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Building better biochronology: New fossils and $^{40}Ar/^{39}Ar$ radioisotopic dates from Central Anatolia

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Türkiye's geographic position between Europe, Asia, and Africa gives it pivotal importance for understanding the local, interregional, and intercontinental dynamics of Neogene vertebrate evolution. Although rich in vertebrate fossil deposits spanning the Middle and Late Miocene, associated geochronology has been limited by the lack of available volcanic materials that allow radioisotopic dating and geochemical correlation. As a result, calibrating mammalian evolution has been largely restricted to the semicircular application of paleomagnetic inferences combined with temporally ill-constrained and geographically remote biochronological deductions. For example, fossils from three Greek localities and one Anatolian locality assigned to the primate genus *Ouranopithecus* lack datable samples, leaving its ages poorly constrained. Chronological calibration based on the $^{40}Ar/^{39}Ar$ results reported here demonstrates how a fauna-focused, precision geochronology can enhance a better understanding of evolving species lineages and the ecosystems they comprise.

biochronology | geochronology | paleontology | Miocene | Türkiye

Significance

Fossil-rich Anatolia is a key region for understanding mammalian evolution during the last 10 million years of changing ecosystems and biogeography. Age estimates for these paleontological assemblages were traditionally inferred from geographically remote and poorly constrained faunas in Europe and Eurasia. However, these have proven to be insufficiently precise to adequately calibrate and explore this paleobiology. Achieving fuller understanding requires accurately dated, abundant, and taxonomically diverse fossils. Recently discovered, richly fossiliferous central Anatolian study areas lying close to volcanic centers of the Central Anatolian Volcanic Province have now provided these ingredients. Targeted application of the radioisotopic Argon–Argon method ($^{40}Ar/^{39}Ar$) geochronologically calibrates this faunal evolution and thereby allows more accurate and precise biochronological placements of regional fossil occurrences lacking associated volcanics.

Anatolia's dynamic Middle and Late Miocene topography generated many sedimentary repositories with vertebrate fossils. Richly fossiliferous horizons (particularly bone beds) in many locations record a long evolutionary history for dozens of mammalian species lineages. During the last 40 y, a few of these central Anatolian localities have also yielded key primate fossils whose evolutionary biology is a continuing focus of intense interest and contention (e.g., ref. 1). Here, we present the results of our approach to building a precise geochronological foundation on which Miocene biochronology of central Anatolia can rest, an approach inspired and validated by parallel efforts in African paleoanthropology.

Historical Background

The 1960s potassium-argon dating of Tanzania's Olduvai Gorge was a crucial early step in creating the foundation for understanding African vertebrate evolution. Subsequent radioisotopic, tephrachronological, and paleomagnetic calibration of the Omo Shungura Formation in southern Ethiopia was stimulated (and ultimately resolved) by biochronologically identified mismatches within the Formation (2); across the Turkana Basin (3) and between eastern and southern Africa (4–6). Today, chronostratigraphic control via multiple independent chronometers (e.g., ref. 7) has become essential in African paleoanthropology for calibrating key localities that lack materials for radioisotopic dating.

Approaches to Biochronology

Volcanic horizons closely associated with Late Miocene vertebrate assemblages are relatively rare in Türkiye. Paleontologists have consequently been forced to rely on traditional long-distance biochronological correlations with distant faunas despite the many uncertainties and imprecisions involved (8). The largely arbitrarily defined "MN" zones (Mammal Neogene Zones; 9) used to place Anatolian Late Miocene fossils are temporally wide (MN9 spans 1.4 Ma; MN10 is 1.0 Ma long; MN11 is 1.2 Ma; "Vallesian" is 2.6 Ma; "Turolian" is 3.7 Ma). These time divisions are based mostly on geographically and ecologically remote western European faunas.

As noted by Hilgen et al. (10), there are two basic approaches to biochronology. The first involves comparing the stage of morphological evolution within select evolving species lineages represented in fossil assemblages. This method has proven particularly useful in

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African biochronology (4) but has fallen into relative disfavor with the rise of cladistics (11). The second approach is based on comparing taxonomic presence or absence of taxa (or matches among faunal lists compiled from printed or online sources). The accuracy of either biochronology depends on two factors, namely 1) the accuracy of the links to external faunas and 2) the accuracy and precision of the ages assigned to those faunas.

The ready availability of large digital faunal databases has dramatically increased the number of comparative quantitative studies in paleobiology. These computational meta-approaches have extended to issues well beyond biochronology. However, quantitative studies based on such digital resources often involve hidden and unwarranted assumptions about taxonomy and reference locality ages. For example, the NOW online database [New and Old World, https://nowdatabase.org; (12) is frequently employed to investigate subjects as diverse as macroevolution (13); extinction (14); ecomorphology (15); paleoecology (16); biogeography (17–19); biome assessment (e.g., ref. 20 vs. ref. 21); biochronology (9, 22); and the ecological and evolutionary effects of climate change or mountain building (23, 24)]. Critiques of such approaches include considerations of biome-related work (25) and the origin and extinctions of hominid taxa (26).

