Supplementary information

Neogene hyperaridity in Arabia drove the directions of mammalian dispersal between Africa and Eurasia

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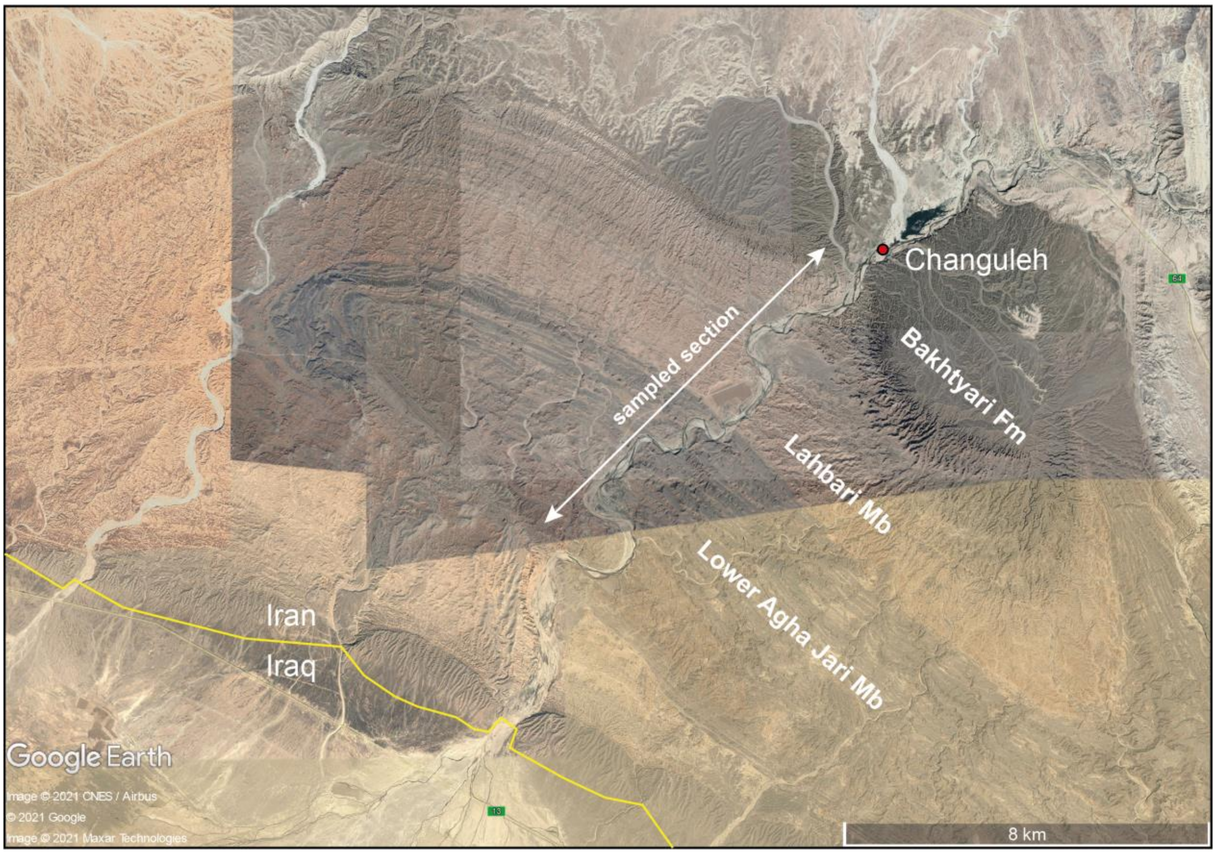
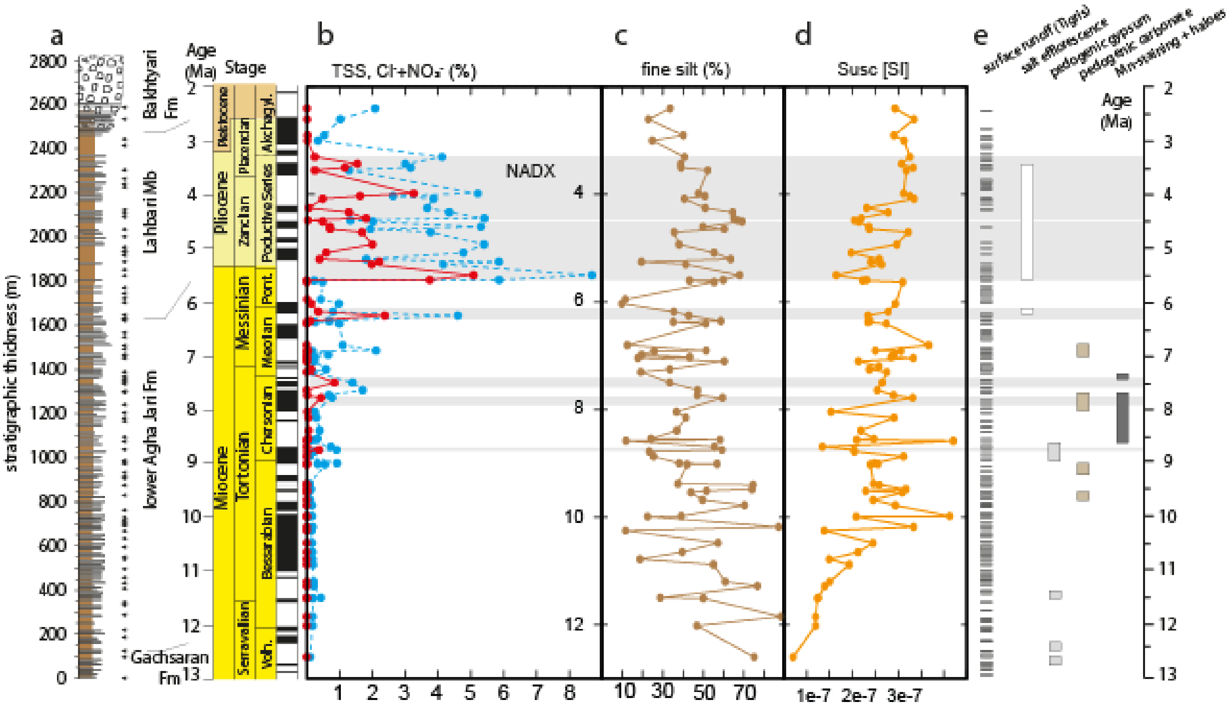
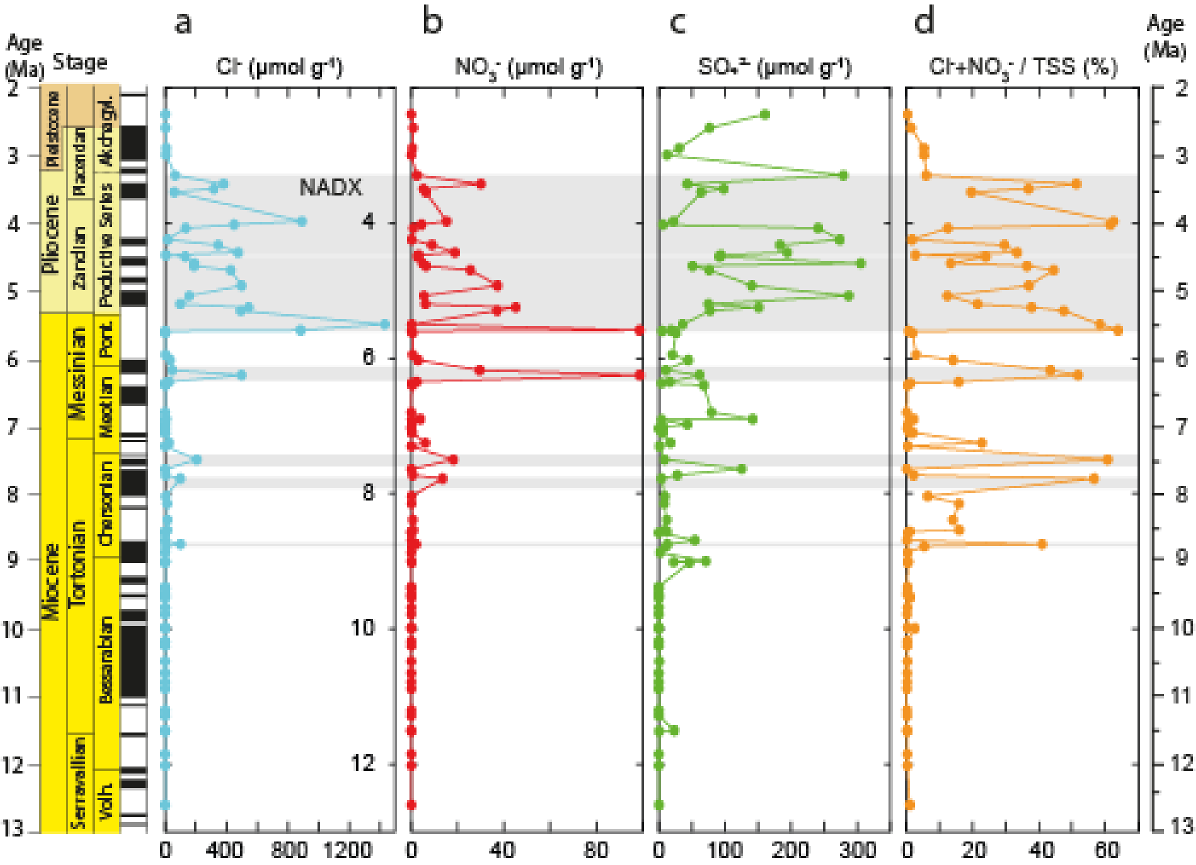
1. Supplementary figures geochemistry



