<https://helda.helsinki.fi>

The rise and fall of the Old World savannah fauna and the origins of the African savannah biome

Kaya, Ferhat

2018-02

Kaya , F , Bibi , F , Zliobaite , I , Eronen , J T , Hui , T & Fortelius , M 2018 , ' The rise and fall of the Old World savannah fauna and the origins of the African savannah biome ' , Nature Ecology & Evolution , vol. 2 , no. 2 , pp. 241-+ . <https://doi.org/10.1038/s41559-017-0414-1>

<http://hdl.handle.net/10138/326196>

<https://doi.org/10.1038/s41559-017-0414-1>

---

unspecified

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

TITLE PAGE

**Rise and Fall of the Old World Savanna Fauna and the Origins of the
African Savanna Biome**

Author affiliations:

Ferhat Kaya^{1*}, Faysal Bibi², Jussi Eronen^{1,3,4}, Tang Hui⁵, Mikael Fortelius^{1,2,6}

^{1*}Department of Geosciences and Geography, University of Helsinki, P.O. Box 64 (G.
Hälströminkatu 2), FI-00014 Helsinki, Finland

²Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science,
Invalidenstrasse 43, Berlin 10115, Germany

³BIOS Independent Research Unit, Kalliolanrinne 4, 00510 Helsinki, Finland

⁴Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberg Gesellschaft
für Naturforschung, Senckenberganlage 25, 60325 Frankfurt, Germany

⁵Department of Geosciences, University of Oslo, P.O. Box 1047 Blindern, NO-0316 Oslo,
Norway

⁶Centre for Ecological and Evolutionary Synthesis, Dept. of Biosciences, University of Oslo,
P.O. Box 1066 Blindern, NO-0316 Oslo, Norway

Corresponding author: Ferhat Kaya, Department of Geosciences and Geography, University
of Helsinki, P.O. Box 64 (G. Hälströminkatu 2), FI-00014 Helsinki, Finland. Email:
ferhat.kaya@helsinki.fi

Keywords: mammals, fossils, evolution, ecometrics, climate, Africa, Eurasia

Abstract

Despite much interest in the ecology and origins of the extensive grassland ecosystems of the modern world, the biogeographic relationships of savanna paleobiomes of Africa, India, and mainland Eurasia have remained obscure. We assemble the most recent data from the Neogene fossil record in order to map the biogeographic development of Eurasian and African (Old World) mammal faunas in relation to paleoenvironmental conditions. Using genus-level faunal similarity and mean ordinated hypsodonty paleoprecipitation proxy analysis in combination with paleoclimate modeling we show that these faunas developed as a spatially and temporally connected entity that we term the Old World savanna paleobiome (OWSP). The OWSP flourished under the influence of the middle and late Miocene global cooling and aridification that resulted in the spread of open habitats across vast continental areas. This extensive biome fragmented to Eurasian and African branches due to pressure of increased aridification in North Africa and Arabia during the latest Miocene. Its Eurasian branches had mostly disappeared by the end of the Miocene but the African branch survived and eventually contributed to the development of Plio-Pleistocene African savanna faunas, including their early hominins. The modern African savanna fauna is thus a continuation of the extensive Old World savanna biome, which at its peak covered much of the Old World.

Introduction

The savannas are home to many emblematic plants and animals, prominent in the public conception of nature and global change due to their threatened conservational status – they may disappear during our lifetimes (1, 2). African savannas are among the most intensely studied ecosystems which encompass tropical and subtropical grasslands and woodlands typically characterized by a highly seasonal climate and annual precipitation of 100 to 1200 mm (3, 4). In Eurasia and Africa today, savannas are mainly found in sub-Saharan Africa and South Asia, but savanna-like wooded grasslands were more extensive in past times. Understanding the paleobiogeographical origins of savanna biomes at geological timescales and how herbivores, vegetation, and climate interacted in these environments would provide powerful tools for conservation in the face of future climatic changes. However, the origin of African savannas and the biogeographic relationships of savanna-like biomes in the Old World remain obscure.

