in these regional clusters is possible but unlikely.

The results show two megaclusters, one grouping the Early and Middle Miocene faunas (Fig. 2A) and the other Late Miocene faunas (Fig. 2B). This holds for all four similarity indices used in this analysis (see Appendix 1). The only exceptions are the early Late Miocene (MNEQ 9) Western and central European (WEUCEU) and Siwalik localities, which are clustered within the Early–Middle Miocene megacluster

This clearly indicates the different paleoecological and paleoenvironmental settings in these localities, which were different from the predominantly more open settings of the Late Miocene. Apparently, localities and faunas showing more closed, forested settings are clustered together in the Early–Middle Miocene megacluster and those adapted to more open, nonforested environments are grouped in the Late Miocene megacluster.

The megaclusters (Fig. 2A,B) show the formation of subclusters named by geographical regions and their temporal attributes that can be used for dividing the areas into different bioprovinces. Thus, the following bioprovinces can be defined for the Early and Late Miocene: Western and central Europe (WEUCEU), Western Asia including Anatolia, Iran, the Arabian Peninsula, Afghanistan, and the Indian subcontinent (WAS), northern China and central Asia (CHNCAS), and Africa and Arabia (AFRARB).

Table 3. Faunal provinces (for the Miocene of the Old World) and geographic subdivisions, and their areal extensions proposed and used in previous studies and the present research.

Name of Province/Geographical area	Areal Extension
Western Asia	Turkey (east), Caucasus, Iran, Iraq, Syria, Lebanon, Israel, Saudi Arabia, United Arab Emirates, Pakistan, Afghanistan, Tajikistan
Western Europe	Spain, France, Germany, Italy
central Europe	Austria, Czech, Slovakia, Hungary, Poland
Balkans	Croatia, Bosnia, Serbia, Montenegro, Macedonia, Kosovo, Albania, Bulgaria, Greece
North Black Sea	Romania, Moldova, South Ukraine
Southeast Asia	India, Nepal, Thailand, Burma, Vietnam, South China
Eastern Mediterranean	Balkan, North Black Sea, Anatolia, Caucasus, NW Iran
BAANIR ^M	Balkan, North Black Sea, Anatolia, Caucasus, Iran, Afghanistan, Tajikistan
CHNCAS ^M	North China, Mongolia, Kazakhstan, Kyrgyzstan
SIWSEAS ^M	Pakistan, India, Nepal, Thailand, Burma, Vietnam, South China
AFRARB ^M	Libya, Chad, Tanzania, Kenya, Ethiopia, Israel, Lebanon, Saudi Arabia, United Arab Emirates, Iraq
Western and Southern Europe Province ^B	Spain, France, Italy
East and central European Province ^B	Germany, Austria, Czech, Slovakia, Hungary
Romania-Western USSR Province ^B	North Black Sea, Caucasus region
Sub-Paratethyan Province ^B	Balkans, Anatolia, Western Asia (excluding Caucasus, possible extension to central Asia and China)
North African Province ^B	Morocco, Algeria, Libya, Egypt
Siwalik Province ^B	Pakistan (possible extension to Southeast Asia)
Greco-Irano-Afghane Province ^D	Greece, Anatolia, Iran, Afghanistan
Western Europe ^F	Spain, France
central Europe ^F	Germany, Switzerland, Austria, Poland, Czech, Slovakia, Hungary
Southeastern Europe ^F	Balkans, Romania, Georgia, Turkey-Thrace
Southwestern Asia ^F	Anatolia, Iran
West ^F	Western and central Europe
East ^F	Southeastern Europe, Southwestern Asia, Afghanistan, Kazakhstan
central European Province ^N	France, Germany, Austria, Czech, Slovakia, Hungary, Poland, Romania
Eastern European/Western Asia Province ^N	Greece, Turkey, Iran, Caucasus region

^M Present work, ^B Bernor 1983, ^D de Bonis *et al.* 1992, ^F Fortelius *et al.* 1996, ^N Nargolwalla 2009

As mentioned before, the Late Miocene Siwalik and Southeast Asian localities are also a distinct bioprovince (SIWSEAS) within this megacluster (SIW in Fig. 2A). Figure 2B shows the clusters for the Late Miocene episode. The major difference at this time is the fact that Western Asia cannot be defined as a distinct province and most of it, is part of the Balkan-Anatolia-Iran (BAANIR) province. Indeed, Western Asia is the crossroads of main provinces (BAANIR, CHNCAS, SIWSEAS and AFRARB) at this time. This indicates the availability of permanent land connections in Western Asia, as well as the presence of high mountain ranges that served as geographic barriers.

4.2 Discussion

4.2.1 Balkan-Anatolia-Iran province

Although the results of provinciality analysis in this research are in major agreement with previous studies, some modifications are proposed. Bernor (1984, 1983) proposed the Sub-Paratethyan province mainly for the Vallesian and Turolian localities in Greece, Turkey, and Iran, pointing to its possible continuation into China. Discovery of Turolian faunas in Afghanistan (Brunet *et al.* 1981, Heintz *et al.* 1981, 1979, 1978) inspired de Bonis *et al.* (1992) to propose a Greco-Irano-Afghane province that was synonymous with Bernor's Sub-Paratethyan province.

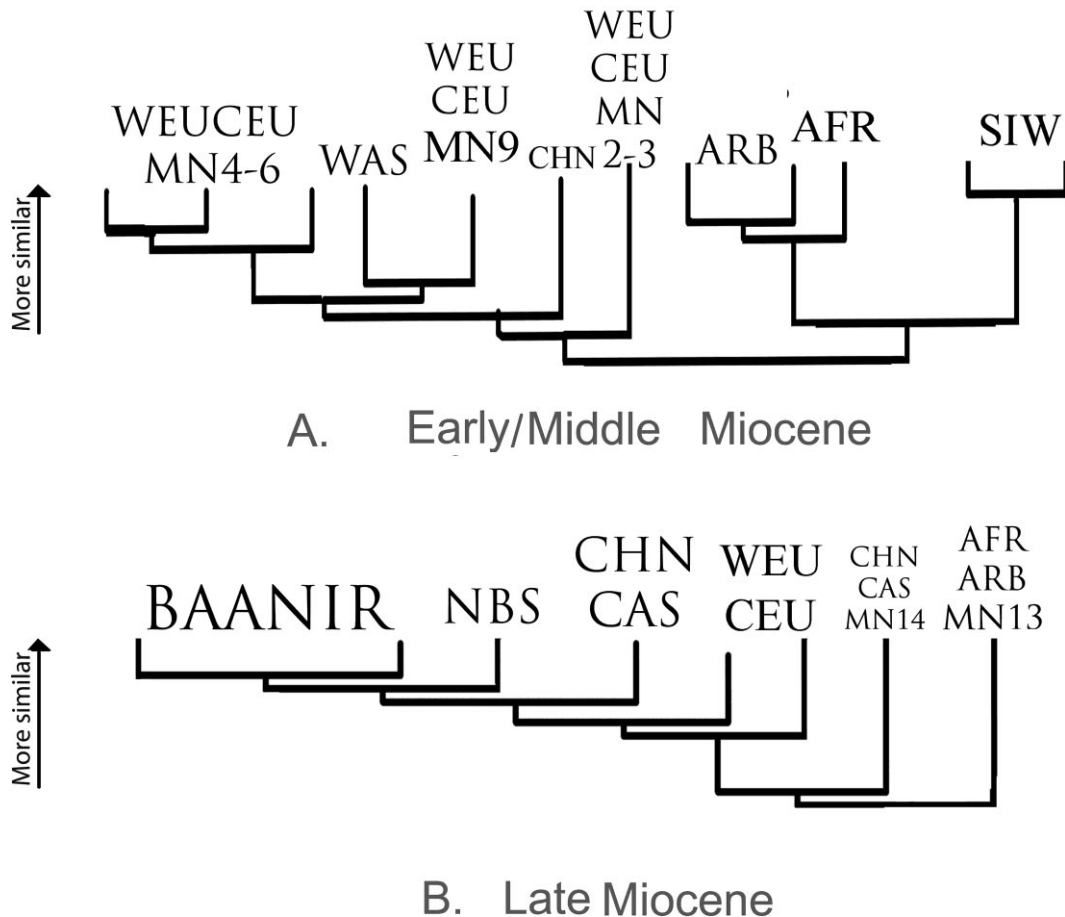


FIGURE 2. Clusters of localities showing the relationships of faunal provinces in the Miocene of the Old World. Clusters are from an analysis of 407 Miocene localities, using the Raup-Crick similarity index. **A:** Early–Middle Miocene clusters, **B:** Late Miocene clusters, **WEUCEU:** Western Europe-central Europe, **WAS:** Western Asia, **CHN:** North China, **ARB:** Arabia, **AFR:** Africa, **SIW:** Siwaliks, **BAANIR:** Balkan-Anatolia-Iran, **NBS:** North Black Sea, **CAS:** central Asia.

Fortelius *et al.* (1996) described a similar Balkan and Anatolia-Iran province for these regions and Casanovas-Vilar *et al.* (2005) used the Greek-Iranian name for it. Nargolwalla's Eastern European/Western Asian province addresses the same area (Nargolwalla 2009). The so-called Balkan-Anatolia-Iran province (BAANIR in Fig. 1) can also be regarded as synonymous with the previous terms and divisions to some extent. The main difference here is the inclusion of the North Black Sea (NBS) fossil localities in BAANIR, which were assigned to a separate province by Bernor (1983). This inclusion is supported by the cluster analysis and distribution history of the "Pikermian" chronofauna (II), which dominated this province in the Late Miocene.

4.2.2 Africa-Arabia province

Unlike Bernor (1978) and Bernor and Pavlakis (1987), other studies do not extend their analyses to most of the (east) Asian and African localities. In the present study, I included data from these areas. The results indicate some differences from previous research. Bernor (1984, 1983) proposed a North African province that included exclusively localities from that region. Later discovery of Miocene fossil localities in the Arabian Peninsula (see Whybrow and Hill 1999 for a review) and Djurab Desert, Chad (Brunet *et al.* 2000) and detailed studies of some important Middle and Late Miocene North and East African faunas such as Sahabi, Libya (Boaz *et al.* 2008, 1987), Wadi Moghara, Egypt (Miller 1999), Lothagam, Kenya (Leakey and Harris 2003) and Middle Awash, Ethiopia (Haile Selassie and Wolde Gabriel 2009) also offered a better opportunities for quantitative and qualitative provinciality study of the African and Arabian faunas.

Bernor (1984) included the Arabian Late Miocene localities in his sub-Paratethyan province. However, later studies (Bernor and Rook 2008, Leakey and Harris 2003, Bernor *et*

al. 2001, Whybrow and Hill 1999, Whybrow 1987) demonstrated higher similarity of these localities with the North and East African localities than the "Pikermian" chronofaunas. Cluster and faunal resemblance (GFRI) analyses also support the closer relationship of the Arabian faunas both in the Middle and Late Miocene with African faunas. In addition, the presence of several lineages in common at these localities, such as Canthumerycinae in North Africa and Arabia (Geraads and Aslan 2003, Thomas *et al.* 1999), proboscideans in Ad Dabtiyah, Arabia; Wadi Moghara, Egypt, and Jabal Zaltan (Gebel Zelten), Libya (Sanders 2008a, Sanders and Miller 2002) in the Middle Miocene, and in Baynunah, Arabia; Sahabi, Libya and Lothagam, Kenya (Sanders 2008b, Tassy 2003, 1999) in the Late Miocene, and even nonmammalian groups, such as ratit birds (Bibi *et al.* 2006), support this idea. Hence, it is better to define this area along with North and East Africa in a single province: Africa-Arabia (AFRARB, Fig. 1).

Nevertheless, evidence for the presence of subprovinces within AFRARB such as a Chado-Libyan (Boaz 2008, Lihoreau *et al.* 2006) or possibly an East African province (Bernor and Pavlakis 1987, Bernor 1978) is evident. In addition, interprovincial connections between this province and Balkan-Anatolia-Iran also existed. The African-Arabian faunas clearly had "Pikermian" elements that were vicariant and evolved independently, subsequent to early-middle Late Miocene extensions (Bernor *et al.* 2009, Bernor and Rook 2008, Werdelin 2003). However, due to geographical barriers, the northward migration of lineages (to the Palearctic realm) was probably less frequent than the east-west (between the Ethiopian and Oriental realms) directions (Hill and Whybrow 1999, Van der Made 1999).

4.2.3 China-central Asia province

The Chinese Miocene faunas are East Asian expressions of the Pan-Eurasian *Hispanotherium*

and *Hipparion* faunas, which correspond to their Western counterparts (IV, II). Although Bernor (1983) pointed to the presence of a Northern Asian province (*sensu* Qiu *et al.* 1979), he refrained from defining this province, due to its undeveloped geochronology in the modern sense. However, the results of our cluster and GFRI analysis (IV) as well as of some previous studies (Sotnikova *et al.* 1997, Vislobokova 2009) shows that the central Asian (Russia, Mongolia, Kazakhstan, and Kyrkyzstan) faunas are very similar to the northern Chinese localities and should be included in the same province (hence the CHNCAS province, Fig. 1). On the other hand, the fauna from Tajikistan are more similar to the west and south (Sotnikova *et al.* 1997) and are better grouped together with Afghanistan in the Balkan-Anatolia-Iran province. The CHNCAS Middle Miocene chronofauna originated in and extended from Western Europe (see also Fig. 10B) in response to continental drying and increased seasonality. They followed the widening arid belt towards the East (IV); however, their strongest expression in East Asia was at the very end of their history.

The Late Miocene localities of CHNCAS are clearly part of the Pan-Eurasian chronofaunas (IV, see also Fig. 10B). Nevertheless, there is evidence showing their distinction from their Western counterparts. This consists mainly of taxonomic and chronological differences, that express their development via a stage-of-endemism in harsh environmental settings. This was followed by expansion when summer rainfall brought richer resources and immigrants to northern China (Fortelius and Zhang 2006, Watabe 1992).

4.2.4 Siwalik-Southeast Asia province

The Siwalik province was delineated by Bernor (1983, after Barry *et al.* 1982). He pointed to the remarkably endemic character of this province and illustrated its possible

extension to Southeast Asia and southern China (Bernor 1984: Fig. 1). Here, the results of cluster and GFRI analyses (see section 6 under Siwalikan chronofauna and Fig. 8) support the high level of endemism of the Siwalikan faunas. In recent years there have been several discoveries of new Miocene localities in Southeast Asia (Chavasseau *et al.* 2006, Htike *et al.* 2005, Pillansa *et al.* 2005, Marivaux *et al.* 2004, Nakaya *et al.* 2003, Sehgal and Nanda 2002, Covert *et al.* 2001, Ducrocq *et al.* 1994,1995, Ginsburg *et al.* 1992, West *et al.* 1991,1978, and Ginsburg and Tassy 1985), which were used in the analysis here. The results show that they are grouped together with the Siwalik localities and thus form the Siwalik-Southeast Asia province (SIWSEAS in Fig. 1). The southern Chinese localities (e.g. Lufeng) should be included in this province, since they were separated from the northern localities in the Middle Miocene by a dry midlatitude belt (Liu *et al.* 2009, and IV). The possible interprovincial relationships of SIWSEAS with other provinces will also be discussed later (see section 6 discussion, under the Siwalikan chronofauna).

4.3 Conclusions

The present study demonstrates the formation of two megaclusters of localities in the Miocene of the Old World. One cluster (Fig. 2A) groups the faunas of the Early–Middle Miocene, which were best adapted to more forested settings, while the other (Fig. 2B) assembled the Late Miocene faunas, adapted to more open conditions. In agreement with previous studies, but with some modifications, four main faunal bioprovinces are proposed that interacted in Western Asia: 1) the Balkan-Anatolia-Iran (BAANIR) province, including the faunas of Iran, Afghanistan, and Tajikistan together with those of Anatolia, Caucasus, Balkans, and the North Black Sea, 2) the China-central Asia (CHNCAS) province for the northern Chinese, Mongolian, and central Asian localities, 3) the Africa-Arabia (AFRARB)

province for the North and East African and Arabian Peninsula localities, and 4) the Siwalik-Southeast Asia (SIWSEAS) for the Siwalik, Indian subcontinent, and Southeast Asian localities.

Although this provinciality pattern existed in late Early–Middle Miocene times, it is better expressed and defined in the Late Miocene. The Western Asian localities that formed a separate cluster in the Middle Miocene do not appear as a separate entity in the Late Miocene. Indeed, they became parts of other provinces at this time. This is evidence for increased provinciality in Western Asia in the Late Miocene, which was due to the changing climate and paleogeographic conditions.

5. Relative abundance history of the closed- and open-adapted taxa

The faunal and floral developments in the Miocene of Eurasia are well known. A shift from tropical/subtropical evergreen forest conditions of the Early and early Middle Miocene to more seasonal and open, deciduous woodlands and grasslands of the Late Miocene was recorded by several authors (e.g. Solounias *et al.* 2010, 1999, Bruch *et al.* 2007, Mosbrugger *et al.* 2005, Fortelius *et al.* 2006, 2003, 2002, Agustí *et al.* 2003, 1999, 1997, Gabunia and Chochieva 1982, Dorofeyev 1966). As marked by the climatic and environmental records of the Miocene and also exhibited in the results of the clustering analysis of the previous section, the Miocene can be divided unequivocally into two parts: an Early–Middle Miocene part that is associated with the development of closed-adapted (forest) taxa and a Late Miocene part that corresponds to the enhanced evolution of open-adapted (nonforest; woodland and grassland) taxa.

Here, a taxic (taxon-counting) approach (Levinton 1988) toward quantification of the Miocene mammalian groups and their

environments (closed/open), and a survey of their relative abundance in space and time was carried out. The “Pikermian” large mammal assemblages that were composed of open-country-adapted taxa that dominated the later part of the Miocene in Eurasia are characterized by dominance of the families Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae**, and poor representation of the families Cervidae, Tragulidae, and Suidae (Solounias *et al.* 2010, 1999, Bernor 1984).

Thus, in the present work, the open-adapted taxa are defined as members of the families Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae**. On the other hand, families with poor representation in the “Pikermian” chronofaunas were not favored by the increasingly open and seasonal environments of the Late Miocene. As a result, the closed-adapted taxa are defined as members of the families Cervidae, Suoidae, Tragulidae, and other clearly closed/humid-adapted groups such as Anthracotheriidae, Hippopotamidae, Moschidae, Palaeomerycidae, Tapiridae, and Proboscidea.

Kurtén (1952), in his quantitative study of the Chinese Hipparion fauna, listed the frequency of species in the closed (*Gazella gaudryi*), mixed, and open (*Gazella dorcadoides*) faunas of the Shanxi region of northern China. His results showed the high percentage of Equidae, Giraffidae, Bovidae, and Carnivora in the open-adapted faunas while Cervidae and Suidae were abundant in the closed-adapted faunas (Kurtén 1952: Fig. 2). More recently, Nakaya and Tsujikawa (2006) used the average percentage of open-country taxa in sub-Saharan Africa to show a significant increase in the relative abundance of these taxa from the Early to the Late Miocene.

The analysis of mean hypsodonty (HYP) values in the groups termed here open- and closed-adapted (Fig. 3A) reveals the predominance of brachyodont taxa in the

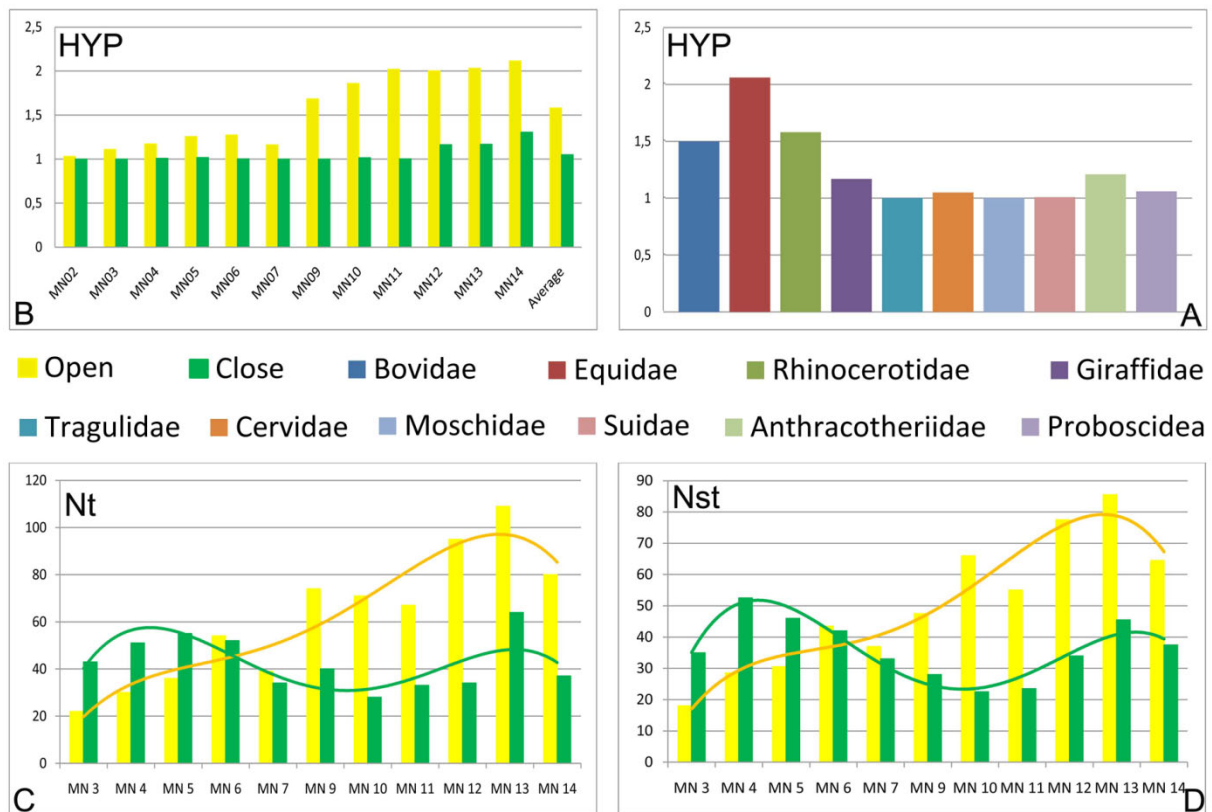


FIGURE 3. Mean hypsodonty (HYP) in the Miocene of: (A) families and orders assigned to open- and closed-adapted classes in this work and (B) open- and closed-adapted classes. (C) Total diversity (Nt) and (D) standing diversity (Nst) of the open- and closed-adapted categories in the Miocene of the Old World. The trend lines are polynomial 4th order.

Open-adapted: Bovidae, Equidae, Giraffidae, and **Rhinocerotidae** (+ Felidae and Hyaenidae in the diversity curves)

Closed-adapted: Anthracotheriidae (+ Hippopotamidae), Cervidae, Moschidae (+ Palaeomerycidae), Suidae (+ Tapiridae), Tragulidae, and Proboscidea

closed-adapted category (HYP = 1), while most of the mesodont and hypsodont species are found within the open-adapted classes (HYP > 1). The mean HYP trends of these groups in the Miocene shows that the closed-adapted taxa had a mean HYP value of 1 for most of their history, showing only slightly higher values during the Late Miocene. Conversely, the open-adapted taxa are strongly coupled with mean HYP values of more than 1 during their entire history, which significantly increased in the Late Miocene (Fig. 3B).

Hypsodonty is the adaptive response of the dentition to the need for more wear tolerance and functional durability, which is related to more open, less forested habitats with fibrous,

abrasive vegetation (Eronen *et al.* 2010a, Fortelius *et al.* 2006, 2003, 2002, Fortelius and Solounias 2000, Solounias *et al.* 1994, Janis and Fortelius 1988, Fortelius 1985). In contrast, brachydont (low-crowned) teeth are present in herbivores eating relatively nonabrasive food in grit-free environments (soft browse in closed environments). The data of Janis *et al.* (2002) showed that the HYP indices in living ungulates of woodland and forest habitats are app. 1.5. Therefore, it seems that mean HYP values of less than 1.5 would probably correlate well with more closed environments, while higher values would correspond to more open conditions. The Late Miocene average HYP values of the open- and

closed-adapted groups ($HYP > 1.5$ vs. $HYP < 1.5$) in the present research (Fig. 3B) agree well with this idea and support this grouping.

Thus, the open- and closed-adapted categories described here are credible and realistic, and are good representatives of their designated environments. Although some of these families and orders were not exclusively adapted to the closed or open environments, it appears that exceptions are present in all groups, while the majority of species of these groups were adapted to the environments assigned to them. So, this fact does not devalue the patterns seen in the relative abundance of these open- and closed-adapted groups in space and time.

The total (Nt) and standing (Nst) diversity (richness) of the open- and closed-adapted groups for each MNEQ unit throughout the study area (Old World) were also calculated, based on the formula used in Fortelius *et al.* 1996 (after Maas *et al.* 1995 and Barry *et al.* 1995). Total diversity (Nt) here (Fig. 3C) is based on counts of the number of open- and

closed-adapted genera in each MNEQ unit while standing richness (Nst) is the number of genera known before and after the MNEQ interval, plus the sum of the first, last, and only occurrences in the MNEQ interval, divided by 2 (Fig. 3D). The diversity patterns (Fig. 3C,D, see also discussion) are similar to the relative abundance pattern (Fig. 4A), indicating that the relative abundance patterns are not biased by oversampling of a few taxa. The frequencies of the closed- and open-adapted groups, as defined above, were calculated in each locality, as recorded in the NOW database. The sum of these taxa was recorded and their percentages in each locality were calculated (see Appendix 2 for raw data). The graphs showing the relative abundance of open- and closed-adapted taxa during the Miocene are presented in Figure 4. The graphs include one plot (Fig. 4A) for the Old World Miocene localities of the NOW database that met the criterion for selection (see methods) and four plots for the major faunal provinces presented in this work (Fig. 4B–F).

FIGURE 4. Relative abundance (percentage) of the (C) closed- and (O) open-adapted taxa (% O/C), and number of localities and species during the Miocene in different geographical and provincial regions: (A) O/C percentage in the Old World, (B) O/C percentage in Western and central Europe (WEUCEU), (C) O/C percentage in Balkan-Anatolia-Iran (BAANIR) province, (D) O/C percentage in the north China-central Asia (CHNCAS) province, (E) O/C percentage in Africa-Arabia (AFRARB) province, (F) O/C percentage in Siwalik-Southeast Asia (SIWSEAS) province. The green and yellow dots represent fossil localities. The trend lines are polynomial 4th order. (G) All regional trend lines of open-adapted taxa percentage, (H) All regional trend lines of closed-adapted taxa percentage. Dots represent average points. (I) Number of localities and (J) species in each regional subdivision and province. MN units in areas other than Europe are MNEQ.

Open-adapted taxa: Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae.**

Closed-adapted taxa: Anthracotheriidae, Cervidae, Hippopotamidae, Moschidae, Palaeomerycidae, Suoidea, Tapiridae, Tragulidae, and Proboscidea.

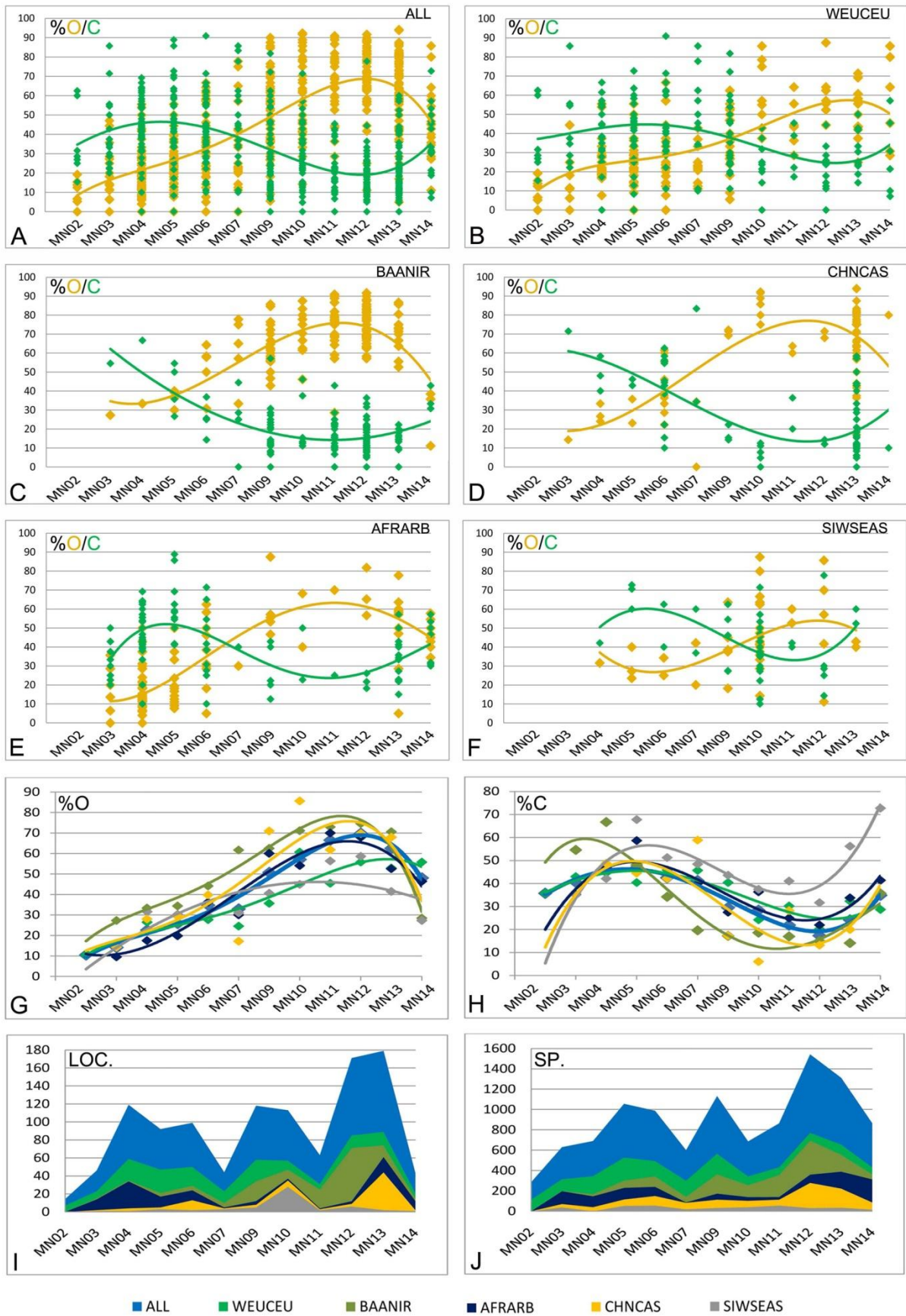


Figure 4. See caption on page 33

5.1 Results

5.1.1 Miocene relative abundance history of the closed- and open-adapted taxa

As seen in Figure 4A, the trend of open- (nonforest; woodland-grassland) adapted taxa (hereafter open-adapted taxa) over the Miocene in the Old World are completely different from that of closed (forest) adapted taxa (hereafter closed-adapted taxa). The percentage of open-adapted taxa from the Early to Late Miocene continuously increased until they decreased in the late Late Miocene. There was an initial rise during the late Early–early Middle Miocene, due to *Hispanotherium* fauna, while the trend accelerated over the Middle and Late Miocene until it peaked at MNEQ 12. The open-adapted taxa comprised 20% or less of the faunas during the Early Miocene, but from the early Late Miocene they began to dominate until they reached their acme in MNEQ 12. The turning point for the open-adapted taxa to prevail over the closed-adapted taxa was probably the late Middle Miocene (MNEQ 7+8), although they only began to dominate the faunas from MNEQ 9.