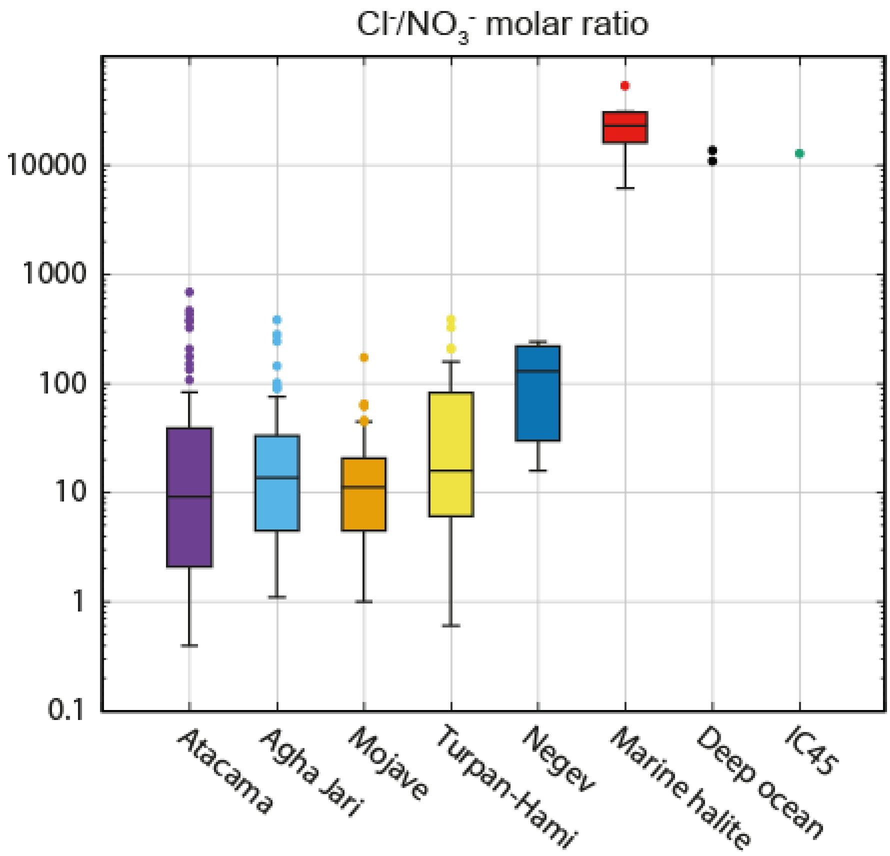
Supplementary Fig. S1. Aerial image of the Changuleh syncline shows the excellent outcrop conditions of the Agha Jari Fm (upper part), Lahbari Mb, and the Bakhtyari Fm, dated magnetostraphically to between 9 and 2 Ma[1]. Note that the darker colours of Agha Jari and Bakhtyari Fms are related to dominance of coarse-grained, fluvial sediments (sandstones and conglomerates).



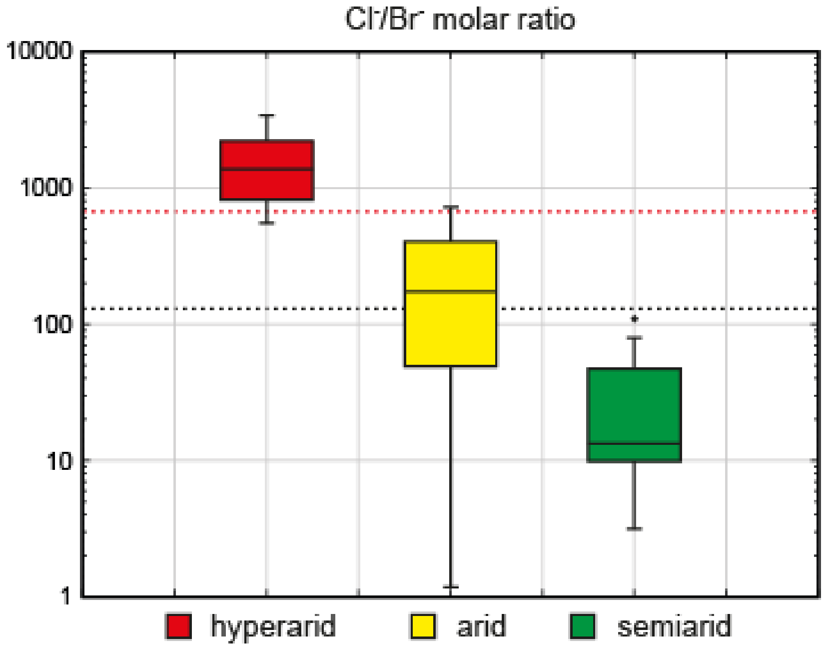
Supplementary Fig. S2. Neogene of the Zarrinabad and Changuleh synclines: chronological, geochemical, sedimentological, geophysical and pedologic data and observations. a – Lithology, stratigraphy (following [1]) and sampling points. b – Ionic composition of palaeosoils (see Supplementary Data 1; TSS – blue broken line, $Cl^{-}+NO_3^{-}$ – red line), c – fine-silt fraction (2-30 μm). d – Magnetic susceptibility. e – ‘Barcoding’ of fluvial run-off (density of palaeo-Tigris channels) and field observations of soil humidity indicators.



Supplementary Fig. S3. Concentration of anions. a – Chloride, b – nitrate, c – sulphate, d – relative contribution of highly soluble chloride and nitrate to total soluble salt (TSS; see Supplementary Data 1).



Supplementary Fig. S4. Chloride and nitrate concentrations from mid-latitudinal arid and hyper-arid desert soils (Atacama, n=76; Mojave, n=66; Turpan Hami, n=41; Negev, n=10). Data are from refs.[2-8]. The chloride/nitrate molar ratios from continental deserts do not exceed 700 (median value 12.3, n=193; see Supplementary Data 2) comparable to our results from the Agha Jari Fm (median value 14.0, n=80; Fig. 5d, Supplementary Data 2), except sample IC45 (5.50 Ma). This ratio is $12.77 \cdot 10^3$ (Fig. 5d), similar reduced in nitrate as oceanic deep water[9] and Phanerozoic marine halite (own data, n=8; Supplementary Data 2). All box plots show the centre line (median), box limits (upper and lower quartiles), whiskers (range) and outliers (circles).

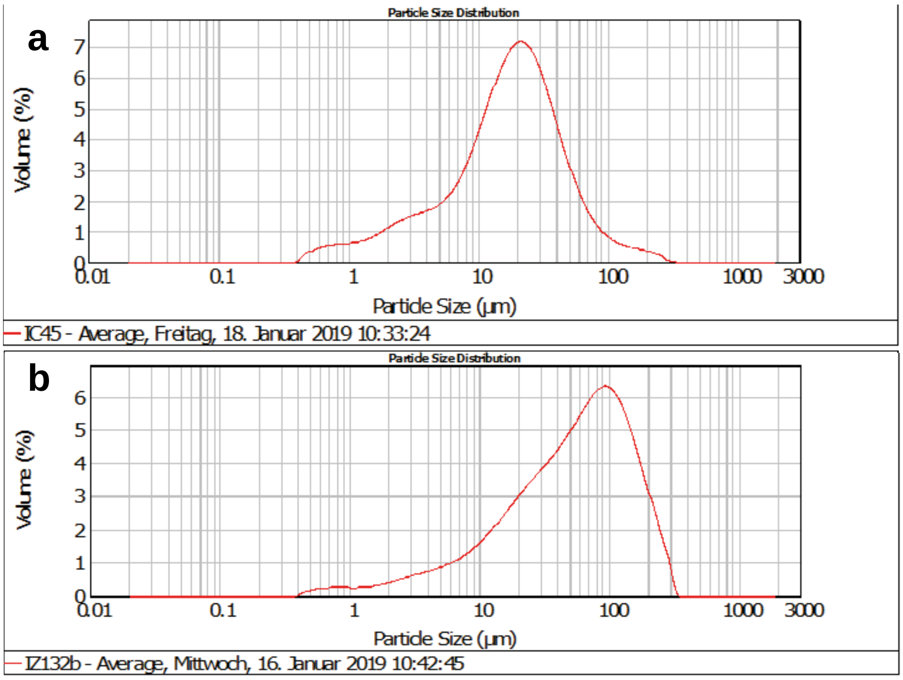


Supplementary Fig. S5. Chloride-bromide molar ratios of 80 Neogene soil samples from Agha Jari Fm grouped according their chloride and nitrate concentrations into hyper-arid, arid, and semi-arid climates (Tab. 1; [2,10]). The Cl^-/Br^- ratios follow theoretical expectations of aerosol contributions (Methods), falling above (below) seawater ratio (650, red dotted line) in hyper-arid (arid) samples and below upper tropospheric ratio (125, black dotted line) in semi-arid-samples. All box plots show the centre line (median), box limits (upper and lower quartiles), whiskers (range) and outliers (circles).

2. Grain-size distribution and end-member analysis

2.1. Grain-size distribution

Grain-size distribution was measured from 84 mudstone samples. Fine- to medium-sized silt content (2-30 µm) ranges between 10-90%, with high amplitude fluctuations in the older (Miocene) part of the profile and low amplitude fluctuations and a decreasing trend in the younger (Pliocene) part (Supplementary Fig. S2c). Grain-size distribution of both silt-rich and silt-poor samples are predominantly unimodal, with peaks between 70-90 µm (silt-poor, Supplementary Fig. S6b) and 10-20 µm (silt-rich, Supplementary Fig. S6a). Weak sub-populations with modal values around 3 µm can be present in silt-rich samples. The unimodal distribution of fine silt (with occasional small sub-population of very fine silt) is found in loess deposited by westerlies (e.g. Tajik loess, Chinese Red Clay) and is usually interpreted as long-distance aeolian transport (‘small dust’; refs.[11,12]).



