



Human pre-adaptation to leishmania parasites: Insights from twelve Plio-Pleistocene fossil and archaeological sites in Africa

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ABSTRACT

This study aims to assess the climatic suitability patterns of cutaneous and visceral leishmaniasis in Africa over the last 4.5 Myr. To achieve this, the climatic suitability values of sand fly vectors, mammalian reservoir hosts, and cutaneous and visceral leishmaniasis were modelled in relation to 12 Plio-Pleistocene hominin and archaeological sites across Africa, using palaeoclimatic data from the PALEO-PGEM-Series. The results suggest that climatic conditions could have allowed cutaneous leishmaniasis transmission at Uraha Hill in the late Piacenzian and at Broken Hill and Jebel Irhoud during the second half of the Chibanian. Similarly, the mid-Zanclean Middle Awash and Woranso-Mille regions show high climatic suitability for visceral leishmaniasis. The early Gelasian Sterkfontein and the early-mid-Gelasian Ledi-Geraru also exhibit relatively high climatic suitability values for both leishmaniasis forms, whereas the early-late Gelasian Ileret and the early Calabrian Upper Burgi Koobi Fora appear less suitable for cutaneous leishmaniasis. During the Zanclean-Piacenzian transition, Koro-Toro shows suboptimal conditions for visceral leishmaniasis. Patterns of high present-day Y-A and Y-B allele frequencies overlap with regions that exhibited high climatic suitability during their expansion around 150–100 kya. These patterns are interpreted as reflecting demographic continuity in ecologically stable, leishmaniasis-endemic regions rather than suggesting any form of genetic susceptibility. Taken together, the findings indicate that early human evolution in Africa likely occurred under climatic conditions that could have supported both cutaneous and visceral leishmaniasis transmission.

1. Introduction

Leishmaniasis is a major neglected tropical disease endemic to more than 90 countries (André et al., 2020; Montaner-Angoiti and Llobat, 2023). Of roughly 1000 known phlebotomine sand fly species, about 100 are proven or suspected vectors (Cecilio et al., 2022), and more than 20 *Leishmania* species can infect humans worldwide (Aronson et al., 2016). In Europe, Asia, and Africa, *Phlebotomus*—and less commonly *Sergentomyia*—species serve as vectors (Maia and Depaquit, 2016; Owino et al., 2021; Phumee et al., 2024), while in the Americas the main vectors are *Lutzomyia* species (Labbe et al., 2023). Globally, more than one million new cases of leishmaniasis occur each year, leading to around 30,000 deaths (Barbero-Moyano et al., 2024), and over one billion people remain at risk (Wamai et al., 2020). Cutaneous leishmaniasis (CL) affects 0.7–1.2 million people annually and often results in disfiguring lesions (Flanley et al., 2018). Visceral leishmaniasis (VL), with 50,000–90,000 cases each year (Dhamnetiya et al., 2021), is potentially fatal without treatment (Elaagip et al., 2020). Ethiopia alone has over 3.2 million people at risk of VL and records 4000 cases annually

(Gadisa et al., 2015). Mucocutaneous leishmaniasis (MCL), mainly in the Americas, is caused by New World *Leishmania* species such as *Leishmania panamensis* (Abadías-Granado et al., 2021). As this study focuses on Africa, New World leishmaniasis are not discussed in detail.

Leishmania parasites rely on diverse vectors and reservoirs, which vary by species and region. In North Africa, *Leishmania infantum* is maintained largely by domestic and wild dogs, while *Leishmania major* circulates mainly in rodents. Some forms are anthroponotic, such as *Leishmania donovani* transmission in northern East Africa (Abadías-Granado et al., 2021). In established regional transmission cycles, the principal vectors and reservoir hosts may vary. Local transmission systems can be complex: for example, although the *Leishmania major-Phlebotomus duboscqi*-rodent cycle dominates in West Africa, dogs may also serve as reservoirs (Blaizot et al., 2024). East Africa hosts a particularly rich sand fly fauna. Ethiopia has 65 recorded species (Aklilu et al., 2023), Kenya has 48 species within *Phlebotomus* and *Sergentomyia* (Anjili et al., 2011), Tanzania has at least eight sandflies in northern regions (Clark et al., 2013), and Sudan has at least five *Phlebotomus* species in endemic areas (Elaagip et al., 2020).

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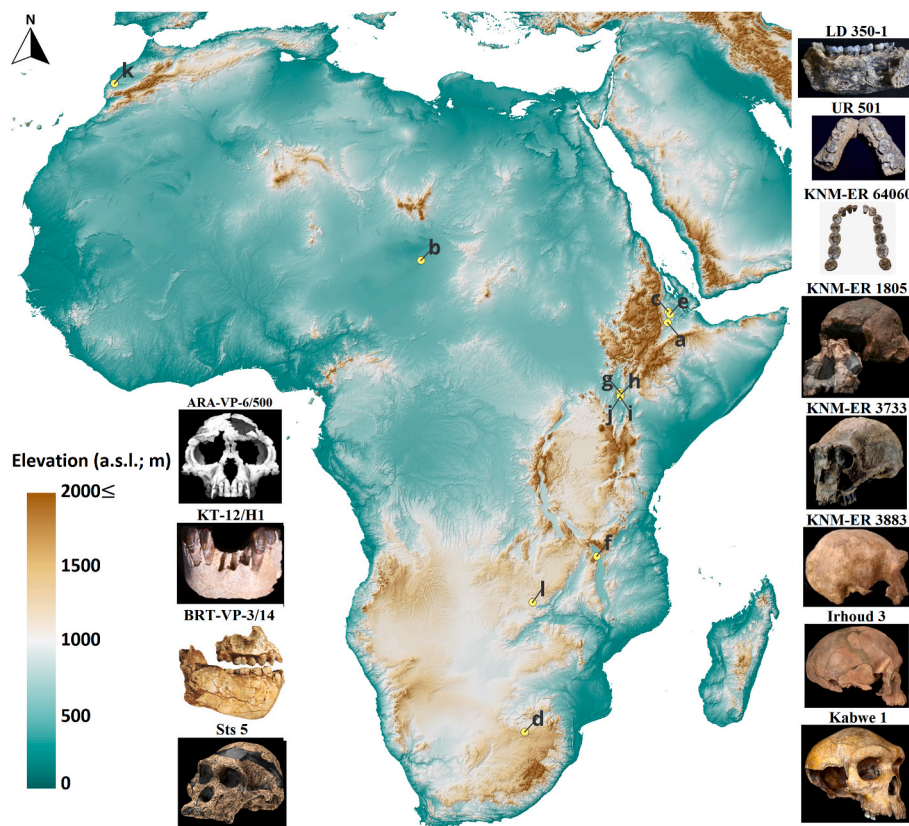


Fig. 1. Distribution of the studied Pliocene and Pleistocene hominin sites in Africa. a: Middle Awash (ARA-VP-6/500); b: Koro-Toro (KT-12/H1); c: Woranso-Mille (BRT-VP-3/14); d: Sterkfontein (Sts 5); e: Ledi-Geraru (LD 350-1); f: Uraha Hill (UR 501); g: Ileret (KNM-ER 64060); h: Upper Burgi (KNM-ER, 1805); i: Koobi Fora (KNM-ER 3733); j: Koobi Fora (KNM-ER 3883); k: Jebel Irhoud (Irhoud 3); l: Broken Hill (Kabwe 1).

Despite its modern public health relevance, the origins of leishmaniasis remain poorly understood. The oldest Afro-Eurasian evidence of human infection—DNA of *L. donovani*—was identified in Middle Kingdom Egyptian and Nubian mummies (Zink et al., 2006). In the Americas, pre-Columbian populations also suffered from the disease (Sabbatani et al., 2021). The evolutionary history of leishmania parasites and their phlebotomine vectors has been more extensively researched.

Understanding long-term leishmaniasis ecology also requires considering the environments in which hominins evolved. Africa's Pliocene–Pleistocene climatic variability shaped both early human diversification (Ramírez-Pedraza et al., 2024) and the distribution of phlebotomine vectors (Cruaud et al., 2021). Thus, reconstructing the geographic and climatic settings of early human populations may clarify how ancient human–Leishmania interactions emerged. Although the earliest *Homo sapiens* fossils (~315 ka) come from Jebel Irhoud, Morocco (Hublin et al., 2017), genetic evidence supports an extended, structured African origin in which different populations intermittently expanded and interbred (Meneganzin et al., 2022).

The distributions of the earliest-diverging Y-chromosome haplogroups (A00, A, and B) reflect deep population structure in Africa (Karmin et al., 2015; Cruciani et al., 2002). While not linked to leishmaniasis susceptibility, these lineages act as demographic–geographic markers for likely refugia between ~250 and 100 ka (Cabrera, 2022; Sirak et al., 2022). Comparing paleoclimate-based suitability for cutaneous and visceral leishmaniasis with the centers of these lineages helps explore whether ancient human refugia overlapped with regions favourable for *Leishmania* transmission.

The trypanosomatid genus *Leishmania* is an old branch of the class Kinetoplastea. Molecular clocks estimate a divergence from *Trypanosoma* around 327–205 Ma (Douzery et al., 2004; Parfrey et al., 2011).

The oldest fossil evidence for the *Leishmania*-like protozoan parasite *Paleoleishmania proterus* was found in mid-Cretaceous Myanmar amber (Poinar Jr. and Poinar, 2004). The phlebotomine clade is similarly old (Poinar, 2004): early Barremian Lebanese amber preserves fossils such as *Eophlebotus gezei*, *Mesophlebotomites hennigi*, and *Libanophlebotomus lutfallahi* (Azar et al., 1999). More recent Old World clades, including *Paraphlebotomus*, originated around 12.9–8.5 Ma in the Paratethys Region (Trájer 2022a; 2023a), and they spread southward during the Messinian Event (Cruaud et al., 2021), when special geographical and climatic conditions facilitated expansion (Trájer et al., 2021). Progressive aridification of the Mediterranean and Sahara over the last 7–11 Myr (Zhang et al., 2014; Crocker et al., 2022) likely accelerated sand fly diversification in Africa (Cruaud et al., 2021) and led to repeated habitat contractions and genetic bottleneck events during the Quaternary glaciations (Mahamdallie et al., 2011; Trájer and Sebestyén, 2019).

1.1. Aim

The aim of this study was to investigate the possibility of the persistence of human cutaneous and VL related to 12 hominin fossils and archaeological sites in Africa, which covers the period from the Zanclean to the Chibanian, considering the distribution-limiting climatic requirements of leishmaniasis, their vectors, and reservoirs. In addition, the climatic suitability of the two main leishmaniasis forms was studied in the times of the divergence of the Y-A00, Y-A, and Y-B haplogroups of Africa.

Table 1

Data of the studied hominin specimens and sites in Africa.

Fossil specimen	Fossil site	Country	Species	Age	Reference
ARA-VP-6/500	Middle Awash	Ethiopia	<i>Ardipithecus ramidus</i>	4.51–4.32 mys	Kalb et al. (1982)
KT-12/H1	Koro Toro	Chad	<i>Australopithecus bahrelghazali</i>	3.85–3.31 mys	Brunet et al. (1995)
BRT-VP-3/14	Woranso–Mille	Ethiopia	<i>Australopithecus deyiremeda</i>	3.596–3.330 mys	Haile-Selassie et al. (2015)
Sts 5	Sterkfontein	South Africa	<i>Australopithecus africanus</i>	2.05–2.58 mys	Herries and Shaw (2011)
LD 350-1	Ledi-Geraru	Ethiopia	<i>Homo sp.</i>	2.80–2.75 mys	Villmoare et al. (2015)
UR 501	Uraha Hill	Malawi	<i>Homo rudolfensis</i>	2.5–2.3 mys	Bromage et al. (1995)
KNM-ER 64060	Ileret	Kenya	<i>Homo habilis</i>	2.03–2.02 mys	Rozzi et al. (1997)
KNM-ER 1805	Upper Burgi	Kenya	<i>Homo habilis</i>	1.85–1.60 mys	Harris (1983)
KNM-ER 3733	Koobi Fora	Kenya	<i>Homo ergaster</i> /early African <i>H. erectus</i>	1.78–1.48 mys	Lepre and Kent (2015)
KNM-ER 3883	Koobi Fora	Kenya	<i>Homo erectus</i>	1.65–1.49 mys	Feibel et al. (1989)
Irhoud 3	Jebel Irhoud	Morocco	<i>Homo sapiens</i>	0.349–0.281 mys	Richter et al. (2017)
Kabwe 1	Broken Hill	Zambia	<i>Homo heidelbergensis</i>	0.324–0.274 mys	Grün et al. (2020)

2. Materials and methods

2.1. The workflow of the study

The main steps were as follows.