The closed-adapted taxa trend showed two increasing periods in the Miocene: one early and one late. Nonetheless, the second rise was not very significant, attaining only the levels of the early Early Miocene. The percentage of closed-adapted taxa increased rapidly in the mid-Early Miocene and peaked in the late Early–early Middle Miocene (MNEQ 4–6). During MNEQ 3–MNEQ 7+8, they dominated the faunas by more than 40%. Later, they experienced a constant fall over the mid-Middle and Late Miocene until MNEQ 12, when they showed their lowest percentage (20%) in the faunas. The closed-adapted taxa began to increase again in MNEQ 13 and 14, but they did not attain significant levels.

5.1.1.1 Western and central Europe

The trend of the open- and closed-adapted taxa in Western and central Europe (WEUCEU) is shown in Fig. 4B. The general trend in Europe was similar to that of global developments. This is probably due to the good sampling in WEUCEU, which predominates in the dataset. The percentage of open-adapted taxa in the faunas gradually increased, but not as sharply as the Old World trend. There was an early increase and minor peak in the percentage of the open-adapted taxa in MN 4–6 (due to the *Hispanotherium* fauna), while the next and major peak was in the Late Miocene (MNEQ 12, 13). The closed-adapted taxa, on the other hand, reached their acme in MN 4–6, with more than 40% of the faunas, and later steadily decreased until MN 13. Unlike the global trend, the turning point for the open-adapted taxa to rise above the closed-adapted taxa in WEUCEU was in MN 9. This shows that the dominance of the closed-adapted taxa in these faunas lasted longer. The open-adapted taxa began to predominate here after the Vallesian Crisis, which marked the extinction of the closed-adapted taxa in WEUCEU (Agustí *et al.* 2003, Agustí and Moya Sola 1990). The open-adapted taxa continued their acme here for a longer time (until MN 13) and declined only in MN 14.

5.1.1.2 Balkan-Anatolia-Iran province

Figure 4C shows the trend of open- and closed-adapted taxa in the Balkan-Anatolia-Iran (BAANIR) province. Regardless of poor sampling in the Early Miocene, the open-adapted taxa in this area showed a trend similar to that in the global graph. They increased from the Middle to the Late Miocene until MN 12 and then began to decrease over MN 13 and 14. The closed-adapted taxa, on the other hand, behaved differently. The percentage of these taxa was more than 50% during MN 3–5 and then decreased from the Middle to the Late Miocene. This drop was sharp until MNEQ 10.

and there was a slight increase over MN 13 and 14. The turning point in this province was the mid-Middle Miocene (MN 6), when open-adapted taxa began to dominate the faunas (by more than 50%). However, their acme was in MN 10–12, by more than 70% in some faunas. They decreased abruptly in MN 14.

5.1.1.3 China-central Asia province

The trend of open- and closed-adapted taxa in this province is shown in Figure 4D. The general trends here are very similar to those of Balkan-Anatolia-Iran. The open-adapted taxa increased steadily until the Late Miocene and the closed-adapted taxa decreased at the same time. The open-adapted taxa dominated the faunas in the Late Miocene and climaxed in MNEQ 13. The closed-adapted taxa predominated in the faunas in the Early and Middle Miocene, by more than 40%. There was an increase in the percentage of closed-adapted taxa in MNEQ 13 and 14, but they were still well below the open-adapted taxa.

5.1.1.4 Africa-Arabia province

The open- and closed-adapted taxa trends in this province are illustrated in Figure 4E. The graphs are generally similar to those of the global trends. The open-adapted taxa here were in sharp, steady increase until reaching climax in MNEQ 10–12 by more than 60%. They decreased over MNEQ 13 and 14. The closed-adapted taxa increased sharply in the Early Miocene and peaked in MNEQ 4 and 5, then decreased until the Late Miocene (MNEQ 11). They increased again in MNEQ 12–14. Although they were predominant only in MNEQ 4 and 5, they always comprised a significant percentage of the faunas. The only significant decrease in closed-adapted taxa below the open-adapted taxa was in MNEQ 11 and 12. This is the time of poor sampling in Africa. Only a few sites in Africa (e.g. the Tugen Hills and Lothagam) represent this time interval in which a major change in the African sub-Saharan terrestrial vertebrate fauna

evolved (Hill 1995) and the ecological transition from equatorial forests to savanna grasslands occurred (Leakey and Harris 2003). This is also coincident with the transition of C₃ to C₄ vegetation in Africa (Segalen *et al.* 2007). Nonetheless, faunal evidence suggests that forest vegetation was present in the region of the western Rift Valley during the Late Miocene and Early Pliocene (Hill 1999, Pickford 1990a).

5.1.1.5 Siwalik-Southeast Asia province

In the Siwalik-Southeast Asia (SIWSEAS) province, the general trend in closed- and open-adapted taxa (Fig. 4F) was similar to that of other provinces and the global trend, although the sampling is admittedly poor compared with that of other provinces (Fig. 4I, J). The abundance of open-adapted taxa increased from the Early to the Late Miocene, while the closed-adapted taxa decreased. However, the detail of patterns indicates that the open-adapted taxa did not increase their percentage significantly until MNEQ 9. The percentage of the closed- and open-adapted taxa in the faunas was similar during MNEQ 9 and 10. The open-adapted taxa only predominated in MNEQ 11 and 12, while the closed-adapted taxa prevailed until the early Late Miocene, longer than in other provinces and similar to the situation in Western and central Europe.

5.2 Discussion

The distribution of the Old World Miocene fossil mammal localities is not uniform in space and time (sampling bias) and this may complicate the trends observed in the relative abundance of the open- and closed-adapted taxa. In recent article, Saarinen *et al.* (2010) used the locality-based occurrence data of the NOW database and grid-based modern mammal distribution data to determine whether fossil locality point data result in favorable estimates of the total fauna known

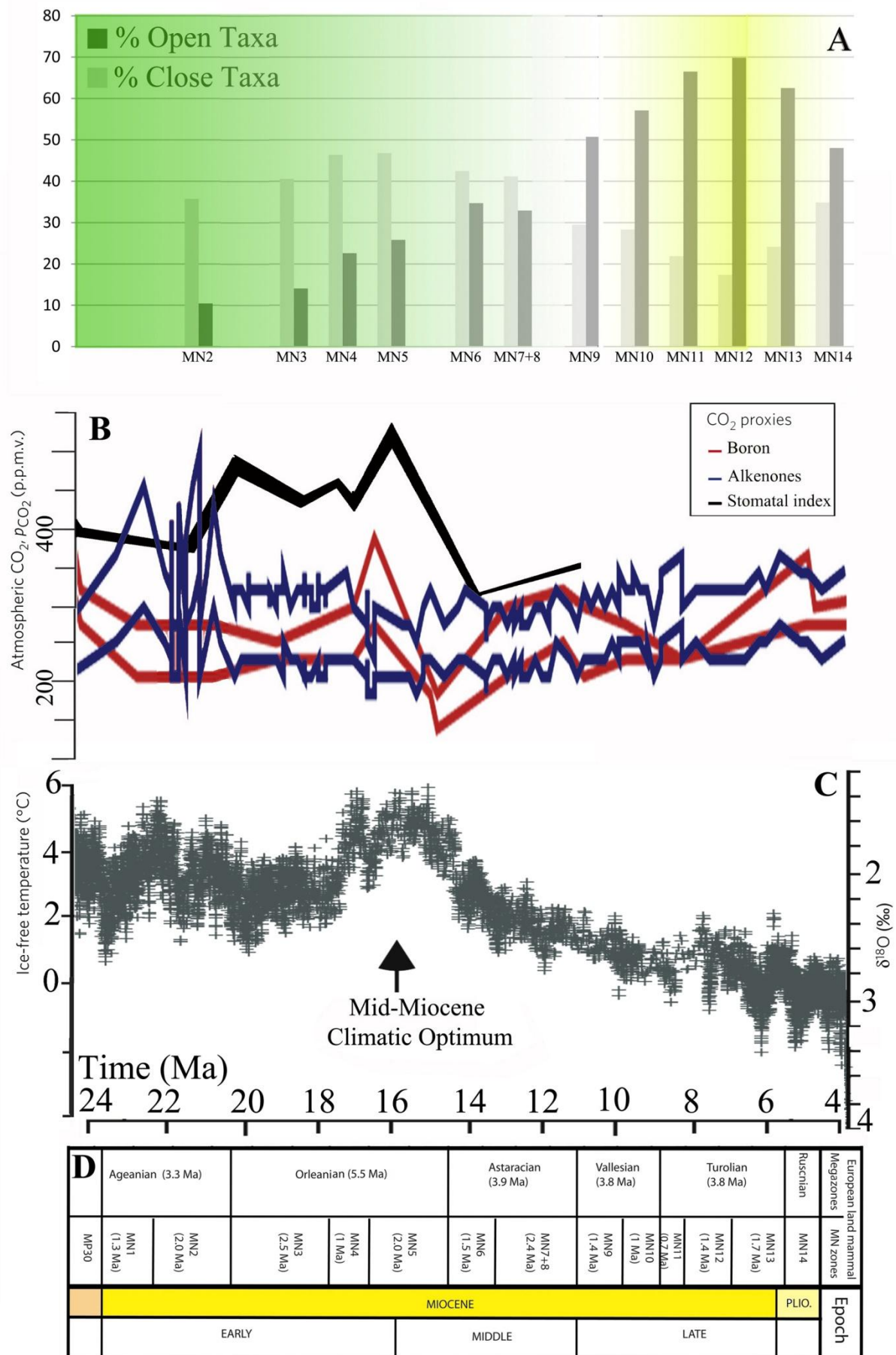


Figure 5. See captions on page 38

FIGURE 5. (A) Relative abundance (percentage) of closed- and open-adapted taxa in the Old World, (B) evolution of atmospheric CO₂ concentration after Kürschner *et al.* 2008 (stomatal index) and Zachos *et al.* 2008 (boron and alkenones), (C) global ice-free temperature and oxygen isotopes after Zachos *et al.* 2008, and (D) MN zones after Steininger 1999, during the Miocene.

Open-adapted taxa: Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae**

Closed-adapted taxa: Anthracotheriidae, Cervidae, Hippopotamidae, Moschidae, Palaeomerycidae, Suoidea, Tapiridae, Tragulidae, and Proboscidea

from the grid cells. Their results showed that the fossil localities they studied captured almost 60% of the known species richness, and the community structure could be accurately estimated from these locality data. Thus, the NOW data are almost certainly good representatives of the real faunas from which they were drawn. The open- and closed-adapted taxa during the Miocene, even in provinces with small numbers of localities, clearly showed the general trends. These trends are probably robust patterns that were not altered by sampling bias.

After an initial cooling phase at the transition of the Oligocene to Miocene (Kürschner *et al.* 2008), warm climates with dense vegetation prevailed in Eurasia during the first half of the Miocene (Alçiçek 2010, Akgün *et al.* 2007, Bruch *et al.* 2007, Mosbrugger *et al.* 2005, Kovar-Eder 2003, Zubakov and Borzenkova 1990), Siwaliks (Quade and Cerling 1995), and Africa (Jacobs 2004, Pickford 2004, Nesbit Evans *et al.* 1981, Van Couvering 1980, Axelrod and Raven 1978, Andrews and Van Couvering 1975). A temperature peak known as the Middle Miocene Climatic Optimum occurred between 17–15 Ma ago (Böhme 2003, Zachos *et al.* 2001). Between 15–14 Ma ago a major cooling step occurred that was associated with East Antarctic Ice Sheet growth (Zachos *et al.* 2001). As a result, midlatitude drying increased (Kutzbach *et al.* 1993). The levels of CO₂ also decreased (Fig. 5B) at this time (Kürschner *et al.* 2008), marking the passage from the greenhouse climate, which had prevailed so far, into the icehouse period (Holbourn *et al.* 2005). The CO₂ fluctuations probably had an important effect on Cenozoic

climate trends and changes in terrestrial ecosystems (Kürschner *et al.* 2008). After these events, significant progressive drying and cooling of the midlatitudes in Late Miocene time caused the expansion of more open vegetation and increased aridity and seasonality (Fortelius *et al.* 2006, 2003, 2002, 1996, Agustí and Antón 2002).

On the global (Old World) scale, the closed-adapted taxa dominated the faunas by more than 40% from MNEQ 3 to MNEQ 6. However, their acme was in MNEQ 4–6 for the global trend as well as most of the provinces (Fig. 4H). The diversity patterns of the closed-adapted taxa (Fig. 3C and D) showed peaks in the richness of this group of mammals in the late Early–early Middle Miocene (MNEQ 4 and 5). Mammalian faunas in the Great Plains region of North America also showed an extraordinary richness of browsing taxa in the late Early Miocene that decreased steadily through the Middle and Late Miocene (Janis *et al.* 2000, 2002, 2004).

The peak in relative abundance of the closed-adapted taxa as shown in Figure 5A (and also their taxonomic richness as shown in Figure 3C and D) coincides with the Middle Miocene Climatic Optimum (Fig. 5C). A period of climax resulted in temperatures believed to be 6 °C warmer than present conditions (Zachos *et al.* 2001). This is also the period of highest atmospheric CO₂ concentration in the Miocene, based on some proxy data (Kürschner *et al.* 2008, Retallack 2001), and may reflect higher primary productivity levels of the vegetation at this time (Janis *et al.* 2000, 2002, 2004). Therefore, the peak of the closed-adapted taxa and their

environments probably was closely related to the climatic conditions of the Middle Miocene.

The succeeding cooling event caused the decrease in relative abundance and diversity of the closed-adapted taxa and a subsequent increase in abundance and richness of the open-adapted taxa in the faunas. This may also have been due to a gradual decline in primary productivity of vegetation, which would be consistent with the decrease in atmospheric CO₂ concentrations (Fig. 5B) from higher early Middle Miocene levels (Kürschner *et al.* 2008) and opening of the environments. From the early Middle Miocene to the end of this epoch, a distinct shift occurred in European floras (Bruch *et al.* 2007, Mosbrugger *et al.* 2005, Kovar-Eder 2003, Bernor 1983). The subtropical (warm-temperate forests with low seasonality) that predominated during the first half of the Miocene gave place to warm-temperate taxa (open-country floras with higher seasonality). Nevertheless, the closed-adapted taxa still showed a significant percentage during MNEQ 9 and 10 (about 30%) while their diversity was severely reduced. This was due to the Western-central European and Siwalik-Southeast Asian faunas that retained their humid/closed environments longer than other parts of Eurasia (Barry *et al.* 2002, Agustí *et al.* 1999, 1997).

The onset of Miocene cooling and the subsequent increase in aridity and seasonality apparently favored the open-adapted taxa, which began to increase their diversity and numbers significantly after the Middle Miocene Climatic Optimum. Throughout the dataset, the time for the open-adapted taxa to predominate over the closed-adapted taxa and become taxonomically diverse is the early Late Miocene. However, the relative abundance patterns may be different in the provinces due to regional differences. In Western-central Europe and Siwalik-Southeast Asia, this occurred after MNEQ 9 (Fig. 4B, F), which was the time after the Vallesian Crisis in Western Europe (Agustí *et al.* 1999).

In north China-central Asia and Africa-Arabia this occurred in MNEQ 9 (Fig. 4D and E), even though sampling is poor during MNEQ 7+8 in both regions. It has been suggested that the mammalian assemblages of sub-Saharan Africa significantly changed during the Middle Miocene (Astaracian) by an increase in the number of open-country taxa (Nakaya and Tsujikawa 2006).

The trends in Balkan-Anatolia-Iran (Fig. 4C) were quite different in this context. The open-adapted taxa in this province began to predominate during MN 6, much earlier than in other areas and immediately after the Climatic Optimum. In this area the number of Early and Middle Miocene localities was significantly lower than in the Late Miocene. However, some of the major fossil localities of this time (e.g. Çandır and Paşalar, Turkey) documented the beginning of seasonality and opening of the environment by an increase in number of hyaenids, bovids, and giraffids (Bernor 1978). A mosaic landscape with relatively dry and seasonal, subtropical woodland was proposed for these localities (Geraads and Aslan 2003, Andrews 1990) although some taxa in these localities showed adaptations to more open environments (Quade and Cerling 1995). This region was also the core area in which the classic “Pikermian” chronofauna of the Late Miocene would later thrive. The open-adapted taxa here became predominant in the Late Miocene (MN 9–13) by more than 50% in the faunas. However, they were significant even before and after this time. This pattern coincided with the acme of “Pikermian” chronofauna and was closely associated with climatic phenomena, such as the late Neogene cooling trend (Zachos *et al.* 2001), midlatitude drying (Kutzbach *et al.* 1993), development of physical drivers such as the Tibetan Plateau uplift and the retreat of the Paratethys (Eronen *et al.* 2010b), and changes in the North Atlantic climatic system with increased northward heat transport (II, Micheels *et al.* 2010).

The overall abundance patterns of open- and closed-adapted taxa in north China-central Asia were very similar to those of Balkan-Anatolia-Iran. This indicates similar history and success of open-adapted taxa in these areas. The distribution history of several chronofaunas from these regions was also similar (see also Fig. 10B) and indicates broad mutual association of these regions. On the other hand, Siwalik-Southeast Asia was similar in overall pattern to Africa-Arabia. This was likely due to longer predominance of closed-adapted taxa in these provinces or (less likely) it may have been an artifact of sampling. Nonetheless, as proposed by some authors (Pickford 1990b, Pickford and Morales 1994, Van der Made 1999), the presence in the Miocene of biogeographical zones (e.g. CHNCAS-BAANIR and SIWSEAS-AFRARB) similar to present-day Palearctic and Paleotropic (Ethiopian and Oriental realms) bioprovinces can be emphasized here.

5.3 Conclusions

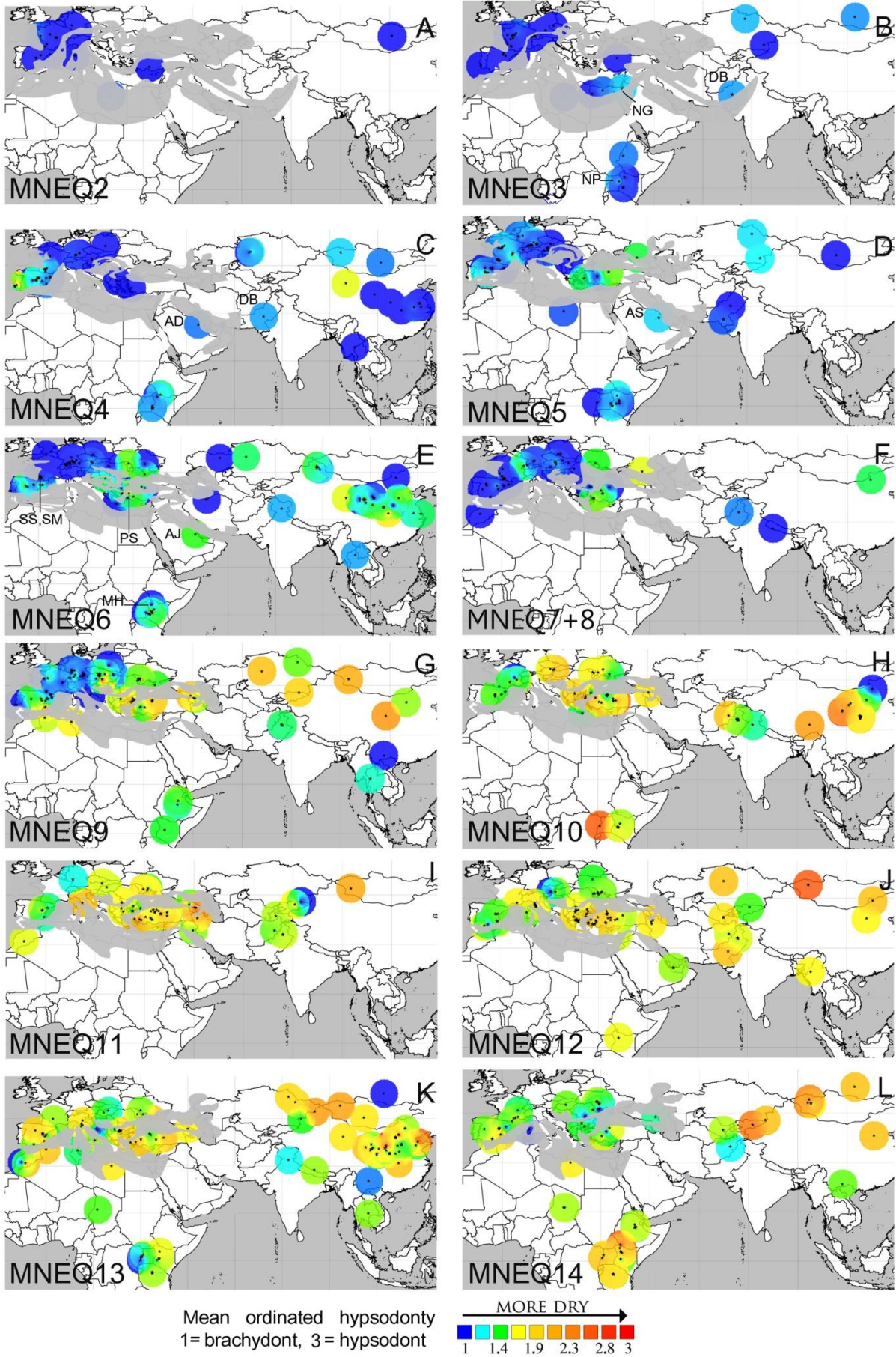
The relative abundance history patterns of closed- and open-adapted taxa during the Miocene of the Old World reveal the close relationships of these trends with major climatic events during this epoch. The dominance of closed-adapted taxa as defined here (i.e. Suoidae, Cervidae, Tragulidae, Moschidae, Hippopotamidae, Anthracotheriidae, Palaeomerycidae, Tapiridae, and Proboscidea) is well correlated with the Middle Miocene Climatic Optimum and possibly increased

atmospheric CO₂ concentrations. The timing of the shift from a closed to an open environment varies in different regions and is highly diachronous. Nonetheless, it is related to the subsequent cooling event of the Middle Miocene which caused the decline in percentage of the closed-adapted taxa and increase in the number of open-adapted taxa. The later predominance of the open-adapted taxa is related to the midlatitude drying and increased aridity in Eurasia as well as to paleogeographical and paleoclimatological configurations. The trends observed in distribution and relative abundance history of open- and closed-adapted taxa appear to be realistic and straightforward signals that are not likely to be critically affected by sampling inconsistency.

6. Distribution history of the Western Asian Miocene chronofaunas

Olson (1952) developed the concept of the chronofauna as “a geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time” (Olson 1952:181). A computational (quantitative) equivalent of this concept in terms of faunal resemblance was recently developed, which characterizes a chronofauna as a set of localities united by faunal similarity to an arbitrarily selected type or standard locality (**II, IV**).

FIGURE 6. Mean ordinated hypsodonty (HYP) values mapped for each MN-equivalent (MNEQ) unit during the Miocene. **A)** MNEQ 2, **B)** MNEQ 3 (NP: Napak, NG: Negev, DB: Dera Bugti), **C)** MNEQ 4 (AD: Ad Dabtiyah, DB: Dera Bugti), **D)** MNEQ 5 (AS: As Sarrar), **E)** MNEQ 6 (SS: Sansan, SM: Simorre, PS: Paşalar, MH: Muruarot Hill, AJ: Al Jadidah), **F)** MNEQ 7+8, **G)** MNEQ 9, **H)** MNEQ 10, **I)** MNEQ 11, **J)** MNEQ 12, **K)** MNEQ 13, **L)** MNEQ 14. Red and yellow patterns (high HYP) indicate increased aridity while blue patterns (low HYP) represent humid conditions. Paleogeographic setting of the European and Eastern Mediterranean areas are from Popov *et al.* 2004 (redrawn after Eronen 2006).



The dynamics of land mammal provinciality was recently addressed, using faunal similarity to chart the rise and fall of the several Miocene Eurasian chronofaunas, including “Pikermian” (II), Baodean, and Tunggurian (IV) chronofaunas.

These studies showed that the westward expansion of the “Pikermian” chronofauna from the late Middle Miocene to the middle Late Miocene correlates closely with the expansion of arid habitats, as well as some paleogeographical and paleoclimatological configurations (II). We also demonstrated that both the Tunggurian and the Baodean chronofaunas moved into Eastern Asia from the West, apparently shifting their range across the continent in response to changing climate (IV).

Eronen *et al.* (2010a,b), Fortelius *et al.* (2006, 2003, 2002), Eronen (2006), and Eronen and Rook (2004) previously showed that the mean ordinated hypsodonty (i.e. molar crown height assigned to hypsodonty classes, see methods) of large herbivorous mammals can be used as a proxy for humidity, yielding both qualitative and quantitative estimates. These studies indicate major regional differences in the chronology of the general trend of Neogene midlatitude aridification. It is known that these patterns are due to the genera and species with the highest occupancy or relative locality coverage (Eronen 2006, Jernvall and Fortelius 2002).

Here, I focused on the development of the late Early and early Middle (MNEQ 4 and 5), early Late (MNEQ 9 and 10) and middle Late Miocene (MNEQ 11 and 12) mammal assemblages of Western Asia. I refer to these assemblages as the Arabian, Siwalikan, and Maraghean chronofaunas, after their localities of occurrence, respectively (Ad Dabtiyah and As Sarrar, Saudi Arabia, Siwaliks of Pakistan, and Maragheh, Iran (see also Fig. 1). As demonstrated in sections 4 and 5, the Miocene can be divided into two large cycles: the Early–Middle Miocene, dominated mainly by

closed-, forest-adapted taxa and the Late Miocene, dominated by open-adapted, nonforest taxa. Therefore, the Western Asian chronofaunas investigated are representative of these closed and open environments.

The rise and fall of these major Western Asian chronofaunas were mapped and described over a series of time steps, based on correlation with the MNEQ system (see methods for details). The aim was to observe the relationships of these chronofaunas to their neighboring provinces through the faunal resemblance patterns and determine whether these patterns were related to regional differences in environmental conditions. For this purpose, I investigated the spatial and temporal distribution of two attributes that reflect the regional development of faunas and environments: faunal resemblance and humidity estimated from mean hypsodonty.

I mapped the distribution in space and time of the Arabian, Siwalikan, and Maraghean chronofaunas using Dice (1945), Jaccard (1912), Simpson (1960), and Raup-Crick (1979) similarity indices. All indices gave similar patterns; hence, to be consistent with previous studies (IV), I present the maps depicting Dice index values and the other raw results in Appendix 2. The Dice index weights shared taxon occurrences more profoundly than unique (unshared) taxa, and produced some of the best results among a number of similar indices (Maples and Archer 1988, Archer and Maples 1987). It is calculated as $2C/A+B$, where C is the number of shared taxa between two faunas, and A+B are the total number of taxa in the faunas compared. I also presented the hypsodonty maps (Fig. 6) to follow the patterns of change in humidity and to determine whether there were any relationships between the development of the chronofaunas studied (Fig. 7–9) and the humidity/aridity patterns.