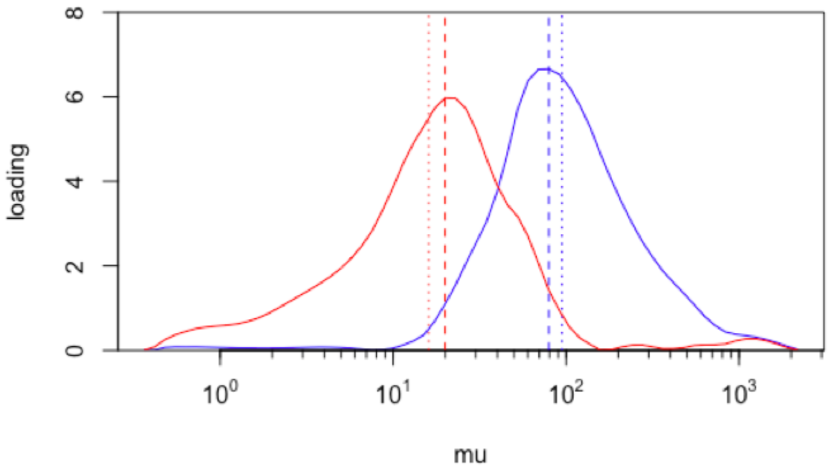
Supplementary Fig. S6. Grain-size distribution of silt-rich (a, sample age 5.50 Ma) and silt-poor (b, sample age 11.85 Ma) sediment samples.

2.2. End-member analysis

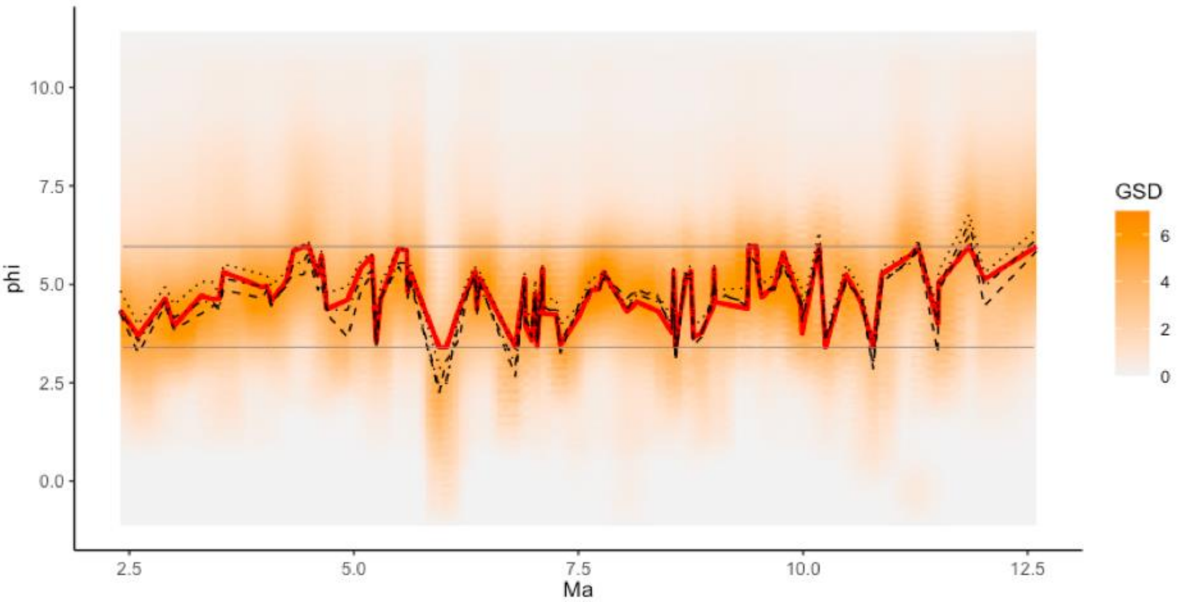
From the grain-size distributions of 84 independent samples of the composite profile, we determined end-member components using the R package EMMAgeo[13]. In brief, the purpose of end-member analysis is to identify a few characteristic spectral components (end members) which can explain most of the variability in the grain-size spectra across all samples of the stratigraphic profile. We found that already two end members (Supplementary Fig. S7, Supplementary Tab. S1) – silt (20 µm) and sand (80 µm) – explain as much as 73% of the total variance, with a sample wise correlation coefficient of 88% (84 samples) and a grain-size class correlation coefficient of 54% (64 bins). Inclusion of a third end member would explain 81% of the total variance, but comes with the cost of higher model complexity, which is why we selected the most parsimonious model with two end members. As can be seen in Supplementary Fig. S8, the variability of the mean grain size curve along the profile is captured by the variability of the silt end member score (i.e., relative contribution to a given sample). The silt end member can be regarded as a proxy for aeolian dust transport.

Endmembers	*Mean grain size*	*Mode position*	*Median grain size*	*Explained variance*
#1 (silt)	*16.0 µm (5.96 phi)*	*20.0 µm (5.64 phi)*	*18.6 µm (5.75 phi)*	*50% (of 73%)*
#2(sand)	*94.6 µm (3.40 phi)*	*79.4 µm (3.65 phi)*	*98.1 µm (3.35 phi)*	*50% (of 73%)*

Supplementary Table S1. Statistical properties of the two identified end member grain-size spectra shown in Fig. S1. The mean and modal grain size refer to the differential grain-size distribution (i.e., grain-size spectrum), the median is defined with respect to cumulative grain size distribution. In case of two end-members, the explained variance is partitioned equally between the two.



Supplementary Fig. S7. The two end-member grain-size spectra (differential grain-size distribution) identified in 84 independent samples of the profile (1 sample per stratum); red: silt EM, blue: sand EM. The dashed and dotted lines indicate the mode positions and mean grain size, respectively, see Tab. S1 for statistical parameters.



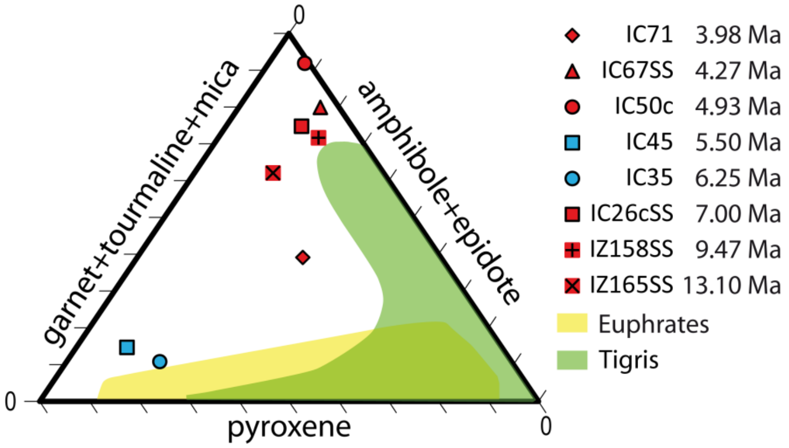
Supplementary Fig. S8. Density-coded grain-size spectrum (phi scale) vs. age. The grey horizontal lines at phi=5.96 and at phi=3.40 indicate the mean grain size of end member 1 and 2, respectively. The variation of the silt end-member score (red solid curve) tracks the variation of the mean grain size (dotted), median grain size (dash-dot), and modal grain size (dashed), and explains 92%, 91%, 85% of the respective variance. Note that the silt end member (eolian dust) is altogether absent at 6 Ma, but exclusively present at 4.4 Ma. Other dust maxima are at 9.5 Ma, 10.2 Ma, 11.2, 11.8 Ma, 12.5).

3. Heavy mineral analysis

A total of 18.124 heavy mineral spectra with grain sizes between 2 to 630 µm were obtained from eight samples (IZ165SS, IZ158SS, IC26cSS, IC35, IC45, IC50c, IC167SS, IC71; see Supplementary Data 3). Statistically sufficient numbers of more than 200 transparent grains (ref.[14]) per grain size fraction were mostly found for the 6.3-20 µm, 20-63 µm, and 63-200 µm fractions (Supplementary Figs. S9 and S10). The sandstone samples contain higher proportions of coarse-grained material than the palaeosol samples.

Comparatively high amounts of celestine (‘others’) in the entire non-opaque heavy mineral spectra were found in samples IC45 (5.57%), IC67SS (6.69%), and IC71 (1.27%). However, this mineral dominantly occurs in the grain-size fractions > 63 µm, where it can account for more than 70% of the entire transparent heavy mineral spectrum.

The heavy mineral compositions of six of the eight samples (IZ165SS, IZ158SS, IC26cSS, IC50c, IC167SS, IC71) appear almost similar in general aspects, but also in all of the studied grain size fractions. These samples contain minor portions of mica, high amounts of garnet, some tourmaline, very little zircon and rutile and varying amounts of ‘other’ minerals (see Materials and Methods). Pyroxene and – usually more abundant – amphibole vary in occurrence, but mostly make-up more than 20% of the transparent heavy minerals (Supplementary Fig. S10). Such spectra are characteristic for the Tigris River system that drains large parts of the Zagros Orogen and therefore has a strong garnet-mica-amphibole signal (ref.[15]), Supplementary Fig. S9). Thus, the (palaeo-)Tigris is interpreted as the main source of the sedimentary rocks IZ165SS, IZ158SS, IC26cSS, IC50c, IC67SS, IC71, implying a NW-SE directed sediment transport, which is in agreement to published channel orientation and palaeoflow directions towards southeast (ref.[1]). This hypothesis is further corroborated by occurrences of less abundant minerals like olivine (‘others’). The latter is absent in samples IC35, IC45 and IC71, except for two olivine grains in IC71. On the other hand, olivine accounts for 1.16 to 7.71% in the remaining samples. The published heavy mineral spectra of the upper reaches of the modern Euphrates and most parts of the Tigris rivers indicate olivine contents between 0.5% and 8.6% (ref.[13-15]). All older terraces of the Euphrates are lacking olivine, whereas this mineral is known from sediments of the palaeo-Tigris (ref.[15]).