The bedrock variables of NOW and similar databases are two, namely estimated ages and zoological nomina. Despite the recent celebration of the NOW database effort (12), when the basic taxonomic or chronological data input to such databases are imprecise or inaccurate, resultant meta-analytical study conclusions will be correspondingly compromised. This phenomenon is referred to by the acronym GIGO in computer science (27). The philosophy espoused by the NOW principals is summarized by their recent statement that *"It doesn't have to be right, consistency is everything!"* (28). Ensuring that ages and taxa are "right" (i.e., accurate and precise) is crucial in biochronology. We now briefly consider how biochronological results are routinely compromised by inaccurate and/or imprecise chronology and systematics.

The biological reality of the taxonomic labels used in biochronological estimations (mostly genus and species names imported to databases from specialist literature) is often questionable. Here, the inherently dichotomous structural underpinnings of cladistic classification combine with rampant taxonomic inflation in contemporary vertebrate paleontology to produce ambiguous systematics (11, 29–33). Comparisons of taxa across wide geographic and ecological distances can further decrease accuracy unless diligent longitudinal studies of species lineages are undertaken (34).

Furthermore, claimed faunal matches based on biochronological inferences have often been employed to choose among the many paleomagnetic reversals recorded in the encapsulating (but otherwise uncalibrated) sedimentary rocks. For example, the ages assigned hominoid-bearing Miocene bone accumulations in central Anatolia (e.g., Sinap, Paşalar, Çandır, Sivas, and Çorakyerler) (Fig. 1*A*) were routinely estimated by this combinatory biochronology-plus-paleomagnetism approach.

In Türkiye, Late Miocene fossiliferous sedimentary successions lacking radioisotopic control usually do retain paleomagnetic polarity signals that are potentially linkable to the chronologically calibrated Geomagnetic Polarity Time Scale. However, there were 7 normal and 7 reversed global paleomagnetic intervals between 5.0 and 8.0 Ma, some densely spaced in time. Using ambiguous