6.1 Results

6.1.1 Arabian chronofauna

Due to the small number of Miocene localities in Western Asia (see Table 3 for regional

extent and Appendix 2 for list of localities), the choice of localities for analytical studies was limited. For the late Early–early Middle Miocene analysis, the Ad Dabtiyah (Whybrow 1987) and As Sarrar (Thomas *et al.* 1982) fossil localities from the continental equivalents

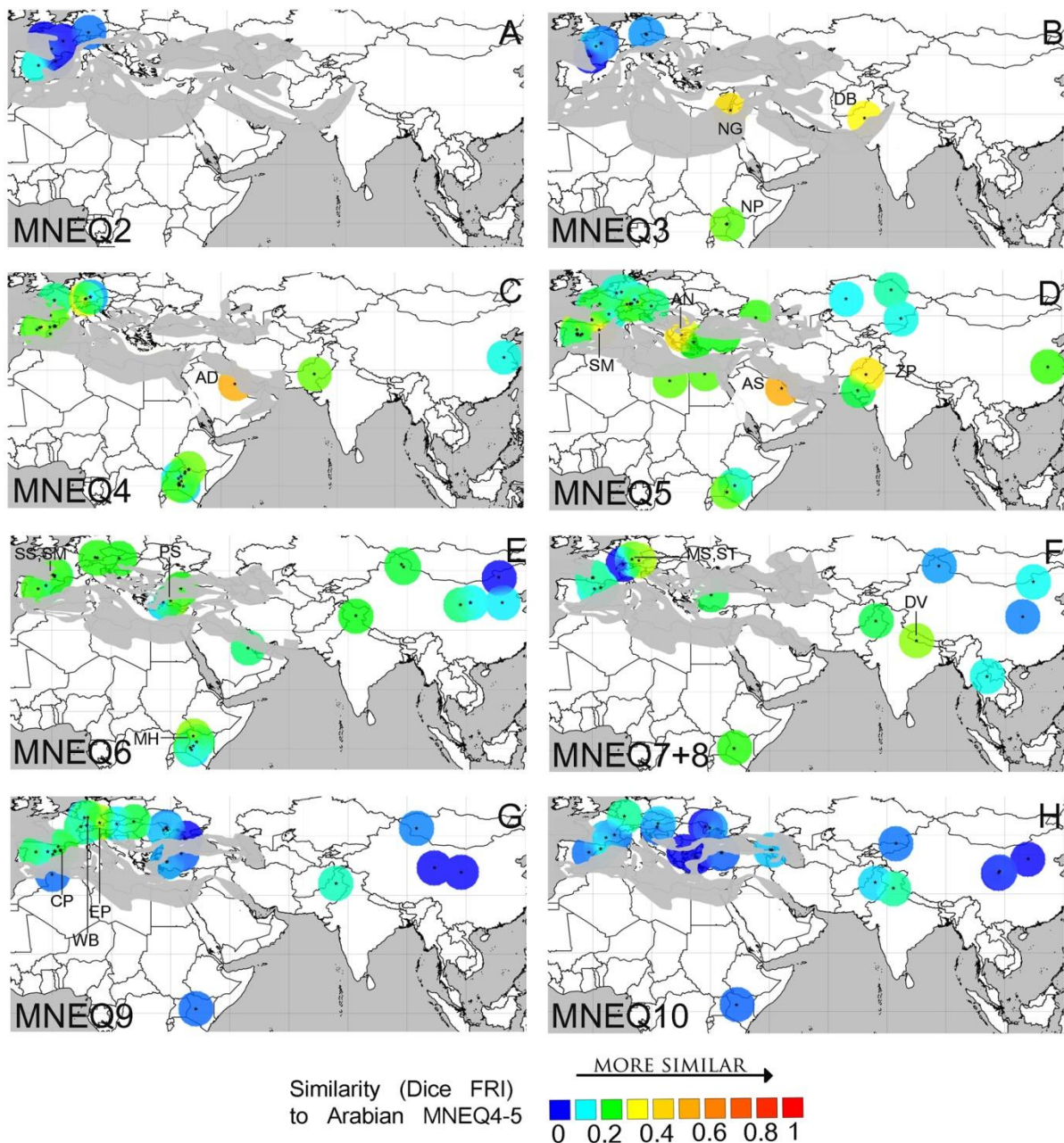


FIGURE 7. Faunal similarity (Dice GFR) to the Arabian MNEQ 4 and 5 faunas at the genus level, mapped for each MN-equivalent (MNEQ) unit during the Miocene. **A)** MNEQ 2, **B)** MNEQ 3 (NP: Napak, NG: Negev, DB: Dera Bugti), **C)** MNEQ 4 (AD: Ad Dabtiyah), **D)** MNEQ 5 (SM: Sant Mamet, AN: Antonios, AS: As Sarrar, ZP: Zinda Pir), **E)** MNEQ 6 (SS: Sansan, SM: Simorre, PS: Paşalar, MH: Muruarot Hill), **F)** MNEQ 7+8 (MS: Massenhausen, ST: Steinheim, DV: Dang Valley), **G)** MNEQ 9 (CP: Can Ponsic, EP: Eppelsheim, WB: Wartenberg), **H)** MNEQ 10. Red and yellow patterns (high GFR) indicate high similarity while blue patterns (low GFR) represent insignificant similarity. Paleogeographic setting of the European and Eastern Mediterranean areas are from Popov *et al.* 2004 (redrawn after Eronen 2006).

of the Dam formation in Saudi Arabia, situated near the western coasts of the Persian Gulf, were used. The age of these localities are placed between 19–16 Ma ago (Whybrow and Clements 1999). Since the MNEQ 4 and 5 are lumped here, the problem of assigning these localities to one of these MNEQ units is not relevant. The early and middle Miocene localities of Pakistan are also present among the Western Asian data. However, they were not selected as the reference chronofaunas, due to their more endemic and distinct provincial nature.

Figure 7 shows the result of the GFRI (Dice index) of the Arabian chronofauna. Figure 7B shows that MNEQ 3 areas similar to Arabia are present in Western Asia. These are the Negev locality (NG in Fig. 7B) in Israel (Dice 0.36) and Dera Bugti 4 (DB in Fig. 7B) of Pakistan (Dice 0.3). Both faunas share "*Dicerorhinus*", *Dorcatherium*, *Eotragus*, and *Gomphotherium* with Arabia. The Negev locality also shares *Canthumeryx* with Arabia, while Bugti shares *Amphicyon*, *Brachypotherium*, and *Bunolistriodon*.

Another locality with moderate similarity is Napak (NP in Fig. 7B) in East Africa (Dice 0.27). Common genera (i. e. those with incidence over 25% throughout the data matrix for the relevant MNEQ zone) at this time are *Amphicyon*, *Brachypotherium*, "*Dicerorhinus*", *Dorcatherium*, *Gomphotherium*, and *Martes*. The humidity according to hypsodonty analysis (Fig. 6B) showed humid conditions for these areas. However, conditions in the localities mentioned above are slightly more arid than in other localities.

More similarity appears during MNEQ 4, where sampling is very good in Europe and Africa, but poor in Asia. Regardless of Ad Dabtiyah, which has a Dice index of 0.6 and is one of the reference points, the area of highest similarity with Arabia in Western Asia is Dera Bugti 6 (Dice 0.24) of Pakistan. Areas highly similar to Arabia (Dice 0.3–0.34) appeared in Western Europe in Spain (Can Canals,

Artesilla, Els Casots) and Germany (Langenau 1) and also in Eastern Africa in Kenya (Rusinga (Kiyune), Uyoma 2 (Chianda N)) and Uganda (Bukwa). Common genera that drove the similarity at this time are: *Aceratherium*, *Brachypotherium*, *Bunolistriodon*, *Canthumeryx*, *Deinotherium*, "*Dicerorhinus*", *Dorcatherium*, *Gomphotherium*, and *Pseudaelurus*.

Hypsodonty analysis at this time (Fig. 6C) also showed cells of increased aridity in Western Europe, Eastern Africa and Western Asia. Nonetheless, the mean hypsodonty values in the above-mentioned localities show that the highest similarity with Arabia is between 1 and 1.2 and hence, these areas are not significantly arid.

During MNEQ 5, when the As Sarrar fauna (Dice 0.6) was present in Arabia, the highest similarity (Dice 0.35) was shown in Antonios (AN in Fig. 7D), Greece, Sant Mamet (SM in Fig. 7D), Spain, and Zinda Pir 3 (ZP in Fig. 7D), Pakistan. In both MNEQ 4 and MNEQ 5, many localities other than these with Dice indices > 0.2 (green patterns in Fig. 7C and D) are also present. Common genera encountered at this time were mostly those of the previous time slice, including: *Brachypotherium*, *Bunolistriodon*, *Canthumeryx*, *Deinotherium*, *Dorcatherium*, *Gomphotherium*, and *Pseudaelurus* with addition of *Amphicyon* and *Eotragus*. The humidity pattern (Fig. 6D) showed the predominance of humid conditions in most of the areas. The exceptions were localities in Anatolia and Caucasus, which were less humid than others.

After MNEQ 5, there were no localities with high similarity (Dice \geq 0.3) to Arabia. Even the Al Jadidah fauna of Saudi Arabia is not similar to the MNEQ 4 and 5 faunas (Dice 0.15). Even so, several localities with Dice = 0.23–0.26 remained until MNEQ 9, mostly in Western Europe. In MNEQ 6 these localities were: Paşalar (PS in Fig. 7E) in Turkey, Sansan and Simorre (SS and SM in Fig. 7E) in France, and Muruarot Hill (MH in Fig. 7E), Kenya. In MNEQ 7+8 Massenhausen and

Steinheim (MS and ST in Fig. 7F), Germany and the Dang Valley (DV in Fig. 7F), Nepal showed the highest similarity and in MNEQ 9 Can Ponsic I (CP in Fig. 7G), Spain and Eppelsheim and Wartenberg (EP and WB in Fig. 7G), Germany were the most similar. The common taxa during MNEQ 6 were: *Amphicyon*, *Brachypotherium*, *Dorcatherium*, *Eotragus*, *Gomphotherium*, *Listriodon*, and *Pseudaelurus*. During MNEQ 7+8, *Eotragus* was out of the list and *Deinotherium* was included. In MNEQ 9 *Amphicyon*, *Brachypotherium*, and *Pseudaelurus* exited the list and *Aceratherium* entered it. The humidity pattern (Fig. 6E) in MNEQ 6 was similar to that of the previous time slice but with more increased aridity, especially in the Eastern Mediterranean and China-central Asia. During MNEQ 7+8, when sampling is quite low, the humid pattern (Fig. 6F) was predominant but the situation changed significantly in the well-sampled MNEQ 9. During this time, the first signs of midlatitude drying become visible. One exception was most of Western Europe, which retained its significantly humid conditions. This is the refugial area for the lingering similarities to Arabia.

6.1.2 Siwalikan chronofauna

The Siwalik series of Pakistan records an exceptionally continuous Neogene record of 18–2 Ma (Pilbeam *et al.* 1996). Significant studies have been carried out on this fauna by American universities and the Geological Survey of Pakistan teams in recent decades (e.g. Barry *et al.* 2002, 1995, 1982). The bulk of fossil material in Siwaliks is from the early Late Miocene localities (Barry *et al.* 2002), which can be correlated with MNEQ 9 and 10 intervals. Hence, the early Late Miocene (MNEQ 9 and 10) fauna of the Siwaliks has been used to study the development of early Late Miocene faunas in Western Asia. The Siwaliks data are being added to the NOW database and will soon become public.

Although the faunas of India-Pakistan

during MNEQ 5 and 6 (e.g. Manchar 1, Zinda Pir 3, and Ramangar) showed slight similarity (Dice 0.15) with the early Late Miocene Siwalikan faunas, the early incarnation of these faunas can be traced to MNEQ 7+8 of India-Pakistan and Southeast Asia. These include the Dang Valley (DV in Fig. 8B), Nepal (Dice 0.19), Chiang Muan (CM in Fig. 8B), Thailand (Dice 0.23), and Siwalik Y0076 (SY in Fig. 8B), Pakistan (Dice 0.26). The common Siwalikan genera during the Middle Miocene were: *Deinotherium*, *Dorcatherium*, *Eotragus*, and *Listriodon*. The humidity analysis during this time (Fig. 6F) showed the prevalence of humid conditions in the areas of higher similarity, even though the midlatitude drying had already started in Eurasia.

During MNEQ 9 and 10, the peak of similarity to the Siwalikan fauna is observed (Fig. 8C and D) in the India-Pakistan area. Low similarity (Dice 0.1–0.13) is observed outside this territory, mainly in Anatolia and Western Europe. Common genera encountered at this time were: *Deinotherium*, *Dorcatherium*, *Gazella*, *Hipparion*, *Listriodon*, and *Propotamochoerus*, while *Elachistoceras*, *Selenoportax*, *Sivapithecus*, and *Tragoportax* also became common in MNEQ 10. Although midlatitude drying continued during this time and increased aridity was visible in Eurasia, the areas of high similarity were still significantly humid (Fig. 6G and H).

During the Late Miocene (MNEQ 11–13), the areas of high similarity were confined again to the India-Pakistan area (Fig. 8E–G). However, some lingering slight similarities to the Siwalikan fauna were visible outside this area, including the MNEQ 11 locality of Injana (IJ in Fig. 8E) in Iraq, MNEQ 12 of Lufeng-Shihuiba (LF in Fig. 8F) in southern China and Baynunah (BY in Fig. 8F) of Arabia, and MNEQ 13 localities of Gravitelli (GV in Fig. 8G), Italy; Sahabi (SH in Fig. 9G), Libya, and Tha Chang 2 (TC in Fig. 8G) of Thailand. All of these localities shared hippopotamids and some other common taxa with the Siwalikan

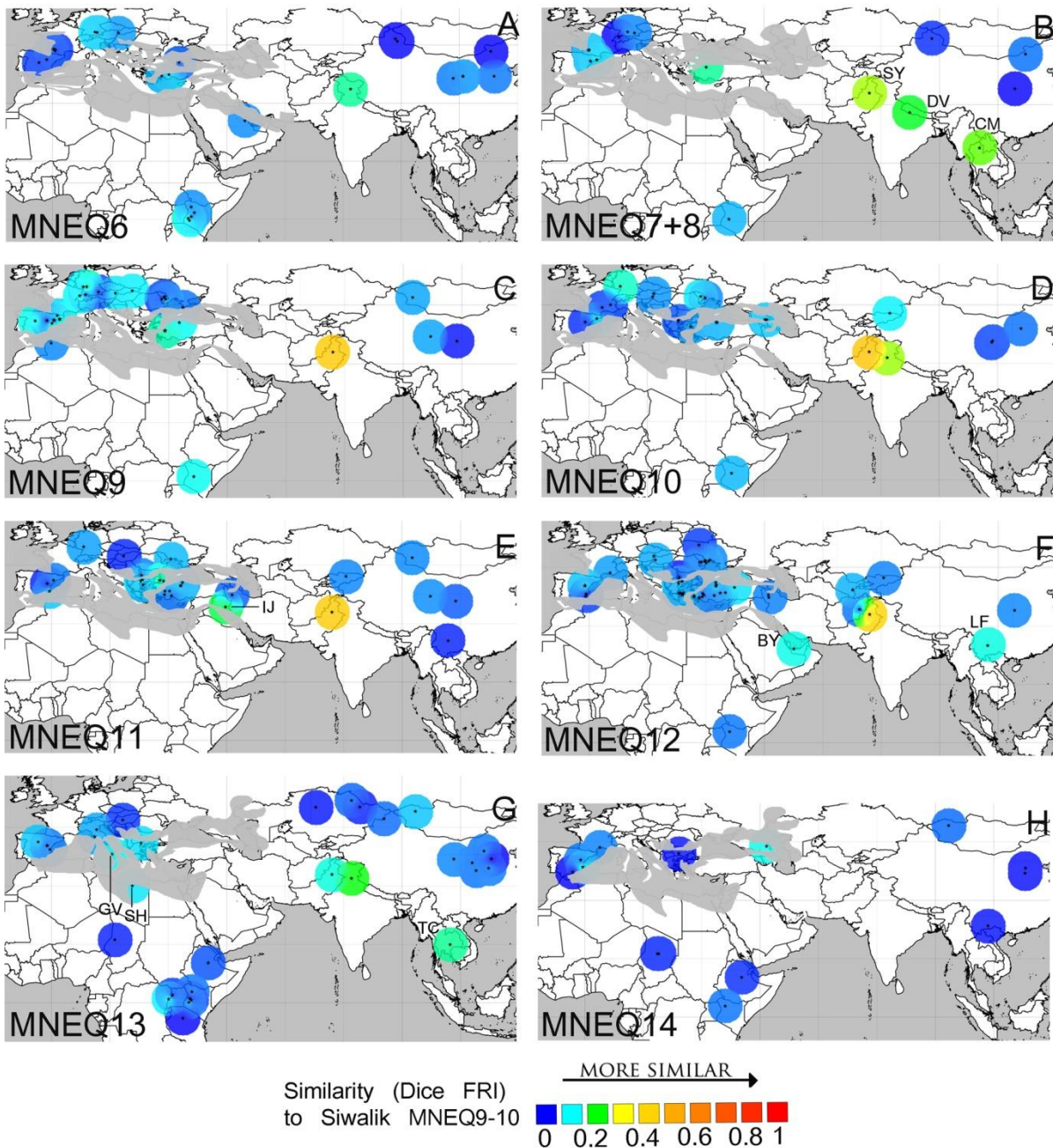


FIGURE 8. Faunal similarity (Dice GFR) to the Siwalik MNEQ 9 and 10 faunas at the genus level, mapped for each MN-equivalent (MNEQ) unit during the Miocene. **A)** MNEQ 6, **B)** MNEQ 7+8 (SY: Siwalik, DV: Dang Valley, CM: Chiang Muan), **C)** MNEQ 9, **D)** MNEQ 10, **E)** MNEQ 11 (IJ: Injana), **F)** MNEQ 12 (BY: Baynunah, LF: Lufeng), **G)** MNEQ 13 (GV: Gravitelli, SH: Sahabi, TC: Tha Chang), **H)** MNEQ 14. Red and yellow patterns (high GFR) indicate high similarity, while blue patterns (low GFR) represent insignificant similarity. Paleogeographic setting of the European and Eastern Mediterranean areas are from Popov *et al.* 2004 (redrawn after Eronen 2006).

fauna. Common taxa during this time were: *Deinotherium*, *Gazella*, *Hipparion*, and *Tragoportax*. *Hexaprotodon* also became more common during MNEQ 13. Hypsodonty maps (Fig. 6I–K) showed increasing aridity during this time. Nevertheless, the faunas showing the greatest similarity with the Siwalikan fauna lived under more humid conditions than the average.

6.1.3 Maraghean chronofauna

The Maraghean fauna of northwestern Iran, along with Samos and Pikermi in Greece, has long been considered as one of the three finest Western Eurasian Late Miocene “Pikermian” chronofaunas (II, V). In Western Asia, even though fossil assemblages are not very abundant, localities similar to the Maraghean fauna were also found in other parts of the region (e. g. Afghanistan and Caucasus). Nonetheless, due to the sheer abundance and diversity of its fauna, Maragheh was chosen as the reference locality. We have recently updated the list of the Maraghean fauna and have addressed some biochronological problems in the correlation of the classical “Pikermian” chronofaunas (V). Although presence of the fauna in MNEQ 11 is possible in the Lower and Middle Maragheh subdivisions, we believe the bulk of fossils from Maragheh can be safely correlated with MNEQ 12.

The early incarnation of the Maraghean fauna can be traced to the MNEQ 9 faunas of Anatolia. The Middle Sinap (MS in Fig. 9C) fauna showed the earliest moderate similarities (Dice 0.24 and 0.28) to the Maraghean fauna. Similarities were also seen in the faunas from other regions, such as Naklai (NK in Fig. 9C) of Kenya (Dice 0.25), Kalfa (KF in Fig. 9C) of Moldova (Dice 0.23), and Can Ponsic I (CP in Fig. 9C) of Spain (Dice 0.23). Common taxa of the Maraghean fauna at this time were: *Deinotherium*, *Gazella*, *Hipparion*, *Hippotherium*, *Miotragoceros*, *Palaeotragus*, and *Thalassictis*.

The humidity patterns (Fig. 6G) showed

strong midlatitude drying in central Asia, but the pattern in the Eastern Mediterranean and Balkan-Anatolia-Iran provinces also showed less humid conditions than areas such as Western Europe, which was quite humid.

During MNEQ 10, the first areas with high similarity emerged in Anatolia, Caucasus, and the northern Black Sea (NBS) area. The localities with the highest similarity were: Grebeniki (GB in Fig. 9D); Dice 0.42, of Ukraine, Sinap 49 (S49 in Fig. 9D); Dice 0.42, Sinap 12 (S12 in Fig. 9D); Dice 0.36, and Gülpınar (GP in Fig. 9D); Dice 0.41, in Turkey, Eldari I (EL in Fig. 9D); Dice 0.34 and Udabno I (UD in Fig. 9D); Dice 0.3, in Georgia, and Can Purull (CP in Fig. 9D); Dice 0.32, Spain. Common Maraghean taxa encountered at this time were: *Chilotherium*, *Choerolophodon*, *Deinotherium*, *Gazella*, *Hipparion*, *Hippotherium*, *Microstonyx*, *Palaeotragus*, and *Tragoportax*. Areas with high similarity to Maragheh appeared strongly arid (Fig. 6H).

During MNEQ 11, areas of high similarity to the Maraghean fauna became expanded and more localities with high similarities (Dice > 0.3) were seen. These localities were present in the same areas as the previous time slice (i.e. EMED, NBS, BAANIR and Spain). Thermopigi (TP in Fig. 9E) and Ravin des Zouaves 5 (RZ in Fig. 9E) of Greece (Dice 0.47 and 0.45), Novaja Emetovka (NE in Fig. 9E) of Ukraine (Dice 0.44), and Karacahasan (KC in Fig. 9E) of Turkey (Dice 0.41) showed the highest similarities to the Maraghean fauna. More Maraghean taxa appeared at this age and became common, including:

Adcrocuta, *Chilotherium*, *Choerolophodon*, *Cremohipparion*, *Deinotherium*, *Gazella*, *Hipparion*, *Hippotherium*, *Ictitherium*, *Indarctos*, *Microstonyx*, *Oioceros*, *Palaeoreas*, *Palaeotragus*, *Prostrepsiceros*, *Samotherium*, and *Tragoportax*. Increased aridity was now widespread in the midlatitudes of Eurasia (Fig. 6I).

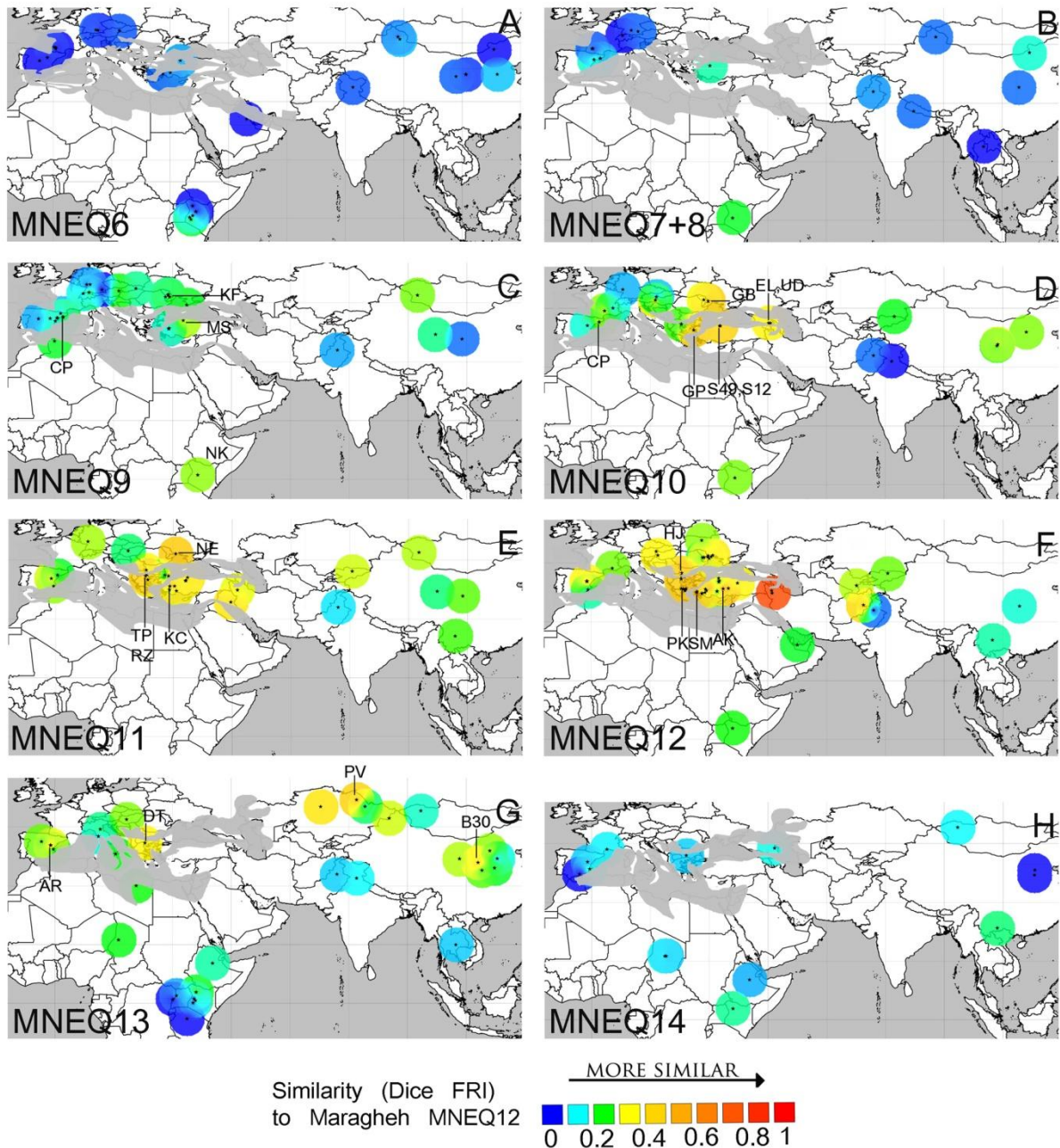


FIGURE 9. Faunal similarity (Dice GFR) to the Maragheh MNEQ 11 and 12 faunas at the genus level, mapped for each MN-equivalent (MNEQ) unit during the Miocene. **A)** MNEQ 6, **B)** MNEQ 7+8, **C)** MNEQ 9 (CP: Can Ponsic, KF: Kalfa, MS: Middle Sinap, NK: Nakali), **D)** MNEQ 10 (CP: Can Purull, GB: Grebeniki, S49: Sinap 49, S12: Sinap 12, GP: Gülpinar, EL: Eldari, UD: Udabno), **E)** MNEQ 11 (TP: Thermopigi, RZ: Ravin des Zouaves, NE: Novaja Emetovka, KC: Karacahasan), **F)** MNEQ 12 (HJ: Hadjidimovo, PK: Pikermi, SM: Samos, AK: Akkaşdağı), **G)** MNEQ 13 (AR: Arquillo, DT: Dytiko, PV: Pavlodar, B30: Baode loc. 30), **H)** MNEQ 14. Red and yellow patterns (high GFR) indicate high similarity, while blue patterns (low GFR) represent insignificant similarity. Paleogeographic setting of the European and Eastern Mediterranean areas are from Popov *et al.* 2004 (redrawn after Eronen 2006).

MNEQ 12 was the climax time of the Maraghean chronofauna. High similarity to this fauna was now visible from Spain to Afghanistan. However, localities with the highest similarity were found in Greece and Anatolia. These localities were: Samos (SM in Fig. 9F), Pikermi (PK in Fig. 9F), and Halmyropotamos in Greece (Dice 0.5-0.6), Hadjidimovo-1 (HJ in Fig. 9F) in Bulgaria (Dice 0.55), and Akkaşdağı (AK in Fig. 9F) in Turkey (Dice 0.56). Common Maraghean taxa of this age included:

Adcrocuta, *Amphimachairodus*, *Ancylotherium*, *Chilotherium*, *Choerolophodon*, *Cremohipparion*, *Deinotherium*, *Gazella*, *Hipparion*, *Hippotherium*, *Ictitherium*, *Mesopithecus*, *Metailurus*, *Microstonyx*, *Oioceros*, *Orycteropus*, *Palaeoreas*, *Palaeoryx*, *Palaeotragus*, *Prostrepsicerus*, *Protragelaphus*, *Samotherium*, *Thalassictis*, and *Tragoportax*. Most of these were present in the previous time slice as well. Aridity was now widespread in all Eurasia, with the exception of a few areas (green patterns in Fig. 6J).

MNEQ 13 was a critical time for the Maraghean fauna. Strangely, there is no significant locality at this time in the core area (BAANIR province), which witnessed the predominance of the Maraghean chronofauna in the previous time. As far as current data suggest, the Maraghean chronofauna moved mostly toward the East to the central Asia and north China, where now the highest similarities to Maragheh are observed. The most localities similar to Maragheh at this time were: Pavlodar (PV in Fig. 9G), Kazakhstan (Dice 0.4), Qingyang loc.115 and Baode loc. 30 (B30 in Fig. 9G), China (Dice 0.37), Dytiko 1 (DT in Fig. 9G), Greece (Dice 0.39), and Arquillo 1 (AR in Fig. 9G), Spain (Dice 0.33). Of the common Maraghean taxa of the previous time slice, *Adcrocuta*, *Chilotherium*, *Cremohipparion*, *Gazella*, *Hipparion*, *Hippotherium*, *Ictitherium*, *Indarctos*, *Metailurus*, *Palaeotragus*, *Samotherium*, *Thalassictis*, and *Tragoportax* continued to thrive at this time. The aridity pattern at this time (Fig. 6K) also showed predominance of

arid cells in the areas of high similarity with Maragheh across Eurasia. Where more humid conditions prevailed, the similarity to Maragheh was quite low.

MNEQ 14 is the end of the Maraghean chronofauna history, with no locality with significant similarity seen across the Old World, even though arid cells continued to be present in some areas (Fig. 6L).

6.2 Discussion

6.2.1 Arabian chronofauna

The high similarity pattern in the MNEQ 3 localities of Negev and Bugti (Pakistan) with the Arabian MNEQ 4 and 5 faunas showed the presence of a mixture of African and Asian elements in Arabia. The Negev fauna, which represented the first evidence for exchange of faunas between Africa and Asia (Koufos *et al.* 2005, Tchernov *et al.* 1987) and also the proboscidean datum in Pakistan, which is now believed to be older than 20 Ma (Lindsay *et al.* 2005), indicated a connection between Arabia and Western Asia well before the “*Gomphotherium* landbridge” in MNEQ 4. Such an earlier (Late Oligocene–earliest Miocene) connection between Africa and Eurasia was proposed previously (Morlo *et al.* 2007, Pickford 2001, Morales *et al.* 2000, Adams *et al.* 1999, 1983, Van der Made 1999, Whybrow 1984) and new paleogeographic reconstructions (Popov *et al.* 2006, 2004) indicated its feasibility.

In MNEQ 4 the landbridge connection to Europe resulted in areas with high similarity in Western and central Europe. During MNEQ 5, although the landbridge temporarily vanished, areas of high similarity were present in Western-central Europe, Eastern Mediterranean and Western Asia. This indicated either an interchange of taxa between these areas well before MNEQ 5 or pulses of land connections during MNEQ 5. The presence of several

species of Canthumerycinae (Giraffidae) with mutually close affinities at this time in the above-mentioned areas and Africa-Arabia (Geraads and Aslan 2003, Thomas *et al.* 1999) support this idea. By MNEQ 6, the areas of high similarity were gone, but some localities with moderate similarity continued to thrive, especially in Western Europe, until they also disappeared at the end of MNEQ 9. This coincided with the Vallesian Crisis, which caused the extinction of the Western European forest faunas (Agustí *et al.* 2003, Agustí and Moya-Sola 1990). This was further evidence for the closed-adapted nature of the Arabian MNEQ 4 and 5 faunas and contrasted with previously suggested more open woodland/bushland environments for the Early Miocene of Arabia (Kingston and Hill 1999).

The humidity pattern based on hypsodonty analysis showed no significant association of the Arabian MNEQ 4 and 5 faunas with more arid conditions. Conversely, the increased aridity reflected in the sabkha and dune deposits of Arabia during Middle Miocene time (Kingston and Hill 1999) and opening of the environment, which was inferred from the MNEQ 6 Al Jadidah fauna (Sen and Thomas 1979, Thomas *et al.* 1978) may explain the demise of the Arabian MNEQ 4 and 5 chronofaunas. This shows that the Arabian faunas in particular and the Western Asian faunas in general were not similar to the *Hispanotherium* fauna. This chronofauna inhabited the seasonal dry conditions of the lower Middle Miocene of the Iberian Peninsula in Europe (Agustí and Antón 2002, Antunes 1979). They extended their range to Eastern Asia later in the terminal Middle Miocene, following the widening arid belt towards the East (IV). The Arabian MNEQ 4 and 5 faunas were probably adapted to humid conditions. Therefore, increased humidity in Europe and development of midlatitude aridity may explain the lingering similarities to Arabia in Western and central Europe until MNEQ 9.