Supplementary Fig. S9. Ternary diagram illustrating the heavy mineral composition of the studied samples versus those of the Euphrates and Tigris rivers.[15-18]

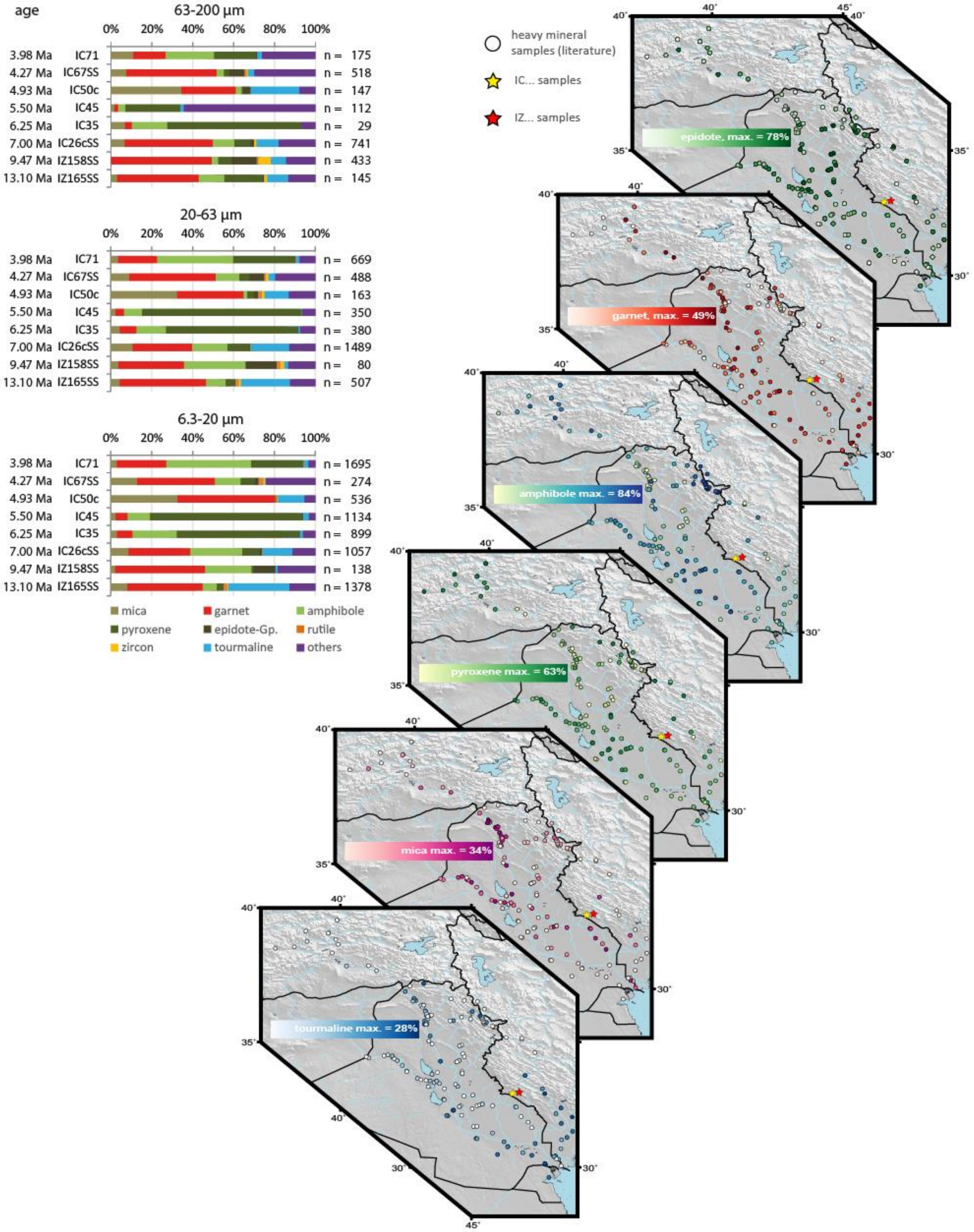
In contrast, hyper-arid silt samples IC35 and IC45 are dominated by pyroxene, while garnet is very rare and tourmaline and zircon are negligible. Comparable spectra are reported from the Euphrates River system, which is known for its increased pyroxene signal, while garnet and tourmaline are very scarce (ref.[15], Supplementary Fig. S3). Samples IC35 and IC45 are dated at 6.25 and 5.50 Ma, respectively, thus deriving from the pre-Messinian Salinity Crisis (MSC) hyper-arid period and the beginning of the NADX period during stage 2 of the MSC. Their pyroxene dominated heavy mineral spectra are suggestive for a massive aeolian sediment input from the west, e.g. the plains of the (palaeo-) Euphrates. Coevally, the heavy mineral spectrum that characterises the (palaeo-) Tigris is not detectable, pointing to very limited runoff and decreased sediment input from this region.

Very arid conditions can additionally be deduced from celestine found in the three NADX samples IC45, IC67SS (a very fine-grained sand- to siltstone), and IC71. The formation of this mineral is restricted to certain processes, which drastically limit its occurrence to few pelagic, hypersaline or carbonate rock settings[19]. Celestine occurrences in palaeosols are often interpreted as secondary formation from hypersaline fluids under arid conditions (refs.[20-22]). This is further corroborated by abundant celestine reported from modern dune sands south of Basra, Iraq (ref.[18]). The assumed arid conditions that triggered celestine formation and its abundance in sediments dated between 5.50 and 3.98 Ma fit quite well to the proposed NADX period.

(next page) **Supplementary Fig. S10. Heavy mineral composition of sand and silt fractions** of four fluvial sandstone samples (numbers ending in SS) and four palaeosoil samples from the Zarrinabad and Changuleh synclines, plotted on published heavy mineral spectra of fine-sand from present-day Mesopotamian rivers and dune fields with subordinate data from up to mid Miocene siliciclastic rocks[15-18]. Topographic map is created using generic mapping tools of [23] and the topographic dataset ETOPO1 of [24].

Transparent heavy minerals of the fine sand and silt fraction, this study

Selected heavy minerals of the fine sand fraction of modern to mid Miocene siliciclastics

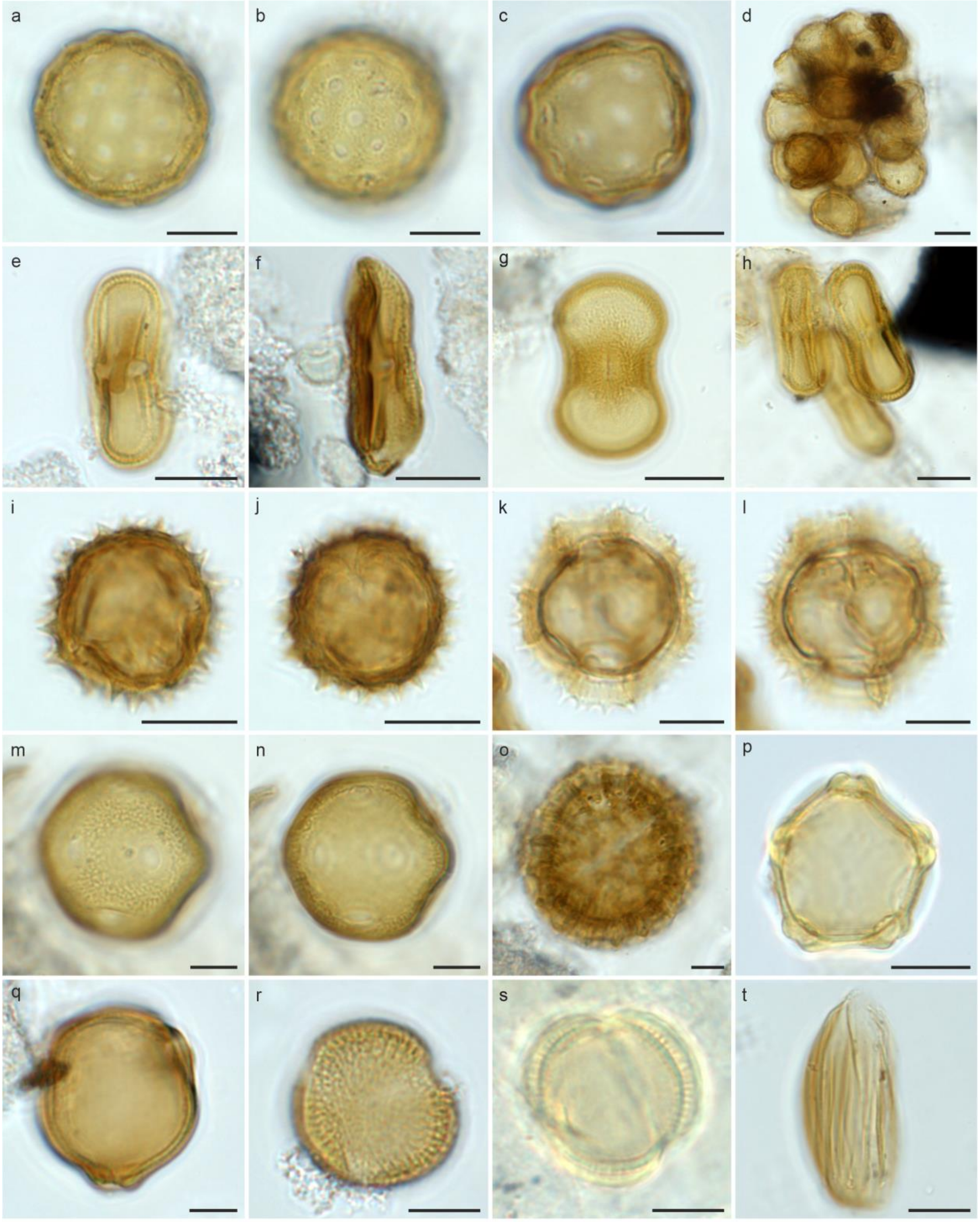


4. Palynology

To determine past vegetation prevailed during the beginning of NADX, sample IC44b, dated to 5.59 Ma, has been selected and studied palynologically. The results reveal common occurrence of pollen grains (mostly angiosperms) and rare spores (Supplementary Fig. S5). The pollen concentration is relatively high and taxonomically moderately diverse. Most of the recorded microfloral elements represent herbs (70%), whereas shrubs and woody angiosperms are rare. Frequent pollen assemblages are preserved as clumps or clusters (e.g. Supplementary Fig. S11 **d**, h) supporting a proximity to vegetation source.