As a result of global cooling and aridification during the late Miocene (11.6 to 5.3 million years ago, Ma), open and dry paleobiomes with mixed woodland-grassland covered large parts of Eurasia in what has been called the Pikermian paleobiome (5–10). This paleobiome was characterized by mammals with novel ecological adaptations to a range of open habitats from woodlands to grasslands (11), savanna in the broad sense. It reached its peak in the latest Miocene, about 9-6 Ma, extending at that time from westernmost Europe to central China, with an extension into the Indian subcontinent (5, 6, 10). It has been argued that some Pikermian elements, with the advantage of their adaptations to open habitats, may have extended their range into northern and eastern Africa between 8-7 Ma, thereby giving rise to the Plio-Pleistocene African savanna fauna, including early hominids (7, 12, 13). It has also been proposed that the contribution of the Pikermian paleobiome to the development of

the African Mio-Pliocene savanna fauna was limited to intercontinental biogeographical exchange prior to 9 Ma that later declined, especially for closed-habitat adapted species like primates (13-16). According to the latter scenario, Eurasian taxonomic input to the African savanna was minimal but cannot be entirely ruled out. Under this view, the modern African savanna fauna evolved through increasing endemism through the Pliocene and Pleistocene (17). We here investigate the Miocene origins of the African savanna biome by quantitatively reconstructing faunal relationships between African and Eurasian large mammal faunas through the Neogene, within the context of continental-scale humidity and productivity. From the perspective of the geological timescale (here 1-2 my intervals), we focus on broad patterns of geographic interconnection (faunal similarity), rather than attempting to resolve directionality of dispersal, or to identify particular exchange events.

Materials and Methods

We assembled and analyzed an updated dataset of the Eurasian and African Neogene mammalian fossil record (18), taking advantage of recent progress in African and Asian fossil taxonomy and stratigraphy (19, 20). The dataset includes all sites between 23 to 1.8 Ma, encompassing European Mammal Neogene (MN) units 1 to 17 (21). Faunal lists from sites across the Old World were used to reconstruct biogeographic relationships of the last 23 Ma using genus-level faunal similarity (GFRI). Just as with the Pikermian chronofauna, which was used to map the Pikermian paleobiome (5), we here define an analogous computational entity, the Nawatian chronofauna, based on the assemblage of large mammals from the Lower Member of the Nawata Formation at Lothagam (~7.44-6.54 Ma, West Turkana, Kenya) (22). Faunal resemblance was calculated only using localities with a minimum of five large mammals identified to at least genus rank (see materials and methods for details). African localities were updated according to ref. 19, with age assignment following ref. 23. The NOW database biochronology system is based on refs. 24, 25. All

localities were assigned an age according to the mean age of their respective MN unit, following ref. 21. We calculated genus level faunal resemblance indices (GFRI) between the Lower Nawata and 1193 localities using PAST 3.11 (26). Raup-Crick, Jaccard, Dice, Simpson and Tversky indices all yielded similar results, and here we show only the Raup-Crick GFRI (27). Similarity results were imported into LeapFrog Geo 3.0.1 (28) as point data to create a three-dimensional geospatial interpolation block using the spheroidal interpolant function with the following settings: Alpha=3, Sill=0.08, Nugget=0.0, Base Range=60, Drift=Constant, and Accuracy=0.005, Plunge=+20, and Azimuth=045. LeapFrog Geo 3.0.1 uses Kriging interpolation technique with a mathematical model called FastRBF, a geostatistical method that quickly generates an estimated output isosurface from a scattered set of points with age (z) values. From the GFRI block we took slices along the age (z) axis for each MN unit between MN 6 to 17 (14.2 to 1.8 Ma) and for mean ordinated hypsodonty between MN9 to MN13 (11.2 to 5.3 Ma). LeapFrog 3.0.1 Geo calculates and contours the entire map surface using interpolation based on available data. This means that similarity is still calculated even for areas where little fossil data is available (e.g. southern Africa, Siberia, South East Asia), and such results should be taken as tentative. This does not affect the main results presented in this paper because sites across the Old World savanna biome are well-sampled at all times (Fig. 1).