- 1) At first, 12 fossil hominin and archaeological sites were selected in Africa, covering the period extending from the Zanclean to the Chibanian.
- 2) Then, the palaeoclimatic conditions related to the 12 hominin specimens were reconstructed based on PALEO-PGEM-Series data.
- 3) Using the KNN algorithm, Köppen-Geiger climatic classes of the fossil hominin specimens were identified.
- 4) After that, the distribution-limiting climatic extrema of cutaneous and VL forms, six potential mammal hosts, and 5 sand fly species were determined. As an African wild dog host model species of *Leishmania donovani* (Hassan et al., 2009), *Canis lupaster* was selected.
- 5) The climatic suitability values of cutaneous and VL were projected to the current frequencies of human Y-chromosome DNA haplogroups A00, A, and B to assess how suitable the area of modern humans' origin within Africa was for the two forms of leishmaniasis for 250, 150, and 100 kya (Karmin et al., 2015). In other words, Y-haplogroups were used solely as neutral population-lineage indicators and were not interpreted as functional immune-related alleles.

2.2. Occurrence data

2.2.1. Hominin sites

A total of 12 Pliocene-Pleistocene hominin sites were studied (Fig. 1). These sites, in a geographical sense, cover Northern Africa (1 site in Morocco), Central Africa (1 site in Chad), East Africa (8 sites), and South Africa (2 sites in the state of South Africa; Fig. 1). Four specimens represent the subtribe Australopithecina, which includes the genera of *Ardipithecus* and *Australopithecus* in this study, and eight specimens belong to the subtribe Homoina, which includes the genus of *Homo* (Table 1).

ARA-VP-6/500 is a part of a partial skeleton of a female *Ardipithecus ramidus* and one of the earliest-known hominins dated back to the Zanclean stage. The anatomical reconstruction related to this partial skeleton supports the hypothesis that the foot anatomy of early hominins resembled that of modern African apes (Prang, 2022). The KT-12/H1 skull fragment, found in Kenya, represents a *Kenyanthropus platyops* individual. The dietary reconstruction of this species suggests that this species has subsisted on a diet of predominantly sedges and lived in a refugium, which was the part of the Central African fault-basin chain (Macho, 2015). The dental analysis of the *Australopithecus deyiremeda*-related BRT-VP-3/14 fossil, Ethiopia, revealed early developed dentognathic features that became characteristic for later *Paranthropus* and *Homo* species (Haile-Selassie et al., 2015). The statistical analysis of the endocast of the Sts 5 fossil and other *Australopithecus africanus*

endocasts suggests that this species' endocranial shape generally approximated the *Pan* condition (Beaudet et al., 2018).

The LD 350-1 specimen from Ledi-Geraru, Ethiopia, is the oldest-known possible remain attributed to *Homo* (Villmoare et al., 2015). The UR 501 specimen, found in the Chiwondo Beds at Uraha, northern Malawi, is attributed to *Homo rudolfensis*. The dental analysis of the specimen revealed transitional conditions between East Turkana australopithecines and early *Homo* (Rozzi et al., 1997). The specimen KNM-ER 64060, which was found in the upper Burgi Member of Area 13, Ileret, northern Kenya, is one of the few early Pleistocene *Homo* remains. Its mandibular dentition exhibits the greatest overall similarities in size to representatives of *Homo habilis* (Grine et al., 2019). The special cranial attributes of KNM-ER 1805, found in Upper Burgi, Kenya, provided the first evidence for sexual dimorphism in *Homo habilis* (Thompson, 1993).

The hominin fossil KNM-ER 3733, which was discovered in central Area 104, is one of the earliest representative fossils of early African *Homo erectus* (alternatively *Homo ergaster*) (Lepre and Kent, 2015). The *Homo erectus* specimen KNM-ER 3883 was found in Koobi Fora, Kenya. Interestingly, the craniometric measures of this African fossil and Ngandong 12, found in Java (this specimen is not part of this study), exhibit great similarities (Kidder and Durband, 2004).

The Irhoud 3 cranium, found in Jebel Irhoud, Morocco, is one of the earliest specimens that belong to our species, *Homo sapiens* (Richter et al., 2017). The Kabwe 1 specimen found in Broken Hill, Zambia, has been the subject of detailed biomechanical analysis of its frontal sinus (Godinho and O'Higgins, 2018), and comparative morphological studies classify it within the African *Homo heidelbergensis* clade (Grün et al., 2020). It should be noted that recent proposals dispute the taxonomic affiliation of the finding (e.g., Schroeder and Komza, 2025) (Fig. 1).

The main related data of these fossil hominin species was obtained from the Paleobiology Database (Peters and McClellenn, 2016) and can be found in Table 1.

2.2.2. Occurrence data of leishmania reservoirs and vectors

To evaluate the host element of the leishmaniasis vector chain, five potential *Leishmania* vector rodents and two hyrax species were selected. The presence of the genera *Acomys*, *Gerbillus*, *Heterohyrax*, *Procavia*, and *Tatera* in Africa during the Pliocene is supported by both fossil and phylogenetic evidence. A multilocus phylogenetic study suggests that the origin of the genus *Acomys* dates to the late Miocene (ca. 8.7 Ma) and is geographically rooted in East Africa (Aghová et al., 2019). Fossils of this genus are known from early Pliocene deposits at Lemudong'o, Kenya (6.08–6.12 Ma; Manthi, 2007; Manthi and Winkler, 2020); the early Pliocene strata of Langebaanweg, South Africa (Denys, 1990); and the 3 Ma layers at Transvaal, South Africa (Denys, 1999), indicating a continuous Pliocene presence on the continent.

Gerbilline rodents, including forms assignable to *Gerbillus* and *Tatera*, are documented in several middle-to late-Pliocene fossil assemblages in East Africa (Wessels, 1998). A mitochondrial phylogeny places the origin of *Tatera* at 8.14 Ma (Colangelo et al., 2005). The earliest

Table 2

The *Leishmania* reservoir competence of the studied mammal species, and the confirmed vector competence of the studied sand fly species in Africa selected for the indicators of sand fly vectors of *Leishmania* species. CL = cutaneous leishmaniasis, VL = visceral leishmaniasis, Z = zoonotic, A = anthroponotic, A/Z = anthroponotic or zoonotic. Ph. = *Phlebotomus*.

Leishmania sp.	Form (manifest.)	Form (host)	Phlebotomus spp.	Reservoirs	Reference
<i>L. aethiopica</i>	CL	Z	<i>Ph. sergenti</i>	<i>Heterohyrax</i>	Lemma et al. (2009); Gebre-Michael et al. (2004)
<i>L. donovani</i>	VL	A/Z	<i>Ph. alexandri</i> , <i>Ph. orientalis</i>	<i>Canis</i>	Hassan et al. (2009); Al-Koleby et al. (2022)
<i>L. major</i>	CL	Z	<i>Ph. bergeroti</i> , <i>Ph. duboscqi</i> , <i>Ph. papatasi</i>	<i>Tatera</i>	Ikeh et al. (1995); Elaagip et al. (2020); Gebre-Michael and Lane (1993); el-Hassan et al. (2001)
<i>L. tropica</i>	CL	A/Z	<i>Ph. sergenti</i>	<i>Acomys</i> , <i>Gerbillus</i> , <i>Procavia</i>	Gebre-Michael et al. (2004); Svobodová et al. (2006)
<i>L. tropica</i>	CL	A/Z	<i>Ph. sergenti</i>	<i>Procavia</i>	Talmi-Frank et al. (2010); Kassahun et al. (2015); Gebre-Michael et al. (2004); Svobodová et al. (2006)

known *Tatera* fossils come from the early Pliocene deposits at Lemudong'o (Manthi, 2007), Langebaanweg (Hendey, 1981), and the early Pliocene (4.19 Ma) fossil small mammal assemblage of Kanapoi, Kenya (Manthi and Winkler, 2020), while subsequent occurrences have been documented at multiple Pliocene and Pleistocene sites across East and South Africa (Wessels, 1998).

The oldest reasonably well-supported *Gerbillus* in Africa is likely *Gerbillus bibersoni* from the late Pliocene strata of Ahl al Oughlam, Atlantic Morocco (~2.5 Ma; Geraads, 2002). Early Pliocene fossils of a closely related taxon, *Gerbilliscus*, were unearthed at Kanapoi (Manthi and Winkler, 2020). Phylogenetic studies indicate that the emergence of *Gerbillus* dates back to the end of the Miocene, with most of its evolutionary history occurring in Africa (Ndiaye et al., 2016). Another molecular clock study suggests that the appearance of the genus *Gerbillus* coincided with the Miocene–Pliocene expansion of African arid biomes (Abiadh et al., 2010).

The earliest known procaviid hyracoid, *Heterohyrax auricampensis*, was recovered from a late Miocene (11.1–9.7 Ma) fissure-fill breccia at the Berg Aukas Site I, Namibia (Rasmussen et al., 1996). *Procavia antiqua* has been discovered in late Pliocene (3.03–2.61 Ma) breccia deposits at Taung, South Africa, associated with the Taung Child 1 specimen of *Australopithecus africanus* (McKee, 1993). Fossil hyracoids from the Transvaal and Taung deposits document the continuous occurrence of these mammals in southern Africa from the late Pliocene into the Pleistocene (Churcher, 1956).

Together, these records demonstrate that all five genera were established components of African mammalian communities by the Late Pliocene. Therefore, it can be concluded that these genera already existed in the Pliocene in Africa based on the fossil record, and their divergence times should not be recalculated. Table 2 shows the associated *Leishmania* species in the current era.

To evaluate the former potential presence of the sand fly vectors, six *Phlebotomus* species as extant indicators of the distribution of different *Leishmania* vectors in Africa were selected. Two of them are the potential vectors of VL-causing *L. donovani* in sub-Saharan Africa, and four of them are the vectors of *L. tropica* and *L. major*, which are the causative agents of CL in this large region. The selection of the vectors and the *Leishmania* species is justified by the phylogenetic time tree results (see subchapters 3.3.1 and 3.2.1 below). It is worth noting that the selected sand fly species are sand fly vector indicators in the climatic sense; several other sand fly species can be the vectors of leishmaniasis in Africa. Table 2 shows the vector competence of the selected sand fly species.

2.3. Source of palaeoclimate data and its procession

Palaeoclimate data was obtained from the PALEO-PGEM series, which contains spatial time series of global climate over the last 5 Myr covering the Plio-Pleistocene era (Barreto et al., 2023). This database contains data with a time interval of 1 kys temporal and $1^\circ \times 1^\circ$ spatial resolution. Each palaeoclimatic data point was averaged before

Table 3

The used bioclimatic variables in K-nearest neighbour classification.

Bioclimatic variable	Abbreviation	Unit
Annual Mean Temperature	Tma	°C
Temperature Seasonality (standard deviation $\times$ 100)	Ts	°C
Mean Temperature of Wettest Quarter	Tmweq	°C
Mean Temperature of Driest Quarter	Tmdq	°C
Mean Temperature of Warmest Quarter	Tmwaq	°C
Mean Temperature of Coldest Quarter	Tmcq	°C
Annual Precipitation	Pa	mm
Precipitation of Wettest Month	Pwm	mm
Precipitation of Driest Month	Pdm	mm
Precipitation Seasonality (Coefficient of Variation)	Ps	mm
Precipitation of Wettest Quarter	Pweq	mm
Precipitation of Driest Quarter	Pdq	mm
Precipitation of Warmest Quarter	Pwaq	mm
Precipitation of Coldest Quarter	Pcq	mm

processing based on the time interval of the hominoid specimens (see Table 1).