The studied assemblage has been grouped based on their ecological significance as follows: 1. Herbs, which represent the most dominant group, particularly Amaranthaceae–Chenopodiaceae (56.0%), Apiaceae (6.0%), Asteraceae Asteroideae (4.0%), Asteraceae Cichorioideae (1.2%), Caryophyllaceae (2.5%), Polygonaceae (1.2%) with complete absence of Poaceae. 2. Mesothermic (warm-temperate) deciduous elements of *Alnus* (10.0%), *Betula* (2.5%), *Carpinus* (1.9%), *Carya* (2.5%), *Ostrya* (1.2%) and *Salix* (0.6%). 3. Steppe elements comprise only *Artemisia* (2.5%) and *Ephedra* (1.2%). 4. Mediterranean xerophytes which is represented exclusively by *Olea* (2.5%). 5. Mega-mesothermic (subtropical) elements of rare Taxodiaceae-Cupressaceae (0.6%) and 6. Pinaceae (1.2%) with a rare record.

The dominance of herbs in the pollen assemblage points to an open vegetation were halophytic Chenopodiacae prevail. *Artemisia*, like Chenopodiaceae, grows in open, continental sites with a Mediterranean rainfall regime, but requires more moisture. The predominance of Chenopodiaceae at the advent of *Artemisia* implying intense aridity in continental regions in the middle East[25]. In dry climates (<450 mm mean annual precipitation, MAP) where the total sum of *Artemisia* (A) and chenopods (C) is >45-50% the A/C ratio correlates positively with humidity[26]. The A/C ratio is found to be <1 when MAP is <200 mm[26], <0.3 in arid desert sites in the Middle East[25,27] and <0.5 in Chinese deserts[28,29]. The total sum of A+C is 58.5% in sample IC44b and A/C ratio is 0.04, pointing therefore to very dry conditions at the beginning of NADX. This is corroborated by the complete absence of grass pollen, because Poaceae growth where conditions are less arid during summer[25,27]. A low percentage of arboreal pollen has also been found in recent pollen spectra from completely open (desertic) sites in Iran, where they are interpreted as wind transported from Hercynian forest in higher altitudes[27].



Supplementary Fig. S11. Herbaceous and arboreal pollen from sample IC 44b. a-d, Chenopodiaceae; e-h, Apiaceae; i-j, Asteraceae-Asteroideae; k-l, Asteraceae-Cichorioideae; m-n, Caryophyllaceae; o, *Polygonaceae*; p, *Alnus*; q, *Betula*; r, Oleaceae; s, *Artemisia*; t, *Ephedra*. (scale bars equal 10 µm)

5. Mammalian megafaunal exchange between Eurasia and Africa from late Miocene till late Pliocene times

5.1. Ages of Neogene mammalian faunas from Africa and southern Arabia

Early Messinian

Lower Nawata Member (Lothagam, Turkana Basin)

The magnetostratigraphic constraints on the sedimentary succession of Lothagam is only vague and no unambiguous correlation to the GPTS is possible yet (ref.[30]). This has probably also due to comparably low sedimentation rate estimates of about 8 cm/kyr (ref.[30]), suggesting the existence of hiatuses. Geochronologic ages of the lower Nawata Mb are therefore constrained by ^{40}Ar-^{39}Ar dating of volcanic tuffs (ref.[30]). The Lower Marker tuff, 43 m above the base of the member, gives an age of 7.49 Ma (recalibrated according to new ages for GA1550 biotite standard, ref.[31]), indicating a probable age for the base of the lower Nawata Mb of ~8 Ma. The Marker tuff at the top of the member has a recalibrated age of 6.58 Ma. The bulk of the fauna from the lower Nawata Mb derives from its upper part (ref.[32]), which can therefore be constrained to 7.3-6.6 Ma.

Mpesida beds, Kabarnet Trachyte Formation (Tugen Hills, Kenya)

The Mpesida beds represent intercalated sediments within the volcanoclastic Kabarnet Trachyte Fm. Kabarnet trachytes underlying the fossiliferous strata gave radiometric ages of 7.3 Ma (refs.[33,34]; recalibrated ages according to revised ages of FCs standard, ref.[35]), whereas a Kabarnet trachyte immediately below the overlying Lukeino Fm is dated to 6.6 Ma (ref.[34], recalibrated ages according to revised ages of FCs standard, ref.[35]). Consequently, the Mpesida beds are contemporary to the lower Nawata Mb at Lothagam.

Toros Menalla, Anthracothere unit (Chad)

The Anthracothere Unit from site TM 266 has been dated biochronologically to 7-6 Ma by Vignaud, et al. [36] and later, using cosmogenic nuclides (^{10}Be/^{9}Be), to between 7.34 ± 0.12 Ma and 7.10 ± 0.14 Ma (refs.[37,38]). However, caution is advisable concerning the suggested precision, because it could be shown that authigenic ^{10}Be/^{9}Be ratios can be highly variable in fluvial settings (ref.[39]) and because of the "exclusion of the outliers" by Lebatard et al.[38], whereby individual sample ages for TM 266 scattered between 5.92 and 8.24 Ma in two samples separated by 10 cm stratigraphy. We therefore accept here a conservative age of ~7 Ma for the Anthracothere Unit at Toros Menalla, at the lower end of initial biochronologic estimates.

Sahabi Formation (Libya)

The fluvial to littoral/lagoonal Sahabi Fm erosively overly the nearshore (sabkha) Formation P, which itself overlies the shallow marine Formation M (lithostratigraphy according De Heinzelin & El-Arnauti[40]). Most mammalian fossils have been found in Sahabi Fm member U-1 and to a lesser extent in members U-2 and V (ref.[40]). Marine Formation M has been dated by nannoplankton, Sr-Isotopy and K-Ar method to the late Tortonian (refs.[41,42]). Glauconite grains from Formation M give K-Ar ages between 7.7 and 7.5 Ma (ref.[41]). A magnetostratigraphic investigation (ref.[41]) of Formations M, P and the Sahabi Formation revealed seven magnetic chrons correlated from C4n.1r to C3Br.2r., e.g. from 7.7 to 7.2 Ma, thus constraining the age of mammal fossils from members U-1 to V to the Tortonian-Messinian transition between 7.3 and 7.2 Ma.

Chorora Formation, Upper Chorora fauna (Ethiopia)

The Chorora Fm has been dated with ^{40}Ar-^{39}Ar method to between 9 and 7 Ma (ref.[43]). The fauna deriving from the younger stratigraphic levels (above ‘series 2’) is called Upper Chorora fauna[44] and shared many taxa with the lower Nawata Mb. Their age is radiometrically constrained to between 7.5 and 7 Ma (ref.[43]).

Baynunah Formation, Abu Dhabi (United Arabian Emirates)

Biostratigraphic constraints place the Baynunah Fm between 8 and 6 Ma (ref.[45]). A magnetostratigraphic study identified a ~2m long normal polarity chron in between otherwise exclusively reversed polarity (ref.[46]). In their study, the authors point out that a confident correlation with the GPTS cannot be achieved. However, they point out a possible correlation of the normal polarity chron with chrons between ca. 6 and 7.5 Ma. A sedimentological study within the same collection (ref.[45]) points out a likelihood of carbonate formation controlled by orbital precession within the Baynunah Fm. This would imply a sediment accumulation rate of ~14cm/kyr (taking the mean thickness of 35 m), which would indicate a duration of the 2m normal chron of ~14 kyrs. This duration is not in agreement with any of the proposed chrons, which are at least double to ten times the duration. Furthermore, the long reverse polarity intervals above and below do not match the GPTS for the proposed time. The short duration of the observed chron might rather suggest it to be a so far unknown short subchron or even an excursion. These features are also known from this time interval (ref.[47]). Taking the overall duration of the reversed polarity interval would only match the chron C3An.2r between 7.14 and 6.733 Ma within the early Messinian[48], which would also allow a correlation of the normal polarity interval with the excursion identified by Okayama et al.[47].

Late Messinian

Lemudong‘o (Kenya)

The fossil localities of Lemudong‘o are deposited at a lake margin environment. The fossiliferous sediments encase a volcanic ash dated by ^{40}Ar-^{39}Ar method to 6.084 Ma (ref.[49]), leading to a recalibrated age (revised ages of FCs standard, ref.[35]) of 6.12 Ma.

Lukeino Formation, Tugen Hills (Kenya)

The age of the Lukeino Fm is constrained by magnetostratigraphy (C3An.1n – C3r) and radiometric dates to between 6.1 to 5.76 Ma ([34,50,51]; recalibrated ages according to revised ages of FCs standard, ref.[35]).

Kossom Bougoudi (Chad)

The mammal fauna from Kossom Bougoudi (KB 1) was estimated on biochronologic grounds to be of terminal Miocene age ~5.3 Ma (ref.[52]). Lacustrine sediments overly the bone layers have later been dated using authigenic ^{10}Be/^{9}Be method to 5.44 ± 0.62 Ma (ref.[38]). The lacustrine episode of KB 1 has further been correlated to nearby lake sediments dated as old as 5.9 Ma (ref.[38]: fig. 5), suggesting that the age of the KB 1 fossiliferous level fall rather at the older end of the error provided by the ^{10}Be/^{9}Be dating at ~6 Ma.

Asa Koma Member, Middle Awash (Ethiopia)

The up to 40 m thick fluvial Asa Koma Mmr (Adu-Asa Fm) have been radiometrically dated to 5.77 to 5.54 Ma (ref.[53]), recalibrated to 5.81-5.58 Ma according to the revised ages of FCs standard (ref.[35]).

Mid-Piacenzian

Shungura B2/3, Shungura Formation, Member B; Usno 12, Usno Formation; lower Lomekwi, Nachukui Formation; Tulu Bor, Koobi Fora Formation; (Turkana-Omo Basin, Kenya and Ethiopia)

Chronostratigraphy of Pliocene-Pleistocene sediments in the Turkana-Omo Basin are based on a combination of magnetostratigraphy and ^{40}Ar-^{39}Ar dating (refs.[54,55]). Ages of the >340 m thick Shungura Formation have been obtained by magnetostratigraphy (ref.[55]). The <20 m thick sediments of Shungura submembers B2 and B3 show an inverse polarization, correlated to the Mammoth chron (3.330-3.207 Ma). Similarly, Member U12 of the Usno Formation correlates to the same chron, as did the lower Lomekwi Member (ref.[56]). Fossils from all three (sub-) members therefore indicate a mid-Piacenzian age of 3.33-3.2 Ma.