We calculated the mean ordinated molar crown height (hypsodonty) of large herbivore mammal communities (Artiodactyla, Perissodactyla, Proboscidea, and Primates) (29) to map spatial changes in continental-scale humidity and productivity (30) and compared these with a global climate model simulation for the late Miocene. 2418 localities in total with a minimum of two crown height scores available from the same time bracket defined for the GFRI analysis included in mean hypsodonty analysis. We generated interpolated slices for the mean ordinated hypsodonty data by using spheroidal interpolant function in LeapFrog

Geo 3.0.1 with the following settings: Alpha=3, Sill=0.1, Nugget=0.0, Base Range=70, Drift=Constant, and Accuracy=0.01, and with adaptive resolution on.

To demonstrate the climate processes involved in the evolution of African mammalian fauna, the results from a late Miocene climate model simulation (31, 32) were also employed. This simulation is based on a fully-coupled atmosphere-ocean general circulation model ECHAM5/MPIOM. The resolution of the model is T31L19 (~3.75°, 19 level) for the atmosphere and GR30L40 (~3°, 40 level) for the ocean. The boundary conditions (e.g., the paleogeography, paleovegetation) for the Tortonian (11 to 7 Ma) simulation are described in detail in ref. 31. Briefly, the palaeogeography was generally lower than today. For instance, the height of the Tibetan Plateau during the Tortonian was about 70% of its recent elevation, and Greenland was also much lower on account of the absence of the present-day ice-sheet. The paleogeography is largely equal to the modern land-sea distribution, except that the Paratethys and an open Central American Isthmus are present. Atmospheric CO₂ is set to 360 ppm for the Tortonian simulation, which is equivalent to that of the present-day. The model was integrated over 2,500 years to reach dynamic equilibrium. We use the averages of the last10-years simulation for comparison with the present-day climate.

Results and Discussion

Faunal similarity comparisons to the Lower Nawata reveal that the earliest elements of the Nawatian chronofauna are first detected between ~13 and 10 Ma in both Eurasia and Africa (Fig. 1B). By 9 Ma, the Nawatian chronofauna united eastern and northern Africa with the Pikermian savanna paleobiome in central and western Asia. This combined Old World savanna palaeobiome expanded to reach its greatest geographic extent between 9 and 6 Ma,

stretching as far west as present-day Spain and France, north to Ukraine, Kazakhstan and Mongolia, and east to China (Fig. 1B, Fig. 2).

Consistently high faunal and ecological similarity among the African Nawatian, the West Eurasian Pikermian (5) and the East Asian Baodean chronofaunas (33) indicate that these late Miocene chronofaunas must have developed within a broadly similar climatic (and almost certainly vegetational) environment that we call the Old World savanna paleobiome (OWSP). Our hypsodonty analyses show that the development of the OWSP is largely owed to increasingly arid conditions that first developed in Central and Western Asia by the beginning of the late Miocene, expanding to match the peak extent of the Old World savanna paleobiome at 9-6 Ma (Fig. 3).

By the early Pliocene (5.3-4.5 Ma), the Nawatian chronofauna had begun to contract, reflecting the severing of African-Eurasian connections around the Miocene-Pliocene boundary, or ~5 Ma. This point effectively marks the separation of the African (Nawatian) and Eurasian (Pikermian and Baodean) savanna paleobiomes from each other. The Pikermian chronofauna went extinct at the end of the Miocene and the Baodean in the Pliocene (5, 33). In contrast, the Nawatian chronofauna survived and, through the course of the Pliocene and Pleistocene, gradually evolved into the modern African savanna fauna.

Climate modeling suggests that the Saharo-Arabian arid belt was already in existence in the early late Miocene (~10 Ma), though its extent was somewhat narrower, with higher rainfall along its subtropical (southern) and temperate (northern) limits (Fig. 4 A versus B). This may not seem a major difference with respect to the present climatic situation but presumably the slightly greater rainfall over the critical areas (Fig. 4C) was sufficient to produce the required freshwater and vegetation to support savanna faunas across the desert belt. This interpretation fits with geological and fossil evidence indicating that diverse late

Miocene savanna faunas in North Africa (e.g. Sahabi), the Sahel (e.g. Toros-Menalla), and Arabia (e.g. Baynunah) subsisted on perennial water sources located within direct proximity to desert conditions (34-37).