6.2.2 Siwalikan chronofauna

Bernor (1984, 1983) pointed to the zoogeographically distinct nature of the Siwalik faunas and province. I performed locality clustering that also showed the endemic character of the Siwaliks. However, faunas showing high similarity to the early Late Miocene Siwalik fauna are found within Southeast Asia and the Indian subcontinent. The subtropical, forested conditions apparently lasted longer in the Siwaliks, even longer than in Western Europe (Agustí *et al.* 1999). Only in the middle Late Miocene did the open-adapted taxa also affect the Siwalik province. The longer persistence of forested conditions in the Siwaliks may have reflected strong monsoonal influence in the area (Leakey and Harris 2003, Agustí *et al.* 1999). Results of a new fullycoupled atmosphere-ocean model simulation for the Tortonian (11–7 Ma ago) showed increased monsoon rainfall over the Indian subcontinent (Micheels *et al.* 2010).

Nonetheless, previous evidence for intensification of the Indian monsoons postdated the early Late Miocene (An *et al.* 2001), which more likely coincided with the expansion of C₄ grasses in the region (Cerling *et al.* 1997, Quade and Cerling 1995, Quade *et al.* 1992, 1989). A major ecological change also occurred during the late Late Miocene (Badgley *et al.* 2008, Barry *et al.* 2002, Pilbeam *et al.* 1996), while hypsodonty analysis (Fig. 6I and J) indicates increased aridity in the region.

Evidence for interprovincial connections between Siwalik-Southeast Asia (SIWSEAS) and other provinces, especially with Africa-Arabia (AFRARB) were noted from both large (e.g. Koufos *et al.* 2003, Werdelin 2003, Pickford 2001, Gentry 1999, Van der Made 1999, Barry *et al.* 1991) and small (e.g. Wessels 2009, López-Antonanzas and Sen 2003, 2004, Flynn and Jacobs 1999) mammal data. From nonmammalian groups, crocodiles are good examples of interprovincial,

paleoenvironmental, and paleoecological connections and similarities between the SIWSEAS and AFRARB localities (e.g. Storrs 2003, Rauhe *et al.* 1999). They were present in many localities in these provinces, but are rarely found in other areas.

This is supported by provinciality analysis of this research, which showed clusters of most of the Siwaliks and Indian subcontinent faunas close to the AFRARB assemblages. In addition to the Early and Middle Miocene interchange of taxa between these provinces, which was discussed in the previous section, the late Miocene also witnessed a number of exchanges. The hipparionine horses of the *Sivalhippus* group are one of the examples, which entered Africa during the middle Late Miocene and are closely related to the African *Eurygnathohippus* lineages (Bernor and Harris 2003, Bernor and Armour-Chelu 1999). The Hippopotamidae are another example of association between these regions (Weston 2003). They drove the lingering similarity observed between the Siwaliks and some MNEQ 13 faunas of AFRARB and Eastern Mediterranean (see section 6 results under Siwalikan chronofauna).

The role played by high mountains as an obstacle to migration of the Siwalikan elements northward is evident. The Turolian locality of Molayan in Afghanistan showed that even at close proximity, the mammalian faunas on opposite sides of the mountains are completely different (Brunet *et al.* 1984, Heintz and Brunet 1982). Indeed, one can mark a borderline between the SIWSEAS and Balkan-Anatolia-Iran (BAANIR) provinces through the mountains separating these two localities. The alpine mountains within Western Asia (i.e. the Taurids, Zagrids, Beloutches, and Himalayas) apparently played a major role in preventing northward immigration of taxa between AFRARB, the Siwaliks, and BAANIR. Good examples include the cervids, which did not enter the Indian subcontinent until the Pliocene-

Pleistocene, due to this barrier (Heintz *et al.* 1990, Heintz and Brunet 1982), and the anthracotheres such as *Merycopotamus* which were limited to the south of the Asian alpine arc (Lihoreau *et al.* 2007). Nevertheless, some taxa passed through this barrier. The gerbil *Abudhabia* is an example that was found in the late Late Miocene of Africa (Wessels 2009, Winkler 2003), Arabia (Bruijn and Whybrow 1994), Pakistan (Flynn and Jacobs 1999), Afghanistan (Sen 1983), and China (Qiu *et al.* 2004). *Prostrepsiceros* aff. *vinayaki* is another example, now believed to have been present in Maragheh (V). Recently, a new species of *Sivatherium* was also recorded from the Late Miocene-Pliocene of Macedonia, which showed association with Africa and Western Asia (Geraads 2009).

The most likely route for such migrations was along the southern paths of these alpine mountain belts, from Baluchistan to southern Iran and along the Persian Gulf and Zagross Mountains to Anatolia and Africa.

Merycopotamus, app. 10 Ma ago, followed a similar direction through the connection of the drainage systems to disperse from the Indian subcontinent to the Injana locality in Iraq (Lihoreau *et al.* 2007). This locality clearly had broad associations with the “Pikermian” chronofaunas of its surroundings (Bouvrain *et al.* 1995, Bouvrain and Thomas 1992, Brunet and Heintz 1983) and Arabia (Friend 1999), and may have been a hub for the interaction of Late Miocene Western Asian province

6.2.3 Maraghean chronofauna

The Maraghean chronofauna is clearly not distinct from the “Pikermian” chronofauna, either in its taxonomic content (V) or in its distribution history (II). Figure 10A shows the trend of mean similarity of Old World localities to Pikermi and Maragheh in the Miocene. The graph clearly illustrates the high mutual similarity of these chronofaunas over time. The development of these chronofaunas

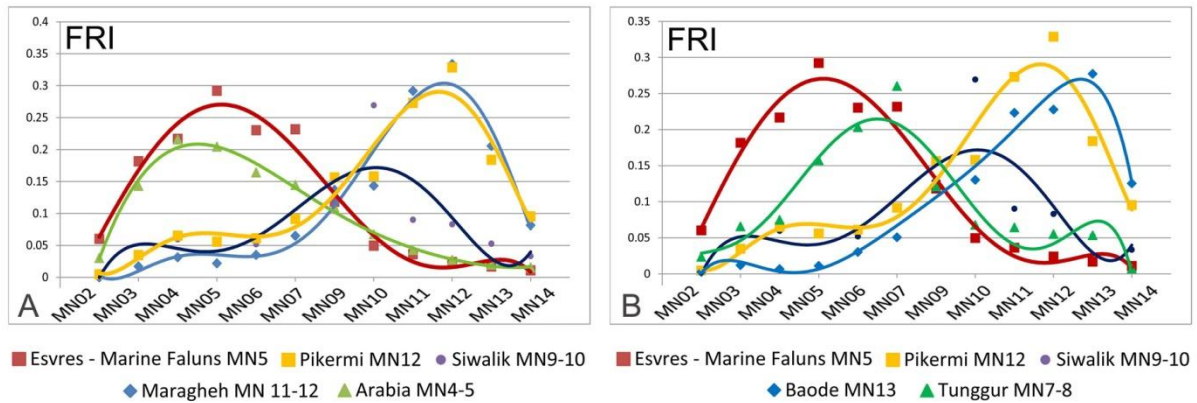


FIGURE 10. Trend lines of average similarity to the: **(A)** Western Asian chronofaunas (Arabian, Siwalikan, and Maraghean) and **(B)** Eastern Asian chronofaunas (Baodean and Tunggurian), compared with the “Pikermian” and European Middle Miocene (Esvres-Marine Falunes) chronofaunas. Trend lines are polynomial 4th order. Dots represent average points. the MN units are MN-equivalents (MNEQ).

during the Late Miocene was closely related to the expansion and contraction of seasonal aridity across Eurasia. The onset of midlatitude drying apparently marked the early development of these chronofaunas, and subsequent environmental, climatic, and paleogeographic processes facilitated their time-transgressive expansion (II).

The evidence indicates high faunal similarity between Pikermi, Samos, and Maragheh as the classical representatives of the “Pikermian” chronofauna (V). Maragheh is paleoecologically located somewhere between Pikermi and Samos (Koufos *et al.* 2009). Maragheh, like Pikermi (Solounias *et al.* 1999), had more wooded settings (V) than Samos (Koufos *et al.* 2009), but on the other hand, like Samos had enough open habitats to sustain its high number of mixed-feeders and hypsodont grazers. It is worth mentioning that the evidence for the presence of C₄ grasses was also found in Maragheh (Strömberg *et al.* 2007). Solounias *et al.* (2010) proposed a model for the “Pikermian” chronofauna (Pikermi and Samos) that is similar to present day Kanha Park in India. This habitat is woodland with large areas of small trees, as well as dense forest and grassy regions that can support a significant number of browsing and

mixed-feeding herbivores.

The latest Miocene climatic and environmental changes, such as the demise of the Paratethys in central Asia and the Messinian Salinity Crisis, were apparently detrimental to the open-adapted chronofaunas of Eurasia (Kostopoulos 2009). Probably, increased humidity and forestation after a period of increased seasonality and regional differentiation caused the extinction of these chronofaunas from their core areas (II). These chronofaunas could have been the precursors of those of the African woodlands, since some of their species extended their ranges into Africa (Bernor *et al.* 2009, Bernor and Rook 2008, Werdelin 2003) and likely evolved into the Pliocene-Pleistocene and recent biomes of East Africa (Solounias *et al.* 1999).

6.3 Conclusions

Chronofaunas, such as individual species and genera, typically appear to have unimodal histories including buildup, climax, and decline. The chronofaunas investigated here developed in two different ways. The closed-adapted chronofaunas (e.g. Arabian chronofauna) appear to have undergone rapid buildup and gradual decline (Fig. 10A). On the

other hand, the open-adapted chronofaunas (e.g. Maraghean, “Pikermian”, Baodean chronofaunas) evidently experienced a gradual buildup and an abrupt decline (Fig. 10A and B). This is in contrast to the individual genera and species of these faunas, in which rise and fall appeared symmetrical (Jernvall and Fortelius 2004). For the closed-adapted chronofaunas, the reason for the rapid buildup could have been the unique or older histories of their taxa, which were not sampled or were excluded from the data studied. Their gradual decline, on the other hand, indicated continuous change from a more closed forested habitat toward more open conditions, as a result of the increase in seasonality after the Middle Miocene cooling event. As the numbers of closed-adapted taxa decreased progressively, the numbers of open-adapted taxa rose to fill the unoccupied niches. The abrupt decline in the open-adapted chronofauna may have indicated their strong dependence on specific environments. Consequently, an environmental reversal towards more humid and closed conditions caused their sudden decline. The Siwalikan chronofauna is unique, because it appears to have been more symmetrical than others (Fig. 10A and B). The significantly lower peak of this chronofauna is apparently the result of its geographical confinement and limited regional extension.

7. Concluding remarks

As a summary of the various results and discussions, the following conclusions are presented:

-With the paucity of body fossil localities in vast areas of Western Asia, mammalian trace fossils such as the footprints discovered in the northern parts of Iran can provide information on mammalian faunas and their habitats during the Miocene.

-Discovery of new fossil localities much further north than the famous Maragheh sites, in northwestern Iran, is increasing our understanding of the Late Miocene mammalian faunas in the area. The presence of fossil mammal localities other than Maragheh shows the favorable potential of northwestern Iran for new findings.

-New excavations and multidisciplinary research in the Maragheh area is updating our understanding of the mammalian fauna of Maragheh and will facilitate better comprehension of critical topics, such as geo- and biochronology, habitats, paleodiets, and paleoecology.

-Clustering of 407 Miocene large mammal fossil assemblages from the Old World resulted in two megaclusters, one grouping mostly the Early–Middle Miocene faunas and the other, the Late Miocene localities.

-The early Late Miocene faunas of Western European and the Siwaliks clustered in the Early–Middle Miocene. This reveals that the Early–Middle Miocene cluster represented the closed-adapted (forest) faunas and the other, the open-adapted (nonforest) faunas.

-Four mutually interacting faunal provinces in Western Asia (Balkan-Anatolia-Iran, north China-central Asia, Siwalik-Southeast Asia, and Africa-Arabaia) can be distinguished according to the clusters. Some of these faunal provinces were previously known to some extent, and are modified here.

-The Western Asian localities in the Early–Middle Miocene formed a single cluster, but in the Late Miocene they failed to do so. This reflects the increased provinciality of the later Miocene in this region, due to paleoclimatic and paleogeographic configurations.

-To quantify the relative abundance history of mammals in the closed (Early–Middle Miocene) and open (Late Miocene) habitats, two groups of mammals were defined: closed-adapted taxa including Anthracotheriidae, Cervidae, Hippopotamidae, Moschidae, Proboscidea, Palaeomerycidae, Suoidea, Tapiridae, and Tragulidae and open-adapted taxa including Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae**.

-The relative abundance patterns of the open- and closed-adapted taxa showed the climax of the closed-adapted taxa during the Middle Miocene Climatic Optimum and the acme of the open-adapted taxa in the Late Miocene.

-Warmer climatic conditions and probably high atmospheric CO₂ concentrations could have increased the primary productivity in the late Early–Middle Miocene that sustained the forested environments and hence the abundance of closed-adapted taxa.

-The subsequent cooling event and the progressive increase in seasonality caused the decline in the closed-adapted taxa. The onset of midlatitude drying and the expansion of seasonally arid environments in Eurasia facilitated the success of the open-adapted taxa.

-The “Pikermian” chronofauna developed in response to the increased aridity and seasonality patterns in the Eastern Mediterranean region. This occurred due to midlatitude drying and a number of changes in paleogeography, as well as climatic configurations, that caused changes in the precipitation patterns.

-The Baodean and Tunggurian chronofaunas both came to China from the West, in association with moving patterns of aridity. They were subsets of the “Pikermian” and *Hispanotherium* chronofaunas of the West. However, the Baodean chronofauna, unlike its Western counterpart, had numerous endemic taxa.

-The distribution history of the late Early–early Middle Miocene Arabian chronofauna includes a rapid buildup and climax in MNEQ 4 and 5, in relation to humid conditions, and a gradual decline. This pattern was similar to that of the Western European localities such as Esvres-Marine-Faluns and means that the Arabian chronofauna can be regarded as a subset of the Western European chronofaunas.

-The early Late Miocene Siwalikan chronofauna is restricted in distribution to the Siwaliks and Southeast Asia with very limited connections to the outside.

-The Late Miocene (Turolian) Maraghean chronofauna developed as did the “Pikermian” chronofauna. It showed a gradual buildup and climax in MNEQ11 and 12. It later moved eastward before an abrupt decline in the latest Miocene–Pliocene. The history of this chronofauna is closely associated with aridity and seasonality patterns.

-The closed-adapted chronofaunal buildup was rapid and their decline gradual in contrast to those of the open-adapted chronofaunas. This could have been due to the unique or unrecorded history of the closed-adapted taxa and strong dependence of the open-adapted taxa on their seasonal, arid environments that were severely disrupted and reversed in the terminal Miocene.

References

- Abbassi**, N. and Amini, A. 2008. Ichnology of Miocene Vertebrate footprints in the Upper Red Formation, Evan-e-key section, east of Tehran, Iran. *Geosciences* 17:54-67 (In Persian with English abstract).
- Abbassi**, N. and Shakeri, S. 2005. Miocene vertebrate footprints from the Upper Red Formation, Mushampa area, Zanjan province: *Geosciences* 12:76-89 (In Persian with English abstract).
- Abich**, H. W. 1858. Tremblement de terre observe a Tebriz en Septembre 1856, notices physiques et gographiques de M. Khanykof sur l'Azerbeidjan. *Bulletin de l'Academie (Imperiale) des Sciences de Saint Petersburg, Classe Physico-Mathematique*. 382 XVI-22 notes 27:339-352.
- Adams**, C. G., Bayliss, D. D. and Whittaker, J. E. 1999. The terminal Tethyan event: a critical review of conflicting age determinations for the disconnection of the Mediterranean from the Indian Ocean. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), New Haven, Yale University Press, p. 477-484.
- Adams**, C. G., Gentry, A. W. and Whybrow, P. J. 1983. Dating the terminal Tethyan events. In: *Reconstruction of Marine Environments* (ed. Meulenkamp, J.), *Utrecht Micropaleontological Bulletins* 30:273-298.
- Aghanabati**, A. 2004. Geology of Iran. Geological Survey of Iran Press (In Persian).
- Agustí**, J., Sanz de Siria, A. and Garcés, M. 2003. Explaining the end of the hominoid experiment in Europe. *Journal of Human Evolution* 45:145-153.
- Agustí**, J. and Antón, M. 2002. Mammoths, Sabertooths, and Hominids; 65 Million Years of Mammalian Evolution in Europe. New York, Columbia University Press.
- Agustí**, J., Cabrera, L., Garcés, M. and Llenas, M. 1999. The late Miocene terrestrial record in the Vallès-Penedès Basin: Mammal turnover and Global climate change. In: *The Evolution of Neogene Terrestrial Ecosystems in Europe* (eds. Agustí, J., Rook, L. and Andrews, P.), Cambridge University Press, p. 397-412.
- Agustí**, J., Cabrera, L., Garcés, M. and Parés, J.M. 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133:149-180.
- Agustí**, J. and Moya-Sola, S. 1990. Mammal extinctions in the Vallesian (Upper Miocene). *Lecture Notes in Earth Science* 30:425-432.
- Akgün**, F., Kayseri, M. S., Akkiraz, M. S. 2007. Palaeoclimatic evolution and vegetational changes during the Late Oligocene-Miocene period in Western and Central Anatolia (Turkey). *Palaeogeography, Palaeoclimatology, Palaeoecology* 253:56-90.
- Alçiçek**, H. 2010. Stratigraphic correlation of the Neogene basins in southwestern Anatolia: Regional palaeogeographical, palaeoclimatic and tectonic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291:297-318.
- Alavi**, M. 2004. Regional stratigraphy of the Zagros fold-thrust belt of Iran and its proforeland evolution. *American Journal of Science* 304:1-20.
- Alavi**, M. 1994. Tectonics of the Zagros orogenic belt of Iran: new data and interpretations. *Tectonophysics* 229:211-238.
- Alroy**, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography Palaeoclimatology Palaeoecology* 127:285-311.
- Amini**, A. 1997. Provenance and Depositional Environment of the Upper Red Formation, Central Zone, Iran. Ph.D. dissertation, University of Manchester.
- Andrews**, P. 1990. Palaeoecology of the Miocene fauna from Paşalar, Turkey. *Journal of Human Evolution* 19:569-582.
- Andrews**, P. J. and Van Couvering, J. H. 1975. Palaeoenvironment in the East African Miocene. In: *Approaches to Primate Paleobiology* (eds. Szalay, F. S. and Karger, B.), p. 62-103.
- An**, Z., Kutzbach, J. E., Prell, W. L. and Porter, S. C. 2001. Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan Plateau since Late Miocene times. *Nature* 411:62-66.
- Antunes**, M. T. 1979. *Hispanotherium* fauna in Iberian Middle Miocene, its importance and paleogeographical meaning. *Annales Geologiques Des Pays Helleniques*: 19-26.
- Archer**, A.W. and Maples, C. G. 1987. Monte Carlo simulation of selected binomial similarity coefficients (1): effect of number of variables.

Palaios 2:609-617.

-Axelrod, D. I. and Raven, P. H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In: *Biogeography and Ecology of Southern Africa* (ed. Werger, M. J. A.), Junk, p. 77-129.

-Badgley, C., Barry, J. C., Morgan, M. E., Nelson, S. V., Behrensmeyer, A. K., Cerling, T. E. and Pilbeam, D. 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences* 105:12145-12149.

-Bajgusheva, S. V. and Titov, V. V. 2006. About teeth of *Deinotherium giganteum* Kaup from eastern Paratethys. *Hellenic Journal of Geology* 41:177-182.

-Barry, J. C., Morgan, M. E., Flynn, L. J., Pilbeam, D., Behrensmeyer, A. K., Raza, S. M., Khan, I. A., Badgley, C., Hicks, J. and Kelley, J. 2002. Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Paleobiology* 28:1-71.

-Barry, J. C., Morgan, M. E., Flynn, L. J., Pilbeam, D., Jacobs, L. L., Lindsay, E. H., Raza, S. M. and Solounias, N. 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:209-226.

-Barry, J. C., Morgan, M. E., Winkler, A. J., Flynn, L. J., Lindsay, E. H., Jacobs, L. L. and Pilbeam, D. 1991. Faunal interchange and Miocene terrestrial vertebrates of southern Asia. *Paleobiology* 17:231-245.

-Barry, J. C., Lindsay, E. H. and Jacobs, L. L. 1982. A biostratigraphic zonation of the Middle and Upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:95-130.

-Bernor, R. L., Rook, L. and Haile-Selassie, Y. 2009. Paleobiogeography. In: *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia* (eds. Haile-Selassie, Y. and Wolde Gabriel, G.), University of California Press, p. 549-563.

-Bernor, R. L. and Rook, L. 2008. A Current View of As-Sahabi Large Mammal Biogeographic Relationships. In: *Circum-Mediterranean Geology and Biotic Evolution during the Neogene Period: The Perspective from Libya* (eds. Boaz, N.T., El-Arnauti, A., Pavlakis, P. and Salem, M.J.), Garyounis Scientific Bulletin, Special Issue 5:285-

292.

-Bernor, R. L. and Harris, J. M. 2003. Systematics and Evolutionary Biology of the Late Miocene and Early Pliocene Hipparionine Equids from Lothagam, Kenya. In: *Lothagam, The Dawn of Humanity in Eastern Africa* (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 387-439.

-Bernor, R.L., Fortelius, M. and Rook, M. 2001. Evolutionary Biogeography and Paleoecology of the *Oreopithecus bambolii* Faunal Zone (Late Miocene, Tusco-Sardinian Province). *Bollettino della Societa Paleontologica Italiana* 40:139-148.

-Bernor, R. and Armour-Chelu, M. 1999. Family Equidae. In: *The Miocene Land Mammals of Europe* (eds. Rössner, G. E. and Heissig, K.), Verlag Dr Friedrich Pfeil, p. 193-202.

-Bernor, R. L., Solounias, N., Swisher III, C. C. and Van Couvering, J. A. 1996. The correlation of three classical "Pikermian" mammal faunas-Maragheh, Samos and Pikermi-with the European MN unit system. In: *The Evolution of Western Eurasian Neogene Mammal Faunas* (eds. Bernor, R. L., Fahlbusch, V. and Mittmann, H. W.), Columbia University Press, p. 137-156.

-Bernor, R. L. and Pavlakis, P. P. 1987. Zoogeographic relationships of the Sahabi large mammal fauna. In: *Neogene Paleontology and Geology of Sahabi* (eds. Boaz, N. T., El-Arnauti, A., Gaziry, A. W., De Heinzelin, J. and Boaz, D. D.), Alan Liss Press, p.349-384.

-Bernor, R. L. 1986. Mammalian biostratigraphy, geochronology, and zoogeographic relationships of the Late Miocene Maragheh fauna, Iran. *Journal of Vertebrate Paleontology* 6:76-95.

-Bernor, R. L. 1985. Systematic and evolutionary relationships on the hipparionine horses from Maragheh, Iran (Late Miocene, Turolian age). *Palaeovertebrata* 15:173-269.

-Bernor, R. L. 1984. A zoogeographic theater and a biochronologic play: the time/biofacies phenomena of Eurasian and African Miocene mammal provinces. *Paléobiologie Continentale* 14:121-142.

-Bernor, R. L. 1983. Geochronology and zoogeographic relationships of Miocene Hominoidea. In: *New Interpretations of Ape and Human Ancestry* (eds. Ciochon, R. L. and Corruccini, R. S.), Plenum Press, p. 21-64.

-Bernor, R. L., Woodburne, M. O. and Van Couvering, J. A. 1980. A contribution to the

chronology of some Old World faunas based on hipparionine horses. *Geobios* 13:25-59.

-Bernor, R.L. Andrews, P.A., Solounias, N. and Van Couvering, J.A. 1979. The evolution of Pontian mammal faunas: some zoogeographic, paleoecological and chronostratigraphic considerations. *Annales Geologiques Des Pays Helleniques*: 81-89.

-Bernor, R. L. 1978. The Mammalian Systematics, Biostratigraphy and Biochronology of Maragheh and its Importance for Understanding Late Miocene Hominoid Zoogeography and Evolution. Ph.D. dissertation, University of California, Los Angeles.

-Bibi, F., Shabel, A. B., Kraatz, B. P. and Stidham, T. A. 2006. New Fossil Ratite (Aves: Palaeognathae) Eggshell Discoveries from the Late Miocene Baynunah Formation of the United Arab Emirates, Arabian Peninsula. *Palaeontologia Electronica* 9:http://palaeoelectronica.org/paleo/2006_1/eggshell/issue1_06.htm

-Boaz, N. T. 2008. A View to the South: Eo-Sahabi Palaeoenvironments Compared and Implications for Hominid Origins in Neogene North Africa. In: *Circum-Mediterranean Geology and Biotic Evolution during the Neogene Period: The Perspective from Libya* (eds. Boaz, N. T., El-Arnauti, A., Pavlakis, P. and Salem, M. J.), *Garyounis Scientific Bulletin*, Special Issue 5:292-308.

-Boaz, N. T., El-Arnauti, A., Pavlakis, P. and Salem, M. J. (eds.) 2008. Circum-Mediterranean Geology and Biotic Evolution during the Neogene Period: The Perspective from Libya. *Garyounis Scientific Bulletin*, Special Issue 5.

-Boaz, N. T., El-Arnauti, A., Gaziry, A. W., De Heinzelin, J. and Boaz, D. D. (eds.) 1987. Neogene Paleontology and Geology of Sahabi. Alan R. Liss. Inc.

-Bonis, L. de, Brunet, M., Heintz, E. and Sen, S. 1992. La province greco-irano-afghane et la repartition des faunes mammaliennes au Miocene superieur. *Paleontologia i Evolucio* 24-25:103-112.

-Bouvrain, G., Sen, S. and Thomas, H. 1995. *Parurmiatherium rugosifrons* Sickenberg 1932, Ovibovine (Bovidae) from the late Miocene of Injana (Jebel Hamrin, Irak). *Geobios* 28:719-726.

-Bouvrain, G. and Thomas, H. 1992. Une antilope chevilles spirales: *Prostrepsiceros zitelli* (Bovidae). Miocene superieur du Jebel Hamrin en Irak.

Geobios 25:525-533.

-Böhme, M. 2003. Miocene Climatic Optimum: evidence from lower vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195:389-401.

-Brandt, J. F. 1870. Ueber die von Herrn Magister Adolph Goebel auf Seiner Persischen Reise bie der Stadt Maragha in der Provinz Azerbeidjan gefundenen Säugethier-Reste. *Denkschrift Naturforscher-Vereins zu Riga*, 1-8.

-Bruch, A. A., Uhl, D. and Mosbrugger, V. 2007. Miocene climate in Europe -patterns and evolution:a first synthesis of NECLIME. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253:1-7.

-Bruijn, H. de. and Whybrow, P. J. 1994. A Late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 97:407-422.

-Brunet, M., Beauvillain, A., Billiou, D., Bocherens, H., Boisserie, J. R., de Bonis, L., Branger, P., Brunet, A., Coppens, Y., Daams, R., Dejax, J., Denys, C., Douring, P., Eisenmann, V., Fanoné, F., Fronty, P., Gayet, M., Geraads, D., Guy, F., Kasser, M., Koufos, G., Likius, A., Lopez-Martinez, N., Louchart, A., Maclatchy, L., Mackaye, H. T., Marandat, B., Mouchelin, G., Mourer-Chauviré, C., Otero, O., Peigné, S., Pelaez Campomanes, P., Pilbeam, D., Rage, J. C., De Rutter, D., Schuster, M., Sudre, J., Tassy, P., Vignaud, P., Viriot, L. and Zazzo, A. 2000. Chad: discovery of a vertebrate fauna close to the Mio-Pliocene boundary. *Journal of Vertebrate Paleontology* 20:205-209.

-Brunet, M., Heintz, E. and Battail, B. 1984. Molayan (Afghanistan) and the Khaur Siwaliks of Pakistan: An example of biogeographic isolation of Late Miocene mammalian faunas. *Geologie en Mijnbouw*: 31-38.

-Brunet, M. and Heintz, E. 1983. Paleoecological interpretation and biogeographical relationships of a late Miocene vertebrate fauna from Injana, Iraq. *Paleogeography, Paleoclimatology, Paleoecology* 44:283-293.

-Brunet, M., Heintz, E. and Sen, S. 1981. Datations paleontologiques et sequence biochronologique dans le Neogene continental d'Afghanistan. *Comptes Rendus Acadmie des Sciences de Paris*

293:305-308.