In contrast, the Tulu Bor Member of the Koobi Fora Formation is slightly older. Sediments are normal polarized (correlated to lower Gauss chron, ref.[55]) and bracketed by tuffs dated to 3.44 and 3.31 Ma (α-Tulu Bor and Toroto tuffs, ref.[57]), indicating an age between 3.44-3.33 Ma (ref.[55]).

Denem Dora Member, Hadar Formation (Ethiopia)

According to Campisano & Feibel [58] the ~30 m thick Denem Dora Mb is bracketed by two tuffs dated to ~3.26 Ma (Triple Tuff 4) and ~3.22 (Kada Hadar Tuff; both ages recalibrated according ref.[35]).

Koro Toro 13 (Chad)

This site has been dated by biochronology to 3.5-3.0 Ma (ref.[59]). Rhinos (*Diceros praecox,* ref.[60]) resample the stage of evolution during the Sidi Hakoma Mb of Hadar Fm (3.4-3.26 Ma, ref.[58], recalibrated according ref.[35]) and the co-occurrence of both suids *Notochoerus euilus* and *Kolpochoerus afarensis* is typical in the Hadar Fm from 3.5 to 2.9 Ma (refs.[61,62]).

5.2. Ages of Neogene mammalian faunas from northern Arabia

The only north Arabian (Mesopotamian) fossil mammal locality of Neogene age comes from Injana at Jebel (=Jabal, Djebel) Hamrin (=Hemrin) in Iraq, 120 km northeast of Baghdad and 230 km west-northwest of the Changuleh section investigated here. Fossils derive from 600 m above the base of the ~2.000 m thick Mukdadiya Fm (formerly named Agha Jari Fm in Iraq, refs.[63,64]). In the Mesopotamian basin, the Mukdadiya Fm concordantly overlies the >620 m thick Injana (= Upper Fars) Fm. The Mukdadiya Fm is characterized by first conglomeratic channel-lags, strongly cross-bedded sandstone bodies, some pedogenic carbonates and clay-balls.[65] The lithostratigraphic transition from Injana to Mukdadiya Fms corresponds in our Iranian composite section (Fig. 2) to stratigraphic meter 430 (magnetostratigraphically dated to 10.8 Ma, ref.[1]), the position of the fossiliferous layer (assuming comparable sedimentation rates between Jebel Hamrin and Changuleh) corresponds to an age of 8.4 Ma, which is in agreement to the common occurrences of all typical lithologic features of the Mukdadiya Fm at stratigraphic meter 1.030 in our composite section (Fig. 3).

The Injana fauna at Jebel Hamrin contains the anthracotheriid *Merycopotamus medioximus* (refs.[66,67]), known also from the Chinji Fm (Siwaliks) in sediments dated to between 10.4 and 8.6 Ma (refs.[67,68]). We therefore conclude that the Injana/Jebel Hamrin fossil horizon has an approximate age between 8.6-8.4 Ma, which agrees with previous estimates.[63,66,69] This period characterizes the most humid interval in our studied section (including temporary ponds, see Fig. 3E-H), which fits well with palaeoenvironmental requirements of the recorded mammals (e.g. suids, anthracotheriids, tragulids; ref.[66]).

The biogeographic affinities of this fauna are Eurasiatic (ref.[63]), as evidenced, besides the anthracotheriid[67], by bovids (*Prostrepsiceros zitteli,* ref.[69]), proboscidians and giraffids (*Choerolophodon, Injanatherium*; refs.[63,70]) and the tragulid *Dorcatherium* (ref.[66]).

5.3. Neogene Afro-Eurasian mammal dispersals

5.3.1. Late Tortonian faunal exchange between Eurasia and Africa

Late Tortonian African mammal fauna rather indigenous (e.g. from Chorora Fm, ‘series 2’; ref.[43]). However, our knowledge of potential faunal exchange between Africa and Eurasia during this time is quite scarce. This may have to do that the African mammal record between 9 and 7.3 Ma is limited. However, while the European (early Turolian and Pikermian faunas) and Asian (Dhok Pathan in Siwaliks and several Chinese faunas) records during the late Tortonian are extremely abundant, no mammal taxon with clear African affinities is known during that extended time interval. To our knowledge, there is only one case, the rhino *Brachypotherium,* which may need consideration in this respect.

Brachypotheriun**.** Geraads & Spassov[71] describe a large *Brachypotherium* from Ahmatovo, and a juvenile skull from Kalimantsi (Southern Bulgaria). The deposits of Ahmatovo (Ahmatovo Fm) are slightly younger than the hominid locality of Azmaka, which derive from the base of this formation (ca. 7.2 Ma, ref.[72]). The age of the main Kalimantsi fauna is roughly contemporaneous to Pikermi (ref.[71]) dated to between 7.33 and 7.27 Ma (ref.[72]) and Gorna Sushitsa (ref.[73]) dated to between 7.44 and 7.31 Ma (ref.[74]). Geraads & Spassov[71] suggest that the Bulgarian *Brachypotherium* could be the last survivor of the supposed Vallesian representatives of the genus from Western and Central Europe, or represent African immigrant. We also think that the late occurrence of *Brachypotherium* could potentially be related to a dispersal from Africa, since large *Brachypotherium* existed in Eastern and Northern Africa at that time. It is worth noting, however, that the upper M2 tooth morphology from Ahmatovo differs from that of Sahabi, despite its very similar stratigraphic age (ref.[75]). Nevertheless, at the same time a large *Brachypotherium* (*B. primense*) is known from the late middle Miocene and early late Miocene of the Siwaliks (Chinji and Nagri Fms of the Middle Siwaliks, Pakistan as well as from Perim island, the type locality, India; ref.[76] and references herein). The upper boundary of its chronological distribution in Asia is not very clear, but the Nagri Fm extends until ~9 Ma (ref.[68]). It is therefore also not impossible that the *Brachypotherium* penetration into the Balkans during the final Tortonian (?~7.4 Ma) started from South Asia, together with the documented entry of taxa, which led, shortly after, to a post-Pikermian faunal turnover in the Balkans (ref.[72]). This question needs further research.

5.3.2. Early Messinian faunal exchange between Eurasia and Africa

Stegodontidae and Gomphotheriidae

Stegodon. *Stegodon* remains are fairly abundant in Plio-Pleistocene across Asia (ref.[77]) and the genus must be of Asian origin (ref.[78]). The oldest known *Stegodon* localities in Yunnan, China, are correlated to 9 Ma (ref.[79]). The first occurrence of the genus in Africa is documented from early Messinian Mpesida Beds of Tugen Hills (Kenya, refs.[77,78,80]).

Anancus. The premise by Pickford et al.[81] of a dispersal of *Anancus* from Africa to Eurasia during Messinian is not supported by the paleontological facts. Remains of *Anancus* are known from the Middle Siwalik (Dhok Pathan) Haritalyangar locality (India), where *Anancus* is reported from 8.6–8.1 Ma (ref.[82]). The first occurrence of the genus in Europe, related to an invasion of a number of new mammals from the east, is recorded in the post-Pikermian locality of Azmaka, Bulgaria[83], at the very end of the Tortonian, at 7.26 Ma (ref.[72]). It is recently described also from the slightly younger locality of Chomateri, Greece (ref. [84]**),** with an age of 7.16 Ma (ref.[72]). The oldest records of *Anancus* in Africa are from lower Nawata Mb (7.3-6.6 Ma, Lothagam, Kenya), Toros-Menalla (~7 Ma, Chad) and the Mpesida beds (7.3-6.6 Ma, Tugen Hills, Kenya; ref. [78]). *Anancus* entered Africa at about the same time, or shortly after its entry into Europe. The late Miocene *Anancus* from the Balkans is a more plesiomorphic form than the Late Miocene African species (see ref.[85]). In both Europe and Africa, *Anancus* must be an early Messinian immigrant from Asia (refs.[84,86]).

Hystricidae

Hystrix. The oldest fossil porcupines are documented from the late Middle Miocene of the Indian Subcontinent (ref.[87]). The first representative of *Hystrix* (*H. parvae*) is known from the Vallesian/Turolian transition (~8.7 Ma) of Europe.[87] This small-sized species is replaced by the larger *H. primigenia*, the typical porcupine of the Pikermian biome. Porcupines are also known since 8 Ma from West Asia (*H. aryanensis*, ref.[88]) and the Siwaliks (*H. sivalensis*), where it is only rarely recorded.[88] *Hystrix* first occurs in Africa during the early Messinian in the lower Nawata Mb and in Toros Menalla, and is here considered as a Eurasian immigrant.[89] Because of the poor taxonomic resolution of Miocene African *Hystrix* remains, it is difficult to assess if these porcupines represent immigrants from western or eastern Eurasia. But since *Hystrix* is a common element in the Pikermian biome (including West Asia), we regard this taxon, in accordance to Geraads et al.[90], as a western Eurasian immigrant into Africa.

Leporidae

The family Leporidae is of North American origin.[91] It is first recorded in Eurasia at the Vallesian-Turolian transition (early Khersonian) of Eastern Europe (ref.[92]) with an age of about 8.7 Ma. During the early and middle Turolian (late Tortonian to basal Messinian) leporids (*Alilepus*) are commonly reported from Eastern Europe, north of the Black Sea.[92] The first leporids in Asia (*Alilepus*, ref.[93]) are known at 7.4 Ma from the Siwaliks (ref.[91]). The family penetrates Africa during the early Messinian, where it is first recorded from Toros Menalla (*Serengetilagus*, ref. [94]) and from Gutosadeen, Upper Chorora fauna (*Alilepus*, refs.[43,44]). The Gutosadeen fossiliferous level is inversely magnetized, overlying a normal polarization (ref.[43]:

fig. 3) and below an inversed magnetized ash layer dated to 6.94 ± 0.17 Ma. Fossils should therefore be assigned to magneto-chron C3Ar, constraining the age of the Upper Chorora *Alilepus* to between 7.14 and 6.94 Ma, being therefore roughly contemporaneous with the Toros Menalla *Serengetilagus*. We therefore assume that leporids enter Africa at the base of Messinian from Western Eurasia.