While aridification may have spurred the initial development of the OWSP and the subsequent separation of the Nawatian from the Eurasian paleobiomes, the final demise of the Pikermian can be attributed to a 'reversal of fortune', namely an early Pliocene increase of humidity (5). This, together with the decline of temperature in the same period, may have destabilized the savanna vegetation (36), leading to a closure of woody canopy in the Eastern Mediterranean and thus the replacement with faunas adapted to more humid forest environments (5, 10). The majority of Pikermian mammal genera shared with Africa went extinct at the end of the Miocene. In the Indian subcontinent as well as in Central Asia, minor remnants of the OWSP survived into the Pliocene, as shown by isolated spots of continued similarity centered on localities such as Uttarbeni and Tatrot in India, and Zhabyrtau and Esekartkan in Kazakhstan (Fig 1B).

Shared taxonomic characteristics between Eurasian and African Miocene taxa have long given rise to several (competing) biogeographic and phylogenetic hypotheses, particularly in the primate literature, including "Out of Europe/Back to Africa", "Intra-African", "filter", and "stepping stone" scenarios (38-43). While dispersal scenarios might be invoked among biomes with disjunct distributions, our results indicate that the OWSP should be viewed as a single cohesive paleobiome, in which faunas evolved together. This conclusion does not contradict biogeographic provinciality that can be discerned by analyses at the species level (33, 44-46). Rather, genus and species level data both agree that there was differentiation as well as continuity within the OWSP, reflecting both lineage evolution and ecological sorting. Such expected biogeographic patterning should not obscure the main pattern of connectedness in space and time. Hypotheses invoking single, unidirectional

events of intercontinental dispersal, filtering, or other forms of limited exchange appear moot, at least until the fragmentation of the OWSP by enhanced desertification in the terminal Miocene. The origin of bipedal hominins in Africa certainly postdates this separation.

Conclusions

The Old World savanna biome arose in the middle Miocene, and expanded during the late Miocene to reach its peak extent at 9-6 Ma. The OWSP flourished during the progressive drying of the late Miocene but was replaced in Eurasia by species adapted to forested or cooler habitats in the early to middle Pliocene (5, 10). The South Asian savanna fauna was an offshoot of the OWSP, remnants of which lingered in favorable locations in southern and central Asia at least until the middle Pliocene. Similarly, the African branch of the OWSP, the Nawatian chronofauna, eventually contributed to the unique development of the Plio-Pleistocene African savanna fauna, including early hominins. The modern African savanna fauna is therefore effectively the surviving branch of a late Miocene savanna biome, which at its peak covered much of the Old World.

Acknowledgements

We thank Aleksis Karne and Gabriel Berni for their kind guidance with the 3D geology software and University of Helsinki, Department of Geosciences and Geography for providing the LeapFrog Geo. To A. H. Kaya, we are grateful for the language improvement. Jussi T. Eronen acknowledges support from EU Marie Curie Fellowship and from Kone Foundation. Mikael Fortelius acknowledges funding from the Academy of Finland and an award from the Alexander von Humboldt Stiftung. Ferhat Kaya's work was supported by an Academy of Finland grant to Mikael Fortelius.

References

1. Watson JEM, et al. (2016) Catastrophic declines in wilderness areas undermine global environment targets. *Curr Biol* 26:1–6.
2. Ceballos G, Ehrlich PR (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proc Natl Acad Sci USA* 103(51):19374–19379.
3. Kingdon, J (1997) *Field Guide to African Mammals*. Academic Press, San Diego, California. 464 pp.
4. White, F (1984) *The Vegetation of Africa: A Descriptive Memoir to Accompany the Unesco/Aetfat/Unso Vegetation Map of Africa and Map*. United Nation Educational.
5. Eronen J, et al. (2009) Distribution history and climatic controls of the Late Miocene Pikermian chronofuana. *Proc Natl Acad Sci USA* 106(29):11867–11871.
6. Kostopoulos DS (2009) The Pikermian Event: Temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. *Palaeogeogr Palaeoclimatol Palaeoecol* 274:82–95.
7. Solounias N, Plavcan JM, Quade J, Witmer L (1999) in *The evolution of Neogene terrestrial ecosystems in Europe*, eds Agusti J, Rook L, Andrews P (Cambridge Univ Press, Cambridge), pp 436–453.
8. Solounias N, Semprebon GM, Muhlbachler M, Rivals F (2013) in *Fossil mammals of Asia: Neogene biostratigraphy and chronology*, eds Wang X, Fortelius M, Flynn L (Columbia University Press, New York), pp 676–692.
9. Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–93