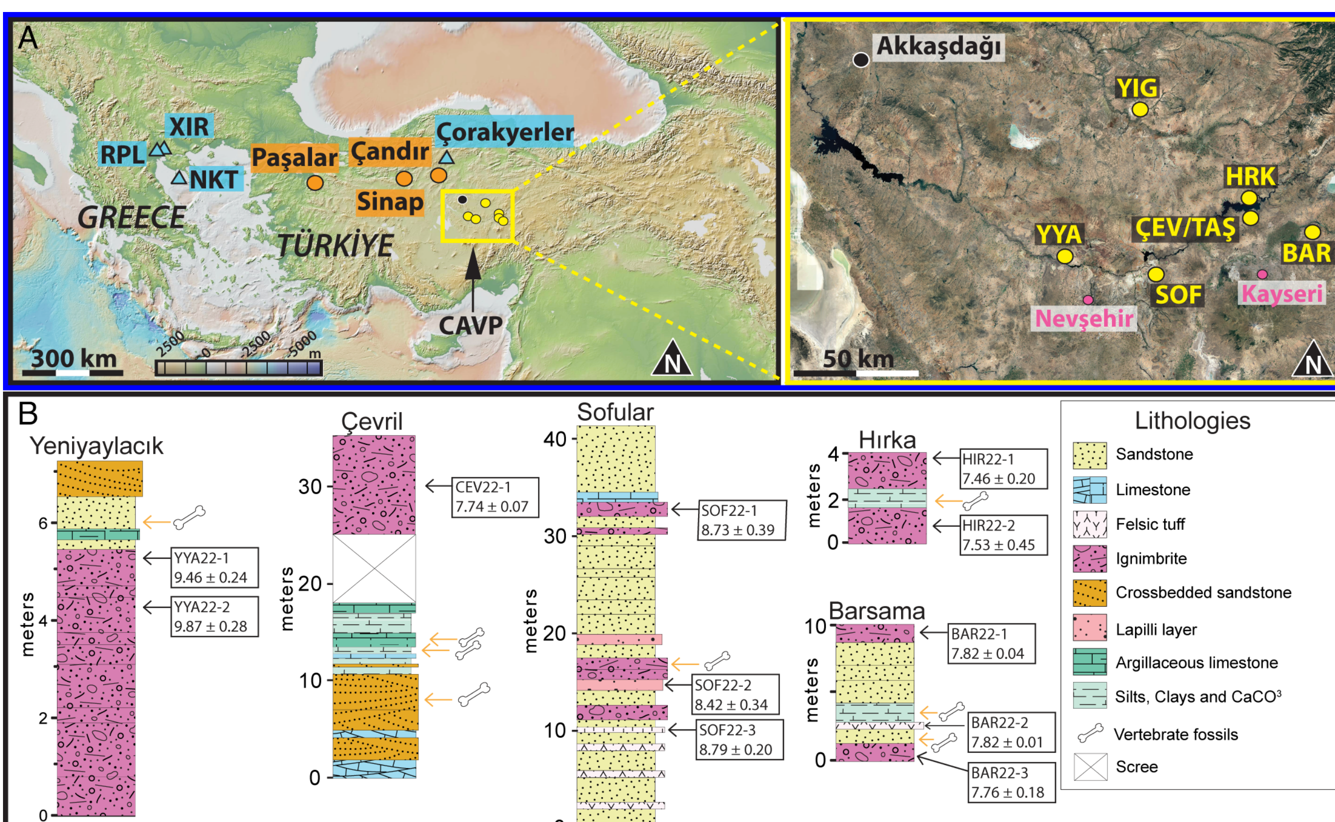

Fig. 1. Spatial and stratigraphic positions of fossils and $^{40}Ar/^{39}Ar$ dates. (*A*) Topographic map of Anatolia and Greece highlighting Miocene hominoid primate occurrences shown in blue (*Ouranopithecus*) and (other Miocene primate genera) in orange. The topographic map is made with GeoMapApp (www.geomapapp.org) under a CC BY license and topographic map color code is shown with the color-scale. The Central Anatolian Volcanic Province (CAVP), shown in the yellow box in the satellite imagery to the *Right* (Google Earth). Newly dated paleontological localities are marked by three-letter abbreviations in yellow. The cities of Kayseri and Nevşehir are marked in magenta. (*B*) Stratigraphic positions of the new $^{40}Ar/^{39}Ar$ dates calibrating the nearest fossil horizons in each study area. Additional details are provided in Fig. 2 and *SI Appendix*.

biochronological estimates to choose among them injects a degree of circularity to the process, particularly when the temporally wide circum-Mediterranean "MN Zones" are invoked in such attempts.

Applying MN divisions to choose among paleomagnetic reversals is a risky, semicircular process often further burdened by the unwarranted but widespread misconception that sedimentary thickness in terrestrial depositional settings reliably reflects the passage of time. While this is more often the case in oceanic and deep lake deposits, sediment accumulation, nondeposition, erosion, and compaction in terrestrial settings is highly variable (35–38). Under such conditions of highly dynamic, nonlinear depositional environments, age claims based on assumptions involving inferred depositional rates can be misleading.

For example, packages of sediment bracketing fossiliferous horizons cannot be simplistically equated to or described as "…a long period of normal polarity followed by a short reversed chron" of time (e.g., ref. 1; in *SI Appendix*, p. 59), particularly in facies-variable sediments like those of Çorakyerler, deposited under conditions of tectonically influenced landscape hydrology. The words "long" and "short" denote intervals of time, whereas sedimentary thickness is merely a crude correlate of time in fluvial depositories where, for example, 10 m of normal sediment in one location may be entirely missing in a different facies or nearby depository.

Together, these sets of confounding factors and misleading assumptions can obscure and/or distort age-dependent inferences about evolutionary pattern and process. In the end, the widespread use of imprecise zonal biochronology combines with flaws in taxonomic identification and age estimations to preclude the practical or precise biochronological use of database compilations to accurately and precisely determine the ages of central Anatolian fossils.

The *Ouranopithecus* Example

The primate genus *Ouranopithecus* provides a prominent and current example of how insufficiently precise biochronological information from digital databases can combine with ambiguous paleomagnetic linkages to limit evolutionary interpretations. This large-bodied Late Miocene primate is advocated by some as the ancestor of African apes and humans (39, 40) or even an exclusive ancestor to humans (41). Known only from three localities in Greece (42) and one in Türkiye (43) (Fig. 1), two generic and three specific names have already been proposed for this small sample of fossils (1).

The age of Greek *Ouranopithecus* fossils is usually reported via the traditional biochronological approaches described above. Age claims for its Greek localities presently available in the online NOW database range between 8.9 and 9.9 Ma. However, such repeatedly published estimates are based only on imprecise biochronological placements by a single team (44). According to Koufos (45), the most important *Ouranopithecus* locality, Ravin de la Pluie, has a short stratigraphic section whose sedimentary successions are uniformly normal in geomagnetic polarity. He biochronologically assigns the fossils they hold to the Late Vallesian (MN10, ~9.3 Ma). The nearby Xirochori 1 locality is similarly ascribed to the Late Vallesian (MN10; ~9.6 Ma) and Nikiti 1 to the Terminal Vallesian (MN10; 8.7 to 9.3 Ma). Unfortunately, chronometric placement by radioisotopic analyses is simply absent for these Greek localities.

The recently published age claim for the single Turkish *Ouranopithecus* locality (Çorakyerler) also lacks radioisotopic control. Estimates of 7.15 to 8.13 Ma (MN11-12; early Turolian) (46) and ~8.7 Ma (early MN 11) (1) have been advanced. The latter team recently proposed the new name "*Anadoluvius*" for these fossils, and the NOW database has already adopted this taxon and places the four involved fragmentary COR fossils in a >2.0 Ma interval between 7.6 and 8.9 Ma. The current *Ouranopithecus* hypodigm therefore exemplifies the challenges of imprecision and uncertainty involved in assessing the evolutionary biology of fossil vertebrates in the eastern Mediterranean. Even the relative chronological seriation of the four known *Ouranopithecus* localities is still undetermined despite their paleoanthropological prominence.