Ursidae

Indarctos**.** In Africa the genus is known only from the late Miocene of Menacer, Algeria.[95,96] Fossils from this locality, where *Dinocrocuta* and cf. *Macaca* have also been found, are most probably heterochronous (D. Geraads, pers. comm.). The genus *Indarctos* from Menacer is referred to as Messinian in age by ref.[96], but given the presence of *Dinocrocuta* this taxon must be older than the remaining fauna. The oldest record of *Indarctos* are known from the early Late Miocene (Vallesian, 11-10 Ma) of Europe and Asia Minor. In the second half of the Late Miocene (Turolian of Europe and Turolian equivalent of Asia) it was widespread in southern, central, and eastern Europe, as well as in Western, Southern and Eastern Asia, reaching North America.[97,98] There is no doubt that *Indarctos* is a Western Eurasian immigrant in North Africa, reaching the continent probably at the end of the Tortonian or at the beginning of Messinian. *Indarctos* from Menacer shows morphological affinities with *I. atticus* (*I. punjabiensis atticus*, ref.[97]), well known from South Europe and the Balkan-Iranian zoogeographic province in the second part of the late Miocene.

Agriotherium. The origin of the genus *Agriotherium* is not well documented in the fossil record. Although badly dated, the oldest species may occur in the Late Miocene of the Siwaliks (*A. palaeindicum*, Hasnot, Dhok Pathan Fm after Matthew 1929 and Colbert 1935; 9.8-3.5 Ma, ref.[99]), China (*A. inexpectans*, Jiegou, upper 4th member of Liushu Fm, Baodean Asian Land Mammal Age, Messinian, 7.2-5.3 Ma, ref.[100]) and in late Miocene-early Pliocene of Myanmar (*A. myanmarensis*, Irrawaddy Fm, ref.[101]). During the latest Miocene, at ~6 Ma, the genus appears in North America (*A. hendeyi*, ref.[102]) and at 6.23 Ma in Europe (*A. roblesi*, ref.[103]). The first African record of *Agriotherium* is known from few fossils coming from the early Messinian (7.3-7.2 Ma) of Sahabi (refs.[96,104]) and the late Messinian of Middle Awash (Kuseralee Mb, 5.8-5.2 Ma; ref.[105]). Better African material is known from the Mio-Pliocene transition or earliest Pliocene of Uganda and Kenya (*A. aecuatorialis*; Nkondo and Magabet Fms; ref.[106]) and South Africa (*A. africanum*, Langebaanweg, ref.[107]). *Agriotherium* probably originates from *Indarctos* (see refs.[95,102]), but it is not very clear, according to existing palaeontological data, whether the earliest *Agriotherium* are Asian or African, although we can suppose an Asian origin for this genus, given the significant number of *Agriotherium* localities in the Late Miocene of Asia. It is clear, however, that in the late Miocene (probably during early Messinian) there was a dispersal of this ursid between Eurasia and Africa.

Canidae

Vulpes**.** The pre-Pleistocene fossil record of *Vulpes* is one of the most fragmentary within the subfamily Caninae. The stratigraphically oldest data are from the Hemphillian (8.2 Ma) of North America where the genus seems to be represented by two species *Vulpes stenognathus* and *V. kernensis* (refs.[108,109]). The oldest remains from Eurasia are from the Early and the Middle Pliocene (ref.[109]). *Vulpes riffautae* is described from early Messinian of Toros Menalla

(Chad, ref.[110]) and if the remains really belong to *Vulpes*, then this species documents the earliest entry of the genus into Africa (refs.[96,110]), probably from Eastern Eurasia.

Mustelidae

***Plesiogulo*.** The genus is wide spread in Eurasia, North America and Africa and includes several species. *Plesiogulo*, which could be of Asian origin (first appearance in middle Miocene of Paşalar, Turkey) migrated to the New World between 7.0 and 6.5 million years ago and is well represented in the late Miocene from the Balkans to Central Asia and Pakistan (refs.[111-113]). Its first appearance in Africa, evidently from Western Eurasia via the Arabian Peninsula, is described as ?*Plesiogulo praecocidens* from the early Messinian Baynunah Formation (UAE, Arabian Peninsula, ref.[114]). The presence of *Plesiogulo* is better documented from the late Messinian of Africa with ?*Plesiogulo praecocidens* from the 6.1–5.8 Ma old site of Lukeino in Kenya (ref.[106]), *P. botori* in Lemudong'o, (Kenya) and Adu Dora Mb (Middle Awash, Ethiopia) dated between ~6 and 5.81 Ma (refs.[115,116], recalibrated according to the revised ages of FCs standard, ref.[35]).

Hyaenidae

"Ictitheres": The large ictithere group was widespread in the late Miocene and includes numerous taxa, known mainly from the Pikermian Hipparion fauna. Paradoxically, although discussed and described in a large number of works, its taxonomy remains strongly controversial (see ref.[117]).

Hyaenotheriini, *cf. Hyaenotherium*. *Ictitherium ebu* from Lower Nawata Mb (ref.[118]) is placed by Semenov[119] in Hyaenotheriini, and could represent a species in the genus *Hyaenotherium.* The African *Hyaenictitherium* from the early Messinian of Toros Menalla and the Pliocene (refs.[96,120]) may represent another taxon (see ref.[119]). In any case, it is clear that the Hyaenotheriini entered in Africa during the early Messinian from Western Eurasia, where this group is widespread in the *Hipparion* fauna of the Late Miocene (from the Vallesian and the Turolian and their Asian analogues) of the Balkan-Iranian zoogeographic province and Central Asia (see ref.[119]).

***Chasmaporthetes*.** The taxon is known from the late Miocene to the Pleistocene and is widespread, especially in the Pliocene of Eurasia, reaching Africa and North America. The time of its appearance is not very clear and its taxonomy possibly needs revision, but it seems that the earliest representative is *C. exitelus* from China (ref.[121]), whose age could correspond to the European Middle Turolian, ~8.0-7.3 Ma (ref.[122]). The first appearance of the genus in Africa is during the early Messinian of Toros Menalla (refs.[96,123]). In Africa *Chasmaporthetes* is an immigrant from Western Eurasia.

***Adcrocuta eximia*.** In Africa the species is known only from the early Messinian of Sahabi, Libya (refs.[96,104]) and demonstrates the features of the evolved late stage of the species (sensu ref.[117]) typical of early Messinian faunas. The species is widespread in the *Hipparion* fauna from South Europe, the Balkan-Iranian zoogeographic province (including the Northern peri-Pontic region) to Central Asia (China) during the Vallesian and the Turolian (refs.[117,122]) and must be a Eurasian immigrant in North Africa at the early Messinian.

Suidae

Suinae. The African FOD of the Suinae is traditional placed in the latest Messinian (6-5.3 Ma), when *Kolpochoerus deheinzelini* is present at Kossom Bougoudi (~6 Ma, Chad) and Middle Awash, Ethiopia (ref.[124]). Suinae is a Eurasian subfamily and Brunet & White[124] suggest affinities with *Propotamochoerus hysudricus* from Siwaliks (Dhok Pathan Fm) and the early Messinian Baynunah Fm of Abu Dhabi, Emirates (ref.[125]). Because Baynunah is in southern Arabia, it belongs to the tropics (today Afrotropics; Fig. 1). Consequently, Suinae have been present in the Afro-Arabian tropics since early Messinian (*Propotamochoerus*), representing eastern Eurasian (Siwaliks) immigrants. The genus *Kolpochoerus* later evolved in Afro-Arabia during the late Messinian.

Giraffidae

The Giraffids of the Pikermian biome and appearance of *Giraffa*. The extant genus *Giraffa* first appears in Africa at the beginning of the Pliocene. It could have been derived from *Bohlinia* or *Palaeotragus rouenii* (ref.[126]) suggesting the probable dispersal of at least one of the mentioned taxa of the Pikermian biome into Africa during the latest Miocene (Messinian). Marra et al (ref.[127]) note the presence of *Bohlinia* cf. *B. attica* at the southernmost Italian locality Cessaniti during latest Tortonian (ref.[128]) and argue for a faunal exchange at this time between southern Europe and northern Africa via Calabria, but a Calabrian-African land connection at this time is so far unsupported by geologic data. A giraffin from the early Messinian of Toros-Menalla (Chad) has been referred to *Bohlinia* (ref.[129]), but the assignment of these remains to *Bohlinia* has been questioned (ref.[126]). Haile-Selassie (refs.[130,131]) referred sparse material from the late Messinian Asa Koma Mb (Middle Awash) to *Palaeotragus* sp. and *Giraffa* sp., but Harris et al.[126] noted that in the absence of an associated set of teeth, they may be better assigned to Giraffidae indet. cf. *Giraffa* sp. In any case, the appearance of a giraffine similar to *Bohlinia* in the early Messinian of Chad point to a dispersal of *Giraffa* ancestors from western Eurasia (refs.[129,132]).

Sivatherium. The genus is the only sivatheriine known from Africa. Until recently *Sivatheriun* was known from three species: one Asiatic form, the type Species *Sivatherium giganteum* from the Plio-Pleistocene of the Upper Siwaliks (Tatrot-Pinjor transitional fauna, Nanda 1994), and two African species, *S. maurusium* (Middle Pliocene to Pleistocene of North and East Africa) and *S. hendeyi* (Early Pliocene of South Africa, refs.[126,133]). A Balkan species *Sivatheriun garevskii* was recently described from the Pliocene (?) of Stamer (Republic of Northern Macedonia, ref.[133]). The other sivatheriinae *Helladotherium* and *Bramatherium* (the former genus a possible synonym of the latter according to some authors) was widespread in the late Miocene from the Balkans to the Siwaliks ([134,135]). Old reports of cf. *Helladotherium duvernoyi* from North Africa (ref.[136]) probably constitute misidentified *Sivatherium* remains (ref.[126]) but it is logical to assume, in these circumstances, that the ancestor of the oldest African *Sivatherium* entered Africa not later than the early Messinian or the Tortonian-Messinian boundary, since the oldest African *Sivatherium* remains, although scant, are known from the early Messinian Lower Navata Fm (ref.[137]) and from Toros Menalla (refs.[138,139]).