- Campbell, B. G., Amini, M. H., Bernor, R. L., Dickenson, W., Drake, W., Morris, R., Van Couvering, J. A. and Van Couvering, J. A. H.** 1980. Maragheh: A classical late Miocene vertebrate locality in northwestern Iran. *Nature* 287:837-841.
- Casanovas-Vilar, I., Moya-Sola, S., Agustí, J. and Köhler, M.** 2005. The geography of a faunal turnover: tracking the Vallesian Crisis. In: *Migration of organisms: climate, geography, ecology* (ed. Elewa, A.T.), Springer-Verlag Publishers, p. 247-301.
- Cerling, T. E., Harris, J. R., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V. and Ehleringer, J. R.** 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389:153-58.
- Chavasseau, O., Chaimanee, Y., Tun, S. T., Soe, A. N., Barry, J. C., Marandat, B., Sudre, J., Marivaux, L. Ducrocq, S. and Jaeger, J. J.** 2006. Chaungtha, a new Middle Miocene mammal locality from the Irrawaddy Formation, Myanmar. *Journal of Asian Earth Sciences* 28:354-362.
- Covert, H., Hamrick, M. W., Dzanh, T. and Mckinney, K. C.** 2001. Fossil mammals from the Late Miocene of Vietnam. *Journal of Vertebrate Paleontology* 21:633-636.
- Crusafont, M. and Golpe, J.** 1971. Biozonation des Mammifères tertiaires d'Espagne. *Congres de Lyon*.
- Dice, L. R.** 1945. Measures of the amount of ecological association between species. *Ecology* 26:297-302.
- Dorofeyev, P. I.** 1966. Flora of Hipparion epoch. *International Geology Reviews* 8:1109-1117.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V. and Jaeger, J. J.** 1995. Mammalian faunas and the ages of the continental Tertiary fossiliferous localities from Thailand. *Journal of Southeast Asian Earth Sciences* 12:65-78.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V. and Jaeger, J. J.** 1994. Ages and paleoenvironments of Miocene mammalian faunas from Thailand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108:149-163.
- Dupont-Nivet, G., Krijgsman, W., Langereis, C. G., Abels, H. A., Dai, S. and Fang, X.** 2007. Tibetan plateau aridification linked to global cooling at the Eocene-Oligocene transition. *Nature* 445:635-638.
- Eisenmann, V., Alberdi, M. T., de Giuli, C. and Staesche, U.** 1988. Methodology. In: *styding fossil horses, collected papers after the New York International Hipparion Conference, 1981* (eds. Woodburne, M. and Sondaar, P.), E. J. Brill, p. 1-71.
- Erdbrink, D. P. B.** 1988. *Protoryx* from three localities East of Maragheh, N.W. Iran. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 91:101-159.
- Erdbrink, D. P. B.** 1982. A fossil reduncine antelope from the locality K 2 east of Maragheh area, N.W. Iran. *Bayerische Staatssammlung für Paläontologie und Historische Geologie Mitteilungen* 22:103-112.
- Erdbrink, D. P. B.** 1978. Fossil Giraffidae from the Maragheh area, N.W. Iran. *Bayerische Staatssammlung für Paläontologie und Historische Geologie Mitteilungen* 18:93-115.
- Erdbrink, D. P. B.** 1977. On the distribution in time and space of three Giraffid genera with Turolian representatives at Maragheh in N.W. Iran. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 80:337-355.
- Erdbrink, D. P. B., Priem, H. N. A., Hebeda, E. H., Cup, C., Dankers, P. O. and Cloetingh, S. A. P. L.** 1976. The bone bearing beds near Maragheh in N.W. Iran. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B* 79:85-113.
- Erdbrink, D. P. B.** 1976a. A fossil Giraffine from the Maragheh region in N.W. Iran. *Bayerische Staatssammlung für Paläontologie und Historische Geologie Mitteilungen* 16:29-40.
- Erdbrink, D. P. B.** 1976b. Early Samotherium and early Oioceros from an Uppermost Vindobonian fossiliferous pocket at Mordaq near Maragheh in N.W. Iran. *Bayerische Staatssammlung für Paläontologie und Historische Geologie Mitteilungen* 16:41-52.
- Eronen, J. T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C. and Fortelius, M.** 2010a. Precipitation and large herbivorous mammals I: estimates from present-day communities. *Evolutionary Ecology Research* 12:217-233.
- Eronen, J. T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C. and Fortelius, M.** 2010b. Precipitation and large herbivorous mammals I: application to fossil data. *Evolutionary Ecology Research* 12:235-248.

- Eronen, J. T.** 2006. Eurasian Neogene large herbivorous mammals and climate. *Acta Zoologica Fennica* 216:1-72.
- Eronen, J. T. and Rook, L.** 2004. The Mio-Pliocene European primate Fossil record: dynamics and habitat tracking. *Journal of Human Evolution* 47:323-341.
- Flower, B. P. and J. P. Kennett.** 1994. The Middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108:537-555.
- Fluteau, F., Ramstein, G. and Besse, J.** 1999. Simulating the evolution of the Asian and African monsoons during the past 30 Myr using an atmospheric general circulation model. *Journal of Geophysical Research* 104:11995-12018.
- Flynn, L. J. and Jacobs, L. L.** 1999. Late Miocene small mammal faunal dynamics: the crossroads of the Arabian Peninsula. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 412-419.
- Forsyth Major, C. J.** 1893. Exhibition of, and remarks upon, a tooth of an ant-bear (*Orycteropus*) from the Upper Miocene of Maragha (Persia). *Proceedings Zoological Society, London*: 239-240.
- Fortelius, M. (coordinator).** 2009. Neogene of the Old World Database of Fossil Mammals (NOW). University of Helsinki.
- Fortelius, M. and Zhang, Z.** 2006. An Oasis in the Desert, History of Endemism and Climate in the Late Neogene of North China. *Palaeontographica A* 277:131-141.
- Fortelius, M., Eronen, J. T., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I., Zhang, Z.** 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238:219-227.
- Fortelius, M., Eronen, J. T., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I., Zhang, Z.** 2003. Continental-scale hypsodonty patterns, climatic palaeobiogeography, and dispersal of Eurasian Neogene large mammal herbivores. In: *Distribution and Migration of Tertiary Mammals in Eurasia, a Volume in Honour of Hans de Bruijn* (eds. Reumer, J. and Wessels, W.), *Deinsea* 10:1-11.
- Fortelius, M., Eronen, J. T., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z. and Zhou, L.** 2002. Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. *Evolutionary Ecology Research* 4:1005-1016.
- Fortelius, M. and Solounias, N.** 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301:1-36.
- Fortelius, M., Werdelin, L., Andrews, P., Bernor, R. L., Gentry, A., Humphrey, L., Mittmann, H. W. and Viranta, S.** 1996. Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the later Miocene of Western Eurasia. In: *The Evolution of Western Eurasian Neogene Mammal Faunas*, (eds. Bernor, R. L., Fahlbusch, V. and Mittmann, H. W.), Columbia University Press, p. 414-448.
- Fortelius, M.** 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zoologica Fennicae* 180:1-76.
- Friend, P. F.** 1999. Rivers of the Lower Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 39-49.
- Gabunia, L. K. and Chochieva, K. I.** 1982. Co-evolution of the Hipparion fauna and vegetation in the Paratethys region. *Evolutionary Theory* 6:1-13.
- Gentry, A. W.** 1999. Fossil pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 290-316.
- Geraads, D.** 2009. Giraffidae (Mammalia) de la fin du Néogène de la République de Macédoine (ARYM). *Geodiversitas* 31:893-908.
- Geraads, D. and Aslan, F.** 2003. Giraffidae from the Middle Miocene hominoid locality of Çandır (Turkey). *Courier Forschungsinstitut Senckenberg* 240:201-209.
- Ginsburg, L., Minh, L. V., Nam, K. Q. and Thuan, D.V.** 1992. Premieres decouvertes de vertebres continentaux dans le Neogene du Nord du Vietnam. *Comptes Rendus Acadmie des Sciences de Paris* 314:627-630.
- Ginsburg, L. and Tassy, P.** 1985. The fossil mammals and the age of the lignites beds in the intramontane basins of northern Thailand. *Journal of the Geolocial Society of Thailand* 8:13-27.

- Grewingk, C.** 1881. Ueber fossile Säugethiere von Maragha in Persien. *Verhandlungen der K. K. Geologischen Reichsanstalt*: 296.
- Haile-Selassie, Y.** and Wolde Gabriel, G. (eds.) 2009. *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press.
- Hammer, Ø.** and Harper, D. A. T. 2006. *Paleontological Data Analysis*. Blackwell publishing.
- Hammer, Ø.,** Harper, D. A. T. and Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4.
- Heintz, E.,** Brunet, M. and Battail, B. 1990. The main features of the Cervid palaeobiogeography. *Quartärpaläontologie* 8:79-82.
- Heintz, E.** and Brunet, M. 1982. Role de la Tethys et de la chaîne alpine asiatique dans la distribution spatio-temporelle des Cervides. *Comptes Rendus Acadmie des Sciences de Paris* 294:1391-1394.
- Heintz, E.,** Brunet, M. and Battail, B. 1981. A cercopithecoid primate from the Late Miocene of Molayan, Afghanistan, with remarks on Mesopithecus. *International Journal of Primatology* 2:273-284.
- Heintz, E.,** Brunet, M., Battail, B., Blicek, A., Brandy, D., Jehenne, Y. and Sen, S. 1979. Resultats biochronostratigraphiques dans le Neogene continental d'Afghanistan. *7e Reunion annale des science de la Terre, Lyon*: 249.
- Heintz, E.,** Brunet, M. and Carbonnel, J. P. 1978. Decouverte du premier grand gisement Mammifères fossils d'Afghanistan. *Comptes Rendus Acadmie des Sciences de Paris* 286:945-947.
- Higgs, W.,** Gardner, D. and Beech, M. 2005. A Fossil Proboscidean Trackway at Mleisa, Western Region of Abu Dhabi, United Arab Emirates. In: *Emirates Heritage, Vol. 1-Proceedings of the 1st Annual Symposium on Recent Palaeontological and Archaeological Discoveries in the Emirates* (eds. Hellyer, P. and Ziolkowski, M.), Zayed Centre for Heritage and History, p. 21-27.
- Hill, A.** 1999. Late Miocene sub-Saharan African vertebrates, and their relation to the Baynunah fauna, Emirate of Abu Dhabi, United Arab Emirates. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 420-429.
- Hill, A.** and Whybrow, P. J. 1999. Arabian fossil vertebrates: a summary and overview of the Baynunah fauna and its context. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 7-14.
- Hill, A.** 1995. Faunal and environmental change in the Neogene of East Africa: Evidence from the Tugen Hills sequence, Baringo district, Kenya. In: *Paleoclimate and evolution, with emphasis on human origins*, (eds. Vrba, E. S., Denton, G. H., Partridge, T. C. and Burkle, L. H.), Yale University Press, p. 178-193.
- Holbourn, A.,** Kuhnt, W., Schulz, M., and Erlenkeuser, H. 2005. Impacts of orbital forcing and atmospheric carbon dioxide on Miocene ice-sheet expansion. *Nature* 438:483-487.
- Hristova, L.,** Kovachev, D. and Spassov, N. 2003. *Hipparion brachypus* Hensel, 1862 from the late Miocene of Hadjidimovo, Southwestern Bulgaria. *Comptes Rendus Acadmie des Sciences de Paris* 56:77-84.
- Htike, T.,** Tsubamoto, T., Takai, M., Natori, M., Egi, N., Maung, M. and Sein, C. 2005. A revision of Tetraconodon (Mammalia, Artiodactyla, Suidae) from the Miocene of Myanmar and description of a new species. *Paleontological Research* 9:243-253.
- Huttunen, K.** 2002. Systematics and taxonomy of the European Deinotheriidae (Proboscidea, Mammalia). *Annalen des Naturhistorischen Museums in Wien A* 103:237-250.
- Jaccard, P.** 1912. The distribution of the flora of the alpine zone. *New Phytologist* 11:37-50.
- Jacobs, B. F.** 2004. Paleobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society of London B* 359:1573-1583.
- Janis, C. M.,** Damuth, J. and Theodor, J. M. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207:371-398.
- Janis, C. M.,** Damuth, J. and Theodor, J. M. 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177:183-198.
- Janis, C. M.,** Damuth, J. and Theodor, J. M. 2000. Miocene ungulates and terrestrial primary

productivity: where have all the browsers gone. *Proceedings of the National Academy of Sciences* 97:7899-7904.

-Janis, C. M. and Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews* 63:197-230.

-Jernvall, J. and Fortelius, M. 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature* 417:538-540.

-Kamei, T., Ikeda, J., Ishida, H., Ishida, S., Onishi, L., Partoazar, H., Sasajima, S. and Nishimura, S. 1977. A general report of the geological and paleontological survey in Maragheh area, North-West Iran. *Memoir of Faculty of Science, Kyoto University* 43:131-164.

-Kingston, J. D. and Hill, A. 1999. Late Miocene palaeoenvironments in Arabia. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 389-407.

-Kittl, E. 1887. Beiträge zur Kenntniss der fossilen Säugethiere von Maragha in Persien. I Carnivoren. *Annalen Naturhistorischen Museums Wien* 11:317-338.

-Kittl, E. 1885. Die fossile Säugethier-fauna von Maragha in Persien. *Verhandlungen der K. K. Geologischen Reichsanstalt*:397-399.

-Kostopoulos, D. S. 2009. The Pikermian Event: temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 274:82-95.

-Koufos, G. D., Kostopoulos, D. S. and Merceron, G. 2009. Palaeoecology and Palaeobiogeography. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (eds. Koufos, G. D. and Nagel, D.), *Beiträge zur Paläontologie* 31:409-428.

-Koufos, G. D. and Vlachou, T. D. 2005. Equidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey. In: *Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia* (ed. Sen, S.), *Geodiversitas* 27:633-705.

-Koufos, G. D., Kostopoulos, D. S. and Vlachou, T. D. 2005. Neogene/Quaternary mammalian migrations in Eastern Mediterranean. *Belgian Journal of Zoology* 135:181-190.

-Koufos, G. D., Zouros, N. and Mourouzidou, O. 2003. *Prodeinotherium bavaricum* (Mammalia, Proboscidea) from early Miocene of Lesvos Island,

Greece; the appearance of deinotheres in Eastern Mediterranean. *Geobios* 36:305-315.

-Koufos, G. D. 1987. Study of the Pikermi hipparions. Part I: Generalities and taxonomy. *Bulletin du Muséum national d'Histoire naturelle Paris* 4e sér., 9, sect. C, 2: 197-252.

-Kovar-Eder, J. 2003. Vegetation dynamics in Europe during the Neogene. In: *Distribution and Migration of Tertiary Mammals in Eurasia. A volume in honour of Hans de Bruijn*, (eds. Reumer J. W. F. and Wessels, W.), *Deinsea* 10:373-392

-Krijgsman, K., Hilgen, F. J., Raffi, I., Sierro, F. J. and Wilson, D. S. 1999. Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400:652-655.

-Kurtén, B. 1952. The Chinese *Hipparion* fauna. *Commentationes Biologicae Societatis Scientiarum Fennicae* 13:1-82.

-Kutzbach, J. E., Prell, W. L. and Ruddiman, W. F. 1993. Sensitivity of Eurasian climate to surface uplift of the Tibetan Plateau, *Journal of Geology* 101:177-190.

-Kürschner, W. M., Kvaček, Z. and Dilcher, D. L. 2008. The impact of Miocene atmospheric carbon dioxide fluctuations on climate and the evolution of terrestrial ecosystems. *Proceedings of the National Academy of Sciences* 105:449-453.

-Leakey, M. G. and Harris, J. M. 2003. Lothagam, Its Significance and Contributions. In: *Lothagam, The Dawn of Humanity in Eastern Africa*, (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 625-670.

-Levinton, J. 1988. Genetics, paleontology, and macroevolution. Cambridge University Press.

-Lihoreau, F., Barry, J., Blondel, C., Chaimanee, Y., Jaeger, J. J. and Brunet, M. 2007. Anatomical revision of the genus *Merycopotamus* (Artiodactyla; Anthracotheriidae): its significance for late Miocene mammal dispersal in Asia. *Palaeontology* 50:503-524.

-Lihoreau, F., Boisserie, J. R., Viriot, L., Coppens, Y., Likius, A., Mackaye, H. T., Tafforeau, P., Vignaud, P., Brunet, M. 2006. Anthracothere dental anatomy reveals a Late Miocene Chad-Libyan bioprovince. *Proceedings of the National Academy of Sciences* 103:8763-8767.

-Lindsay E. H., Flynn, L. J., Cheema, I. U., Barry, J. C., Downing, K., Rajpar, A. R., Raza, S. M. 2005. Will Downs and the Zinda Pir dome.

- Palaeontologia Electronica*, 8: http://palaeo-electronica.org/paleo/2005_1/lindsay19/issue1_05.htm.
- Liu**, X. and Yin, Z. Y. 2002. Sensitivity of East Asian monsoon climate to the uplift of the Tibetan Plateau. *Palaeoclimatology, Palaeogeography, Palaeoecology* 183:223-245.
- Liu**, L., Eronen, J. T., and Fortelius, M. 2009. Significant mid-latitude aridity in the Middle Miocene of East Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 279:201-206.
- López-Antonanzas**, R. and Sen, S. 2004. Ctenodactylids from the Lower and Middle Miocene of Saudi Arabia. *Palaeontology* 47:1477-1494.
- López-Antonanzas**, R. and Sen, S. 2003. Systematic revision of Mio-Pliocene Ctenodactylidae (Mammalia, Rodentia) from the Indian subcontinent. *Eclogae Geologicae Helvetiae* 96:521-529.
- Lydekker**, R. 1886. On the fossil Mammalia of Maragha in Northwest Persia. *Quarterly Journal Geological Society of London* 42:173-176.
- Maples**, C. G. and Archer, A. W. 1988. Monte Carlo simulation of selected binomial similarity coefficients (II): Effect of number of sparse data. *Palaaios* 3:95-103.
- Marivaux**, L., Chaimanee Y., Yamee C., Srisuk P. and Jaeger J. J. 2004. Discovery of *Fallomus ladakhensis* Nanda and Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications. *Geodiversitas* 26:493-507.
- Maas**, M. C., Anthony, M. R. L., Gingerich, P. D., Gunnell G.F. and Krause, D.W. 1995. Mammalian diversity and turnover in the Late Paleocene and Early Eocene of the Bighorn and Crazy Mountains Basins, Wyoming and Montana (USA). *Palaeogeography, Palaeoclimatology, Palaeoecology* 115: 181-207.
- Mecquenem**, R. de. 1924-25. Contribution à l'étude des fossiles de Maragha. *Annales Paléontologie Vertébrés* 13/14:135-160.
- Mecquenem**, R. de. 1911. Contribution à l'étude du gisement des vertébrés de Maragha et de ses environs. *Annales Histoire Naturelle* 1:81-98.
- Mecquenem**, R. de. 1908. Contribution à l'étude du gisement des vertébrés de Maragha et de ses environs. *Annales Histoire Naturelle* 1:27-79.
- Mecquenem**, R. de. 1906. Les Vertébrés fossiles de Maragha. *La Nature* 24:10.
- Mecquenem**, R. de. 1905. Le gisement de vertébrés fossiles de Maragha. *Comptes Rendus Académie des Sciences de Paris* 141:284-286.
- Micheels**, A., Bruch, A. A., Eronen, J. T., Fortelius, M., Harzhauser, M., Utescher, T. and Mosbrugger, V. 2010. Analysis of heat transport mechanisms from a Late Miocene model experiment with a fully-coupled atmosphere-ocean general circulation model. *Palaeogeography, Palaeoclimatology, Palaeoecology* (in press).
- Miller**, E. R. 1999. Faunal correlation of Wadi Moghara, Egypt: implications for the age of *Prohylobates tandyi*. *Journal of Human Evolution* 36:519-533.
- Mirzaie Ataabadi**, M. 2007. Cenozoic mammal footprints of Iran and their significance. In: *Cenozoic Vertebrate Tracks and Traces*, (eds. Lucas, S., Spielmann, D. and Lockley, M.), *New Mexico Museum of Natural History and Science Bulletin* 42:251-259.
- Morales**, J., Pickford, M., Salesa, M. J. and Soria, D. 2000. The systematic status of *Kelba*, Savage, 1965, *Kenyallutra* Schmidt-Kittler, 1987 and *Ndamathaia*, Jacobs *et al.*, 1987 (Viverridae, Mammalia), and a review of Early Miocene mongoose-like carnivores of Africa. *Annales de Paléontologie* 86:243-251.
- Morlo**, M., Miller, E. R. and El-Barkooky, A. N. 2007. Creodonta and carnivore from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 27:145-159.
- Morris**, R. S. 1997. The taphonomy and paleoecology of the Late Miocene Terrestrial Vertebrate Locality near Northwest Iran: *A Framework for Paleoenvironmental Analysis of Late Miocene Hominoidea*. Ph.D. dissertation, University of California, Los Angeles.
- Mosbrugger**, V., Utescher, T. and Dilcher, D. 2005. Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Sciences* 102:14964-14969.
- Motiei**, H., 1993, Geology of Iran: Stratigraphy of Zagros. Geological Survey of Iran Press (In Persian).
- Nakaya**, H., Saegusa, H., Ratanasthien, B., Kunimatsu, Y., Chintasakul, P. and Nagaoka, S. 2003. Neogene mammalian biostratigraphy and age of fossil ape from Thailand. *Asian*

Paleoprimatology 3:66-67.

- Nakaya, H.** and Tsujikawa, H. 2006. Late Cenozoic Mammalian Biostratigraphy and Faunal Change, Paleoenvironments of Hominoid Evolution and Dispersal. In: *Human Origins and Environmental Backgrounds* (eds. Ishida, H., Tuttle, R., Pickford, M., Ogihara, and Nakatsukasa, M.), Springer, p. 59-70.
- Nargolwalla, M. C.** 2009. Eurasian Middle and Late Miocene Hominoid Paleobiogeography and the Geographic Origins of the Homininae. Ph.D. dissertation, University of Toronto.
- Nesbit-Evans, E. M.,** Van Couvering, J. A. and Andrews, P. J. 1981. Paleocology of Miocene sites in western Kenya. *Journal of Human Evolution* 10:98-121.
- Olson, E.C.** 1952. The evolution of Permian Vertebrate Chronofauna. *Evolution* 6:181-196.
- Osborn, H. F.** 1910. The Age of Mammals. Macmillan.
- Papp, A.** and Thenius, E. 1959. Tertiär, Teil 2: Wirbeltier faunen. Ferdinand Enke Verlag.
- Pickford, M.** 2004. Palaeoenvironments of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial mollusks. *Annales de Paléontologie* 90:1-12.
- Pickford, M.** 2001. Africa's smallest ruminant: a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. *Geobios* 34:437-447.
- Pickford, M.** and Morales, J. 1994. Biostratigraphy and palaeobiogeography of East Africa and the Iberian peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology* 112:297-322.
- Pickford, M.,** 1990a, Uplift of the Roof of Africa and its bearing on the Evolution of Mankind. *Human Evolution* 5:1-20.
- Pickford, M.** 1990b. Dynamics of Old World biogeographic realms during the Neogene: implications for biostratigraphy. In: *European Neogene mammal chronology* (eds. Lindsay, E. H., Fahlbusch, V. and Mein, P.), Plenum Press, p. 413-442.
- Pilbeam, D.,** Morgan, M., Barry, J. C. and Flynn, L. 1996. European MN units and the Siwalik faunal sequence of Pakistan. In: *The evolution of western Eurasian Neogene mammal faunas* (eds. Bernor, R. L., Fahlbusch, V. and Mittmann, H. W.), Columbia University Press, p. 96-105.
- Pillansa, B.,** Williams, M., Cameron, D., Patnaik, R., Hogarthe, J., Sahnid, A., Sharma, J. C., Williams, F. and Bernor, R. L. 2005. Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks: implications for the age of the Miocene hominids *Indopithecus* and *Sivapithecus*, with a note on a new hominid tooth. *Journal of Human Evolution* 48:507-515.
- Pohlig, H.** 1886. On the Pliocene of Maragha, Persia, and its resemblance to that of Pikermi in Greece; on fossil elephant remains of Caucasia and Persia; and on the results of a monograph of the fossil elephants of Germany and Italy. *Quarterly Journal Geological Society of London* 42:177-182.
- Popov, S. V.,** Shcherba, I. G., Ilyina, L. B., Nevesskaya, L. A., Paramonova, N. P., Khondkarian, S. O., Magyar, I. 2006. Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. *Palaeoclimatology, Palaeogeography, Palaeoecology* 238:91-106.
- Popov, S. V.,** Rögl, S., Rozanov, A. Y., Steininger, F. F., Shcherba, I. G. and Kovac, M. (eds.) 2004. Lithological-Paleogeographic maps of the Paratethys. *Courier Forschungsinstitut Senckenberg* 250:1-46.
- Poulakakis, N.,** Lymberakis, P. and Fassoulas, C. 2005. *Deinotherium giganteum* (Proboscidea, Deinotheriidae) from the Late Miocene of Crete. *Journal of Vertebrate Paleontology* 25:732-736.
- Qiu, Z. D.,** Zheng, S. H. and Zhang, Z. Q. 2004. Gerbillids from the Late Miocene Bahe Formation, Lantian, Shaanxi. *Vertebrata Palasiatica* 42: 193-204.
- Qiu, Q.,** Li, Q. and Qiu, Q. 1979. The Chinese Neogene. A preliminary review of the mammalian localities and faunas. *Annales Geologiques Des Pays Helleniques*: 263-272.
- Quade, J.** and Cerling, T. E. 1995. Expansion of C₄ grasses in the Late Miocene of Northern Pakistan: evidence from stable isotopes in paleosols. *Palaeoclimatology, Palaeogeography, Palaeoecology* 11: 163-166.
- Quade, J.,** Cerling, T. E., Barry, J. C., Morgan, M. E., Pilbeam, D. E., Chivas, A. R., Lee-Thorp, J. A. and van der Merwe, N. J. 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chemical Geology* 94:183-192.
- Quade, J.,** Cerling, T. E. and Bowman, J. R. 1989.

Development of Asian monsoon revealed by marked ecological shift in the latest Miocene of northern Pakistan. *Nature* 342:163-166.

-Rahimzadeh, F. 1994. Geology of Iran: Oligocene, Miocene, Pliocene. Geological Survey of Iran Press (in Persian).

-Ramstein, G., Fluteau, F., Besse, J. and Joussaume, S. 1997. Effect of orogeny, plate motion and land-sea distribution on Eurasian climate change over the past 30 million years. *Nature* 386:788-795.

-Rauhe, M., Frey, E., Pemberton, D. and Rossmann, T. 1999. Fossil crocodylians from the Late Miocene Baynunah Formation of the Emirate of Abu Dhabi, United Arab Emirates: osteology, taphonomy and palaeoecology. Comparison with African, Asian and South American crocodylians. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 163-185.

-Raup, D. M. and Crick, R. E. 1979. Measurement of faunal similarity in paleontology. *Journal of Paleontology* 53:1213-1227.

-Remeika, P. 2001. The Fish Creek Canyon ichnofauna: a Pliocene (Blancan) vertebrate footprint assemblage from Anza-Borrego desert state park, California. In: *Science and research on public lands, 6th fossil conference proceedings volume*, p.55-75.

-Retallack, G. J. 2001. A 300-million-year record of atmospheric carbon dioxide from fossil plant cuticles. *Nature* 411:287-290.

-Rodler, A. 1890. Ueber *Urmitherium polaki* n. gen., n. sp., einen neuen Sivatheriiden aus dem Knochenfeide von Maragha. *Denkschriften K. Akademie der Wissenschaften, Wien; Mathematisch-Naturwissenschaftlichen Klasse* 56:315-332.

-Rodler, A. and K. A. Weithofer. 1890. Die Wiederkauer der Fauna von Maragha. *Denkschriften K. Akademie der Wissenschaften, Wien; Mathematisch Naturwissenschaftlichen Klasse* 62:753-772.

-Rodler, A. 1887. Der Urmia-See und das Nordwestliche Persien. *Schriften des Vereins zur Verbreitung naturwissenschaftlicher Kenntnisse* 27:535-575.

-Rögl, F. 1999. Circum-Mediterranean Miocene Paleogeography. In: *The Miocene Land Mammals of Europe* (eds. Rössner, G. E. and Heissig, K.), Verlag Dr Friedrich Pfeil, p. 39-48.

-Rögl, F. 1998. Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien A* 99:279-310.

-Saarinen, J., Oikarinen, E., Fortelius, M. and Mannila, H. 2010. The living and the fossilised-how well do unevenly distributed points capture the faunal information in a grid. *Evolutionary Ecology Research* 12: 363-376.

-Sanders W. J. 2008a. Review of Fossil Proboscidea from the Early-Middle Miocene Site of Jabal Zaltan, Libya. In: *Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya* (eds. Boaz, N. T., El-Arnauti, A., Pavlakis, P. and Salem, M. J.) *Garyounis Scientific Bulletin*, Special Issue 5:217-240.

-Sanders, W. J. 2008b. Review of Fossil Proboscidea from the Late Miocene-Early Pliocene Site of As Sahabi, Libya. In: *Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya* (eds. Boaz, N. T., El-Arnauti, A., Pavlakis, P. and Salem, M. J.) *Garyounis Scientific Bulletin*, Special Issue 5:241-256.

-Sanders, W. J. and Miller, E. R. 2002. New proboscideans from the early Miocene of Wadi Moghara, Egypt. *Journal of Vertebrate Paleontology* 22:388-404.

-Segalen, L., Lee-Thorp, J. A. and Cerling, T. 2007. Timing of C₄ grass expansion across sub-Saharan Africa. *Journal of Human Evolution* 53:549-559.

-Sehgal, R. K. and Nanda, A. C. 2002. Age of the fossiliferous Siwalik sediments exposed in the vicinity of Nurpur, District Kangra, Himachal Pradesh. *Current Science* 82:392-395.

-Sen, S. and Purabrishemi, Z. 2010. First porcupine fossils (Mammalia, Rodentia) from the Late Miocene of NW Iran, with notes on late Miocene-Pliocene dispersal of porcupines. *Paläontologisch Zeitschrift* 84:239-248.

-Sen, S. 1998. The age of the Molayan mammal locality, Afghanistan. *Geobios* 31:385-391.

-Sen, S., Blicek, A., Bouvrain, G., Brunet, M., Geraads, D., Heinz, E., Koufos, G.D. 1997. Late Miocene mammals from Taghar, Khurd Kabul Basin, Afghanistan. *Annales de Paléontologie*, 83:233-266.