The *Ouranopithecus* impasse illustrates the need for more solid and precise chronological calibration of biological evolution of all vertebrate species lineages sampled through time in Anatolia. Uncertainties of 2 to 3 Ma have long been the reality for vertebrate paleontologists and geologists working there, but such lengthy chronological intervals are incompatible with understanding the evolutionary biology of species and ecologies through time. A new geochronological approach to central Anatolian paleontological assemblages is therefore essential.

Radioisotopically calibrated eastern African Plio-Pleistocene faunas show that better biochronology is not only essential but is also possible. Understanding evolutionary trajectories and ecological relationships, and relating these to the impacts of geophysical phenomena such as the Messinian event, the formation of the Central Anatolian Plateau, and the effects of global climate change will depend on a better synthesis of geochronological and paleobiological information. Building a better calibrated Anatolian late Neogene biochronology based on increased temporal precision is the way forward. We have therefore embarked on a long-term endeavor to establish an accurate, densely sampled, radioisotopically controlled time-stratigraphic framework for paleontological assemblages this region.

Accordingly, we describe and illustrate a series of recently discovered and excavated Late Miocene fossil assemblages in the CAVP. Proximal explosive volcanism bracketing Late Miocene sedimentary deposition resulted in bone beds interbedded with primary or near-primary deposits of ignimbrites, tephra, and other volcanic materials susceptible to Ar/Ar techniques.

We targeted five previously undated fossiliferous vertebrate assemblages for their stratigraphic proximity to overlying and underlying volcanic horizons (Fig. 1). By spatially and stratigraphically centering our geochronological efforts on the *fossils* rather than the overall stratigraphic *formations*, we have already been able to provide more precise calibration of separate vertebrate assemblages across the Late Miocene. The result is a succession of large, radioisotopically controlled fossil samples of individual mammalian species lineages in central Anatolia. Calibrating the evolution of species lineages and the faunas they comprise now forms the foundations for an accurate, precise, and effective regional biochronology.

The Geological Context

The Central Anatolian Volcanic Province (CAVP) is a 60 × 300 km plateau averaging ~1,400 m above sea level (47, 48). It dominantly comprises ignimbrites and andesitic and basaltic lavas intercalated with fluvio-lacustrine sediments. Syn- and post-depositional tectonism limits lateral correlations (49). Previous stratigraphic and geochronologic studies of the CAVP have come from the Ürgüp Formation exposed within the Nevşehir plateau. These document eruptions between ~2 and ~9 Ma (50–52).

Until now, the only chronometrically controlled Late Miocene bone beds in the region are in the Akkaşdağı I study area, where Late Miocene vertebrate fossils were embedded in a volcanic horizon dated to 7.1 ± 0.1 Ma (53). This is an important calibration point, but more than one is obviously necessary for precision biochronology. For this reason, we turned our attention to calibrating the newly excavated bone beds from the localities and areas presented below in chronological order and results summarized in Fig. 1 and detailed in *SI Appendix*, Figs. S1–S5 and Dataset S1.

Yeniyaylacık (YYA) (A three-letter abbreviation system is used to designate study areas and their successively numbered localities) (Figs. 1*B* and 2 and *SI Appendix*, Fig. S5)

Since 2014, excavations in the YYA study area (54) have yielded 912 cataloged vertebrate fossils. A modern road cut exposed the Miocene fossiliferous unit near the top of a <10 m section comprising several discrete reworked pyroclastic deposits. We sampled the closely underlying ignimbrite and another ignimbrite ~2 m below the fossil horizon and obtained $^{40}Ar/^{39}Ar$ ages of 9.46 ± 0.24 Ma and 9.87 ± 0.28 Ma, respectively, the younger result most applicable to the fossil assemblage. All reported errors are 2σ or 95% CI; full results for all dates are presented in *SI Appendix*. The first published analytical paleontological study is ref. 55.

Sofular (SOF) (Fig. 1*B* and *SI Appendix*, Figs. S1, S4, and S5)

Since 2014, excavations in six designated Neogene localities of this study area (54) have yielded nearly 1,000 cataloged vertebrate fossils, 786 of them from Locality SOF-2. The overall succession measures >100 m. The basal ~50 m contains numerous tuffaceous layers intercalated with sedimentary rocks comprising reworked volcanic material and carbonate horizons. Airfall pumice deposits define rocks directly underlying the bone bed at SOF-2, a silica-cemented sandstone whose upper erosional surface is an uneven 1 to 2 mm carbonate layer below

Fig. 2. (*A*) Excavation of the vertebrate paleontology locality at YYA. Fossils were first encountered during road construction. (*B*) The stratigraphy visible in the roadcut, showing the positioning of the newly dated volcanic horizons and the bone bed just below. (*C*–*E*) Vertebrate fossils excavated in situ, showing the concentrated nature of the remains. (*F*) A panoramic view of the YYA large mammal fossils thus far recovered and cleaned. Bovids to the *Left*, horses in foreground, rhinos center, and proboscideans to the *Right*.

silica-cemented sandstone. Carbonate-dominated rocks are more common higher in the succession, eventually grading into limestones (Fig. 1).