PALEO-PGEM NetCDF files were read and processed in the Scientific Python Environment (Python) v. 3.9, using xarray, matplotlib.pyplot, and numpy program libraries, which is a commonly used environment for scientific computing purposes (Perez et al., 2010). GeoTIFF files were created using rasterio transform program library, and the created models were presented in the WGS84 geodetic (coordinate) system of the United States National Geospatial-Intelligence Agency. Maps were opened and coloured in Quantum GIS (QGIS) v. 3.34.11 (Flenniken et al., 2020) with Grass GIS 8.4.0 software (Neteler et al., 2012). Supplementary Table 1 shows the reconstructed, averaged palaeoclimatic values by site.

2.4. K-nearest neighbour-based climate classification

The Köppen-Geiger (hence: Köppen) climate classification system (Geiger, 1954) was the basis of climatic classification. The Köppen climatic system contains five main groups: tropical (A), arid (B), temperate (C), continental (D), and polar (E). Based on the specific seasonal precipitation trend, 30 climate sub-classes are determined. The Köppen-Geiger data was obtained from Beck et al. (2018). In this study, the palaeoclimatic values of all 12 sites were reconstructed based on the data and method described in subsection 2.4. The reconstructed climatic value types can be seen in Table 3.

A K-nearest neighbour classifier was used in the determination of the fossil hominin specimens-associated paleoclimates. It is a widely used machine learning algorithm for classification purposes (Bansal et al., 2022). Gaining train data, the Köppen-Geiger and recent climatic values of 12134 African and Eurasian random sites were sampled and added to the analyses. WorldClim version 2.1 climate data for 1970–2000 with 2.5 arc-min resolution formed the basis of the reference period's climatic data (Fick and Hijmans, 2017). Eurasian sites were involved to increase the contrast between sites since Eurasia has extensive cold regions that

are missing in Africa. The 12 fossil hominins and archaeological sites played the role of test data. This process was also performed in a Python environment using program libraries performing train-test split, standard scaling, k-neighbors classifying, and accuracy scoring functions.

2.5. Model identification

2.5.1. Determination of lower and upper extrema

Climate values were sampled with the occurrence points of the different species by variables using the sampling tool of QGIS following the general logic of ecological niche modelling for past periods (Myers et al., 2015). [Supplementary Table 2](#) shows the sources of the occurrence data of the studied sand fly, hyrax species, and *Leishmania* diseases. It means a total of 16 samplings, 2 monthly and 14 bioclimatic maps. It can be read in [Supplementary Table 3](#). Before the determination of the lower and upper extrema, 1-1 percent from the highest and lowest values was cut for data purification purposes.

Formally, let X be the set of climate values sampled at occurrence points across n climatic variables $\{X_1, X_2, \dots, X_n\}$. For each variable X_i , let $X_i^{(\text{sorted})}$ represent the ordered values of X_i .

To determine the purified data for each variable X_i :

$$X_i^{cleaned} = X_i^{(sorted)}[k], X_i^{(sorted)}[k+1], \dots, X_i^{(sorted)}[m-k] \quad (1)$$

Where $k = \lceil 0.01 \times m \rceil$ and m is the total number of samples in X_i .

2.5.2. Modelling of climatic suitability patterns

The Climate Envelope Method (CEM) underpins climate suitability models, predicting species distribution based on climatic conditions (Hijmans and Graham, 2006). It assumes species are primarily limited by specific temperature and precipitation thresholds. By defining these climatic "envelopes", CEM predicts potential species locations under varying climate scenarios. CEM is based on Boolean algebra (Whitesitt, 2010), where species presence or absence is determined by whether climatic conditions fall within specified limits. Boolean algebra combines presence-absence maps for each variable, creating an overall suitability map.

The modelling results were visualized using GIS software, integrated with GRASS. The spatial data were projected in the Lambert Azimuthal Equal Area coordinate system (EPSG:3035). The modelling process followed these steps:

A total of 14x2 factors were included in the model for all modelled taxa.

The extrema of these climatic factors defined the range of suitable conditions for species distribution. Specifically, the potential distribution area for a species was determined using a Boolean approach:

The presence or absence of a species (Y) at a given location was modelled as a binary variable, $Y \in \{0, 1\}$, where:

$Y = 1$: Suitable conditions exist for the species.

$Y = 0$: Conditions are unsuitable.

This Boolean characterization considers whether the conditions fall within the suitable range defined by: in each case. [Supplementary Tables 4–7](#) exhibit the limits used in modelling processes.

$$\min (variable_{mean}) \leq variable_{mean} \leq \max (variable_{mean})$$

2.5.3. Human Y-chromosome DNA haplogroup allele frequencies and its processing

The analysis of Y-chromosome haplogroups was conducted independently of the fossil site-based paleo-suitability modelling. The fossil hominin sites served only to examine climatic suitability patterns across the Plio-Pleistocene, whereas the Y-chromosome component exclusively uses present-day allele-frequency data that reflect late Pleistocene population structure. Published Y-DNA haplogroup frequency datasets (Suppl. Table 8) were compiled for haplogroups A00, A, and B,

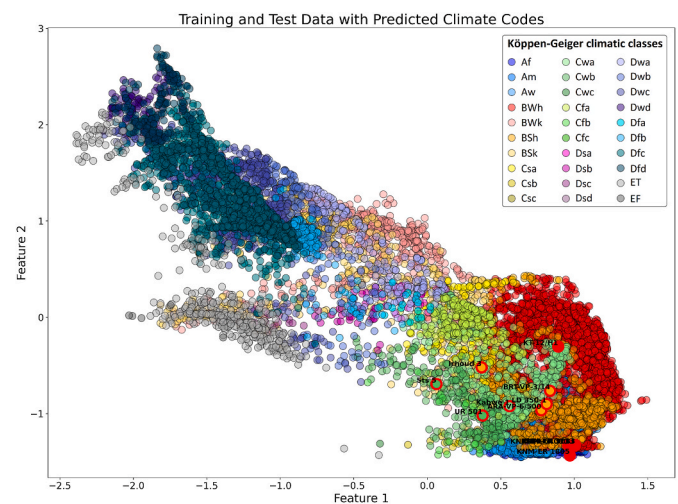


Fig. 2. The results of KNN-analysis, based on the reconstructed palaeoclimatic values of the sites. Red circles mark the hominoid specimens-related points. Af: Tropical rainforest climate, Am: Tropical monsoon climate, As: Tropical dry savanna climate, Aw: Tropical savanna, wet, BSh: Hot semi-arid (steppe) climate, BSk: Cold semi-arid (steppe) climate, BWh: Hot deserts climate, BWK: Cold desert climate, Cfa: Humid subtropical climate, Cfb: Temperate oceanic climate, Cfc: Subpolar oceanic climate, Csa: Hot-summer Mediterranean climate, Csb: Warm-summer Mediterranean climate, Csc: Cool-summer Mediterranean climate, Cwa: Monsoon-influenced humid subtropical climate, Cwb: Subtropical highland climate, Cwc: Cold subtropical highland climate, Dfa: Hot-summer humid continental climate, Dfb: Warm-summer humid continental climate, Dfc: Subarctic climate, Dfd: Extremely cold subarctic climate, Dsa: Hot, dry-summer continental climate: Cold (continental), Dsb: Warm, dry-summer continental climate, Dsc: Dry-summer subarctic climate, Dwa: Monsoon-influenced hot-summer humid continental climate, Dwb: Monsoon-influenced warm-summer humid continental climate, Dwc: Monsoon-influenced subarctic climate, Dwd: Monsoon-influenced extremely cold subarctic climate, EF: Ice cap climate, ET: Tundra: Polar climate. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

representing basal modern human paternal lineages. These frequency values were interpolated across Africa using the Inverse Distance Weighting (IDW) function in QGIS to create continuous spatial allele-frequency surfaces. The resulting surfaces were compared with modelled climatic suitability layers for 250, 150, and 100 ka to explore whether regions of high late Pleistocene leishmaniasis suitability overlapped with the present-day geographic centers of basal Y-chromosome lineages. [Supplementary Fig. 1](#) shows the interpolated Y-A and Y-B allelic frequencies in Africa with isolines.

3. Results

3.1. KNN analysis results

The KNN analysis result indicates that steppe-like or woodland/shrubland biome regions generally host the predicted climate types of hominin specimens. The ancient hominin individuals, including ARA-VP-6/500 (*Ardipithecus ramidus*), BRT-VP-3/14 (*Australopithecus deyiremeda*), LD 350-1 (*Homo* sp.), KNM-ER 64060 (*Homo habilis*), KNM-ER 1805 (*Homo habilis*), KNM-ER 3733 (*Homo ergaster*), KNM-ER 3883 (*Homo erectus*), and the Kabwe 1 (*Homo heidelbergensis*) specimens, lived in hot, semi-arid, steppe climate (Köppen BSh) sites. The Irhoud 3 (*Homo sapiens*) specimen-related individual lived under a cold semi-arid steppe (Köppen BSk) climate. The individual of UR 501 (*Homo rudolfensis*) inhabited a tropical savannah (Köppen Am) site. The Sts 5 (*Australopithecus africanus*) individual lived in a temperate, dry-winter, warm-summer (Köppen Cwb) region. Solely the individual of the specimen of KT-12/H1 (*Australopithecus bahrelghazali*) lived in an oasis formed by

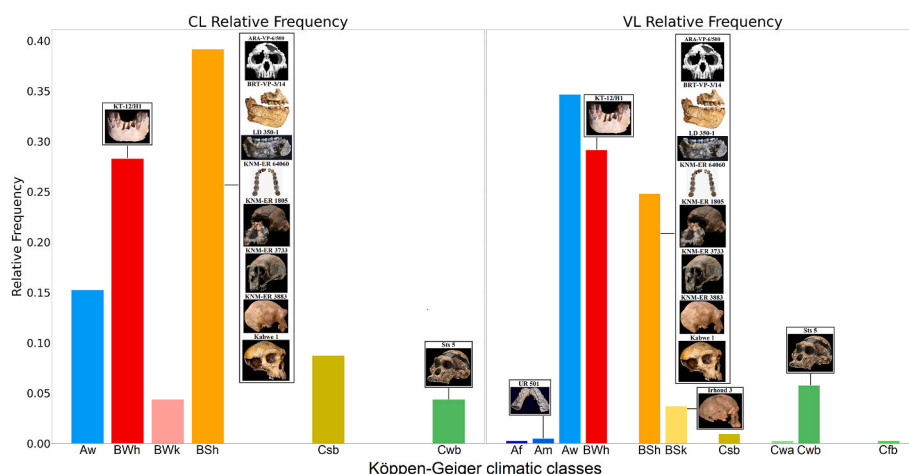


Fig. 3. The projection of the determined palaeoclimates by fossil specimens to the present-day relative frequency of cutaneous (CL) and visceral leishmaniasis (VL) cases in present-day sub-Saharan Africa. Af: Tropical rainforest climate, Am: Tropical monsoon climate, Aw: Tropical savanna, wet, BSh: Hot semi-arid (steppe) climate, BSk: Cold semi-arid (steppe) climate, BWk: Hot deserts climate, BWk: Cold desert climate, Cfb: Temperate oceanic climate, Csb: Warm-summer Mediterranean climate, Cwa: Monsoon-influenced humid subtropical climate, Cwb: Subtropical highland climate.