10. Fortelius M, et al. (2014) Evolution of Neogene Mammals in Eurasia: Environmental Forcing and Biotic Interactions. *Annu Rev Earth Planet Sci* 42:579–604.
11. Strömberg AES (2011) Evolution of grasses and grassland ecosystems. *Annu Rev Earth Planet Sci* 39:517–544.
12. Agustí, J (2015) in *Handbook of Paleoanthropology*, eds Henke W, Tattersal I (Springer Books, Berlin-Heidelberg), pp 979–1010.
13. Nakaya H (1994) Faunal Change of late Miocene Africa and Eurasia: Mammalian Fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *African Study Monographs, Suppl* 20:1–112.
14. Thomas H (1984) Les bovidae (Artiodactyla: Mammalia) du miocene du sous-continent indien, de la peninsule arabique et de l'afrique: Biostratigraphie, biogeographie et ecologie. *Palaeogeogr Palaeoclimatol Palaeoecol* 45 (3,4): 251–299.
15. Bernor RL, Rook L, Haile-Selassie Y (2009) in *Ardipithecus kadabba; Late Miocene Evidence from the Middle Awash, Ethiopia*, eds Haile-Selassie Y, WoldeGabriel G (Univ of California Press, Berkeley) pp 549–563.
16. Katoh S, et al. (2016) New geological and palaeontological age constraint for the gorilla-human lineage split. *Nature* 530:215–218.
17. Bibi F (2011) Mio-Pliocene faunal exchanges and African biogeography: The record of fossil Bovids. *PloS One* 6(2):e16688
18. Fortelius, F (coordinator) (2016) *New and Old Worlds Database of Fossil Mammals (NOW)*. University of Helsinki. <http://www.helsinki.fi/science/now/>

19. Werdelin S, Sanders, WJ (2010) *Cenozoic Mammals of Africa*. University of California Press, Berkeley.
20. Wang X, Flynn LJ, Fortelius M (2013) *Fossil Mammals of Asia*. Columbia University Press, New York.
21. Hilgen F, Lourens L, Van Dam J, (2012) in *The Geologic Time Scale 2012*, eds Gradstein F, Ogg J, Schmitz M, Ogg G (Elsevier, Amsterdam) pp. 923–978.
22. Leakey MG, Harris JM (2003) in *Lothagam: The Dawn of Humanity in Eastern Africa*, eds Leakey MG, Harris JM (Columbia Univ Press, New York) pp 625–655.
23. Werdelin, L (2010) in *Cenozoic Mammals of Africa*, eds Werdelin L, Sanders WJ (University of California Press, Berkeley), pp:27–44.
24. Steininger FF, et al. (1996) in *The evolution of Western Eurasian Neogene Mammal Faunas*, eds Bernor RL, Fahlbusch V, Mittmann HW (Columbia University Press, New York), pp:7–46.
25. Steininger FF, et al. (1999) in *The Miocene Land Mammals of Europe*, eds Rössner GE, Heissig K (Verlag Dr. Friedrich Pfeil, München), pp:9–24.
26. Hammer Q, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electron*, 4(1), 9pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
27. Raup D, Crick RE (1979) Measurement of faunal similarity in paleontology. *J Paleontol* 53:1213–1227.
28. Aranz Geo Ltd (2016) Aranz Geo Ltd. LeapFrog Geo software version 3.1 64bit.
29. Fortelius M, et al. (2002) Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. *Evol Ecol Res* 4:1005–1016.