Three samples were collected for $^{40}Ar/^{39}Ar$ analysis that gave overlapping ages between 8 and 9 Ma. The stratigraphically lowest sample lies ~7 m below the SOF-2 fossils. It is a ~1 m thick felsic tuff dated to 8.79 ± 0.2 Ma. A second sample was collected ~2 m below the SOF-2 bone bed. This ~75-cm-thick lapilli gave an age of 8.42 ± 0.34 Ma. A third sample was collected from an ignimbrite ~17 m above the fossil layer and gave in an age of 8.73 ± 0.39 Ma.

Çevril (CEV) and Taşhan (TAS) (Fig. 1*B* and *SI Appendix*, Figs. S2, S4, and S5)

The filling of the Yamula reservoir north of Kayseri, Türkiye brought increased paleontological attention to this research area previously geologically reported in ref. 50 and 51. On the southern margin of the reservoir lie geographically adjacent and stratigraphically contiguous CEV and TAS areas. Each contains localities and excavations that sample two stratigraphically successive fossiliferous units. The lower stratigraphic division is a poorly sorted coarse sand and gravel deposit that has so far yielded 72 in situ and spatially largely unconcentrated large mammalian remains, primarily proboscideans belonging to species of *Choerolophodon*, *Konobelodon*, and *Mammut* (*SI Appendix*, Fig. S2). The upper stratigraphic horizons occur in a set of finer grained alluvial deposits with carbonate horizons and nodules. Here, small, medium, and large mammals co-occur in true bone beds with a total of 300 in situ cataloged fossils.

Fossiliferous outcrops lie within a ~30 m succession in the CEV and adjacent TAS areas. The lower exposed strata (~10 m) are dominated by cross-bedded sands, gravels, and poorly sorted pebble conglomerates interbedded with limestones. These lithologies fine upward into a second intermittently fossiliferous package of reddish sandstones/siltstones/mudstones with carbonate nodules interbedded among limestones. Resting atop a scree-obscured ~6 m interval is a prominent, resistant ~10-m-thick felsic ignimbrite containing quartz and biotite phenocrysts. We date this ignimbrite with a $^{40}Ar/^{39}Ar$ age of 7.74 ± 0.07 Ma. What is likely to be the same ignimbrite was dated at 7.51 ± 0.07 Ma ($^{40}Ar/^{39}Ar$, amphibole) and 7.52 ± 0.14 Ma ($^{40}Ar/^{39}Ar$, plagioclase; 50) ca. 1.5 km to the west (50).

Hırka (HIR) (Fig. 1*B* and *SI Appendix*, Figs. S3 and S5)

One of four formal areas so far designated within the Yamula (YAM) reservoir research area, HIR comprises a fossiliferous outcrop along the lake's present northern shoreline. Discovered in 2019, the partially excavated HIR Locality 1 bone bed in the YAM research area has yielded 315 vertebrate fossils currently under analysis. Sediments exposed at this locality span a stratigraphic thickness of ~4 m between two discrete ignimbrite layers yielding an overlying age of 7.46 ± 0.2 Ma and an underlying age of 7.53 ± 0.45 Ma.

Barsama (BAR) (Fig. 1*B* and *SI Appendix*, Figs. S3 and S5)

Lying ~25 km to the southeast of the YAM area, the Barsama research area is comparatively less explored. A total of 102 fossils have so far been collected from silty clays with carbonate nodules in 2018 (56 fossils), 2019 (37 fossils), and 2021 (9 fossils). Here, felsic volcanic deposits bound two discrete fossil layers in an outcrop of ~10 m of section. A felsic ignimbrite whose base is 8 m above the upper fossil layer gave an age of 7.82 ± 0.04 Ma. A ~20 cm sanidine-bearing tuff between the fossil layers gave an age of 7.82 ± 0.01 Ma, and a felsic ignimbrite <1 m below the lower fossil layer gave an age of 7.7 ± 0.18 Ma.

Yiğitler (YIG) (Fig. 1*B* and *SI Appendix*, Fig. S3)

Located about 50 km northwest of the YAM reservoir, the single YIG locality contains Late Miocene or early Pliocene fossils embedded in a volcanic lahar. Preliminary unreported Ar/Ar dates suggest that these fossils may have been emplaced no earlier than 5.3 Ma. If confirmed, this locality will further extend the biochronological record in central Anatolia upward from the 7.2 Ma Akkaşdağı locality to nearly the Messinian Event.