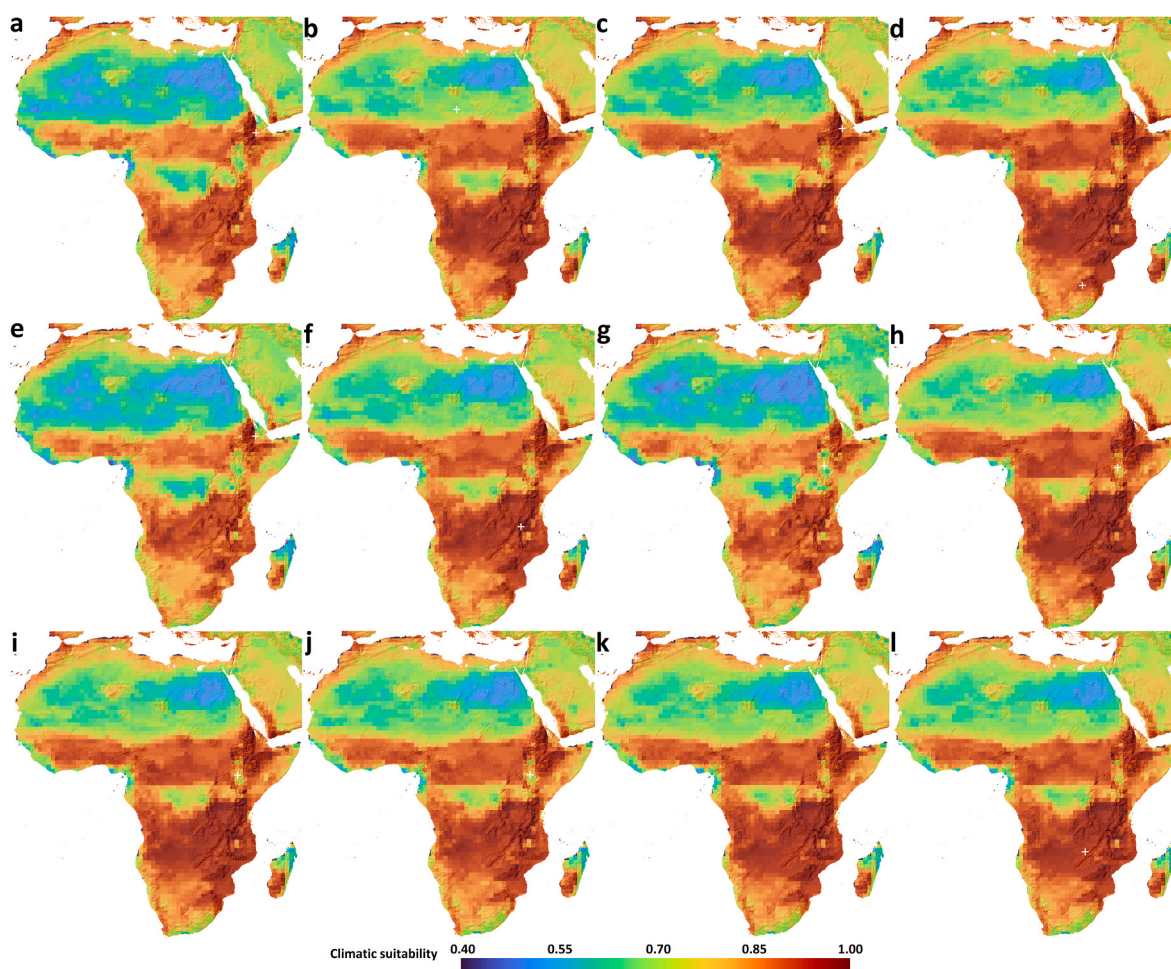


Fig. 4. The modelled average local maximum climatic suitability values of cutaneous leishmaniasis-vector sand fly species in the periods of 4.51–4.32 Ma (a), 3.85–3.31 Ma (b), 3.596–3.330 Ma (c), 2.05–2.58 Ma (d), 2.80–2.75 Ma (e), 2.50–2.30 Ma (f), 2.03–2.02 Ma (g), 1.85–1.60 Ma (h), 1.78–1.48 (i), 1.65–1.49 Ma (j), 0.349–0.281 Ma (k), 0.324–0.274 Ma (l).

Lake Chad, in a hot, arid desert (Köppen BWk) climate environment (Fig. 2).

The comparison of the KNN results with the relative frequency values

of the Köppen-Geiger climate classes in present-day Africa shows that both cutaneous and VL frequently occur in the hot semi-arid (steppe) (Köppen-Geiger BSh) climate under which most (8/12) of the studied

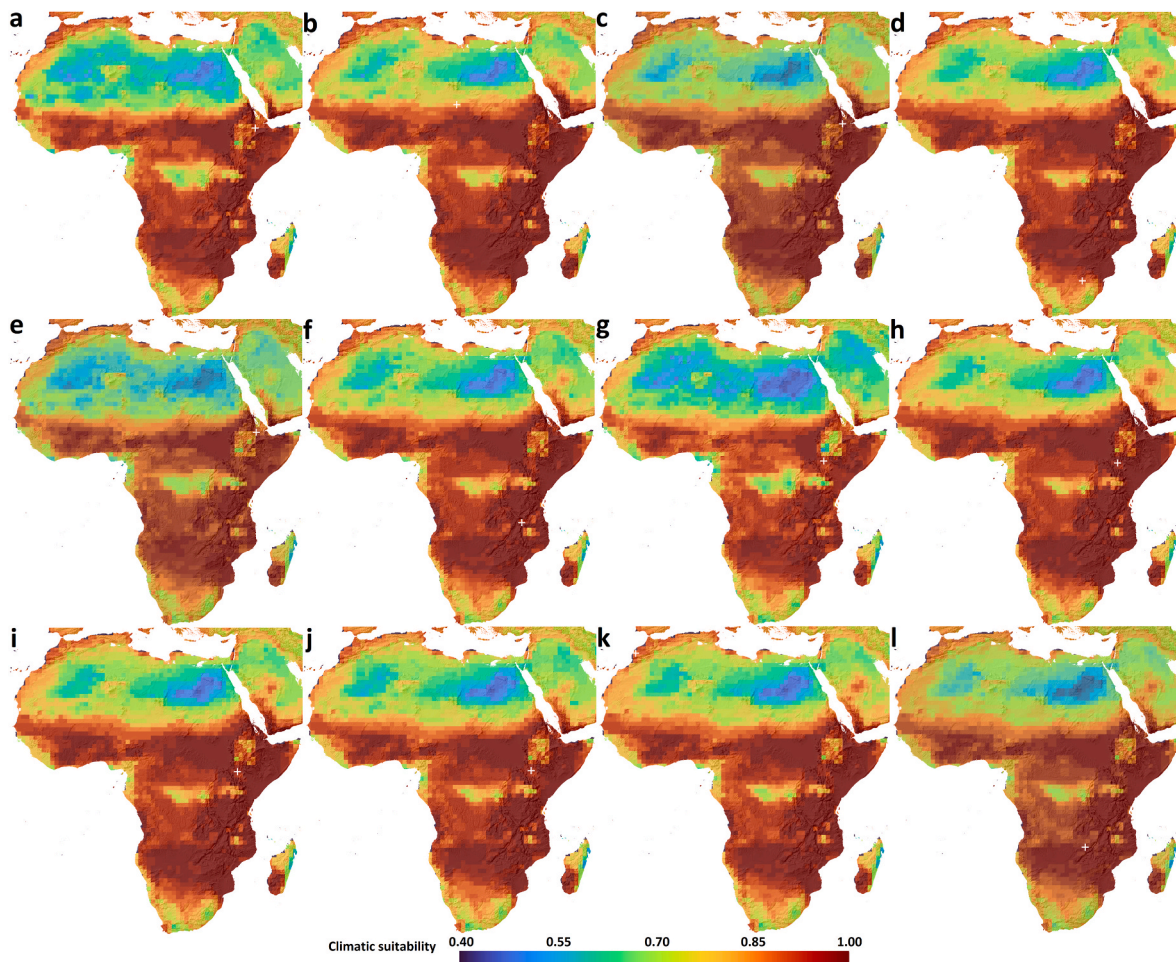


Fig. 5. The modelled average local maximum climatic suitability values of visceral leishmaniasis-vector sand fly species in the periods of 4.51–4.32 Ma (a), 3.85–3.31 Ma (b), 3.596–3.330 Ma (c), 2.05–2.58 Ma (d), 2.80–2.75 Ma (e), 2.50–2.30 Ma (f), 2.03–2.02 Ma (g), 1.85–1.60 Ma (h), 1.78–1.48 Ma (i), 1.65–1.49 Ma (j), 0.349–0.281 Ma (k), 0.324–0.274 Ma (l).

fossil hominin individuals lived. The KT-12/H1 individual lived under a hot desert (Köppen-Geiger BWh) climate, which is also suitable for both leishmaniasis types. It is also valid for the Sts5 individual, which lived in a subtropical highland (Köppen-Geiger Cwb) climate. In contrast, the tropical monsoon (Köppen-Geiger Am) climate, which was characteristic of the site of the UR 501 individual in its life, is currently suitable for VL in sub-Saharan Africa. Similarly, the cold semi-arid (Köppen-Geiger BSk; steppe) climate is currently suitable in this large region only for the VL form (Fig. 3).

3.2. Cutaneous leishmaniasis vectors

The overall maximum climatic suitability patterns of CL vectors indicate that in a climatic sense, CL generally could be stable in Eastern Africa, the southern and northern parts of Central Africa, the southern part of Western Africa, and the northwestern coastal area of North Africa from the Zanclean to the Chibanian. However, there are differences in the modelled periods. The general climatic stability was relatively low considering Africa in 4.51–4.32, 2.80–2.75, and 1.85–1.60 mya, and high, e.g., in 3.85–3.31, 2.05–2.58, 1.85–1.60, or in 1.78–1.48 mya. The modelled periods show that East Africa and the southern part of Central Africa possessed the highest long-term maximum climatic stability for CL-vectors. The Sahara generally was less suitable for the studied vectors of CL in the modelled period (Fig. 4).

3.3. Visceral leishmaniasis vectors

The Sahel region, including the southern part of Western Africa, as well as the northern part of Central Africa and Eastern Africa, was suitable for the VL vectors in the modelled time slices. East Africa and the southern part of Central Africa (the heart of the Congo Basin), as well as the northern regions of South Africa, also exhibit high maximum climatic suitability values related to VL-vector sand fly taxa. Relatively high climatic suitability values can be found also in Northwest Africa. Large regions of the Sahara were uninhabitable for the studied VL vectors, although the extension of these regions shows a decreasing trend parallel to the Quaternary cooling of the global climate (Fig. 5).

3.4. Cutaneous leishmaniasis

The modelled climatic suitability values of CL show that except for the Central Sahara and the core region of Central Africa, this parasitic disease generally exhibits medium or high values at each time. Among them, the northwest part of North Africa, the Sahel Belt, the Horn of Africa, the southern part of East Africa, the southern regions of Central Africa, and the northernmost and the western coastal regions of South Africa exhibit the highest climatic suitability values and long-term stability considering the modelled 12 sites and periods. Both the African and the Arabian Peninsula sides of the Bab-el-Mandeb Gate show high modelled values for CL (Fig. 6).