-Sen, S. 1983. Rongeurs et lagomorphes du

- gisement Pliocene de Pul-e Charkhi, bassin de Kabul, Afghanistan. *Bulletin du Museum National d'Histoire Naturelle, Paris* 5 ser. 1:33-74.
- Sen, S.** and Thomas, H. 1979. Découverte de Rongeurs dans le Miocène moyen de la Formation Hofuf (Province du Hasa, Arabie Saoudite). *Compte Rendus Sommaire des Séances de la Société Géologique de France, Paris* 1:34-37.
- Simpson, G. G.** 1960. Notes on the measurement of faunal resemblance. *American Journal of Science* 258A:300-311.
- Solounias, N., Rivals, F. and Semperebon, G. M.** 2010. Dietary interpretation and paleoecology of herbivores from Pikermi and Samos (Late Miocene of Greece). *Paleobiology* 36:113-136.
- Solounias, N., Plavcan, J. M., Quade, J. and Witmer, L.** 1999. The palaeoecology of the Sub-Paratethyan province and the savanna myth. In: *The Evolution of Neogene Terrestrial Ecosystems in Europe* (eds. Agustí, J., Rook, L. and Andrews, P.), Cambridge University Press, p. 436-453.
- Solounias, N., Fortelius, M. and Freeman, P.** 1994. Molar wear rates in ruminants: a new approach. *Annales Zoologica Fennici* 31:219-227.
- Sotnikova, M. V., Dodonov, A. E., Penkov, A. V.** 1997. Upper Cenozoic bio-magnetic stratigraphy of Central Asian mammalian localities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133:243-258.
- Steininger, F. F.** 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammals Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-zones)". In: *The Miocene Land Mammals of Europe* (eds. Rössner, G. E. and Heissig, K.), Verlag Dr Friedrich Pfeil., p. 9-24.
- Steininger, F. F., Berggren, W. A., Kent, D. V., Bernor, R. L., Sen, S. and Agustí, J.** 1996. Circum-Mediterranean Neogene (Miocene-Pliocene) marine continental chronologic correlations of European mammal units. In: *The evolution of western Eurasian Neogene mammal faunas* (eds. Bernor, R. L., Fahlbusch, V. and Mittmann, H. W.), Columbia University Press, p. 7-46.
- Storrs, G. W.** 2003. Late Miocene-Early Pliocene Crocodylian Fauna of Lothagam, Southwest Turkana Basin, Kenya. In: *Lothagam, The Dawn of Humanity in Eastern Africa*, (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 137-160.
- Stöcklin, J. and Setudehnia, A.** 1970. Stratigraphic lexicon of Iran. Geological Survey of Iran Press.
- Strömberg, C. A. E., Werdelin, L., Friis, E. M. and Saraç, G.** 2007. The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: phytolith evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 250:18-49.
- Stuart, C. and Stuart, T.** 2006. Field guide to the larger mammals of Africa. Struik Publishers.
- Takai, F.** 1958. Vertebrate Fossils from Maragha. *Institute of Oriental Culture, University of Tokyo* 26:7-11.
- Tassy, P.** 2003. Elephantoida from Lothagam. In: *Lothagam, The Dawn of Humanity in Eastern Africa*, (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 331-358.
- Tassy, P.** 1999. Miocene elephantids (Mammalia) from the Emirate of Abu Dhabi, United Arab Emirates; palaeobiogeographic implications. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 209-233.
- Tchernov, E., Ginsburg, L., Tassy, P. and Goldsmith, N. F.** 1987. Miocene mammals of the Negev. *Journal of Vertebrate Paleontology* 7:284-310.
- Thomas, H., Roger, J., Sen, S., Pickford, M., Gheerbrant, E., Al-Sulaimani, Z. and Al-Busaidi, S.** 1999. Oligocene-Miocene terrestrial vertebrates in the southern Arabian peninsula (Sultanate of Oman) and their geodynamic and palaeogeographic settings. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 430-442.
- Thomas, H., Sen, S., Khan, M., Battail, B. and Ligabue, G.** 1982. The Lower Miocene fauna of Al-Sarrar (Eastern Province, Saudi Arabia). *The Journal of Saudi Arabian Archaeology* 5:109-136.
- Thomas, H., Sen, S. and Ligabue, G.** 1980. La faune Miocene de la formation Agha Jari du Jebel Hamrin (Irak). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 83:269-287.
- Thomas, H., Taquet, P., Ligabue, G. and Del'Agnoia, C.** 1978. Découverte d'un gisement de Vertébrés dans les dépôts continentaux du Miocène moyen du Hasa (Arabie saoudite). *Compte Rendu Sommaire des Séances de la Société Géologique de France, Paris*: 69-72.

- Tobien**, H. 1968. Palaeontologische Ausgrabungen nach Jungtertiären Wirbeltieren auf der Insel Chios (Griechenland) und bei Maragheh (N.W. Iran). *Jahrbuch der Vereinigung "Freunde der Universität Mainz"*:51-58.
- Van Couvering**, J. A. H. 1980. Community evolution in East Africa during the late Cenozoic. In: *Fossils in the making; Vertebrate taphonomy and paleoecology* (eds. Behrensmeyer A. K. and Hill A.), University of Chicago Press, p. 272-298.
- Van Couvering** J. A. H. and Van Couvering, J. A. 1976. Early Miocene mammal fossils from East Africa: Aspects of Geology, faunistics and paleoecology. In: *Human origins, Louis Leakey and the east African evidence* (eds. Isaac, G. and Mccown, E. R.), Staples, 155-207.
- Van der Made** J. 1999. Intercontinental relationship Europe-African and the Indian Subcontinent. In: *The Miocene Land Mammals of Europe* (eds. Rössner, G. E. and Heissig, K.), Verlag Dr Friedrich Pfeil., p. 457-472.
- Viranta**, S. 1996. European Miocene Amphicyonidae: Taxonomy, systematics and ecology. *Acta Zoologica Fennica* 204:1-61.
- Vislobokova**, I. A. 2009. The First Record of *Chleuastochoerus* (Suidae, Artiodactyla) in Russia. *Paleontological Journal* 43: 686-698.
- Vlachou**, T. D. and Koufos, G. D. 2009. Equidae. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (eds. Koufos, G. D. and Nagel, D.), *Beiträge zur Paläontologie* 31:207-281.
- Watabe**, M. 1992. Phylogeny of Chinese hipparion (Perissodactylia, Mammalia): their relationships with the Western Old World and North American hipparionines. *Paleontologia i evolució* 24-25:155-174.
- Watabe**, M. and Nakaya, H. 1991a. Phylogenetic significance of the postcranial skeletons of the hipparions from Maragheh (late Miocene), NW Iran. *Memoirs of the Faculty of Sciences, Kyoto University* 56:11-53.
- Watabe**, M. and Nakaya, H. 1991b. Cranial skeletons of *Hipparion* (Perissodactyla, Mammalia) from Maragheh (Turolian, late Miocene), NW Iran. *Memoirs of the Faculty of Sciences, Kyoto University* 56:55-125.
- Watabe**, M. 1990. Fossil Bovids (Artiodactyla, Mammalia) from Maragheh (Turolian, late Miocene), Northwest Iran. *Annual Report of the Historical Museum of Hokkaido* 18:19-56.
- Werdelin**, L. 2008. Biogeographic relationships of African carnivoran faunas. *Comptes Rendus Palevol* 7:645-656.
- Werdelin**, L. 2003. Mio-Pliocene Carnivora from Lothagam, Kenya. In: *Lothagam, The Dawn of Humanity in Eastern Africa*, (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 261-330.
- Wessels**, W. 2009. Miocene rodent evolution and migration, Muroidea from Pakistan, Turkey and Northern Africa. *Geologica Ultraiectina, Mededelingen van de Faculteit Geowetenschappen-departement Aardwetenschappen-Universiteit Utrecht* 307: 1-290.
- West**, R. M., Hutchinson, J. H. and Munthe, J. 1991. Miocene vertebrates from the Siwalik Group, western Nepal. *Journal of Vertebrate Paleontology* 11:108-129.
- West**, R. M., Luckas, J. R., Munthe, J. and Hussain, S. T. 1978. Vertebrate fauna from Neogene Siwalik Group, Dang valley, western Nepal. *Journal of Paleontology* 52:1015-1022.
- Weston**, E. M. 2003. Fossil Hippopotamidae from Lothagam. In: *Lothagam, The Dawn of Humanity in Eastern Africa*, (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 441-484.
- Whybrow**, P. J. and Clements, D. 1999. Arabian Tertiary fauna, flora and localities. In: *Fossil Vertebrates of Arabia* (eds. Whybrow, P. J. and Hill, A.), Yale University Press, p. 460-473.
- Whybrow**, P. J. and Hill, A. (eds.) 1999. Fossil Vertebrates of Arabia. Yale University Press.
- Whybrow**, P. J. 1987. Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia. *Bulletin of the British Museum (Natural History), Geology* 41:367-457.
- Whybrow**, P. J. 1984. Geological and faunal evidence from Arabia for mammal "migrations" between Asia and Africa during the Miocene. *Courier Forschungsinstitut Senckenberg* 69:189-198.
- Winkler**, A. J. 2003. Rodents and Lagomorphs from the Miocene and Pliocene of Lothagam, Northern Kenya. In: *Lothagam, The Dawn of Humanity in Eastern Africa*, (eds. Leakey, M. G. and Harris, J. M.), Columbia University Press, p. 169-200.
- Yechieli**, Y. and Wood, W. W. 2002. Hydrogeologic processes in saline systems: playas,

sabkhas and saline lakes. *Earth Science Reviews* 58:343-365.

-Zachos, J. C., Dickens, G. R. and Zeebe, R. E. 2008 An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451:279-283.

-Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686-693.

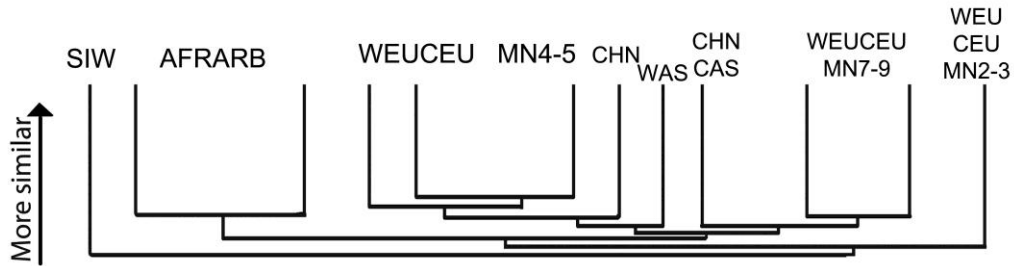
-Zhang, Z. S., Wang, H. J., Guo, Z. T. and Jiang, D. B. 2006. Impact of topography and land-sea distribution on East Asian paleoenvironmental patterns. *Advanced Atmospheric Science* 23:258-266.

-Zubakov, V. A. and Borzenkova, I. I. 1990. Global Paleoclimate of the Late Cenozoic. Elsevier.

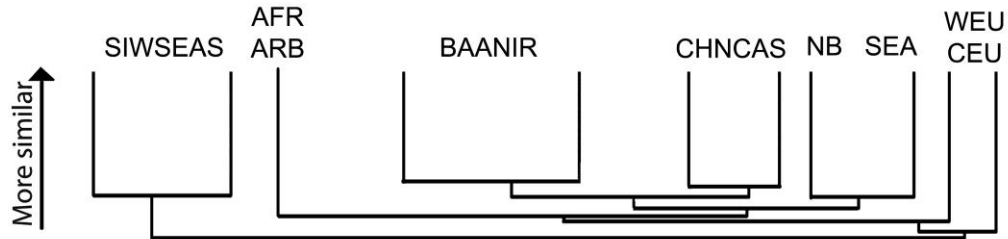
Appendix 1 Clusters of localities showing the relationships of faunal provinces in the Miocene of the Old World. Clusters are from an analysis of 407 Miocene localities, using (A) Dice, (B) Jaccard, and (C) Simpson similarity indices. **A:** Early–Middle Miocene clusters, **B:** Late Miocene clusters.

WEU: Western Europe, **CEU:** central Europe, **WAS:** Western Asia, **CHN:** north China, **ARB:** Arabia, **AFR:** Africa, **SIW:** Siwaliks, **BAANIR:** Balkan-Anatolia-Iran, **NB SEA:** north Black Sea, **CAS:** central Asia, **SIWSEAS:** Siwalik-Southeast Asia.

Appendix 1A. Dice clusters

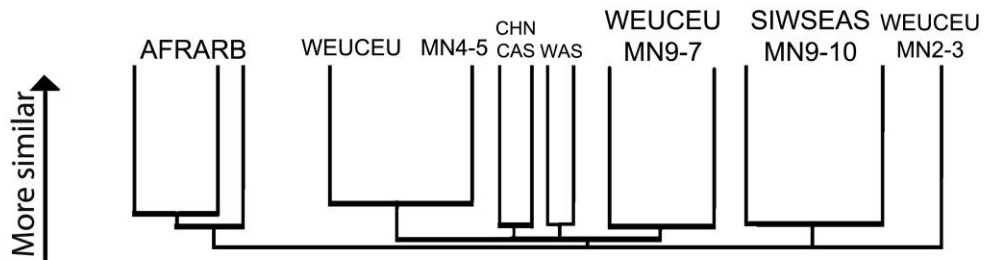


A. Early/Middle Miocene

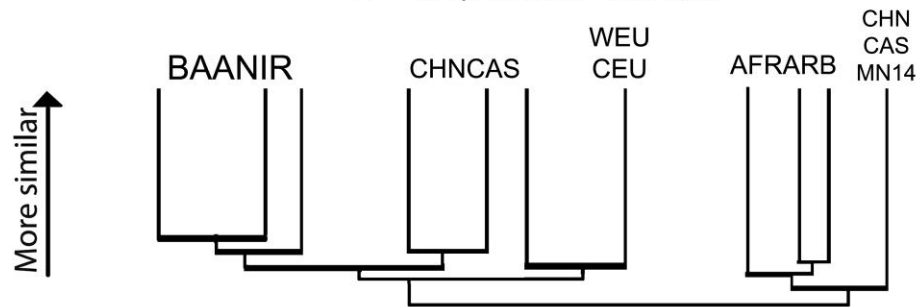


B. Late Miocene

Appendix 1B. Jaccard clusters

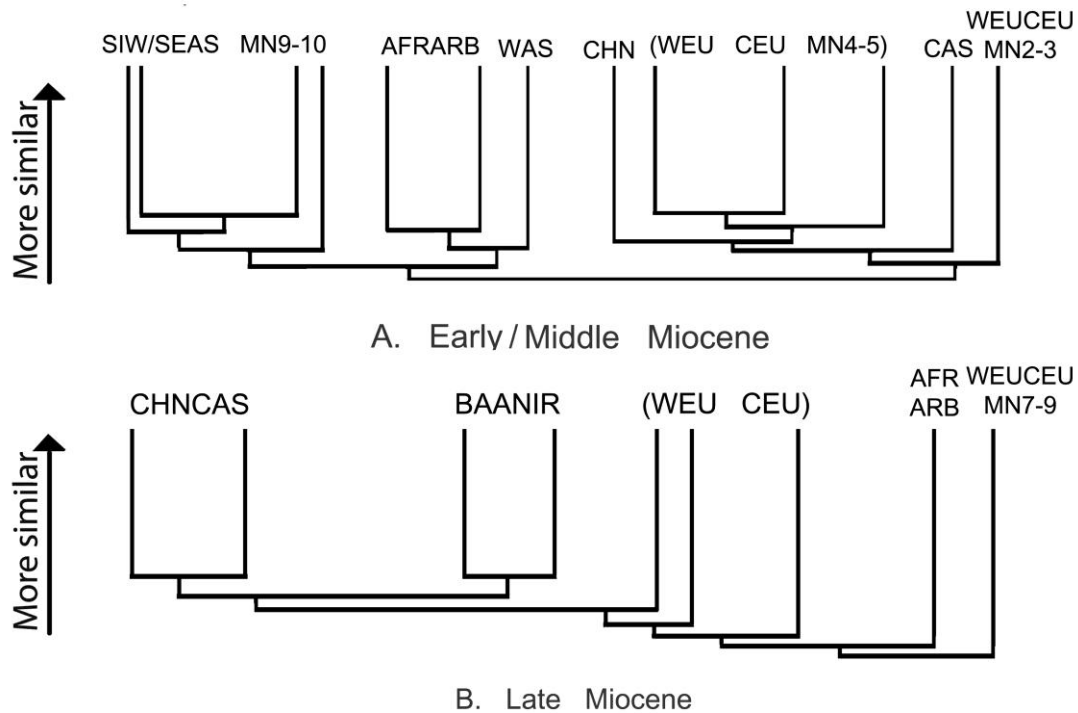


A. Early/Middle Miocene



B. Late Miocene

Appendix 1C. Simpson clusters



Appendix 2. List of the localities used in provinciality, abundance, and similarity analyses of this study with their geographical positions (country and coordinates), age correlation (MN-equivalent: **MNEQ**) and age span, Dice (**DFRI**), Jaccard (**JFRI**), Simpson (**SFRI**), and Raup-Crick (**RCFRI**) genus-level faunal resemblance to Maragheh MNEQ 11 and 12 (**MRG**), Arabia MNEQ 4 and 5 (**ARB**), and Siwalik MNEQ 9 and 10 (**SIW**), percentage of open-adapted (**%OPEN**) and closed-adapted (**%CLOSE**) taxa, and taxa excluded from these categories (**%OTHER**), total number of taxa (**TOTAL**), and mean hypsodonty (**HYP**) values. Localities with blank FRI values had fewer than seven distinct genera and were not used in similarity analysis. Those with no HYP value had fewer than two herbivorous genera.

Open-adapted taxa: Bovidae, Equidae, Felidae, Giraffidae, Hyaenidae, and **Rhinocerotidae**

Closed-adapted taxa: Anthracotheriidae, Cervidae, Hippopotamidae, Moschidae, Palaeomerycidae, Suoidea, Tapiridae, Tragulidae, and Proboscidea

Ad Dabtiyah	Saudi Arabia	MN04	4.80	0.00	0.00	0.00	0.00	0.06	0.60	0.55	0.61	0.96	0.09	0.05	0.11	0.64	50.00	41.67	8.33	12	1.08
Aérotrain	France	MN04	1.00	0.04	0.02	0.13	0.21	0.11	0.11	0.06	0.13	0.75	0.02	0.01	0.02	0.36	60.00	0.00	40.00	10	1.00
Armanes 1	Spain	MN04	1.00	0.00	0.00	0.00	0.06	0.17	0.09	0.19	0.84	0.01	0.00	0.01	0.32	33.33	66.67	0.00	0.00	9	1.22
Arrisdrift	Namibia	MN04	1.80	0.10	0.05	0.16	0.26	0.13	0.07	0.18	0.72	0.07	0.04	0.10	0.45	26.09	21.74	52.17	23	1.46	
Artenay	France	MN04	1.00	0.03	0.02	0.04	0.01	0.19	0.11	0.32	0.88	0.00	0.00	0.00	0.10	17.24	17.24	65.52	29	1.00	
Artesilla	Spain	MN04	1.00	0.07	0.04	0.12	0.17	0.32	0.20	0.42	0.99	0.07	0.03	0.09	0.46	20.00	35.00	45.00	20	1.09	
Baggersee Freudeneegg 2	Germany	MN04	1.00													28.57	57.14	14.29	7	1.00	
Baggersee Freudeneegg 3	Germany	MN04	1.00													22.22	66.67	11.11	9	1.00	
Bézian	France	MN04	1.00	0.03	0.02	0.04	0.00	0.25	0.14	0.43	1.00	0.05	0.03	0.09	0.32	27.59	31.03	41.38	29	1.07	
Bukwa	Uganda	MN04	2.00	0.03	0.02	0.06	0.03	0.33	0.20	0.44	0.99	0.08	0.04	0.10	0.51	15.00	65.00	20.00	20	1.12	
Buluk	Kenya	MN04	1.00	0.00	0.00	0.00	0.00	0.27	0.16	0.39	0.99	0.09	0.05	0.13	0.54	28.57	38.10	33.33	21	1.11	
Buluk (West Stephanie)	Kenya	MN04	1.00	0.04	0.02	0.08	0.13	0.22	0.12	0.24	0.92	0.08	0.04	0.10	0.57	18.18	63.64	18.18	11	1.30	
Buñol	Spain	MN04	1.00	0.00	0.00	0.00	0.00	0.22	0.13	0.31	0.89	0.00	0.00	0.00	0.15	33.33	27.78	38.89	18	1.09	
Can Canals	Spain	MN04	1.00	0.04	0.02	0.06	0.06	0.34	0.20	0.43	1.00	0.09	0.05	0.12	0.57	33.33	44.44	22.22	18	1.23	
Can Julia	Spain	MN04	1.00	0.04	0.02	0.11	0.22	0.16	0.09	0.17	0.84	0.00	0.00	0.00	0.26	18.18	54.55	27.27	11	1.13	
Córcoles	Spain	MN04	1.00	0.00	0.00	0.00	0.06	0.23	0.13	0.25	0.86	0.03	0.01	0.04	0.40	22.22	55.56	22.22	9	1.00	
Dera Bugti 6	Pakistan	MN04	1.00	0.03	0.02	0.05	0.03	0.24	0.14	0.35	0.95	0.04	0.02	0.06	0.33	31.58	42.11	26.32	19	1.13	
Eggingen-Mittelhart 3	Germany	MN04	1.00	0.03	0.02	0.05	0.02	0.27	0.16	0.38	0.98	0.06	0.03	0.09	0.42	19.23	53.85	26.92	26	1.11	
El Canyon	Spain	MN04	1.00	0.04	0.02	0.09	0.12	0.23	0.13	0.25	0.95	0.07	0.03	0.08	0.52	16.67	50.00	33.33	12	1.00	
Els Casots	Spain	MN04	1.00	0.04	0.02	0.08	0.09	0.34	0.20	0.38	1.00	0.08	0.04	0.10	0.55	7.69	61.54	30.77	13	1.00	
Erkertshofen 2	Germany	MN04	1.00	0.04	0.02	0.08	0.08	0.13	0.07	0.14	0.78	0.00	0.00	0.00	0.20	18.75	31.25	50.00	16	1.00	
Illerkirchberg 1	Germany	MN04	4.80													37.50	25.00	37.50	8	1.00	
Kalodirr	Kenya	MN04	4.10	0.00	0.00	0.00	0.01	0.21	0.12	0.31	0.87	0.05	0.03	0.07	0.36	13.64	50.00	36.36	22	1.00	
Karungu (Nira-Kachuk)	Kenya	MN04	1.00	0.03	0.01	0.04	0.00	0.24	0.14	0.43	0.98	0.07	0.04	0.12	0.40	24.00	40.00	36.00	25	1.14	
La Romieu	France	MN04	1.00	0.00	0.00	0.00	0.00	0.27	0.16	0.39	0.99	0.01	0.01	0.02	0.19	30.00	45.00	25.00	20	1.07	
Langenau 1	Germany	MN04	1.00	0.03	0.02	0.05	0.02	0.32	0.19	0.49	1.00	0.07	0.04	0.10	0.43	28.00	32.00	40.00	25	1.07	
Langenau 2	Germany	MN04	1.00													22.22	66.67	11.11	9	1.00	
Les Cases de Valenciana	Spain	MN04	1.00	0.00	0.00	0.00	0.05	0.17	0.09	0.19	0.85	0.08	0.04	0.10	0.60	22.22	55.56	22.22	9	1.14	
Locherangan	Kenya	MN04	1.00	0.00	0.00	0.00	0.05	0.26	0.16	0.27	0.80	0.07	0.04	0.08	0.55	21.43	64.29	14.29	14	1.00	
Mfwangano 1	Kenya	MN04	1.00													0.00	57.14	42.86	7	1.00	
Mfwangano 2	Kenya	MN04	1.00	0.08	0.04	0.17	0.27	0.13	0.07	0.14	0.77	0.11	0.06	0.13	0.68	0.00	42.86	57.14	14	1.14	

Mfwangano 3	Kenya	MN04	1.00	0.07	0.04	0.14	0.25	0.16	0.09	0.19	0.86	0.08	0.04	0.10	0.55	6.67	46.67	46.67	15	1.27
Mfwangano 5	Kenya	MN04	1.00												0.00	0.00	60.00	40.00	10	1.20
Moli Calopa	Spain	MN04	1.00	0.04	0.02	0.08	0.13	0.22	0.12	0.24	0.96	0.07	0.04	0.08	0.52	21.43	50.00	28.57	14	1.10
Montreal-du-Gers	France	MN04	1.00	0.00	0.00	0.00	0.02	0.17	0.10	0.21	0.80	0.01	0.01	0.02	0.24	53.85	38.46	7.69	13	1.42
Moroto II	Uganda	MN04	1.00	0.04	0.02	0.07	0.07	0.08	0.04	0.10	0.56	0.01	0.01	0.02	0.23	5.88	35.29	58.82	17	1.00
Napak IV	Uganda	MN04	1.00	0.00	0.00	0.00	0.04	0.10	0.05	0.11	0.71	0.07	0.04	0.08	0.54	0.00	21.43	78.57	14	1.00
Pellecahus	France	MN04	1.00	0.03	0.02	0.04	0.00	0.21	0.12	0.33	0.95	0.04	0.02	0.07	0.30	20.83	37.50	41.67	24	1.29
Petersbuch 2	Germany	MN04	1.00	0.00	0.00	0.00	0.05	0.06	0.03	0.06	0.54	0.00	0.00	0.00	0.27	25.00	66.67	8.33	12	1.00
Rusinga	Kenya	MN04	1.00	0.03	0.02	0.04	0.02	0.30	0.18	0.49	1.00	0.08	0.04	0.13	0.48	18.52	33.33	48.15	27	1.17
Rusinga (Gumba)	Kenya	MN04	1.00	0.06	0.03	0.09	0.04	0.28	0.16	0.44	0.99	0.09	0.05	0.14	0.53	21.74	39.13	39.13	23	1.18
Rusinga (Hiwegi west)	Kenya	MN04	1.00	0.04	0.02	0.08	0.09	0.26	0.15	0.29	0.98	0.11	0.06	0.14	0.67	13.33	53.33	33.33	15	1.07
Rusinga (Hiwegi)	Kenya	MN04	1.00	0.06	0.03	0.07	0.00	0.20	0.11	0.39	0.93	0.07	0.04	0.13	0.40	9.09	42.42	48.48	33	1.17
Rusinga (Kalim)	Kenya	MN04	1.00												42.86	57.14	0.00	0.00	7	1.14
Rusinga (kathwanga)	Kenya	MN04	1.00	0.06	0.03	0.07	0.02	0.18	0.10	0.35	0.85	0.07	0.04	0.13	0.42	6.06	39.39	54.55	33	1.11
Rusinga (kiahera hill)	Kenya	MN04	1.00	0.07	0.04	0.13	0.18	0.20	0.11	0.25	0.88	0.09	0.05	0.11	0.59	11.76	41.18	47.06	17	1.00
Rusinga (Kiyune)	Kenya	MN04	1.00	0.04	0.02	0.09	0.15	0.33	0.20	0.36	0.99	0.11	0.06	0.13	0.67	15.38	69.23	15.38	13	1.08
Rusinga (kulu)	Kenya	MN04	1.00	0.00	0.00	0.00	0.01	0.16	0.09	0.22	0.75	0.07	0.04	0.10	0.46	16.67	45.83	37.50	24	1.20
Rusinga (Nyamsingula)	Kenya	MN04	1.00	0.07	0.03	0.11	0.06	0.24	0.13	0.33	0.97	0.09	0.05	0.12	0.54	14.29	57.14	28.57	21	1.21
Rusinga (R 113)	Kenya	MN04	1.00	0.00	0.00	0.00	0.04	0.25	0.14	0.27	0.95	0.04	0.02	0.06	0.44	30.00	20.00	50.00	10	1.11
Rusinga (R 114)	Kenya	MN04	1.00												0.00	0.00	50.00	50.00	8	1.00
Rusinga (R105)	Kenya	MN04	1.00	0.00	0.00	0.00	0.04	0.14	0.08	0.16	0.78	0.09	0.05	0.11	0.62	0.00	53.85	46.15	13	1.00
Rusinga (R106)	Kenya	MN04	1.00	0.06	0.03	0.09	0.03	0.15	0.08	0.24	0.84	0.08	0.04	0.12	0.46	4.00	44.00	52.00	25	1.13
Rusinga (R107)	Kenya	MN04	1.00	0.00	0.00	0.00	0.01	0.19	0.10	0.20	0.93	0.09	0.05	0.11	0.62	8.33	41.67	50.00	12	1.00
Rusinga (Wakundu)	Kenya	MN04	1.00												11.11	55.56	33.33	33.33	9	1.00
Rusinga (Wayondo)	Kenya	MN04	1.00	0.00	0.00	0.00	0.01	0.25	0.15	0.33	0.98	0.09	0.05	0.12	0.55	20.00	45.00	35.00	20	1.06
Sihong-songlinzhuang	China	MN04	4.80	0.04	0.02	0.06	0.05	0.11	0.06	0.14	0.68	0.05	0.03	0.07	0.40	26.67	40.00	33.33	15	1.00
Songhor (Main)	Kenya	MN04	2.00	0.06	0.03	0.08	0.04	0.09	0.05	0.15	0.50	0.06	0.03	0.10	0.37	6.45	22.58	70.97	31	1.09
Ulan-Tologoj	Mongolia	MN04	2.85												41.67	50.00	8.33	8.33	12	1.09
Uyoma 12 (Rangoye)	Kenya	MN04	1.00												50.00	10.00	40.00	40.00	10	1.33
Uyoma 2 (Chianda N)	Kenya	MN04	1.00	0.04	0.02	0.09	0.12	0.33	0.20	0.36	0.99	0.10	0.05	0.12	0.65	31.25	43.75	25.00	16	1.00
Wintershof-West	Germany	MN04	2.00	0.07	0.04	0.13	0.16	0.04	0.02	0.04	0.35	0.00	0.00	0.00	0.17	6.25	37.50	56.25	16	1.00