Conclusions

In addition to the assemblages cited above, our ongoing surveys have already located additional fossiliferous horizons sandwiched between datable volcanics across central Anatolia. We anticipate that hundreds of such localities lie undiscovered across the region and sample different time horizons. Intensive exploration guided by high-resolution satellite imagery in the CAVP and beyond can be coupled with the fossil-focused geochronological sampling methods introduced here to effectively narrow the many remaining gaps in this region's fossil record.

In turn, radioisotopic calibration of the lineage-specific evolutionary trajectories of each species through time will allow more accurate and precise biochronological age placements for the many eastern Mediterranean fossil assemblages lacking volcanics for geochronological control, including primate-bearing assemblages. In this manner, understanding of the evolutionary modes and tempos; the biotic impacts of climate and tectonics; and the biogeographic relations among Neogene Eurasia, Europe, and Africa will be enhanced.

Methods

Samples were collected in the field by AJT October 2022 and processed at the Berkeley Geochronology Center where the coarsest inclusion-free feldspars were separated using heavy liquids, magnetic susceptibility, and hand-picking. Feldspar abundance was low and processing resulted in tens of viable feldspar grains per sample. Feldspar grains from each sample were coirradiated in Aluminum disks along with Fish Canyon sanidine neutron fluence monitors in a 3-h irradiation in the Cadmium-Lined In-Core Irradiations Tube facility at the Oregon State University Training, Research, Isotopes and General Atomics reactor. Most samples and all fluence monitors underwent total fusion of individual grains with a carbon dioxide laser operated at 7 W. Some samples that revealed no conspicuous xenocrysts were subsequently analyzed as multiple grains to increase precision. Argon isotope abundances were analyzed on an analog mode electron multiplier fitted to a MAP 215C mass spectrometer at the Berkeley Geochronology Center. Full isotopic and relevant meta-data are given in the accompanying Dataset. Neutron fluence for each sample was determined by planar interpolations between three bracketing standard positions. Ages were determined from isotope data corrected for backgrounds, mass discrimination power law (56), and radioactive decay using the calibration of ref. 57.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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1. A. Sevim-Erol *et al.*, A new ape from Türkiye and the radiation of late Miocene hominines. *Commun. Biol.* **6**, 842 (2023).
2. T. D. White, R. V. Moore, G. Suwa, Hadar biostratigraphy and hominid evolution. *J. Vert. Pal.* **4**, 575–583 (1984).
3. R. Lewin, *Bones of Contention: Controversies in the Search for Human Origins* (University of Chicago Press, 1997).
4. S. R. Frost, F. J. White, H. G. Reda, C. C. Gilbert, Biochronology of South African hominin-bearing sites: A reassessment using cercopithecid primates. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2210627119 (2022).
5. F. Bibi, Telling time with monkeys. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2217198119 (2022).
6. R. Hanon, C. Steininger, Fossil Bovidae (Mammalia: Artiodactyla) from southern Africa: Biochronology and palaeoenvironments. *Quat. Environ. Hum.* **2**, 100010 (2024).
7. E. M. Niespolo *et al.*, Integrative geochronology calibrates the Middle and Late Stone Ages of Ethiopia's Afar Rift. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2116329118 (2021).
8. E. Ünay, H. de Bruijn, G. Saraç, A preliminary zonation of the continental Neogene of Anatolia based on rodents. *Deinsea* **10**, 539–548 (2003).
9. F. F. Steininger *et al.*, "Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European Mammal Units" in *The Evolution of Western Eurasian Neogene Mammal Faunas*, R. Bernor, V. Fahlbusch, H. Mittmann, Eds. (Columbia University Press, 1996), pp. 7–46.
10. F. J. Hilgen, L. J. Lourens, J. A. Van Dam, "Chapter 9 The Neogene period" in *The Geologic Time Scale*, F. M. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, Eds. (Elsevier B.V, 2012) pp. 923–978.
11. T. D. White, "Ladders, bushes, punctuations, and clades: Hominid paleobiology in the late Twentieth Century" in *The Paleobiological Revolution: Essays on the Growth of Modern Paleontology*, D. Sepkoski, M. Ruse, Eds. (University of Chicago Press, 2009), pp. 122–148.