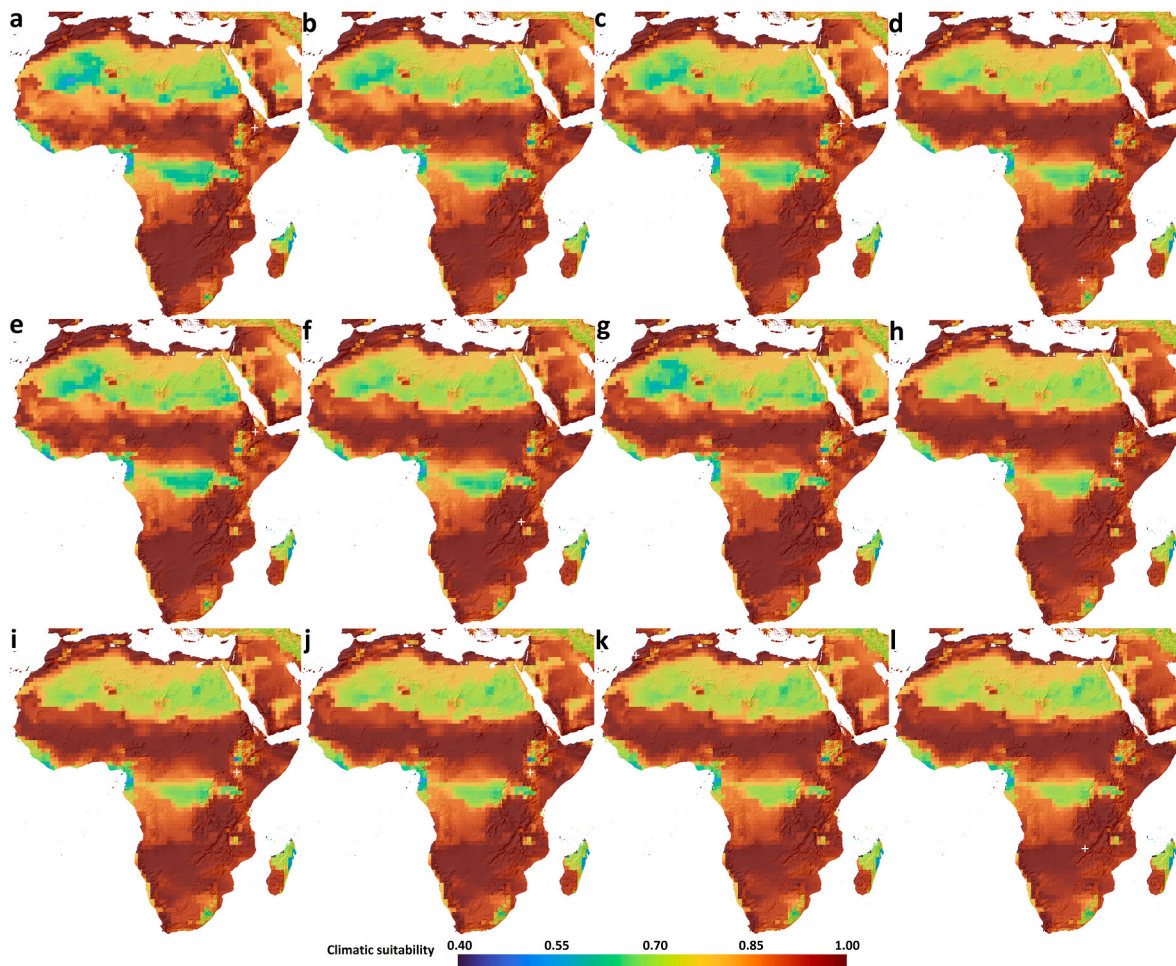


Fig. 6. The modelled climatic suitability values of cutaneous leishmaniasis in the periods of 4.51–4.32 Ma (a), 3.85–3.31 Ma (b), 3.596–3.330 Ma (c), 2.05–2.58 Ma (d), 2.80–2.75 Ma (e), 2.50–2.30 Ma (f), 2.03–2.02 Ma (g), 1.85–1.60 Ma (h), 1.78–1.48 (i), 1.65–1.49 (j), 0.349–0.281 Ma(k), 0.324–0.274 Ma(l).

3.5. Visceral leishmaniasis

The modelled climatic suitability values of VL exhibit high climatic suitability values in Northwest Africa, through the Sahel Belt, in the Horn of Africa, in the southern part of Eastern Africa, and in the southern and northwestern parts of South Africa. The modelled climatic suitability of VL shows an overall decreasing trend in the Sahara between the Zanclean and the Chibanian. The heart of the Sahara, the Congo Basin, and the coastal regions of the Gulf of Guinea were not suitable for VL (Fig. 7).

3.6. *Acomys*, *Gerbillus*, *heterohyrax*, *procavia*, and *tatera*

The modelled average local maximum climatic suitability values of *Acomys*, *Gerbillus*, *Heterohyrax*, *Procavia*, and *Tatera* generally exhibit the highest values in the eastern part of the Sahel Belt, the southern part of Eastern Africa, the southernmost regions of Central Africa, and the northern regions of South Africa. Depending on the period, large regions of the Sahara also show relatively high climatic suitability values. The palaeoclimate of North Africa was less suitable for these species. The climatic suitability values in the Sudanian part of the Sahel show notable fluctuations between the studied time slices. In contrast, the northern part of South Africa provided a more stable palaeoenvironment for the studied rock hyrax and rodent reservoirs of *Leishmania* spp. (Fig. 8).

3.7. Wild canids (*Canis lupaster* model)

The modelled climatic suitability values of a *Canis lupaster*-like ancient wild dog exhibit somewhat different climatic suitability patterns compared to the above-mentioned hyraxes and rodents. The climatic suitability of canid hosts seems to be the highest and the most stable in East and South Africa and in the western, Atlantic coastal regions of Northwest Africa. Also, high climatic suitability values can be seen in the southern regions of the Sahel belt, although the extension of these areas strongly depends on the studied period. The models exhibit a clear increasing climatic suitability trend for the wild canid model species between the Zanclean and the Chibanian in the Sahel. The central part of the Congo Basin was not suitable for a canid vector characterized by the climatic needs of modern *C. lupaster*. Although the climatic suitability values vary by period, certain regions of the Sahara were suitable for this *Leishmania* host (Fig. 9).

Climatic suitability for cutaneous and VL vectors varied across hominin sites (Fig. 10a–b). For CL (Fig. 10c), middle Zanclean *Ar. ramidus* (ARA-VP-6/500, Ethiopia) had high suitability (0.84), indicating a conducive environment. *Australopithecus bahrelghazali* (KT-12/H1, Chad) showed lower suitability (0.67). Piacenzian *Au. deyiremeda* (BRT-VP-3/14, Ethiopia) and *H. rudolfensis* (UR 501, Malawi) exhibited high values (0.86–0.94). Gelasian *Au. africanus* (Sts 5, South Africa) and early *H. habilis* (KNM-ER 64060, Kenya) showed moderate suitability (0.71–0.94). Later Calabrian specimens, including *H. ergaster* (KNM-ER 3733) and *H. erectus* (KNM-ER 3883, Kenya), had moderate values (0.79–0.80). Late Chibanian *H. sapiens* (Irhoud 3, Morocco) and

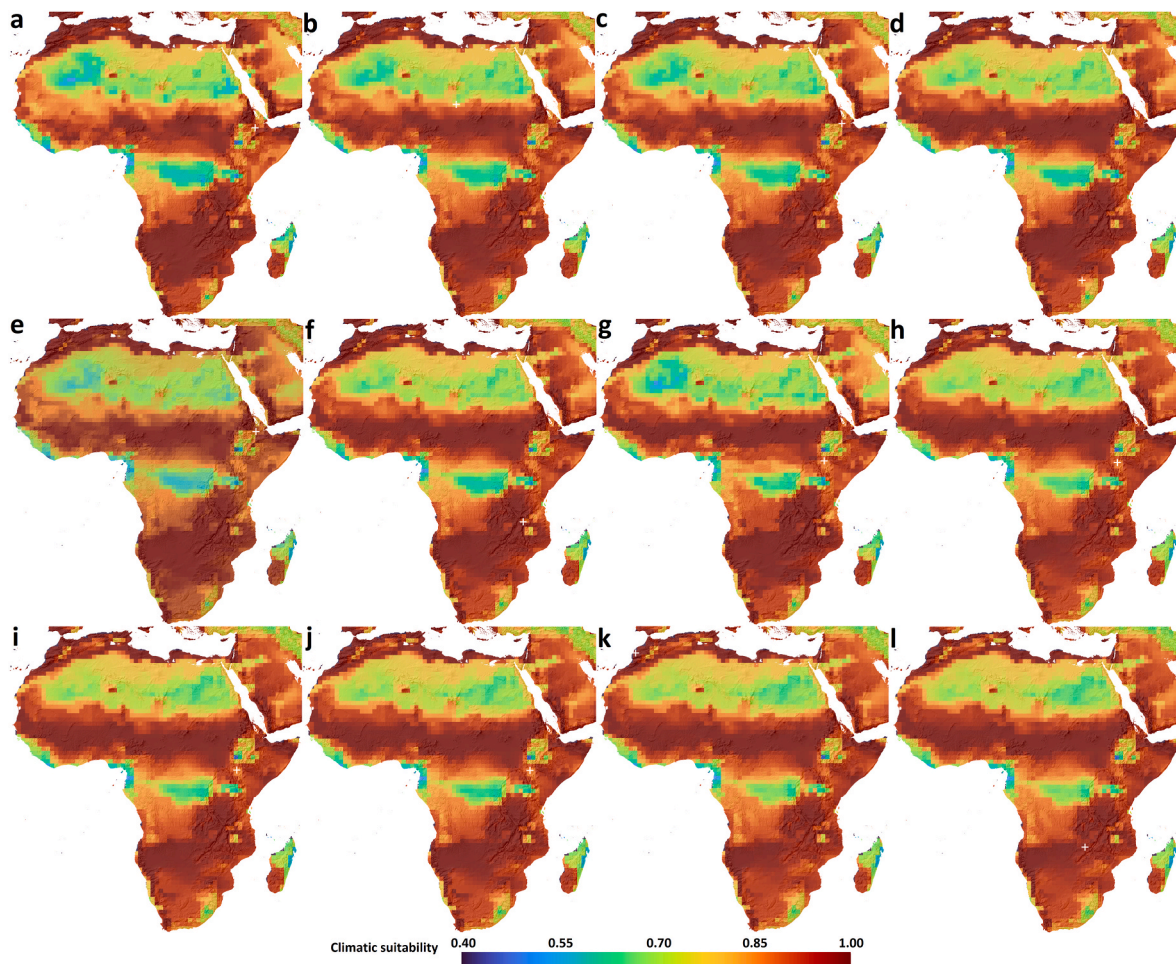


Fig. 7. The modelled average climatic suitability values of visceral leishmaniasis related to hominins of ARA-VP-6/500 (*Ardipithecus ramidus*; a), KT-12/H1 (*Australopithecus bahrelghazali*; b), BRT-VP-3/14 (*Australopithecus deyiremeda*; c), Sts 5 (*Australopithecus africanus*; d), LD 350-1 (*Homo* sp.; e), UR 501 (*Homo rudolfensis*; f), KNM-ER 64060 (*Homo habilis*; g), KNM-ER 1805 (*Homo habilis*; h), KNM-ER 3733 (*Homo ergaster*; i), KNM-ER 3883 (*Homo erectus*; j), Irhoud 3 (*Homo sapiens*; k), Kabwe 1 (*Homo heidelbergensis*; l).

H. heidelbergensis (Kabwe 1, Zambia) showed high suitability (0.84–0.94).

For VL (Fig. 10d), suitability values were generally higher. *Ar. ramidus* (ARA-VP-6/500, Ethiopia) and *Au. deyiremeda* (BRT-VP-3/14) showed maximum values (1.0), suggesting highly suitable environments. *Homo rudolfensis* (UR 501, Malawi) and early Gelasian *Homo* sp. (LD 350-1, Ethiopia) had values near 0.95, while later Gelasian *H. habilis* and Calabrian *H. ergaster* (Koobi Fora, Kenya) maintained high suitability (0.95–0.98). Late Chibanian specimens, such as *H. sapiens* (Irhoud 3, Morocco) and *H. heidelbergensis* (Kabwe 1, Zambia), exhibited values of 0.88–0.98, highlighting persistent risks.

Climatic suitability for rodent and hyrax genera, as well as the *Canis lupaster*-like canid host model associated with fossil hominins also varied regionally (Fig. 10e and f). For example, *Ar. ramidus* (ARA-VP-6/500) had high suitability (0.93), as did *Au. deyiremeda* (BRT-VP-3/14, 0.96). Kenya's specimens, including *H. habilis* and *H. ergaster*, showed moderate suitability (0.84–0.90). Late Chibanian specimens such as *H. sapiens* (Irhoud 3, 0.94) and *H. heidelbergensis* (Kabwe 1, 0.99) demonstrated the highest values.