30. Liu L, et al. (2012) Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and presents. *Proc R Soc B* 279:2793–2799.
31. Micheels, A, et al. (2011) Analysis of heat transport mechanisms from a Late Miocene model experiment with a fully-coupled atmosphere-ocean general circulation model, *Palaeogeogr Palaeoclimatol Palaeoecol* 304: 337–350.
32. Tang H, Eronen JT, Micheels A, Ahrens B (2013) Strong interannual variation of the Indian summer monsoon in the late Miocene. *Clim Dyn* 41(1): 135 –153.
33. Mirzaie Ataabadi M, et al. (2013) in *Fossil mammals of Asia: Neogene biostratigraphy and chronology*, eds Wang X, F. Lawrence F, Fortelius M, (Columbia University Press, New York) pp. 546–565.
34. Boaz NT, (2008) A view to the South: Eo-Sahabi palaeoenvironments compared and implications for hominid origins in Neogene North Africa. *Garyounis Scientific Bulletin, Special Issue* 5:291–308.
35. Bibi F, Hill A, Beech M, Yasin W (2013) in *Fossil mammals of Asia: Neogene biostratigraphy and chronology*, eds Wang X, F. Lawrence F, Fortelius M, (Columbia University Press, New York) pp. 583–594.
36. Sankaran, M, et al. (2005) Determinants of woody cover in African savannas, *Nature*, 438: 846–849.
37. Gilbert CC, Bibi F, Hill A, Beech MJ (2014) Early guenon from the late Miocene Baynunah Formation, Abu Dhabi, with implications for cercopithecoid biogeography and evolution. *Proc Natl Acad Sci USA* 111(28):10119–10124.
38. Schuster M, et al. (2006) The Age of the Sahara. *Science* 311(5762):821

39. Bernor RL, Fortelius M, Rook L (2001) Evolutionary biogeography and paleoecology of the “*Oreopithecus bambolii* Faunal Zone” (late Miocene, Tusco-Sardinian Province). *Bollettino della Società Paleontologica Italiana* 40:139–148.
40. Bernor RL (2007) New apes fill the gap. *Proc. Natl. Acad. Sci. USA* 104(50):19661–19662.
41. Rook, L, Bernor RL (2003) Ancestry of the African a pre-human clade. *Palaeontographia Italica* 89:30–31.
42. Kaya F, et al. (2016) Magnetostratigraphy and paleoecology of the hominid-bearing locality Çorakyerler, Tuglu Formation (Cankiri Basin, Central Anatolia). *J Vert Paleontol* 36:2, e1071710, doi:10.1080/02724634.2015.1071710
43. Eronen JT, Rook L (2004) The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *J Hum Evol* 47:323–341.
44. Bernor RL (1983) in *New Interpretations of Ape and Human Ancestry*, eds Ciochon RL, Corruccini RS (Plenum Press, New York), pp 21–64.
45. Bernor RL (1984) A zoogeographic theater and a biochronologic play: The time/biofacies phenomena of Eurasian and African Miocene mammal provinces. *Paléobiologie Continentale* 14:121–142.
46. Beden M, Brunet M, (1986) Faunes de mammifères et paléobio-géographie des domaines indiens et péri-indiens au Néogène. *Sciences de la Terre* 47:61–87.

Authors' Contributions

F.K., M.F., F.B., and J.E. designed research; F.K. updated taxonomic identifications of African localities in the NOW database and performed research; H.T. performed climate

modelling; all authors participated in the interpretation of results and wrote the paper; M.F. supervised the study.

Figures

Fig. 1 Raup-Crick genus level faunal similarity to the Lower Nawata. Figure shows southwest (A1) view of the three-dimensional spatiotemporal faunal similarity block from 23 to 1.8 Ma, and 36° (A2) vertical slices from the east axis. White circles indicate spatial position of the localities in the blocks. (B) Extracted time-slices from the block with present-day base map with localities from each time slice shown as black dots. A star indicates location of the Lower Nawata at 7Ma slice.

Fig.2 Three-dimensional spatiotemporal Raup-Crick GFRI interpolations with values above 0.7 from 12 to 1.8 Ma for the Nawatian (blue), Pikermian (red), and Baodean (yellow) faunas. Figure shows overlapping biogeographic areas of the chronofaunas in different views (A, from southwest; B, from northeast). See Fig. S1 for a video animation.

Fig. 3 (left). Interpolated time-slices of the mean ordinated hypsodonty maps with present-day base map with localities from each time unit.

367

368 Fig. 4. Climate model simulations for precipitation over the Old World in the present day

369 (A), late Miocene (11 to 7 Ma) (B), and late Miocene minus present day precipitation (C).