12. I. Casanovas-Vilar, L. W. van den Hoek Ostende, C. M. Janis, J. Saarinen, Eds., *Evolution of Cenozoic Land Mammal Faunas and Ecosystems: 25 Years of the NOW Database of Fossil Mammals* (Springer, 2023).
13. I. Žliobaitė, Laws of macroevolutionary expansion. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2314694121 (2024).
14. P. D. Gingerich, Rates of geological processes. *Earth-Sci. Rev.* **220**, 103723 (2021).
15. F. Blanco *et al.*, 60 million years of ecological shifts in large herbivore communities revealed by Network Analysis. EcoEvoRxiv [Preprint] (2024). https://doi.org/10.32942/X2GW4F (Accessed 8 November 2024).
16. T. I. Foister *et al.*, Quantifying heterogeneity of hominin environments in and out of Africa using herbivore dental traits. *Quat. Sci. Rev.* **337**, 108791 (2024).
17. R. L. Bernor *et al.*, "The evolution of western Eurasian Neogene mammal faunas: A chronologic, systematic, biogeographic, and paleoenvironmental synthesis" in *The Evolution of Western Eurasian Neogene Mammal Faunas*, R. Bernor, V. Fahlbusch, H. Mittmann, Eds. (Columbia University Press, New York, 1996), pp. 449–469.
18. M. Fortelius *et al.*, "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*, R. Bernor, V. Fahlbusch, H. Mittmann, Eds. (Columbia University Press, 1996), pp. 414–448.
19. S. Faurby, D. Silvestro, L. Werdelin, A. Antonelli, Reliable biogeography requires fossils: Insights from a new species-level phylogeny of extinct and living carnivores. *Proc. R. Soc. B* **291**, 20240473 (2024), 10.1098/rspb.2024.0473.
20. T. Denk, C. M. Zohner, G. W. Grimm, S. S. Renner, Plant fossils reveal major biomes occupied by the late Miocene Old-World Pikermian fauna. *Nat. Ecol. Evol.* **2**, 1864–1870 (2018).
21. M. Fortelius *et al.*, The nature of the Old World savannah palaeobiome. *Nat. Ecol. Evol.* **3**, 504–504 (2019).
22. N. Spassov, The final Pliocene and Early Pleistocene faunal dispersals from East to Europe and correlation of the Villafranchian biochronology between Eastern and Western Europe. *Quaternary* **7**, 43 (2024).
23. J. T. Faith, J. Tyler, J. Rowan, A. Du, Late Cenozoic faunal and ecological change in Africa. *Ann. Rev. Earth Planet. Sci.* **52**, 379–407 (2024).
24. S. Huang, M. J. M. Meijers, A. Eyres, A. Mulch, S. A. Fritz, Unravelling the history of biodiversity in mountain ranges through integrating geology and biogeography. *J. Biogeogr.* **46**, 1777–1791 (2019).
25. I. W. Krone, K. M. Magoulick, R. M. Yohler, All the Earth will not remember: How geographic gaps structure the record of diversity and extinction. *Paleobiology* **50**, 214–225 (2023), 10.1017/pab.2023.34.
26. S. J. Maxwell, P. J. Hopley, P. Upchurch, C. Soligo, Sporadic sampling, not climatic forcing, drives observed early hominin diversity. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 4891–4896 (2018).
27. R. Stenson, This the first time anyone printed, 'Garbage In, Garbage Out'? *Atlas Obscura*, March 14, 2016. https://www.atlasobscura.com/articles/is-this-the-first-time-anyone-printed-garbage-in-garbage-out. (Accessed 6 November 2024).
28. M. Fortelius *et al.*, "The origin and early history of NOW as it happened" in *Evolution of Cenozoic Land Mammal Faunas and Ecosystems: 25 Years of the NOW Database of Fossil Mammals*, I. Casanovas-Vilar, L. W. van den Hoek Ostende, C. M. Janis, J. Saarinen, Eds. (Springer, 2023), pp. 7–32.
29. N. J. B. Isaac, J. Mallet, G. M. Mace, Taxonomic inflation: Its influence on macroecology and conservation. *Trends Ecol. Evol.* **19**, 464–469 (2004).
30. M. T. Silcox, A pragmatic approach to the species problem from a paleontological perspective. *Evol. Anthrop.* **23**, 24–26 (2014).
31. T. D. White, Delimiting species in paleoanthropology. *Evol. Anthrop.* **23**, 30–32 (2014).
32. J. Van der Made, The Suoidea from the Middle Miocene of Gračanica (Bugojno Basin, Bosnia and Herzegovina)—Evolution, taxonomy, and biostratigraphy. *Palaeobiodiversity Palaeoenvironments* **100**, 321–349 (2020).
33. S. Mahony, R. G. Kamei, R. M. Brown, K. O. Chan, Unnecessary splitting of genus-level clades reduces taxonomic stability in amphibians. *Vertebr. Zool.* **74**, 249–277 (2024).
34. R. L. Bernor, F. Kaya, A. Kakkinen, J. Sarinnen, M. Fortelius, Old world hipparionine evolution, biogeography, climatology and ecology. *Earth-Sci. Rev.* **221**, 103784 (2021).