3.8. Principal component analysis result

The principal component analysis indicates that UR-501 differs from the other sites, as these individuals exhibit high modelled climatic suitability values for CL and the *Acomys*, *Gerbillus*, *Heterohyrax*, *Procavia*,

and *Tatera* genera. In contrast, ARA-VP-6/500, LD 350-1, and Sts 5 show high modelled suitability values for CL vectors and VL. The biplot suggests that the Broken Hill and Irhoud 3 specimens are characterized by relatively high *Acomys*, *Gerbillus*, *Heterohyrax*, *Procavia*, and *Tatera* genera, CL vectors, and VL climatic suitability values. The BRT-VP-3/14 individual displays high values for VL vectors and wild dogs. In contrast, the KNM-ER 1805, 3733, and KNM-ER 3883 individuals exhibit low climatic suitability values for CL-vectors and VL. Similarly, the KT-12/H1 specimen demonstrates low values for wild dogs, CL vectors, VL vectors, and VL vectors (Fig. 11).

3.9. Comparison of human Y-chromosome DNA haplogroup frequencies and past climatic suitability values

The region of northwestern Cameroon where the people carrying the highest Y-A00 haplogroup frequency alive today live was moderately suitable for both visceral and CL in 250 kya, exhibiting 0.71–0.75 climatic suitability values. In contrast, in the region of South Sudan, where currently the Y-A haplogroup frequency is the highest, both the cutaneous and the visceral form's modelled climatic suitability values exhibit the maximum (1.0) value (Fig. 12 a1–a2). Also, moderately high (0.92: CL) and maximum (1.0: VL) climatic suitability values can be seen in Namibia, Burkina Faso, and North Tanzania in 150 kya, where currently the number of people carrying the Y-A haplogroup is relatively high (Fig. 12 b1–b2). In the case of the Y-DNA haplogroup, the center of the

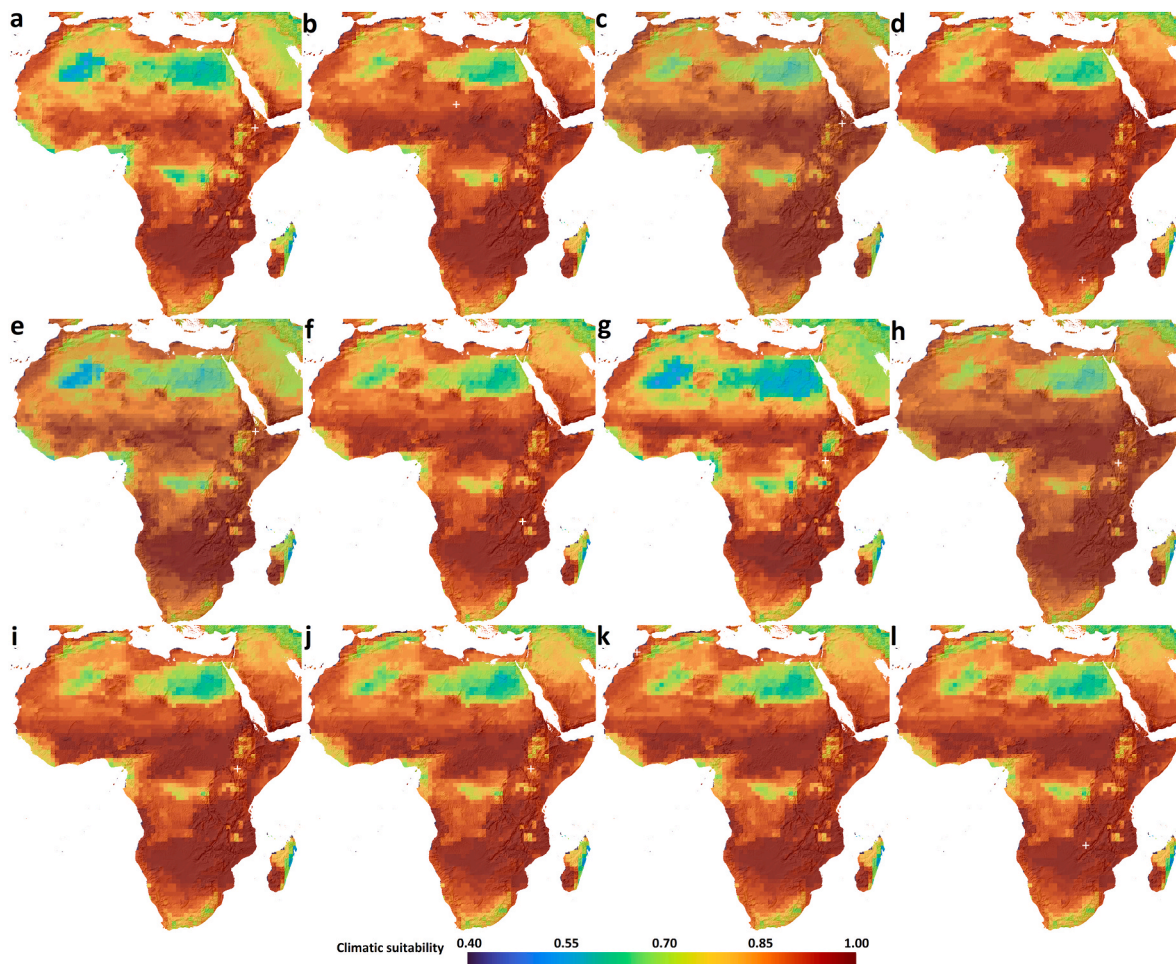


Fig. 8. The modelled average local maximum climatic suitability values of *Acomys*, *Gerbillus*, *Heterohyrax*, and *Procavia* and *Tatera* genera related to hominins of ARA-VP-6/500 (*Ardipithecus ramidus*; a), KT-12/H1 (*Australopithecus bahrelghazali*; b), BRT-VP-3/14 (*Australopithecus deyiremeda*; c), Sts 5 (*Australopithecus africanus*; d), LD 350-1 (*Homo* sp.; e), UR 501 (*Homo rudolfensis*; f), KNM-ER 64060 (*Homo habilis*; g), KNM-ER 1805 (*Homo habilis*; h), KNM-ER 3733 (*Homo ergaster*; i), KNM-ER 3883 (*Homo erectus*; j), Irhoud 3 (*Homo sapiens*; k), Kabwe 1 (*Homo heidelbergensis*; l).

present-day highest frequencies can be found in northern Tanzania. In 100 kya, this region was highly suitable (climatic suitability value: 1.0) for both leishmaniasis forms (Fig. 12 c1-c2).

4. Discussion

The reconstructed paleoclimates of the fossil sites indicate that most studied hominin individuals occupied desert, semi-desert, savanna, and steppe-like habitats (see Figs. 2 and 3). This agrees with palaeozoological evidence showing that in the mid-Pliocene Hadar and early Pleistocene Turkana sites, animals typical of moderately dry or dry environments represented at least three-quarters of the vertebrate faunas (Trájer 2022b). These habitats closely resemble present-day environments where leishmaniasis is most prevalent, such as in Ethiopia (Gadisa et al., 2015) or in Chad (Israël et al., 2022).

Today, Ethiopia, Somalia, South Sudan, and Sudan form one of the major foci of VL (Jones and Welburn, 2021), characterized by arid, semi-arid, or savanna climates (Beck et al., 2018). These regions host several mammalian *Leishmania*-reservoir species, many of which have archaeozoological records from fossil hominin-bearing sites. For example, Zanclean age wild canids occur in the Aramis Member of Middle Awash with the ARA-VP-6/500 specimen (WoldeGabriel et al., 2004), at Woranso-Mille with BRT-VP-3/14, and at Sterkfontein (Sts 5). This is notable because canids serve as key reservoirs of various *Leishmania* species (Hubálek et al., 2011). The type species used in our model,

Canis lupaster, inhabits tropical and semi-arid climate zones—including Sahelian savannas, desert fringes, and rocky habitats (Gaubert et al., 2012). Fig. 9 shows its wide potential distribution in Africa during the last five million years. Hot, relatively dry environments are also typical habitats of several rodent taxa that act as *Leishmania* reservoirs.

The Aramis Member in Middle Awash contains sciurid fossils (Sciuridae indet.; WoldeGabriel et al., 2004), a rodent family that includes potential *L. infantum* hosts (Azami-Conesa et al., 2023). While northern-hemisphere sciurids are often arboreal, such African genera as *Geosciurus* occupy arid and semiarid landscapes (Kopij, 2023). Fossil *Acomys* remains were excavated in the Pliocene hominin fossil site Makapansgat, South Africa (Rayner et al., 1993), and in the Gelasian hominin site Omo (de Heinzelin, 1983). Similarly, *Tatera* fossils were found in the Piacenzian geological layers of Hadar (Johanson et al., 1976), Laetoli (Leakey and Harris, 1987), Omo (de Heinzelin, 1983), Swartkrans (Brain, 1994), and many other Plio-Pleistocene sites in Africa. These faunal records closely support the modelled climatic suitability patterns in Fig. 8.

The origin of human leishmaniasis must also be considered in the context of hominin–sand fly coevolution. The diversification of sand fly vector clades during the Late Neogene aridification and cooling (Owen et al., 2018) coincided with major stages in hominin evolution (Trájer et al., 2023b; Timmermann et al., 2024). Molecular evidence places the *Homo-Pan* split at ~6.4 Ma (CI: 6.0–6.5 mya; derived from 81 phylogenetic studies; Kumar et al., 2022), close to the ages of the earliest known

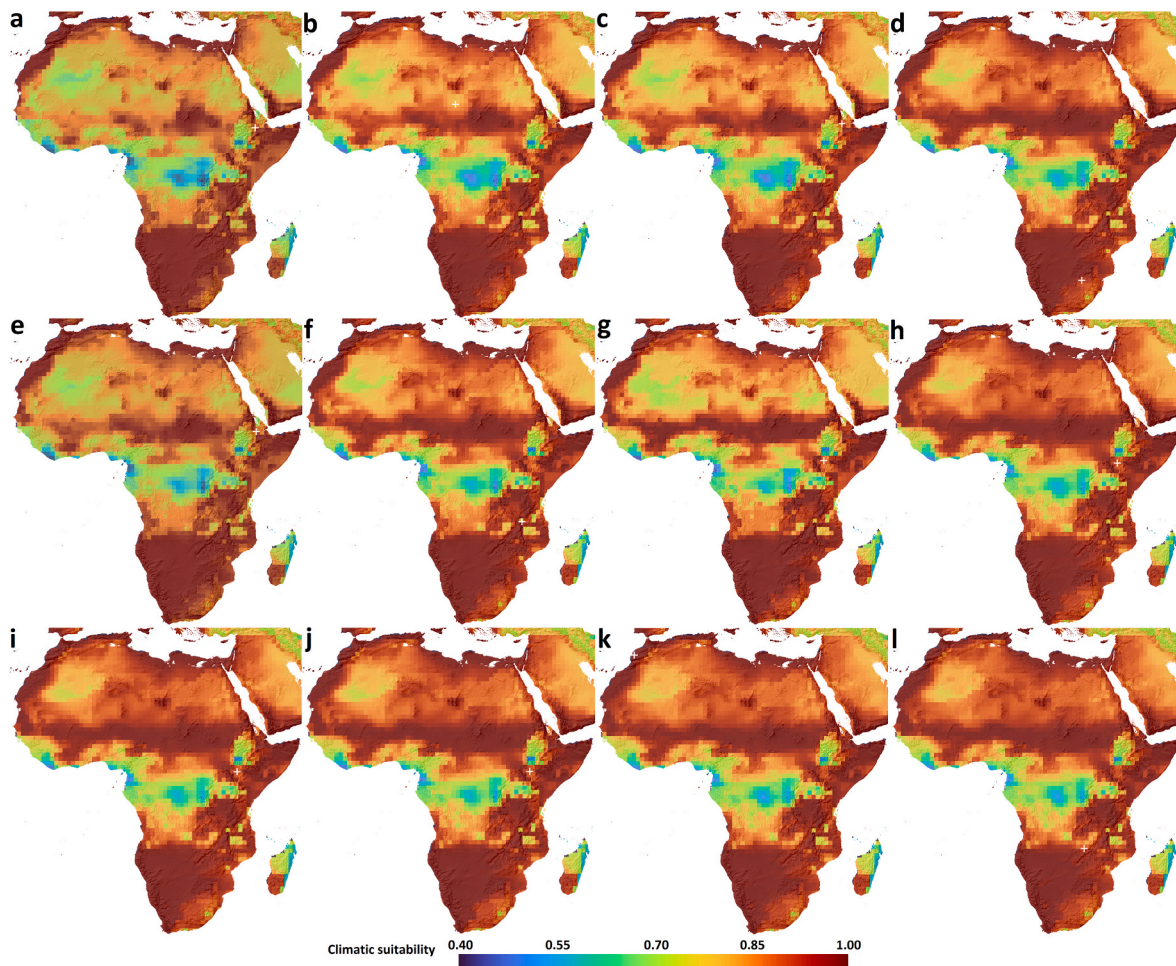


Fig. 9. The modelled climatic suitability values of a *Canis lupaster*-like wild canid host model species in the periods of 4.51–4.32 Ma (a), 3.85–3.31 Ma (b), 3.596–3.330 Ma (c), 2.05–2.58 Ma (d), 2.80–2.75 Ma (e), 2.50–2.30 Ma (f), 2.03–2.02 Ma (g), 1.85–1.60 Ma (h), 1.78–1.48 (i), 1.65–1.49 Ma(j), 0.349–0.281 Ma (k), 0.324–0.274 Ma (l).