Aktau Mountain	Kazakhstan	MN05	2.80	0.04	0.02	0.13	0.24	0.11	0.06	0.13	0.74	0.05	0.02	0.06	0.48	23.08	46.15	30.77	13	1.20
Al-Sarrar	Saudi Arabia	MN05	1.80	0.08	0.04	0.17	0.29	0.60	0.55	0.61	0.96	0.09	0.05	0.12	0.63	23.53	41.18	35.29	17	1.17
Antonios (ANT)	Greece	MN05	0.00	0.00	0.00	0.00	0.03	0.35	0.21	0.37	1.00	0.12	0.06	0.14	0.71	33.33	66.67	0.00	9	1.00
Baigneaux-en Beauce	France	MN05	1.80	0.00	0.00	0.00	0.00	0.16	0.09	0.24	0.86	0.00	0.00	0.00	0.14	29.17	8.33	62.50	24	1.17
Belometchetskaja	Georgia	MN05	1.80	0.06	0.03	0.08	0.03	0.22	0.12	0.36	0.84	0.10	0.06	0.17	0.57	39.29	35.71	25.00	28	1.36
Çandır (Loc. 3)	Turkey	MN05	1.80	0.06	0.03	0.07	0.01	0.20	0.11	0.38	0.94	0.07	0.04	0.13	0.40	40.00	26.67	33.33	30	1.50
Chios	Greece	MN05	1.80	0.08	0.04	0.20	0.41	0.20	0.11	0.21	0.93	0.11	0.06	0.13	0.69	36.36	54.55	9.09	11	1.30
Contres MN 5	France	MN05	1.80	0.03	0.02	0.05	0.01	0.22	0.13	0.35	0.94	0.07	0.04	0.11	0.46	20.83	45.83	33.33	24	1.06
Dzhilanchik	Kazakhstan	MN05	2.85	0.00	0.00	0.00	0.02	0.10	0.05	0.11	0.68	0.00	0.00	0.00	0.24	33.33	58.33	8.33	12	1.25
Edelbeuren-Maurerkopf	Germany	MN05	2.00	0.00	0.00	0.00	0.04	0.22	0.12	0.25	0.96	0.10	0.06	0.13	0.70	7.69	30.77	61.54	13	1.00
Eibiswald	Austria	MN05	1.80													14.29	42.86	42.86	7	1.20
Engelswies	Germany	MN05	2.80	0.00	0.00	0.00	0.02	0.26	0.15	0.31	0.93	0.06	0.03	0.07	0.47	20.00	46.67	33.33	15	1.00
Estación Imperial	Spain	MN05	2.00	0.00	0.00	0.00	0.05	0.10	0.05	0.11	0.70	0.00	0.00	0.00	0.27	30.00	20.00	50.00	10	1.40
Esvres - Marine Faluns	France	MN05	1.80	0.05	0.02	0.05	0.00	0.25	0.14	0.63	1.00	0.05	0.03	0.12	0.22	18.00	34.00	48.00	50	1.11
Faluns of Touraine	France	MN05	1.80	0.00	0.00	0.00	0.08	0.12	0.07	0.13	0.61	0.02	0.01	0.02	0.35	55.56	0.00	44.44	9	1.50
GebelZelten	Libya	MN05	4.80	0.06	0.03	0.08	0.04	0.23	0.13	0.40	0.94	0.08	0.04	0.13	0.46	37.50	41.67	20.83	24	1.05
Georgensmünd	Germany	MN05	1.80	0.00	0.00	0.00	0.03	0.06	0.03	0.06	0.46	0.00	0.00	0.00	0.26	44.44	44.44	11.11	9	1.25
Grund	Austria	MN05	0.65													0.00	60.00	40.00	10	1.00
Göriach	Austria	MN05	1.80	0.00	0.00	0.00	0.00	0.16	0.09	0.24	0.81	0.05	0.02	0.07	0.34	14.81	48.15	37.04	27	1.00
Häder	Germany	MN05	1.80	0.04	0.02	0.13	0.27	0.10	0.06	0.13	0.62	0.00	0.00	0.00	0.28	22.22	55.56	22.22	9	1.00
Hambach 6C	Germany	MN05	1.80	0.00	0.00	0.00	0.01	0.12	0.06	0.15	0.68	0.07	0.03	0.09	0.47	18.18	36.36	45.45	22	1.07
Heggbach	Germany	MN05	1.80	0.00	0.00	0.00	0.04	0.24	0.14	0.26	0.98	0.07	0.04	0.09	0.55	25.00	58.33	16.67	12	1.10
Kalkaman lake	Kazakhstan	MN05	1.60	0.04	0.02	0.10	0.19	0.14	0.08	0.15	0.64	0.01	0.00	0.01	0.27	35.71	42.86	21.43	14	1.18
Kaloma	Kenya	MN05	1.60													14.29	85.71	0.00	7	1.43
Kirimun	Kenya	MN05	1.60													12.50	62.50	25.00	8	1.00
La Hydroelectrica	Spain	MN05	1.80	0.00	0.00	0.00	0.01	0.16	0.09	0.19	0.84	0.00	0.00	0.01	0.20	9.09	72.73	18.18	11	1.00
La Retama	Spain	MN05	2.80	0.00	0.00	0.00	0.02	0.18	0.10	0.19	0.90	0.00	0.00	0.00	0.21	26.67	26.67	46.67	15	1.29
Münzenberg (Leoben)	Austria	MN05	1.80													12.50	37.50	50.00	8	1.00
Maboko	Kenya	MN05	1.60	0.06	0.03	0.06	0.00	0.22	0.12	0.44	0.94	0.06	0.03	0.11	0.31	19.44	41.67	38.89	36	1.20
Majiwa	Kenya	MN05	1.60	0.04	0.02	0.06	0.06	0.22	0.13	0.28	0.94	0.07	0.04	0.09	0.49	18.18	59.09	22.73	22	1.18
Manchar 1	Pakistan	MN05	1.60	0.03	0.02	0.05	0.02	0.15	0.09	0.22	0.71	0.13	0.07	0.20	0.70	23.53	70.59	5.88	17	1.10

Manchar 2	Pakistan	MN05	1.60	0.04	0.02	0.07	0.11	0.20	0.11	0.22	0.81	0.10	0.06	0.13	0.62	27.27	72.73	0.00	11	1.00
Monteagudo	Spain	MN05	2.80													44.44	44.44	11.11	9	1.00
Montejo de la Vega	Spain	MN05	1.80	0.00	0.00	0.00	0.07	0.27	0.15	0.31	0.98	0.01	0.01	0.02	0.34	50.00	25.00	25.00	8	1.00
Moratines	Spain	MN05	2.00	0.00	0.00	0.00	0.04	0.11	0.06	0.13	0.73	0.00	0.00	0.00	0.29	44.44	33.33	22.22	9	1.11
Morourot	Kenya	MN05	1.80													11.11	88.89	0.00	9	1.22
Omo	Kenya	MN05	1.60	0.04	0.02	0.09	0.17	0.27	0.16	0.29	0.97	0.09	0.04	0.11	0.61	33.33	50.00	16.67	12	1.40
Paseo de la Esperanza	Spain	MN05	2.00	0.00	0.00	0.00	0.04	0.17	0.09	0.19	0.83	0.08	0.04	0.10	0.60	25.00	50.00	25.00	8	1.20
Paseo de las Acacias	Spain	MN05	2.00	0.00	0.00	0.00	0.04	0.20	0.11	0.21	0.92	0.07	0.04	0.09	0.56	30.00	40.00	30.00	10	1.00
Pontlevey	France	MN05	1.80	0.03	0.01	0.04	0.01	0.18	0.10	0.32	0.85	0.02	0.01	0.04	0.18	24.14	17.24	58.62	29	1.08
Poudenas-Peyrecrehen	France	MN05	1.80	0.00	0.00	0.00	0.03	0.24	0.14	0.26	0.95	0.08	0.04	0.10	0.58	36.36	63.64	0.00	11	1.09
Puente de Vallecas	Spain	MN05	1.80	0.04	0.02	0.07	0.06	0.24	0.13	0.29	0.96	0.00	0.00	0.01	0.20	31.25	50.00	18.75	16	1.00
Rimbez - Lapeyrie base	France	MN05	1.80	0.00	0.00	0.00	0.01	0.27	0.16	0.31	0.93	0.08	0.04	0.09	0.56	33.33	41.67	25.00	12	1.00
Rothenstein 1	Germany	MN05	1.80	0.00	0.00	0.00	0.02	0.14	0.07	0.15	0.79	0.00	0.00	0.00	0.23	27.27	36.36	36.36	11	1.14
Samburu Hills 1	Kenya	MN05	1.60	0.00	0.00	0.00	0.01	0.13	0.07	0.15	0.74	0.06	0.03	0.07	0.46	7.69	69.23	23.08	13	1.15
Sandelzhausen	Germany	MN05	1.80	0.03	0.02	0.05	0.03	0.26	0.15	0.38	0.98	0.05	0.03	0.07	0.34	21.74	47.83	30.43	23	1.06
Sant Mamet	Spain	MN05	1.80	0.04	0.02	0.08	0.15	0.36	0.22	0.39	1.00	0.06	0.03	0.08	0.50	28.57	42.86	28.57	14	1.00
Savigné-sur-Lathan	France	MN05	1.80	0.00	0.00	0.00	0.00	0.12	0.06	0.15	0.68	0.05	0.03	0.07	0.41	9.09	72.73	18.18	22	1.05
Shanwang	China	MN05	4.80	0.00	0.00	0.00	0.02	0.22	0.12	0.29	0.95	0.04	0.02	0.05	0.31	24.00	48.00	28.00	25	1.05
Sinda	Congo	MN05	1.60													50.00	50.00	0.00	10	1.00
Thymiana B	Greece	MN05	1.80	0.08	0.04	0.22	0.47	0.20	0.11	0.22	0.89	0.11	0.06	0.14	0.73	30.00	50.00	20.00	10	1.38
Wadi Moghara	Egypt	MN05	4.10	0.00	0.00	0.00	0.00	0.23	0.13	0.35	0.94	0.06	0.03	0.09	0.40	28.57	50.00	21.43	14	1.08
Vieux Collonges	France	MN05	2.80													12.90	12.90	74.19	31	1.00
Zinda Pir 3	Pakistan	MN05	1.60	0.04	0.02	0.11	0.22	0.36	0.22	0.39	1.00	0.16	0.09	0.19	0.82	40.00	60.00	0.00	10	1.00
Al Jadidah	Saudi Arabia	MN06	2.70	0.00	0.00	0.00	0.07	0.16	0.09	0.19	0.82	0.05	0.03	0.07	0.50	62.50	25.00	12.50	8	1.43
Ardic-Mordogan	Turkey	MN06	4.50													50.00	25.00	25.00	12	1.75
Arroyo del Val	Spain	MN06	2.70	0.00	0.00	0.00	0.06	0.10	0.05	0.11	0.61	0.01	0.00	0.01	0.30	33.33	22.22	44.44	9	1.50
Castelnau-d'Arbieu	France	MN06	2.70	0.00	0.00	0.00	0.02	0.18	0.10	0.21	0.77	0.01	0.01	0.02	0.26	35.71	35.71	28.57	14	1.00
Catakbagyaka	Turkey	MN06	4.00	0.04	0.02	0.09	0.15	0.09	0.05	0.10	0.65	0.07	0.04	0.09	0.52	58.33	25.00	16.67	12	1.18
Derching	Germany	MN06	4.50													57.14	42.86	0.00	7	1.29
Devinská Nová-Bonanza	Slovakia	MN06	2.70													0.00	28.57	71.43	7	1.00
Devinská Nová-Fissures	Slovakia	MN06	2.70	0.00	0.00	0.00	0.00	0.19	0.11	0.28	0.92	0.07	0.03	0.10	0.44	21.74	34.78	43.48	23	1.07

Devínská Nová-Sandhill	Slovakia	MN06	4.00	0.06	0.03	0.07	0.02	0.21	0.12	0.36	0.83	0.06	0.03	0.10	0.33	23.53	41.18	35.29	34	1.17
Edelbeuren-Schlactberg	Germany	MN06	2.00													12.50	62.50	25.00	8	1.00
Fort Ternan	Kenya	MN06	3.60	0.19	0.10	0.26	0.72	0.09	0.05	0.14	0.58	0.10	0.05	0.16	0.56	31.03	27.59	41.38	29	1.20
Fort Ternan 2 (Serek)	Kenya	MN06	3.60													30.00	50.00	20.00	10	1.48
Griesbeckerzell	Germany	MN06	4.50													0.00	91.67	8.33	12	1.00
Haulies	France	MN06	2.70	0.00	0.00	0.00	0.04	0.21	0.12	0.22	0.94	0.03	0.01	0.04	0.39	33.33	66.67	0.00	9	1.00
Hezheng-laogou	China	MN06	4.00	0.04	0.02	0.07	0.10	0.16	0.09	0.18	0.79	0.05	0.03	0.06	0.40	36.36	45.45	18.18	11	1.40
Inönü I (Sinap 24A)	Turkey	MN06	2.70	0.07	0.03	0.11	0.10	0.20	0.11	0.29	0.95	0.04	0.02	0.05	0.29	57.89	36.84	5.26	19	1.50
Jiulongkou	China	MN06	2.70	0.08	0.04	0.18	0.35	0.09	0.05	0.10	0.68	0.05	0.02	0.06	0.43	60.00	10.00	30.00	10	1.50
Junggar-1	China	MN06	4.00													37.50	56.25	6.25	16	1.43
Junggar-Botamoyin	China	MN06	4.00	0.08	0.04	0.17	0.28	0.18	0.10	0.19	0.89	0.00	0.00	0.00	0.22	33.33	58.33	8.33	12	1.00
Junggar-Tieersihabahe	China	MN06	4.00	0.04	0.02	0.09	0.12	0.19	0.10	0.20	0.90	0.00	0.00	0.00	0.22	46.15	15.38	38.46	13	1.00
Kipsaramon 1	Kenya	MN06	1.60	0.08	0.04	0.20	0.43	0.05	0.02	0.05	0.46	0.01	0.01	0.02	0.30	12.50	62.50	25.00	8	1.25
Kipsaramon 2	Kenya	MN06	1.60	0.04	0.02	0.09	0.15	0.09	0.05	0.10	0.65	0.07	0.03	0.08	0.52	16.67	58.33	25.00	12	1.00
Klein Hadersdorf	Austria	MN06	2.70													14.29	71.43	14.29	7	1.14
Liet	France	MN06	2.70													20.00	60.00	20.00	10	1.00
Lintong-Lengshuigou	China	MN06	4.00													36.36	54.55	9.09	11	1.36
Muruarot Hill	Kenya	MN06	2.00	0.00	0.00	0.00	0.01	0.25	0.15	0.33	0.98	0.05	0.03	0.07	0.40	5.00	65.00	30.00	20	1.00
Ngorora 13	Kenya	MN06	3.60													30.00	10.00	60.00	10	1.33
Nyakach 10 (Kaimogool)	Kenya	MN06	3.60													38.46	30.77	30.77	13	1.42
Nyakach 11 (Kaimogool)	Kenya	MN06	3.60	0.12	0.06	0.30	0.75	0.20	0.11	0.21	0.92	0.13	0.07	0.16	0.75	58.33	41.67	0.00	12	1.38
Nyakach 19 (Pundo)	Kenya	MN06	3.60													50.00	50.00	0.00	8	1.50
Nyakach 8 (Kadianga)	Kenya	MN06	3.60													46.15	38.46	15.38	13	1.23
Nyakach 9 (Kaimogool)	Kenya	MN06	3.60													28.57	71.43	0.00	7	1.29
Paracuellos 3	Spain	MN06	2.70	0.00	0.00	0.00	0.05	0.21	0.12	0.25	0.89	0.04	0.02	0.05	0.43	66.67	11.11	22.22	9	1.20
Paracuellos 5	Spain	MN06	2.70	0.00	0.00	0.00	0.02	0.22	0.12	0.24	0.95	0.02	0.01	0.03	0.31	44.44	33.33	22.22	9	1.00
Paşalar	Turkey	MN06	4.50	0.05	0.03	0.06	0.01	0.24	0.14	0.51	0.97	0.09	0.05	0.18	0.45	30.77	25.64	43.59	39	1.46
Prebreza	Serbia	MN06	2.70													22.22	44.44	33.33	9	1.33
Ramangar	India	MN06	3.60	0.03	0.02	0.04	0.00	0.20	0.11	0.33	0.18	0.14	0.08	0.23	0.09	34.29	40.00	25.71	35	1.13
Samburu Hills 4	Kenya	MN06	4.00	0.00	0.00	0.00	0.01	0.17	0.09	0.19	0.88	0.06	0.03	0.07	0.47	18.18	54.55	27.27	11	1.18
Sansan	France	MN06	2.70	0.05	0.03	0.05	0.00	0.25	0.14	0.61	0.99	0.06	0.03	0.13	0.26	17.78	31.11	51.11	45	1.00

Sevastopol (Sebastopol)	Ukraine	MN06	2.10	0.19	0.10	0.42	0.91	0.00	0.00	0.00	0.24	0.04	0.02	0.05	0.40	64.29	14.29	21.43	14	1.45
Simorre	France	MN06	4.00	0.00	0.00	0.00	0.02	0.23	0.13	0.28	0.93	0.03	0.01	0.03	0.29	25.00	31.25	43.75	16	1.00
Stätzing	Germany	MN06	2.70	0.03	0.02	0.06	0.04	0.21	0.12	0.29	0.94	0.09	0.05	0.13	0.56	23.81	61.90	14.29	21	1.05
Tairum Nor	China	MN06	0.18	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.26	28.57	42.86	28.57	7	1.00
Thannhausen	Germany	MN06	2.70	0.00	0.00	0.00	0.01	0.21	0.12	0.25	0.91	0.07	0.04	0.09	0.51	37.50	62.50	0.00	16	1.13
Tongxin	China	MN06	2.70	0.04	0.02	0.11	0.24	0.06	0.03	0.06	0.52	0.05	0.03	0.06	0.47	22.22	22.22	55.56	9	1.33
Tongxin-dingjaergou	China	MN06	4.00	0.00	0.00	0.00	0.03	0.14	0.08	0.16	0.77	0.07	0.04	0.08	0.52	22.22	55.56	22.22	9	1.00
Walda 2	Germany	MN06	4.50													0.00	90.91	9.09	11	1.00
Anwil	Switzerland	MN07	1.30	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.26	11.11	33.33	55.56	9	1.00
Can Feliu	Spain	MN07	1.30	0.04	0.02	0.13	0.32	0.10	0.06	0.13	0.63	0.03	0.01	0.04	0.39	12.50	62.50	25.00	8	1.00
Castell de Barberà	Spain	MN07	1.30	0.10	0.05	0.14	0.20	0.15	0.09	0.22	0.71	0.12	0.06	0.18	0.66	22.73	45.45	31.82	22	1.00
Chiang Muan	Thailand	MN07	2.70	0.00	0.00	0.00	0.07	0.11	0.06	0.13	0.72	0.23	0.14	0.30	0.94	25.00	62.50	12.50	8	1.13
Dang Valley	Nepal	MN07	1.30	0.04	0.02	0.11	0.21	0.25	0.15	0.28	0.98	0.19	0.11	0.24	0.84	20.00	60.00	20.00	10	1.00
Escobosa	Spain	MN07	1.30													33.33	11.11	55.56	9	1.00
Hostalets de Pierola Inf.	Spain	MN07	1.30	0.12	0.07	0.17	0.22	0.11	0.06	0.18	0.64	0.07	0.04	0.12	0.43	37.04	33.33	29.63	27	1.00
Junggar-duolebulejin	China	MN07	4.00	0.04	0.02	0.13	0.26	0.06	0.03	0.06	0.53	0.02	0.01	0.02	0.36	37.50	62.50	0.00	8	1.63
Kaiyuan-Xiaolongtan	China	MN07	1.30													0.00	83.33	16.67	6	1.00
Kutsaj M	Russia	MN07	0.70													57.14	28.57	14.29	7	1.67
La Grive St. Alban	France	MN07	1.30	0.07	0.03	0.07	0.00	0.13	0.07	0.36	0.67	0.04	0.02	0.11	0.16	23.33	10.00	66.67	60	1.11
Lintong-lengshuigou	China	MN07	4.00	0.04	0.02	0.13	0.24	0.05	0.03	0.06	0.49	0.00	0.00	0.00	0.28	61.54	38.46	0.00	13	1.85
Mannersdorf	Austria	MN07	1.30													42.86	57.14	0.00	7	1.43
Massenhausen	Germany	MN07	3.00	0.04	0.02	0.08	0.14	0.27	0.15	0.29	0.98	0.05	0.03	0.06	0.43	38.46	53.85	7.69	13	1.00
Ngorora	Kenya	MN07	3.00	0.19	0.10	0.38	0.90	0.21	0.12	0.24	0.93	0.07	0.04	0.09	0.50	50.00	21.43	28.57	14	1.33
Nombrevilla-2	Spain	MN07	1.30													42.86	42.86	14.29	7	1.00
Poudenas-Cayron	France	MN07	1.30	0.00	0.00	0.00	0.05	0.15	0.08	0.17	0.82	0.11	0.06	0.14	0.70	11.11	77.78	11.11	9	1.00
Przeworno 2	Poland	MN07	1.30													25.00	50.00	25.00	8	1.00
Saint-Gaudens (Valent.)	France	MN07	1.30													14.29	85.71	0.00	7	1.00
Sant Quirze	Spain	MN07	1.30	0.09	0.05	0.13	0.13	0.18	0.10	0.28	0.86	0.11	0.06	0.18	0.62	20.83	50.00	29.17	24	1.00
Saricay	Turkey	MN07	1.30													33.33	44.44	22.22	9	1.13
Siwaliks Y0076	Pakistan	MN07	0.08	0.06	0.03	0.07	0.01	0.17	0.10	0.32	0.82	0.26	0.16	0.48	0.95	42.11	36.84	21.05	38	1.10
Sofca	Turkey	MN07	1.30	0.14	0.07	0.22	0.55	0.17	0.10	0.24	0.89	0.14	0.08	0.19	0.74	65.00	25.00	10.00	20	1.39

Steinheim	Germany	MN07	1.30	0.03	0.01	0.04	0.00	0.23	0.13	0.42	0.93	0.05	0.03	0.09	0.30	21.88	34.38	43.75	32	1.06
Tunggur	China	MN07	1.30	0.12	0.06	0.15	0.18	0.11	0.06	0.17	0.53	0.04	0.02	0.07	0.27	34.38	34.38	31.25	32	1.35
Yeni Eskihisar 1	Turkey	MN07	1.30													75.00	0.00	25.00	8	2.00
Yenieskihisar	Turkey	MN07	1.30													77.78	0.00	22.22	9	1.80
Vösendorf	Austria	MN09	1.70	0.20	0.11	0.56	0.98	0.10	0.05	0.11	0.60	0.09	0.05	0.11	0.64	62.50	37.50	0.00	8	1.29
Akin	Turkey	MN09	3.00													85.71	14.29	0.00	7	1.83
Alkacaköy (1-6)	Turkey	MN09	1.70	0.18	0.10	0.33	0.86	0.04	0.02	0.04	0.35	0.10	0.05	0.13	0.56	64.71	23.53	11.76	17	1.36
Atavaska	Moldova	MN09	1.70	0.16	0.09	0.44	0.92	0.05	0.03	0.06	0.50	0.02	0.01	0.02	0.33	55.56	22.22	22.22	9	1.33
Awash 1	Ethiopia	MN09	2.20													57.14	42.86	0.00	7	1.50
Ballestar	Spain	MN09	1.70	0.11	0.06	0.20	0.42	0.15	0.08	0.18	0.78	0.13	0.07	0.17	0.73	30.00	40.00	30.00	20	1.21
Bou Hanifia	Algeria	MN09	1.70	0.19	0.10	0.38	0.90	0.04	0.02	0.04	0.41	0.05	0.03	0.06	0.43	87.50	12.50	0.00	8	1.63
Buzhor 1	Moldova	MN09	1.70	0.15	0.08	0.29	0.76	0.08	0.04	0.08	0.51	0.02	0.01	0.03	0.28	60.00	13.33	26.67	15	1.57
Can Lobateres I	Spain	MN09	0.24	0.14	0.08	0.15	0.12	0.15	0.08	0.36	0.75	0.08	0.04	0.18	0.36	24.00	20.00	56.00	50	1.22
Can Ponsic	Spain	MN09	1.70	0.16	0.09	0.24	0.52	0.15	0.09	0.22	0.73	0.05	0.03	0.08	0.34	33.33	23.81	42.86	21	1.00
Can Ponsic I	Spain	MN09	1.70	0.23	0.13	0.28	0.80	0.22	0.13	0.40	0.86	0.10	0.05	0.18	0.54	36.67	30.00	33.33	30	1.16
Charmolle	Switzerland	MN09	1.70	0.11	0.06	0.21	0.49	0.16	0.09	0.18	0.81	0.11	0.06	0.14	0.65	40.00	46.67	13.33	15	1.23
Chorora Fm.	Ethiopia	MN09	1.00													55.56	22.22	22.22	9	1.29
El Firal	Spain	MN09	1.70	0.07	0.04	0.14	0.22	0.16	0.09	0.18	0.79	0.08	0.04	0.10	0.54	26.67	46.67	26.67	15	1.23
Eppelsheim	Germany	MN09	1.70	0.08	0.04	0.10	0.03	0.24	0.14	0.46	0.94	0.15	0.08	0.27	0.74	30.00	40.00	30.00	30	1.19
Esme Akçaköy	Turkey	MN09	1.70	0.08	0.04	0.17	0.30	0.09	0.05	0.10	0.63	0.16	0.09	0.19	0.82	58.33	25.00	16.67	12	1.22
Esselborn	Germany	MN09	1.70	0.04	0.02	0.10	0.17	0.09	0.05	0.10	0.59	0.08	0.04	0.10	0.58	18.18	81.82	0.00	11	1.09
Estevar	Spain	MN09	1.70	0.12	0.07	0.38	0.77	0.10	0.06	0.13	0.62	0.12	0.07	0.16	0.73	50.00	25.00	25.00	8	1.60
Gaiselberg	Austria	MN09	1.70													28.57	28.57	42.86	7	1.40
Gau-Weinheim	Germany	MN09	1.70													28.57	57.14	14.29	7	1.17
Guonigou	China	MN09	1.70	0.04	0.02	0.13	0.24	0.00	0.00	0.00	0.27	0.01	0.00	0.01	0.31	71.43	14.29	14.29	7	2.20
Hostalets de Pierola Sup	Spain	MN09	1.70	0.11	0.06	0.20	0.42	0.07	0.04	0.08	0.52	0.07	0.04	0.09	0.49	47.06	35.29	17.65	17	1.27
Höwenegg	Germany	MN09	1.70	0.16	0.09	0.50	0.95	0.10	0.06	0.13	0.63	0.05	0.03	0.07	0.47	55.56	11.11	33.33	9	1.40
Kalfa	Moldova	MN09	1.70	0.23	0.13	0.35	0.93	0.13	0.07	0.17	0.58	0.09	0.05	0.13	0.55	50.00	27.27	22.73	22	1.25
Kishinev	Moldova	MN09	1.70													57.14	0.00	42.86	7	2.00
Los Valles-Fuentidueña	Spain	MN09	1.70	0.07	0.03	0.11	0.10	0.16	0.09	0.22	0.76	0.11	0.06	0.15	0.62	52.38	19.05	28.57	21	1.40
Middle Sinap	Turkey	MN09	2.20	0.25	0.14	0.44	0.98	0.07	0.04	0.08	0.49	0.13	0.07	0.18	0.73	56.25	12.50	31.25	16	1.38

Nakali	Kenya	MN09	2.20	0.25	0.15	0.50	0.99	0.04	0.02	0.04	0.37	0.11	0.06	0.14	0.64	46.67	40.00	13.33	15	1.38
Nombrevilla	Spain	MN09	1.70	0.12	0.06	0.30	0.70	0.10	0.05	0.11	0.68	0.01	0.00	0.01	0.27	36.36	45.45	18.18	11	1.20
Oshin-I-5 upper	Mongolia	MN09	1.10	0.24	0.14	0.75	1.00	0.05	0.03	0.06	0.49	0.06	0.03	0.08	0.52	70.00	20.00	10.00	10	2.00
Oshin-II-5 upper	Mongolia	MN09	1.10													90.00	10.00	0.00	10	2.20
Qaidam	China	MN09	1.70	0.15	0.08	0.31	0.77	0.00	0.00	0.00	0.20	0.06	0.03	0.08	0.49	72.22	22.22	5.56	18	1.56
Rudabánya	Hungary	MN09	0.85	0.14	0.08	0.18	0.32	0.18	0.10	0.32	0.82	0.09	0.05	0.17	0.52	27.03	24.32	48.65	37	1.21
Santiga	Spain	MN09	1.70	0.11	0.06	0.23	0.55	0.21	0.12	0.22	0.82	0.02	0.01	0.02	0.28	46.67	46.67	6.67	15	1.25
Sinap 108	Turkey	MN09	1.06													46.67	20.00	33.33	15	1.67
Sinap 111	Turkey	MN09	1.70													62.50	0.00	37.50	8	1.40
Sinap 4	Turkey	MN09	1.06													66.67	6.67	26.67	15	1.33
Sinap 45	Turkey	MN09	2.20													42.86	28.57	28.57	7	1.50
Sinap 64	Turkey	MN09	1.06													60.00	0.00	40.00	10	1.29
Sinap 72	Turkey	MN09	1.06	0.29	0.17	0.88	1.00	0.00	0.00	0.00	0.32	0.07	0.04	0.09	0.55	72.22	11.11	16.67	18	1.50
Sinap 88	Turkey	MN09	0.04													100.00	0.00	0.00	7	2.17
Sinap 91	Turkey	MN09	1.06													84.62	7.69	7.69	13	1.73
Sinap 94	Turkey	MN09	1.06													75.00	8.33	16.67	12	1.38
Siwaliks Y0251	Pakistan	MN09	0.05	0.07	0.04	0.15	0.28	0.17	0.09	0.19	0.86	0.52	0.37	0.64	1.00	38.46	46.15	15.38	13	1.50
Siwaliks Y0258	Pakistan	MN09	0.07	0.08	0.04	0.20	0.44	0.10	0.05	0.11	0.65	0.46	0.31	0.55	1.00	63.64	27.27	9.09	11	1.60
Siwaliks Y0259	Pakistan	MN09	0.09	0.00	0.00	0.00	0.06	0.10	0.05	0.11	0.71	0.37	0.25	0.45	0.95	18.18	54.55	27.27	11	1.00
Siwaliks Y0311	Pakistan	MN09	0.07	0.11	0.06	0.12	0.06	0.13	0.07	0.28	0.78	0.43	0.29	0.88	1.00	45.00	27.50	27.50	40	1.43
Sop Mae Tham	Thailand	MN09	1.70													37.50	62.50	0.00	8	1.25
Subsol de Sabadell	Spain	MN09	1.70	0.15	0.08	0.29	0.70	0.20	0.11	0.22	0.82	0.13	0.07	0.16	0.73	35.71	50.00	14.29	14	1.27
Varnitsa	Moldova	MN09	1.70	0.16	0.09	0.44	0.91	0.05	0.03	0.06	0.49	0.04	0.02	0.05	0.42	70.00	20.00	10.00	10	1.67
Wartenberg	Germany	MN09	1.70	0.00	0.00	0.00	0.06	0.27	0.15	0.31	0.98	0.03	0.01	0.04	0.40	40.00	60.00	0.00	10	1.10
Zhelitokamenka	Ukraine	MN09	0.55													42.86	57.14	0.00	7	1.43
Biru-Bulong	China	MN10	4.00													80.00	0.00	20.00	10	2.17
Botamojnak	Kazakhstan	MN10	2.89	0.19	0.11	0.45	0.93	0.04	0.02	0.05	0.44	0.10	0.05	0.12	0.60	69.23	15.38	15.38	13	1.89
Can Purull	Spain	MN10	0.50	0.32	0.19	0.48	1.00	0.06	0.03	0.08	0.41	0.07	0.04	0.10	0.43	57.14	23.81	19.05	21	1.31
Eldari I	Georgia	MN10	1.10	0.34	0.21	0.59	1.00	0.07	0.04	0.08	0.49	0.09	0.05	0.12	0.54	62.50	20.83	16.67	24	1.50
Fugu-Laogaochuan	China	MN10	1.90	0.25	0.14	0.47	0.98	0.00	0.00	0.00	0.14	0.04	0.02	0.05	0.37	76.19	9.52	14.29	21	1.80
Grebeniki	Ukraine	MN10	1.90	0.42	0.27	0.62	1.00	0.06	0.03	0.08	0.38	0.05	0.03	0.07	0.36	62.50	25.00	12.50	24	1.67