35. P. M. Sadler, Sediment accumulation rates and the completeness of stratigraphic sections. *J. Geol.* **89**, 569–584 (1981).
36. M. J. Kraus, T. M. Bown, Short-term sediment accumulation rates determined from Eocene alluvial paleosols. *Geology* **21**, 743–746 (1993).
37. R. Schumer, D. J. Jerolmack, Real and apparent changes in sediment deposition rates through time. *J. Geophys. Res: Earth Surface* **114**, F3 (2009).
38. M. J. M. Meijers *et al.*, Magnetostratigraphy of the Pikermian fauna-bearing late Miocene Sivas Basin (central Anatolia, Turkey): Fluvio-lacustrine sedimentation under stable climatic conditions across the Tortonian-Messinian boundary. *Newsl. Strat.* **55**, 285–310 (2022).
39. D. R. Begun, *Sivapithecus* is east and *Dryopithecus* is west, and never the twain shall meet. *Anthropol. Sci.* **113**, 53–64 (2005).
40. S. Moyà-Solà, M. Köhler, New partial cranium of *Dryopithecus lartet,* 1863 (Hominoidea, Primates) from the upper Miocene of Can Llobateres, Barcelona, Spain. *J. Hum. Evol.* **29**, 101–139 (1995).
41. L. de Bonis, G. D. Koufos, *Ouranopithecus* et la date de séparation des hominoïdes modernes. *C. R. Palevol.* **3**, 257–264 (2004).
42. M. Ioannidou, G. D. Koufos, L. de Bonis, K. Harvati, 3D geometric morphometrics analysis of mandibular fragments of *Ouranopithecus macedoniensis* from the late Miocene deposits of Central Macedonia, Greece. *Am. J. Biol. Anthrop.* **177**, 48–62 (2022).
43. E. Güleç, A. Sevim, C. Pehlevan, F. Kaya, A new great ape from the late Miocene of Turkey. *Anthropol. Sci.* **115**, 153–158 (2007).
44. G. D. Koufos, "The fossil record of the Miocene hominoids (Mammalia: Primates: Hominoidea) in Greece" in *Fossil Vertebrates of Greece Vol. 1: Basal Vertebrates, Amphibians, Reptiles, Afrotherians, Glires, and Primates*, E. Vlachos, Ed. (Springer, 2021), pp. 657–668.
45. G. D. Koufos, Updating the fauna and age of the Neogene-Quaternary large mammal sites of Greece. *Geobios* **85**, 35–57 (2024).
46. F. Kaya *et al.*, Magnetostratigraphy and paleoecology of the hominid-bearing locality Çorakyerler, Tuglu Formation (Cankiri Basin, Central Anatolia). *J. Vert. Paleo.* **36**, e1071710 (2016).
47. E. Aydar *et al.*, Correlation of ignimbrites in the central Anatolian volcanic province using zircon and plagioclase ages and zircon compositions. *J. Volcanol. Geoth. Res.* **213–214**, 83–97 (2012).
48. E. Göz, S. Kadir, A. Gürel, M. Eren, Mineralogy, geochemistry, and depositional environment of a Late Miocene/Pliocene fluviolacustrine succession, Cappadocian Volcanic Province, central Anatolia, Turkey. *Turkish J. Earth Sci.* **23**, 386–411 (2014).
49. D. L. Whitney *et al.*, Breaking plates: Creation of the East Anatolian fault, the Anatolian plate, and a tectonic escape system. *Geology* **51**, 673–677 (2023).
50. M. J. M. Meijers *et al.*, Rapid late Miocene surface uplift of the Central Anatolian Plateau margin. *Earth Planet. Sci. Lett.* **497**, 29–41 (2018).
51. M. J. M. Meijers, G. Y. Brocard, D. L. Whitney, A. Mulch, Paleoenvironmental conditions and drainage evolution of the central Anatolian lake system (Turkey) during late Miocene to Pliocene surface uplift. *Geosphere* **16**, 490–509 (2020).
52. G. Y. Brocard *et al.*, Fast Pliocene integration of the Central Anatolian Plateau drainage: Evidence, processes, and driving forces. *Geosphere* **17**, 1–27 (2021).
53. L. Karadenizli *et al.*, Mammal bearing late Miocene tuffs of the Akkaşdağğ region; distribution, age, petrographical and geochemical characteristics. *Geodiversitas* **27**, 553–566 (2005).
54. O. Başoğlu, *Vertebrate Fossil Beds in the Cappadocia Region and a New Hominid Site: Sofular* (Şükrü Devrez. Bilgin Kültür Sanat Şti. Ltd., 2017).
55. R. L. Bernor *et al.*, *Cormohipparion cappadocium*, a new species from the Late Miocene of Yeniyaylacık, Türkiye, and the emergence of western Eurasian hipparion bioprovinciality. *Ann. Zool. Fennici* **61**, 303–333 (2024).
56. P. R. Renne *et al.*, Data reporting norms for ^{40}Ar/^{39}Ar geochronology. *Quat. Geochron.* **4**, 346–352 (2009).
57. P. R. Renne, G. Balco, K. R. Ludwig, R. Mundil, K. Min, Response to the comment by W.H. Schwarz et al. on "Joint determination of ^{40}K decay constants and ^{40}Ar/^{40}K for the Fish Canyon sanidine standard, and improved accuracy for ^{40}Ar/^{39}Ar geochronology" by P.R. Renne et al. (2010). *Geochim. Cosmochim. Acta* **75**, 5097–5100 (2011).