hominin fossils: *Sahelanthropus tchadensis* (7.2–6.8 Ma; Lebatard et al., 2008), *Orrorin* (6.0–5.7 Ma; Sawada et al., 2002), and *Ardipithecus kadabba* (5.77–5.54 Ma; WoldeGabriel et al., 2004). Although *S. tchadensis* was discovered in the Sahara, the site was part of a wetter Sahelian/Sudanian ecosystem in the past sustained by palaeo-Lake Mega Chad—an area suitable for both leishmaniasis transmission (Israel et al., 2022) and hominin inhabitation (Trájer 2022b).

Later hominin fossils, such as the 2.80–2.75Ma *Homo* specimen LD 350-1 from Ledi-Geraru, Ethiopia (Villmoare et al., 2015), and archaic *Homo sapiens* from Jebel Irhoud, Morocco (349–281 ka; Richter et al., 2017), further confirm Africa's central role in human evolution. Although gene flow with out-of-Africa populations likely influenced modern human genomes (Stringer, 2016), the long-standing African presence of hominins in leishmaniasis-endemic environments suggests repeated opportunities for host–parasite interaction. The modelled climatic suitability patterns of parasites, vectors, and hosts exhibit several consistent features. The Central Sahara, the wettest parts of Central Africa, and the cold southeastern coasts of South Africa were unsuitable for leishmaniasis throughout the Zanclean to present, while surrounding regions represent potential dispersal corridors. It is expected that the potential host ranges exceed the distribution of the pathogens themselves, as seen when comparing CL climatic suitability (see Fig. 6), the sand fly vectors (Fig. 4), and mammalian reservoir groups (Fig. 8). Similar patterns occur for VL (Fig. 7), its vectors (Fig. 5), and the *Canis lupaster* reservoir model (Fig. 9).

Model results (Figs. 4 and 5) suggest several possible sand fly vector

migration routes: (1) from northwestern Africa along the Western African coasts toward the Gulf of Guinea; (2) along the Red Sea coast. It should be noted that 10–4 Ma, the Red Sea was narrower than today, and the Danakil Land was more uplifted (Boone et al., 2021). The third (3), less probable migration route follows the Nile River. Geological and geophysical arguments support the idea that the drainage system of the Nile has existed for 30 Myr (Faccenna et al., 2019).

The *Paraphlebotomus* subgenus, which includes major vectors such as *Ph. alexandri* and *Ph. sergenti*, likely evolved in the Eastern Mediterranean (Cruaud et al., 2021). Their southward spread into Africa coincided with the Messinian Salinity Crisis, which reshaped regional geography and climate (Trájer et al., 2021). Late Miocene environmental changes thus contributed to the diversification of several Afro-Eurasian sand fly subgenera (Kasap et al., 2015; Trájer et al., 2023). Phylogenetic results indicate ancient *Paraphlebotomus* species dispersed both via the Western Saharan, the Nile, and the trans-Bab-el-Mandeb migration routes (Cruaud et al., 2021).

It is important to note that potential host mammals also migrated in the Pliocene from Eurasia to Africa, including—among others—canids (Morales et al., 2005) and *Hystrix* (van Weers, 1994). Related to this study, it is an important topic to discuss the time and the possible origin of human *Leishmania* pathogens, their vectors, and the hosts. As it was mentioned, the *Paraphlebotomus* subgenus of phlebotomine sand flies, which includes such important vector species as *Phlebotomus alexandri* or *Phlebotomus sergenti*, plausibly evolved in the Eastern Mediterranean region (Cruaud et al., 2021). The ancestors of these species started their

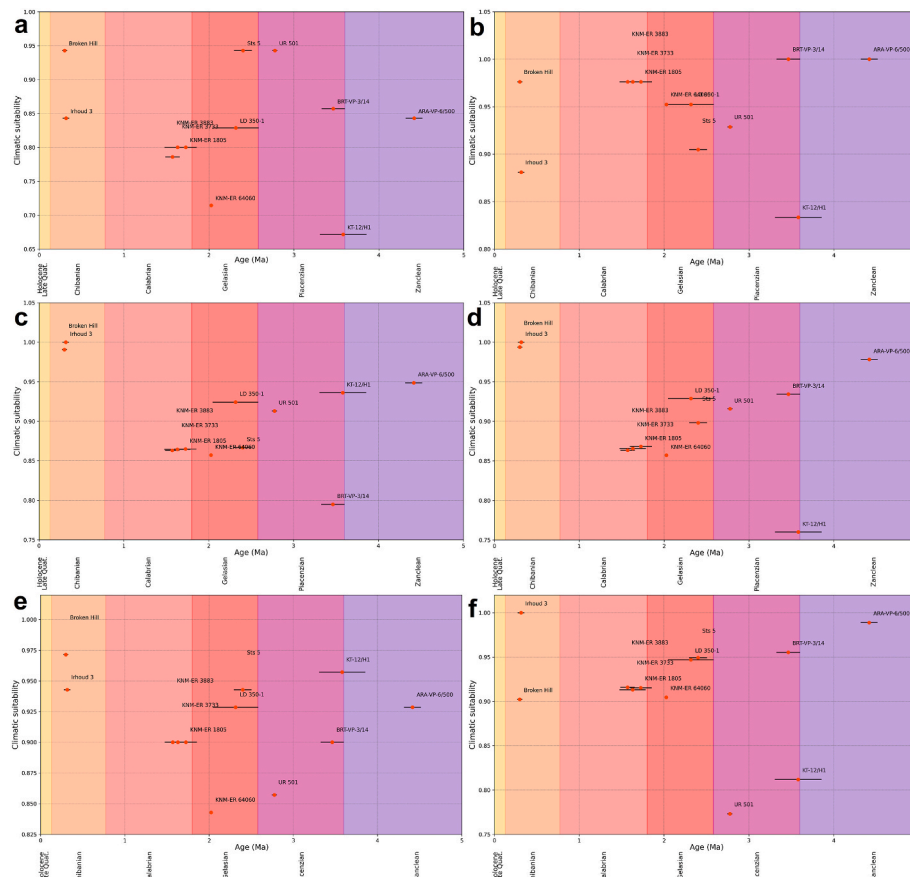


Fig. 10. The modelled average local maximum climatic suitability values of cutaneous leishmaniasis-vector sand fly species (a), visceral leishmaniasis-vector sand fly species related to fossil hominin specimen sites (b); the modelled climatic suitability values of cutaneous leishmaniasis (c), visceral leishmaniasis (d); the local maximum climatic suitability values of *Acomys*, *Gerbillus*, *Heterohyrax*, and *Procavia* and *Tatera* genera (e), and the modelled climatic suitability values of a *Canis lupaster*-like canid host model (f) related to hominins of ARA-VP-6/500 (*Ardipithecus ramidus*; a), KT-12/H1 (*Australopithecus bahrelghazali*; b), BRT-VP-3/14 (*Australopithecus deyremeda*; c), Sts 5 (*Australopithecus africanus*; d), LD 350-1 (*Homo* sp.; e), UR 501 (*Homo rudolfensis*; f), KNM-ER 64060 (*Homo habilis*; g), KNM-ER 1805 (*Homo habilis*; h), KNM-ER 3733 (*Homo ergaster*; i), KNM-ER 3883 (*Homo erectus*; j), Irhoud 3 (*Homo sapiens*; k), Kabwe 1 (*Homo heidelbergensis*; l).

southward expansion to Africa parallel to the shrinking of the Mediterranean Sea in the Messinian Salinity Crisis (Cruaud et al., 2021), which created both the geographic and climatic conditions of this spread (Trájer et al., 2021). It can be summarized that the Late Miocene geographical and climatic changes also acted as the key factors of the diversification of several Afro-Eurasian sand fly subgenera (Kasap et al., 2015; Trájer et al., 2023).

In addition, the African-origin paenungulate order of hyracoids (Benoit et al., 2013), which are reservoirs of *Leishmania* parasites in present-day Africa, appeared in Europe and Asia Minor in the Tortonian and became widespread in the Peri-Tethys region in the Messinian (Pickford, 2009). This coincidence with the emergence of *Paraphlebotomus* taxa roughly in the same Eastern Mediterranean region raises the possibility that several sand fly species adapted to consuming the blood of hyracoids in the Late Miocene, which resulted in the parallel adaptation of *Leishmania* parasites to these hosts. It is important to add that although present-day African apes and the human lineage plausibly are not the direct descendants of the Miocene hominoids of Eurasia, it cannot be ignored that their presence may have resulted in the pre-adaptation of present-day *Leishmania* parasites. For example, in Azmaka, Bulgaria, hyracoids co-persisted with *Graecopithecus* during the Messinian (Spassov et al., 2012).

The long history of human exposure to *Leishmania* is reflected in the complexity of the human immune response. The highest suitability regions for parasites, vectors, and hosts all fall within the tropical forest–savanna–steppe transition zone, adjacent to the highly diverse primate

fauna of Central Africa (Estrada et al., 2017). This region, including the Congo Basin, likely played a major role in the emergence of *Homo* (Trájer 2022b). As it was shown, ancient hominins, archaic *Homo sapiens*, and the present-day foci of ancient Y-haplogroups are centred in regions that are moderately or severely affected by leishmaniasis in present-day Africa, except for present-day South Africa (Pigott et al., 2014) due to an unknown reason, and could have also been influenced by this disease group in the past (see the mapped model results of this study). In other words, areas with enduring populations carrying basal Y-chromosome lineages (A00, A, B) correspond to regions with moderate or high CL/VL suitability during 250–100 ka. While this does not indicate genetic susceptibility, it suggests long-term demographic continuity in disease-endemic environments, supporting a deep coevolutionary relationship between humans and *Leishmania* (Tripathi and Nailwal, 2021).

It can be assumed that many alleles that are currently involved in protection against leishmaniasis may have arisen after human ancestors entered the savannah biotope. Multiple immune-related genes illustrate this long-standing interaction. *Slc11a1* (formerly *Nramp1*, natural resistance-associated macrophage protein 1) restricts iron availability in macrophages and influences resistance to intracellular pathogens, including *Leishmania* (Yasmin et al., 2022). It contributes to host defence against *Leishmania* by limiting iron availability within parasitophorous vacuoles, thereby restricting the parasite's growth. Variations or deficiencies in *Slc11a1* expression can influence susceptibility to these pathogens (Ejghal et al., 2014), and it is also known that *Leishmania* spp.