Siwaliks Y0193	Pakistan	MN10	0.05	0.00	0.00	0.08	0.12	0.06	0.14	0.82	0.46	0.31	0.61	0.99	28.57	71.43	0.00	7	1.57
Siwaliks Y0196	Pakistan	MN10	0.05	0.08	0.04	0.22	0.49	0.00	0.00	0.27	0.41	0.27	0.50	0.99	80.00	10.00	10.00	10	2.13
Siwaliks Y0211	Pakistan	MN10	0.02	0.10	0.05	0.18	0.33	0.11	0.06	0.14	0.67	0.55	0.39	0.73	41.18	47.06	11.76	17	1.50
Siwaliks Y0212	Pakistan	MN10	0.04	0.00	0.00	0.00	0.05	0.11	0.06	0.13	0.75	0.46	0.31	0.57	62.50	12.50	25.00	8	1.43
Siwaliks Y0221	Pakistan	MN10	0.03	0.04	0.02	0.10	0.13	0.10	0.05	0.11	0.68	0.61	0.46	0.74	45.45	45.45	9.09	11	1.45
Siwaliks Y0224	Pakistan	MN10	0.03	0.08	0.04	0.29	0.65	0.12	0.06	0.14	0.78	0.38	0.25	0.51	37.50	50.00	12.50	8	1.25
Siwaliks Y0225	Pakistan	MN10	0.03	0.00	0.00	0.00	0.09	0.11	0.06	0.13	0.76	0.52	0.37	0.65	50.00	37.50	12.50	8	1.29
Siwaliks Y0226	Pakistan	MN10	0.02	0.00	0.00	0.00	0.06	0.12	0.06	0.14	0.78	0.43	0.29	0.57	42.86	28.57	28.57	7	1.67
Siwaliks Y0227	Pakistan	MN10	0.03	0.03	0.02	0.05	0.02	0.07	0.04	0.10	0.52	0.58	0.42	0.81	40.00	35.00	25.00	20	1.38
Siwaliks Y0243	Pakistan	MN10	0.01	0.04	0.02	0.10	0.18	0.05	0.02	0.05	0.46	0.44	0.30	0.53	50.00	30.00	20.00	10	1.22
Siwaliks Y0260	Pakistan	MN10	0.02	0.07	0.04	0.15	0.28	0.09	0.04	0.10	0.61	0.52	0.37	0.64	45.45	45.45	9.09	11	1.31
Siwaliks Y0261	Pakistan	MN10	0.01	0.00	0.00	0.00	0.06	0.12	0.06	0.14	0.79	0.54	0.39	0.71	28.57	57.14	14.29	7	1.67
Siwaliks Y0262	Pakistan	MN10	0.02	0.08	0.04	0.18	0.33	0.14	0.08	0.16	0.80	0.47	0.32	0.57	41.67	50.00	8.33	12	1.42
Siwaliks Y0269	Pakistan	MN10	0.02	0.00	0.00	0.00	0.01	0.12	0.06	0.14	0.74	0.52	0.37	0.65	33.33	53.33	13.33	15	1.46
Siwaliks Y0309	Pakistan	MN10	0.03	0.00	0.00	0.00	0.01	0.09	0.04	0.10	0.59	0.60	0.45	0.74	35.71	35.71	28.57	14	1.36
Siwaliks Y0310	Pakistan	MN10	0.03	0.03	0.02	0.05	0.03	0.07	0.04	0.10	0.46	0.56	0.40	0.79	47.37	36.84	15.79	19	1.50
Siwaliks Y0312	Pakistan	MN10	0.03	0.00	0.00	0.00	0.04	0.11	0.06	0.13	0.70	0.53	0.37	0.66	50.00	37.50	12.50	8	1.57
Siwaliks Y0314	Pakistan	MN10	0.02	0.04	0.02	0.07	0.06	0.12	0.06	0.14	0.74	0.50	0.35	0.62	33.33	40.00	26.67	15	1.09
Siwaliks Y0317	Pakistan	MN10	0.04	0.03	0.02	0.06	0.04	0.11	0.06	0.15	0.67	0.59	0.44	0.80	47.37	36.84	15.79	19	1.50
Siwaliks Y0327	Pakistan	MN10	0.06	0.00	0.00	0.00	0.05	0.11	0.06	0.13	0.75	0.42	0.28	0.53	37.50	37.50	25.00	8	1.67
Siwaliks Y0328	Pakistan	MN10	0.03	0.08	0.04	0.25	0.54	0.00	0.00	0.00	0.28	0.34	0.22	0.42	37.50	37.50	25.00	8	1.57
Siwaliks Y0329	Pakistan	MN10	0.10	0.04	0.02	0.14	0.30	0.05	0.03	0.07	0.54	0.40	0.27	0.53	42.86	42.86	14.29	7	1.67
Siwaliks Y0330	Pakistan	MN10	0.10	0.08	0.04	0.25	0.58	0.06	0.03	0.06	0.53	0.33	0.21	0.41	87.50	12.50	0.00	8	1.88
Siwaliks Y0337	Pakistan	MN10	0.06	0.08	0.04	0.18	0.35	0.04	0.02	0.05	0.42	0.41	0.27	0.49	63.64	27.27	9.09	11	1.45
Soblay	France	MN10	0.50	0.12	0.07	0.38	0.81	0.05	0.03	0.06	0.52	0.03	0.01	0.04	50.00	0.00	50.00	8	1.60
Terrassa	Spain	MN10	0.50	0.26	0.15	0.38	0.94	0.15	0.09	0.22	0.71	0.12	0.07	0.19	50.00	31.82	18.18	22	1.35
Udabno I	Georgia	MN10	1.10	0.30	0.18	0.67	1.00	0.08	0.05	0.08	0.57	0.07	0.04	0.08	61.54	30.77	7.69	13	1.50
Wissberg	Germany	MN10	1.70	0.07	0.04	0.12	0.14	0.14	0.08	0.18	0.76	0.12	0.07	0.17	5.56	72.22	22.22	18	1.00
Xirochori 1 (XIR)	Greece	MN10	0.50	0.16	0.09	0.44	0.92	0.00	0.00	0.00	0.27	0.03	0.02	0.03	77.78	11.11	11.11	9	1.71
Altan-Teli	Mongolia	MN11	0.93	0.27	0.16	0.64	1.00	0.00	0.00	0.00	0.24	0.05	0.03	0.06	78.95	15.79	5.26	19	2.12
Bala Yaylaköy	Turkey	MN11	0.80	0.27	0.16	0.70	1.00	0.00	0.00	0.00	0.27	0.10	0.05	0.12	66.67	16.67	16.67	12	1.45

Corakyerler	Turkey	MN11	0.80	0.35	0.21	0.63	1.00	0.00	0.00	0.00	0.16	0.06	0.03	0.08	0.43	78.95	15.79	5.26	19	1.83
Crevillente 2	Spain	MN11	0.80	0.25	0.15	0.50	0.99	0.12	0.06	0.14	0.75	0.08	0.04	0.10	0.53	44.44	38.89	16.67	18	1.27
Csakvar	Hungary	MN11	0.80	0.16	0.09	0.24	0.60	0.00	0.00	0.00	0.12	0.01	0.01	0.02	0.17	43.48	17.39	39.13	23	1.64
Dorn Dürkheim 1	Germany	MN11	0.80	0.26	0.15	0.29	0.85	0.11	0.06	0.22	0.60	0.06	0.03	0.13	0.32	28.57	28.57	42.86	42	1.22
Dzhuanyark	Kyrgyzstan	MN11	1.24	0.28	0.16	0.78	1.00	0.00	0.00	0.00	0.26	0.05	0.03	0.06	0.47	63.64	36.36	0.00	11	1.70
Garkin	Turkey	MN11	0.80	0.37	0.23	0.61	1.00	0.00	0.00	0.00	0.14	0.06	0.03	0.08	0.38	68.42	15.79	15.79	19	1.64
Injana	Iraq	MN11	0.80	0.36	0.22	0.67	1.00	0.12	0.06	0.15	0.72	0.17	0.10	0.22	0.82	70.00	25.00	5.00	20	1.56
Kalimanci 1	Bulgaria	MN11	0.80	0.31	0.18	0.73	1.00	0.00	0.00	0.00	0.22	0.05	0.03	0.06	0.44	66.67	16.67	16.67	12	1.67
Karacahasan	Turkey	MN11	0.80	0.41	0.26	0.71	1.00	0.00	0.00	0.00	0.16	0.06	0.03	0.08	0.40	78.95	10.53	10.53	19	1.69
Kayadibi	Turkey	MN11	0.80	0.33	0.20	0.64	1.00	0.04	0.02	0.04	0.37	0.04	0.02	0.05	0.36	64.29	21.43	14.29	14	1.42
Kemiklitepe 1.2	Turkey	MN11	1.90	0.48	0.32	0.71	1.00	0.00	0.00	0.00	0.11	0.05	0.03	0.08	0.36	80.00	5.00	15.00	20	1.82
Kemiklitepe D	Turkey	MN11	0.80	0.24	0.13	0.60	1.00	0.00	0.00	0.00	0.24	0.04	0.02	0.05	0.43	90.91	0.00	9.09	11	1.90
Kocherinovo 1	Bulgaria	MN11	0.80													57.14	28.57	14.29	7	1.83
Kocherinovo 2	Bulgaria	MN11	0.80													75.00	25.00	0.00	8	1.63
Kujalnitiskij liman	Ukraine	MN11	2.78													88.89	11.11	0.00	9	2.00
Küçükçekmece	Turkey	MN11	0.80	0.36	0.22	0.55	1.00	0.10	0.05	0.14	0.61	0.11	0.06	0.16	0.63	59.09	22.73	18.18	22	1.38
Lower Maragheh	Iran	MN11	0.80	0.29	0.17	1.00	1.00	0.00	0.00	0.00	0.30	0.04	0.02	0.05	0.43	77.78	22.22	0.00	9	2.00
Nikiti 1 (NKT)	Greece	MN11	0.80	0.38	0.24	0.91	1.00	0.00	0.00	0.00	0.22	0.05	0.03	0.06	0.43	86.67	6.67	6.67	15	1.57
Nikiti 2 (NIK)	Greece	MN11	0.80	0.29	0.17	0.88	1.00	0.00	0.00	0.00	0.28	0.08	0.05	0.11	0.59	90.00	10.00	0.00	10	1.89
Novaja Emetovka	Ukraine	MN11	1.10	0.45	0.29	0.76	1.00	0.03	0.02	0.04	0.34	0.07	0.04	0.10	0.48	63.16	31.58	5.26	19	1.63
Piera	Spain	MN11	0.80	0.19	0.10	0.38	0.90	0.08	0.04	0.08	0.53	0.05	0.03	0.06	0.42	64.29	28.57	7.14	14	1.30
Puente Minero	Spain	MN11	0.80	0.28	0.16	0.50	0.98	0.04	0.02	0.04	0.31	0.01	0.01	0.01	0.21	55.56	22.22	22.22	18	1.50
Qaidam-shenggou	China	MN11	1.00	0.16	0.09	0.40	0.88	0.05	0.02	0.05	0.46	0.05	0.03	0.07	0.49	63.64	18.18	18.18	11	2.00
Ravin des Zouaves 5	Greece	MN11	0.80	0.45	0.29	0.67	1.00	0.00	0.00	0.00	0.12	0.09	0.05	0.14	0.54	76.92	15.38	7.69	26	1.65
Samos-Q6	Greece	MN11	0.80													75.00	12.50	12.50	8	1.86
Sarihasan	Turkey	MN11	2.40													28.57	42.86	28.57	7	1.40
Sinap 34	Turkey	MN11	0.45													81.82	9.09	9.09	11	1.60
Siwaliks Y0024	Pakistan	MN11	0.16	0.15	0.08	0.31	0.71	0.09	0.04	0.10	0.64	0.45	0.30	0.55	0.99	60.00	40.00	0.00	15	1.73
Siwaliks Y0028	Pakistan	MN11	0.15	0.04	0.02	0.07	0.06	0.23	0.13	0.28	0.93	0.43	0.28	0.56	0.99	52.63	42.11	5.26	19	1.50
Strumyani 1	Bulgaria	MN11	0.80													80.00	10.00	10.00	10	1.80
Strumyani 2	Bulgaria	MN11	0.80													69.23	23.08	7.69	13	1.75

Ravin X	Greece	MN12	1.10	0.47	0.31	0.93	1.00	0.00	0.00	0.00	0.20	0.07	0.04	0.09	0.46	78.57	14.29	7.14	14	1.67
Salihpasalar	Turkey	MN12	1.10	0.26	0.15	0.58	1.00	0.00	0.00	0.00	0.20	0.04	0.02	0.05	0.40	84.62	7.69	7.69	13	1.58
Salihpasalar 1	Turkey	MN12	1.10	0.31	0.19	0.80	1.00	0.00	0.00	0.00	0.25	0.05	0.03	0.06	0.46	90.00	10.00	0.00	10	1.57
Salihpasalar 2	Turkey	MN12	1.10	0.27	0.16	0.70	1.00	0.00	0.00	0.00	0.24	0.04	0.02	0.05	0.44	100.00	0.00	0.00	10	1.43
Samos (A-1)	Greece	MN12	1.90	0.60	0.43	0.72	1.00	0.02	0.01	0.04	0.15	0.09	0.05	0.16	0.49	78.79	15.15	6.06	33	1.87
Samos Main Bone Beds	Greece	MN12	0.50	0.65	0.48	0.73	1.00	0.05	0.02	0.10	0.23	0.07	0.04	0.15	0.39	72.73	14.55	12.73	55	1.83
Samos White Sands	Greece	MN12	0.22													87.50	12.50	0.00	8	2.50
Samos-Q5	Greece	MN12	1.10													100.00	0.00	0.00	16	1.69
Sandikli Kinik	Turkey	MN12	2.90	0.50	0.33	0.93	1.00	0.00	0.00	0.00	0.17	0.06	0.03	0.07	0.42	86.67	13.33	0.00	15	1.91
Serefköy	Turkey	MN12	1.10	0.38	0.23	0.83	1.00	0.00	0.00	0.00	0.21	0.06	0.03	0.07	0.47	100.00	0.00	0.00	11	1.83
Sinap 26	Turkey	MN12	0.15	0.27	0.16	0.64	1.00	0.00	0.00	0.00	0.25	0.05	0.02	0.06	0.42	65.00	20.00	15.00	20	1.63
Sinap 27	Turkey	MN12	0.15													77.78	0.00	22.22	9	1.71
Sinap 33	Turkey	MN12	0.15	0.20	0.11	0.50	0.94	0.00	0.00	0.00	0.25	0.05	0.03	0.06	0.45	65.00	20.00	15.00	20	1.56
Siwaliks L0082	Pakistan	MN12	0.11	0.04	0.02	0.14	0.30	0.12	0.06	0.14	0.74	0.37	0.24	0.50	0.98	11.11	77.78	11.11	9	1.25
Siwaliks Y0011	Pakistan	MN12	0.12	0.00	0.00	0.00	0.04	0.10	0.05	0.11	0.68	0.42	0.28	0.51	0.98	41.67	25.00	33.33	12	1.86
Siwaliks Y0017	Pakistan	MN12	0.06	0.08	0.04	0.20	0.42	0.10	0.05	0.11	0.65	0.45	0.30	0.54	1.00	70.00	30.00	0.00	10	1.90
Siwaliks Y0019	Pakistan	MN12	0.11	0.04	0.02	0.14	0.31	0.00	0.00	0.00	0.29	0.34	0.21	0.45	0.97	57.14	28.57	14.29	7	2.00
Siwaliks Y0097	Pakistan	MN12	0.20													85.71	14.29	0.00	7	1.86
Sor	Tajikistan	MN12	1.10	0.27	0.16	0.64	1.00	0.00	0.00	0.00	0.24	0.07	0.04	0.08	0.53	66.67	13.33	20.00	15	1.64
Taraklia	Moldova	MN12	2.90	0.41	0.26	0.52	1.00	0.05	0.03	0.08	0.32	0.04	0.02	0.07	0.26	80.49	14.63	4.88	41	1.67
Tudorovo	Moldova	MN12	1.10	0.24	0.14	0.75	1.00	0.05	0.03	0.06	0.52	0.06	0.03	0.08	0.53	83.33	16.67	0.00	12	1.40
Upper Maragheh	Iran	MN12	1.10	0.76	0.61	1.00	1.00	0.03	0.01	0.04	0.22	0.06	0.03	0.10	0.38	72.22	16.67	11.11	18	1.92
Valdeebro 5	Spain	MN12	1.10													62.50	12.50	25.00	8	1.67
Vathylakkos 2 (VTK)	Greece	MN12	1.10	0.38	0.23	0.83	1.00	0.00	0.00	0.00	0.23	0.07	0.04	0.09	0.51	76.92	15.38	7.69	13	1.55
Vathylakkos 3 (VAT)	Greece	MN12	1.10	0.45	0.29	0.67	1.00	0.06	0.03	0.10	0.41	0.10	0.05	0.15	0.58	71.43	14.29	14.29	21	1.50
Albertine 1	Uganda	MN13	1.80	0.07	0.03	0.11	0.10	0.00	0.00	0.00	0.14	0.02	0.01	0.03	0.23	50.00	34.38	15.63	32	1.80
Albertine 12	Congo	MN13	1.80													57.14	42.86	0.00	7	1.00
Albertine 14	Congo	MN13	1.80	0.00	0.00	0.00	0.04	0.20	0.11	0.21	0.92	0.10	0.05	0.12	0.65	28.57	57.14	14.29	14	1.00
Amasya 2	Turkey	MN13	1.80													71.43	14.29	14.29	7	2.00
Arenas del Rey	Spain	MN13	1.80													50.00	50.00	0.00	10	1.56
Arquillo 1	Spain	MN13	1.80	0.34	0.20	0.56	1.00	0.00	0.00	0.00	0.13	0.06	0.03	0.07	0.40	71.43	23.81	4.76	21	2.00

Asa kuma	Ethiopia	MN13	1.00	0.14	0.07	0.15	0.16	0.02	0.01	0.04	0.11	0.02	0.01	0.03	0.12	48.84	18.60	32.56	43	1.61
Baccinello V3	Italy	MN13	2.90	0.11	0.06	0.23	0.54	0.04	0.02	0.04	0.39	0.07	0.04	0.08	0.49	42.11	42.11	15.79	19	1.43
Brisighella	Italy	MN13	1.80	0.15	0.08	0.33	0.78	0.00	0.00	0.00	0.22	0.07	0.03	0.08	0.51	50.00	25.00	25.00	16	1.83
Casino	Italy	MN13	2.90												25.00	50.00	25.00	8	1.71	
Dytiko 1 (DTK)	Greece	MN13	1.80	0.39	0.24	0.73	1.00	0.00	0.00	0.00	0.17	0.07	0.03	0.08	0.45	73.33	20.00	6.67	15	1.73
Dytiko 2 (DIT)	Greece	MN13	1.80	0.35	0.21	0.90	1.00	0.00	0.00	0.00	0.25	0.07	0.04	0.08	0.52	66.67	16.67	16.67	12	1.33
Dytiko 3 (DKO)	Greece	MN13	1.80	0.19	0.11	0.45	0.96	0.09	0.05	0.10	0.66	0.13	0.07	0.15	0.74	63.64	18.18	18.18	11	1.50
El Arquillo 1	Spain	MN13	1.80	0.33	0.20	0.50	1.00	0.00	0.00	0.00	0.13	0.05	0.03	0.07	0.37	69.23	23.08	7.69	26	1.93
Fugu-Laogaochuan-miao	China	MN13	1.90	0.08	0.04	0.22	0.50	0.00	0.00	0.00	0.27	0.01	0.00	0.01	0.29	41.67	58.33	0.00	12	1.45
Fu-Ku-Lok.51	China	MN13	1.90												87.50	0.00	12.50	8	2.14	
Gravitelli	Italy	MN13	1.80	0.20	0.11	0.50	0.98	0.00	0.00	0.00	0.26	0.10	0.06	0.13	0.68	58.33	25.00	16.67	12	1.63
Gusinyy pereyot	Kazakhstan	MN13	3.70	0.35	0.22	0.52	1.00	0.00	0.00	0.00	0.13	0.01	0.00	0.01	0.14	68.00	12.00	20.00	25	2.00
Hezheng-heilingding	China	MN13	1.90												70.59	11.76	17.65	17	1.67	
Hsin-An-Loc.12	China	MN13	1.90	0.19	0.10	0.42	0.95	0.00	0.00	0.00	0.22	0.05	0.02	0.06	0.43	76.92	15.38	7.69	13	1.50
Huade-Tuchetse	China	MN13	1.90												66.67	33.33	0.00	12	1.67	
Huoxian-anlecun	China	MN13	1.90												71.43	28.57	0.00	7	1.40	
Jilong	China	MN13	1.90												75.00	25.00	0.00	8	1.57	
Jungar-Yaogou	China	MN13	1.90												75.00	8.33	16.67	12	2.00	
Kalmakpaj	Kazakhstan	MN13	1.80	0.28	0.16	0.50	1.00	0.04	0.02	0.04	0.33	0.04	0.02	0.05	0.35	63.16	10.53	26.32	19	2.18
Karabastuz	Kazakhstan	MN13	2.36	0.16	0.09	0.44	0.94	0.00	0.00	0.00	0.26	0.01	0.01	0.01	0.31	58.33	25.00	16.67	12	1.88
Khirgis-Nur II-lower	Mongolia	MN13	1.70	0.12	0.07	0.38	0.79	0.00	0.00	0.00	0.28	0.08	0.04	0.11	0.61	57.89	21.05	21.05	19	2.15
Kuseralie	Ethiopia	MN13	1.00	0.14	0.08	0.17	0.23	0.05	0.03	0.08	0.31	0.04	0.02	0.08	0.25	48.72	25.64	25.64	39	1.50
La Alberca	Spain	MN13	1.80												71.43	14.29	14.29	7	1.60	
Langebaanweg 2 (PPM)	South Africa	MN13	1.80	0.06	0.03	0.09	0.04	0.03	0.02	0.04	0.23	0.02	0.01	0.03	0.18	61.54	15.38	23.08	26	1.94
Langebaanweg 3 (QSM)	South Africa	MN13	1.80	0.09	0.05	0.13	0.11	0.03	0.01	0.04	0.20	0.05	0.02	0.07	0.28	75.00	7.14	17.86	28	1.94
Lantian-42	China	MN13	1.90	0.23	0.13	0.55	0.99	0.00	0.00	0.00	0.22	0.05	0.02	0.05	0.44	75.00	25.00	0.00	12	1.78
Lantian-jiulaopo	China	MN13	1.90												42.86	57.14	0.00	7	1.57	
Lantian-koujiacun-damia	China	MN13	1.90												77.78	11.11	11.11	9	1.67	
Lantian-majiahe-yuanjia	China	MN13	1.90												57.14	42.86	0.00	7	1.71	
Las Casiones	Spain	MN13	1.80	0.23	0.13	0.37	0.90	0.00	0.00	0.00	0.12	0.01	0.01	0.02	0.19	43.48	30.43	26.09	23	1.86
Lemudong'o	Kenya	MN13	1.00	0.03	0.02	0.05	0.03	0.00	0.00	0.00	0.15	0.01	0.01	0.01	0.18	45.45	13.64	40.91	22	1.50

Tha Chang 2	Thailand	MN13	4.10	0.08	0.04	0.22	0.54	0.00	0.00	0.00	0.28	0.14	0.08	0.18	0.75	40.00	60.00	0.00	10	1.60
Titov Veles	Macedonia	MN13	2.90													70.00	10.00	20.00	10	1.29
Toros-Menalla (TM-266)	Chad	MN13	1.80	0.19	0.11	0.29	0.76	0.00	0.00	0.00	0.12	0.01	0.01	0.01	0.17	59.09	22.73	18.18	22	1.47
Wenquan-dakusitai	China	MN13	1.90													75.00	12.50	12.50	8	1.40
Venta del Moro	Spain	MN13	1.80	0.19	0.11	0.27	0.72	0.03	0.02	0.04	0.22	0.05	0.03	0.08	0.34	60.71	14.29	25.00	28	1.69
Villastar	Spain	MN13	1.80													55.56	33.33	11.11	9	1.88
Wudu-longjiagou	China	MN13	1.90													56.67	33.33	10.00	30	1.46
Wu-Hsiang-loc.78	China	MN13	1.90													75.00	25.00	0.00	8	1.38
Wu-Hsiang-Lok.70	China	MN13	1.90													71.43	28.57	0.00	7	1.29
Wu-Hsiang-Lok.73	China	MN13	1.90	0.12	0.06	0.33	0.78	0.00	0.00	0.00	0.27	0.05	0.03	0.06	0.49	60.00	40.00	0.00	10	1.22
Yushe	China	MN13	1.80	0.11	0.06	0.25	0.58	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.21	44.00	44.00	12.00	25	1.25
Zhangqiu-Balouhe	China	MN13	1.90													50.00	50.00	0.00	12	1.45
Alcoy+B556	Spain	MN14	1.10	0.12	0.06	0.30	0.67	0.00	0.00	0.00	0.26	0.11	0.06	0.13	0.70	45.45	45.45	9.09	11	1.90
Aramis	Ethiopia	MN14	0.06	0.07	0.04	0.11	0.12	0.03	0.02	0.04	0.28	0.02	0.01	0.02	0.21	34.48	31.03	34.48	29	1.45
Awash 4	Ethiopia	MN14	1.10													46.67	53.33	0.00	15	1.57
Awash 5	Ethiopia	MN14	1.10													45.00	30.00	25.00	20	1.72
Beresti	Romania	MN14	1.10													11.11	33.33	55.56	9	1.60
Dorkovo	Bulgaria	MN14	1.10	0.08	0.04	0.25	0.52	0.00	0.00	0.00	0.29	0.01	0.00	0.01	0.31	38.46	30.77	30.77	13	1.40
Fonelas	Spain	MN14	1.10	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.20	64.29	21.43	14.29	14	2.00
Yushe-Gaozhuang	China	MN14	2.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.21	0.00	0.00	0.01	0.23	33.33	25.00	41.67	12	1.60
Gona Western Margin 3	Ethiopia	MN14	0.17													50.00	50.00	0.00	10	1.50
Guanghe-shiliudun	China	MN14	1.10	0.16	0.09	0.40	0.91	0.00	0.00	0.00	0.26	0.01	0.00	0.01	0.27	80.00	10.00	10.00	10	1.50
Khrgis-Nur II	Mongolia	MN14	0.40	0.08	0.04	0.20	0.47	0.05	0.02	0.05	0.46	0.01	0.00	0.01	0.27	50.00	18.75	31.25	16	2.31
Khrgis-Nur II-upper	Mongolia	MN14	0.80	0.12	0.06	0.33	0.78	0.00	0.00	0.00	0.28	0.07	0.04	0.10	0.58	60.00	20.00	20.00	20	2.21
Kolle	Chad	MN14	1.10	0.07	0.04	0.14	0.24	0.00	0.00	0.00	0.20	0.01	0.01	0.02	0.24	40.00	46.67	13.33	15	1.57
Kossom Bougoudi	Chad	MN14	1.10	0.10	0.05	0.18	0.26	0.00	0.00	0.00	0.17	0.01	0.01	0.01	0.21	54.55	31.82	13.64	22	1.61
Kosyakino	Russia	MN14	1.10	0.11	0.06	0.21	0.44	0.08	0.04	0.08	0.53	0.11	0.06	0.13	0.66	35.71	42.86	21.43	14	1.30
La Gloria	Spain	MN14	1.10													80.00	10.00	10.00	10	1.43
La Gloria 4	Spain	MN14	1.10	0.08	0.04	0.20	0.48	0.00	0.00	0.00	0.26	0.05	0.03	0.06	0.46	85.71	7.14	7.14	14	2.33
Lothagam 3	Kenya	MN14	1.10	0.14	0.08	0.17	0.23	0.05	0.03	0.10	0.30	0.04	0.02	0.08	0.25	57.78	31.11	11.11	45	1.71
Montpellier	France	MN14	1.10	0.10	0.05	0.14	0.22	0.03	0.02	0.04	0.26	0.05	0.03	0.07	0.34	30.77	30.77	38.46	26	1.35

Shoshmagagai 2	Tanzania	MN14	1.10	42.86	57.14	0.00	7	1.57
Trevoux	France	MN14	1.10	28.57	57.14	14.29	7	1.33

Paper I

Mirzaie Ataabadi, M. and Abbassi, N. 2007.

Affinities and implications of new Miocene mammal footprints from Iran.

Vertebrata Palasiatica 45:128-136.

Paper II

Eronen, J. T., Mirzaie Atabadi, M., Micheels, A, Karme,
A., Bernor, R. L., and Fortelius, M. 2009.

Distribution history and climatic controls of the Late Miocene Pikermian chronofauna.
Proceedings of the National Academy of Sciences 106:11867-11871.

Paper III

Mirzaie Atabadi, M., Zaree, G., and Orak, Z.

Large mammals from the new Late Miocene fossil localities in Varzeghan area,
northwest Iran.

Accepted for publication in *Vertebrata Palasiatica*.

Paper IV

Mirzaie Ataabadi, M., Liu, L., Eronen, J. T., Bernor, R. L., and Fortelius, M.

Continental Scale Patterns in Neogene Mammal Community
Evolution and Biogeography: A Europe-Asia Perspective.

Accepted for publication in *Asian Neogene Mammal Biostratigraphy and Chronology*.

Paper V

Mirzaie Ataabadi, M., Bernor, R. L., Kostopolus, D., Wolf, D., Orak,
Z., Zaree, G., Nakaya, H., Watabe, M. and Fortelius, M.

Recent Advances in the Paleobiological Research of the
Late Miocene Maragheh Fauna, Northwest Iran.

Submitted to *Asian Neogene Mammal Biostratigraphy and Chronology*.

Paper VI

Mirzaie Atabadi, M., Mohammadalizadeh, J., Zhang, Z.,
Watabe, M., Kaakinen, A. and Fortelius, M.

Late Miocene Large mammals from Ivand (northwestern Iran).

Submitted to *Geodiversitas*.



The Miocene Epoch, 23-5.3 million years ago, was a time when the world assumed its modern configuration, and life attained many of its modern aspects. Modern climatic and circulation patterns also have their roots in the Miocene. Being at the crossroads of the Old World continents, Western Asia has a unique position through which the dispersal and migration of fossil mammals and the interaction of faunal bioprovinces occurred. Despite its critical position, the record of Miocene mammals in Western Asia is sporadic and there are large spatial and temporal gaps between the known fossil localities. I undertook fieldwork and systematic study of mammalian trace and body fossils from the northwestern parts of Iran along with analysis of large mammal data from the NOW database. The data analysis was used to study the provinciality, relative abundance, and distribution history of the closed- and open-adapted taxa and chronofaunas in the Miocene of the Old World and Western Asia.

Department of Geosciences and Geography A

ISSN-L 1798-7911

ISSN 1798-7911 (print)

ISBN 978-952-10-6307-7 (paperback)

ISBN 978-952-10-6308-4 (PDF)

<http://ethesis.helsinki.fi/>

Helsinki University Print

Helsinki 2010



UNIVERSITY OF HELSINKI

FACULTY OF SCIENCE