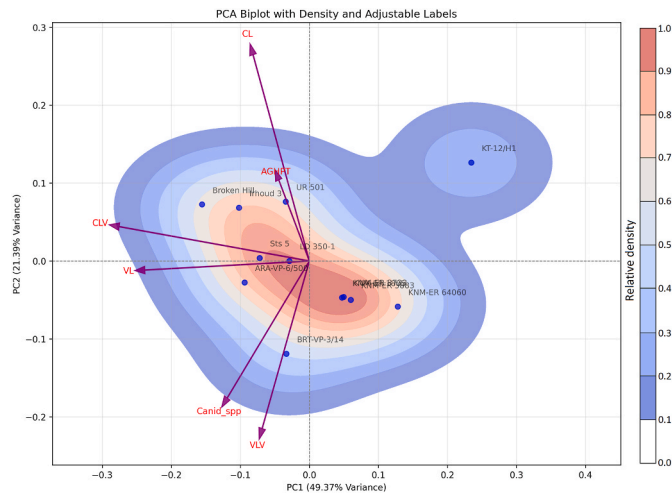


Fig. 11. The result of principal component analysis of the modelled maximum climatic suitability values with kernel density values. Hominin specimens: ARA-VP-6/500 (*Ardipithecus ramidus*; a), KT-12/H1 (*Australopithecus bahrelghazali*; b), BRT-VP-3/14 (*Australopithecus deyiremeda*; c), Sts 5 (*Australopithecus africanus*; d), LD 350-1 (*Homo sp.*; e), UR 501 (*Homo rudolfensis*; f), KNM-ER 64060 (*Homo habilis*; g), KNM-ER 1805 (*Homo habilis*; h), KNM-ER 3733 (*Homo ergaster*; i), KNM-ER 3883 (*Homo erectus*; j), Irhoud 3 (*Homo sapiens*; k), Kabwe 1 (*Homo heidelbergensis*; l). The maximum modelled climatic suitability values of: AGHPT: *Acomys*, *Gerbillus*, *Heterohyrax*, *Procavia*, and *Tatera* genera; Canid_spp.: wild dogs; CL: cutaneous leishmaniasis, CLV: cutaneous leishmaniasis vectors, VL: cutaneous leishmaniasis, VLV: cutaneous leishmaniasis vectors.

have evolved sophisticated mechanisms to bypass this restriction, highlighting the dynamic interplay between host defence and pathogen adaptation (Yasmin et al., 2022).

Immune response varies by *Leishmania* species, reflecting species-specific transcriptional programs (Diotallevi et al., 2024) and SNP (single nucleotide polymorphism) variation (Bharati, 2022). IL-1 β (interleukin-1 beta) polymorphisms affect VL susceptibility; the IL-4 variant rs2243250 contributes to CL self-healing; and IFN- γ + 874 is associated with CL susceptibility (Bharati, 2022). Early macrophage responses involve hundreds of dysregulated genes (Diotallevi et al., 2024), illustrating strong evolutionary selection pressures.

Experimental evidence from non-human primates supports the deep evolutionary roots of primate susceptibility to *Leishmania*. Among Old World monkeys, cercopitheine vervets (*Chlorocebus* spp.) are effective models for *L. major* infection, showing spontaneous lesion healing similar to humans (Olobo et al., 1995). Macaques (*Macaca* spp.) infected with *L. braziliensis* also develop localized skin ulcers that heal spontaneously (Lemos et al., 2008). African cercopitheines—including vervets, Sykes' monkeys (*Cercopithecus mitis*), and baboons (*Papio* spp.)—can be infected experimentally with *L. donovani* or *L. infantum*, producing mild visceral infections lasting 4–8 months before recovery (Githure and Shatry, 1986; Binhazim et al., 1993). Colobines were likewise used as *L. donovani* models.

In contrast, New World monkeys like night monkeys (*Aotus* spp.), squirrel monkeys (*Saimiri* spp.), and marmosets (*Callithrix* spp.) commonly develop severe, rapidly progressing visceral leishmaniasis after intraperitoneal inoculation of amastigotes (Chapman and Hanson, 1981; 1983; Marsden et al., 1981). Rhesus monkeys exhibit systemic VL symptoms, closely resembling human disease (Porrozzi et al., 2006).

The susceptibility of both Old and New World monkeys indicates a broadly conserved primate vulnerability to *Leishmania*, suggesting an ancient host–parasite association predating the ~35 Ma divergence of these lineages (Schrage and Russo, 2003). Old World monkeys typically develop milder, self-limiting infections, possibly reflecting long-term coevolution. This may relate to anti-Gal antibodies in Old World monkeys, apes, and humans, which target the α -gal epitopes

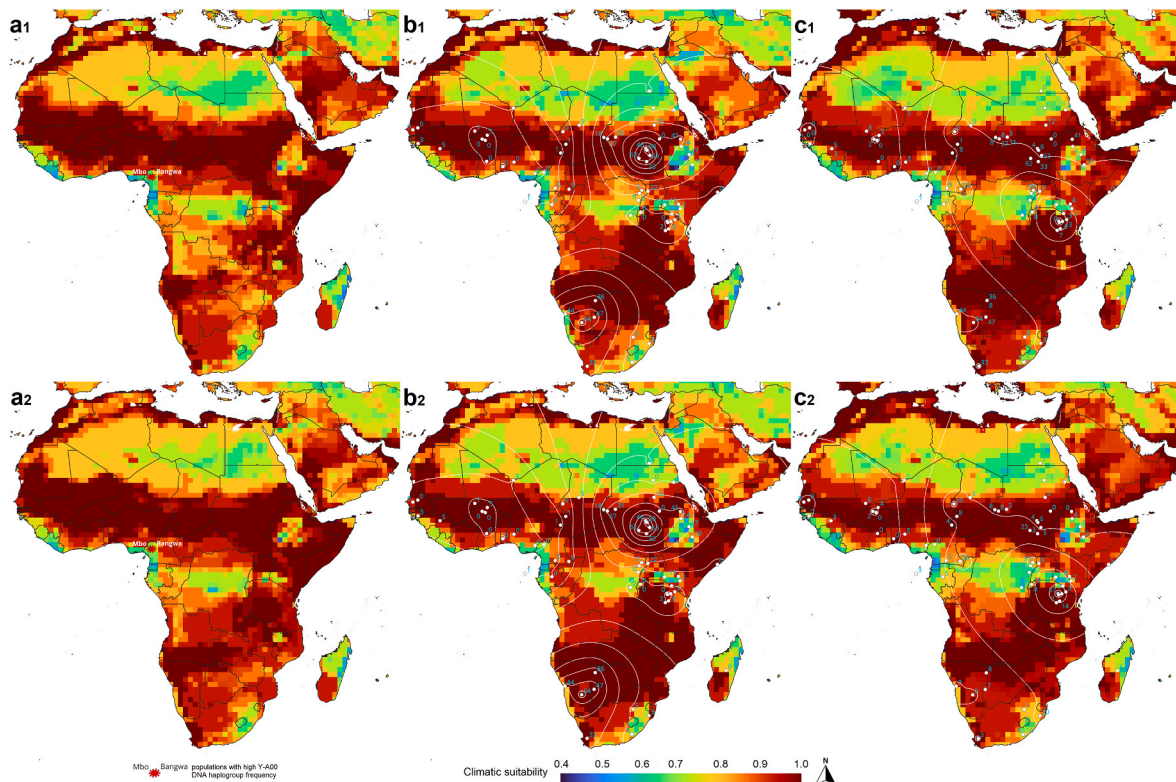


Fig. 12. The geographic position of Bangwa and Mbo people having the highest Y-A00 allelic frequency among modern people (a1-2); the isolines of the IDW-interpolated Y-A (b1-2) and Y-B allele (c1-2) frequencies in Africa projected to the modelled climatic suitability of cutaneous (a,b,c1) and visceral (a2,b2,c2) leishmaniasis forms in 250 kya (a1-2), 150 kya (b1-2), and 100 kya (c1-2).

(Gal α 1-3Gal β 1-4GlcNAc-R). These primates no longer synthesize α -gal due to mutations 20–30 Ma during an extinction event favouring producing anti-Gal antibodies (Galili, 2023). In contrast, New World monkeys and lemurs retain α -gal synthesis and lack anti-Gal antibodies.

This immunological difference likely reflects distinct evolutionary exposures: Old-World primates co-evolved with *Leishmania* in sand fly–endemic regions, developing partial immunity or tolerance. Phlebotomine sand flies evolved in the Nearctic during the Oligocene (34–23 mya; Kerr, 2000), coinciding with primate diversification (Shao et al., 2023). New World primates likely encountered *Leishmania* more recently, after its introduction via infected sigmodontine (New World) rodents and *Lutzomyia* sand flies following the Pliocene formation of the Panama Isthmus (Tuon et al., 2008), which may explain their severe disease responses. The ability of *Leishmania* to infect various primates supports a zoonotic origin for human leishmaniasis, with circulation in non-human hosts preceding human infection. Mild infections in vervets and macaques mirror endemic human disease, suggesting early hominins in *Leishmania*-endemic areas experienced similar selective pressures, potentially shaping immune-related genes such as SLC11A1.

The limitations of this study should be acknowledged. The PALEO-PGEM Series provides high-resolution millennial-scale climatic reconstructions suitable for deep-time analyses, though fine-scale heterogeneity is inevitably smoothed (Holden et al., 2019). As an emulator-based product, it captures large-scale patterns realistically (Barreto et al., 2023), though full climate models offer finer detail (Lord et al., 2017). Nonetheless, PALEO-PGEM remains among the most comprehensive datasets available for continental-scale palaeoclimatic studies.

Suitability thresholds based on modern distributions assume long-term niche conservatism (Wiens and Graham, 2005). While ecological tolerances can shift (Franks et al., 2007), many long-lived taxa—such as African mammals and sand flies—exhibit substantial niche stability (Wiens et al., 2009). Fossil evidence documents both stability and change (Brame and Stigall, 2014). Such assumptions are standard in palaeoecology (Mosbrugger and Utescher, 1997) and remain widely accepted (Blois et al., 2025).

Non-climatic factors such as vegetation, host density, and hydrology may have influenced transmission suitability (Lawing, 2021), but their strong multicollinearity with climate (Campo-Bescós et al., 2013; Arruda et al., 2017; Chen et al., 2020) can increase overfitting risk (Feng et al., 2019). Climate remains the primary predictor of large-scale biotic distributions (Bennett et al., 2020), including zoonotic diseases (Rees et al., 2021). Although the fossil hominin sample is limited, the 12 studied sites span key regions and periods, providing meaningful environmental insights consistent with previous reconstructions (e.g., Bonnefille, 2010; Villaseñor et al., 2023). Together, these considerations outline the scope of inference and highlight opportunities for improved resolution as new palaeoclimate, fossil, and palaeogenomic data emerge.

5. Conclusions

It can be concluded that the regions important for hominin evolution in Africa generally show medium to high climatic suitability for both cutaneous and visceral leishmaniasis. The modelled climatic suitability patterns of mammal reservoirs of *Leishmania* spp. broadly correspond with the fossil record of host hyracoids and rodents. These results suggest that the emerging *Homo* clade could have lived in regions where ecological conditions were favourable for leishmaniasis transmission from the Pliocene onward.

Patterns of present-day human genetic diversity also show that some of the deepest Y-chromosome lineages survive in regions identified as climatically suitable for leishmaniasis in late Pleistocene time-slices, hinting at possible long-term population continuity in disease-endemic settings. While this does not imply genetic susceptibility, it is consistent with the hypothesis that hominin populations repeatedly inhabited

leishmaniasis-endemic habitats.

Homo sapiens evolved in a region where environmental conditions may have been conducive to leishmaniasis. These results highlight the potential value of further research into the phylogenetic patterns of genes involved in leishmaniasis-related immune responses in humans and their closest relatives.

Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2026.110220>.

Data availability

The data that support the findings of this study are openly available in the supplementary materials.

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