S. garevskii is of interest in that regard. It is very probable, according to the other faunal finds, that the Stamer locality is from the final Miocene (ref.[117]). It is interesting to note also the presence of a huge Sivatheriine second phalanx (ref.[140]) in the late Messinian locality of Verduno, N. Italy (5.5-5.33 Ma), which is referred to a large *Helladotherium* sp. because it is believed that *Sivatherium* is not known earlier than the Pliocene. This make it likely to us that *Sivatherium*, or its ancestor, entered Africa from Western Eurasia, since this genus is unknown from southern Asia until the beginning of the Pleistocene.

Bovidae

It seems that during the early Messinian from about 7 Ma the composition of the bovid assemblage on the African continent is already fully African in character (ref.[141]), however, a number of taxa show Eurasian origins (ref.[142]).

***Tragoportax*.** The boselaphin *Tragoportax* is known in Eurasia from the Vallesian/Turolian boundary (~8.7 Ma) to the end of the Turolian (respectively end of Miocene), and represents one of the most widespread Bovids of the so called Hipparion-fauna of the late Miocene, known from the Pikermian biome to the Siwaliks and western China (refs.[73,143]). The genus is known from Messinian African localities. It is represented in the fauna of Sahabi (Libya) by *Tragoportax cyrenaicus* (described as *Miotragocerus cyrenaicus* by Thomas[144], refs.[143,145]), in the fauna of Lothagam (lower Nawata, Kenya) as ?T*ragoportax* sp. (ref.[146]), as well as in the fauna of Middle Awash (Ethiopia), where *T. abyssinicus* is described (refs. [142,147]). Recently the genus is mentioned from the early Messinian Baynunah Formation (UAE, Arabian Peninsula, ref.[45]). All these taxa have been placed in the genus *Miotragocerus* by Gentry[148], but their features correspond to *Tragoportax*, the former likely ancestral to the latter (ref.[73]). *Tragoportax* is apparently an immigrant from western Eurasia, most likely from the beginning of Messinian.

Pachyportax latidens. This large bovid is recorded in the Siwaliks from Dhok Pathan Fm (ref.[149]) at 7.3-7.2 Ma and has also been found in the early Messinian Baynunah Fm (United Arabian Emirates, ref.[150]), but the same species might also be represented in the late Messinian Asa Koma Mb of the Middle Awash (5.81-5.58 Ma), Ethiopia (ref.[45] and references herein). We interpret this species to be an early Messinian immigrant from eastern Eurasia into Africa.

Prostrepsiceros. The antilopin *Prostrepsiceros vinayaki* is recorded in the Siwaliks from the Dhok Pathan Fm (ref.[149]) between 9.3–7.9 Ma and is also known from the Middle Turolian of Molayan (Afghanistan). This form or a direct descent of it (*P. cf. vinayaki*) is found in the early Messinian of the United Arabian Emirates (Baynunah Fm, ref.[45]) and the Middle Awash area (Ethiopia) in levels with an age of 5.7-5.2 Ma, which suggests an early Messinian immigration into Africa, most probably from eastern Eurasia via Arabia (ref.[142] and references therein).

Afrotragus libycus. The antilopin '*Prostrepsiceros' libycus* from Sahabi was referred to the genus *Dytikodorcas* known from the late Turolian of Greece (ref.[151]). Geraads (ref.[146]) suggested that the Sahabi species might belong to the genus *Afrotragus*, erected by him from the early Messinian lower Nawata Formation at Lothagam (*A. premelampus).* Very recently *A. libycus* was recorded in the early Messinian Baynunah Fm (UAE, Arabian Peninsula, ref.[45]). This discovery and generic similarities suggest a probable origin of the species and the genus in Arabia, or possibly in the Middle East/West Asia (ref.[45]).

Dorcadoxa. The reduncin *D. porrecticornis* (='*Kobus' porrecticornis*) was first described by Lydekker from the Dhok Pathan deposits of the Siwaliks (recorded here from 9.3 to 8.0 Ma; refs.[82,142,152]) and was assigned to the genus *Dorcadoxa* by Pilgrim[149]. *D.* cf. *porrecticornis* has been recorded from several Messinian African sites, e.g. from Asa Koma Mb, Middle Awash (ref.[147]), Lukeino Fm (ref.[153]), Manonga (ref.[154]), but its oldest occurrence is from the early Messinian (7.3-6.6 Ma) Mpesida beds (ref.[155]).

Caprini. It is likely that this group first appears in the Miocene of Asia (ref.[142]). Fossil forms that can be unambiguously assigned to this tribe are known in Africa only by the early Messinian at Sahabi in Libya, lower Nawata Fm in Kenya, and Toros Menalla in Chad (refs.[148,156-158]). However, Geraads et al. (ref.[159]) described the new genus *Skouraia* from the late Miocene (Turolian-equivalent) of Morocco, including it in Caprini and hypothesized that the presence of this tribe in Africa is much older, possibly from the Middle/late Miocene boundary.

Bovini. It is assumed that Bovini descended from Boselaphini, but their appearance is rather obscure and it is not impossible that the tribe is polyphyletic (ref.[148]). The oldest remains referred to Bovini on the African continent, are known from the early Messinian at Toros Menalla (refs.[36,160]), Lothagam (Lower Nawata, ref.[157]), and slightly after at Lukeino: *Ugandax* cf. *gautieri* (ref.[161]). Most probably the tribe originate in South Asia and its earliest members are present by at least 8.9 Ma in the Siwaliks (Dhok Pathan Fm., ref.[162]).

5.3.3. Late Messinian faunal exchange between Eurasia and Africa

Canidae

***Eucyon*.** Tedford and Qiu (ref.[163]) erected the genus *Eucyon* for the most of the primitive *Canis*-like forms from the Late Miocene and the Pliocene. The origin of the genus must be North American. Its first clear occurrences in Asia and Europe (if we do not consider the dubious "*E.*" *cipio*) are from Brisigella, Italy and Venta del Moro, Spain (both late Messinian), and apparently also from the probably similar in age levels of the Khirgis-Nur-2 section, Mongolia (ref.[164]). Several remains of primitive *Canis*-like forms are described as representatives of *Eucyon* from the latest Miocene of Africa. They are slightly younger (<6.1 Ma) than the oldest European forms from Venta del Moro (6.23 Ma, ref. [165]). A new species *Eucyon intrepidus* is erected from Lukeino Fm (Tugen Hills, Kenya; ref.[106]). *Eucyon* aff. *intrepidus* were also described from scant remains from the late Messinian of Lemudong'o (Kenya, ref.[166]). Primive *Canis*-like remains from the Latest Miocene of Langebaanweg, probably also represent a primitive *Eucyon* species (see ref.[167]). Latest Miocene *Eucyon* dispersal must be a very rapid event and the entry of the genus from North America to Asia and its dispersal through the continent to Southwest Europe and Africa at the late Messinian was nearly contemporaneous and Old-World-wide (ref.[164]).

Hyaenidae

?*Hyaenictis*. The genus is one of the least known Neogene hyaenids. This genus and its type species, *Hyaenictis graeca* Gaudry, 1861 (ref.[168]), were erected on the basis of scarce dentognathic remains from the well-known middle Turolian locality of Pikermi. Due to the lack of material the taxon has been the subject of debates in relation to its taxonomic status (ref.[122]). Attempts have been made to include in this genus a number of other species, most of which have been rejected in the recent literature (id). *Hyaenictis almerai* Villalta Comella and Crusafont Pairó was erected from the late Vallesian of Spain, but the more specialized, durophagous adaptations in this sample, which is much older than the type species raises some doubts about it belonging to *Hyaenictis* (ref.[169]). *Hyaenictis wehaietu* Haile-Selassie and Howell was erected for the latest Miocene and earliest Pliocene of the Middle Awash, Ethiopia (5.8–5.2 Ma). The inclusion of this species in *Hyaenictis* is questionable (ref.[169]). *Hyaenictis hendeyi* (ref.[170]) was erected based on early Pliocene (ca. 5 Ma) material from Langebaanweg in South Africa, but given the scarity of the material its attribution to *Hyaenictis* is far from certain (ref.[96]). If *Hyaenictis* entered Africa, it must have happened at the end of the Miocene as an immigrant from western Eurasia.

Felidae

Metailurus. Evidence for the presence of the genus and the Eurasian species *M. major* in Africa is weak, especially given new ideas about the taxonomy of the genus (ref.[171]). The attribution of *M. obscurus* from South Africa to *Metailurus* is doubtful and the attribution of a specimen from Olduvai, Bed II to this genus (ref.[172]) is tentative at best (see ref.[96]). The P3 from Tugen Hills (Lukeino Fm) described by Morales et al.[106] is too small for *Metailurus* s. str. and the mandible fragment with p3-p4, referred to *Metailurus major* by Howell and Garcia[166] from Lemudong'o is also insufficient for a definitive determination. The assignment of some fragmental remains to *Metailurus* (*M. major*?) from lower Nawata Mb, Lothagam is also highly tentative (ref.[118]). If this taxon really existed in Africa it must be an immigrant from western Eurasia, where it was a member of the Late Miocene Pikermian biome currently known from Central Asia (China) to southern and central Europe (ref.[173]).

Chalicotheriidae

Ancylotherium. The genus *Ancyloterium* is widespread in the late Miocene from southern Europe to China (ref.[174]) and its origin is most likely Eurasian. The oldest African species of the genus is *A. cheboitense*. Its first appearance is at Cheboit, Tugen Hills (lower Lukeino Fm) at 6.1-5.9 Ma (ref.[175]). This suggests a migration of the genus to Africa, likely during late Messinian times. It is not entirely impossible, however, that the genus dispersed to Africa earlier: Geraads et al. (ref.[176]) identified remains of the genus from the Awash Basin, Chorora Fm. (8.7-7.7 Ma) as *A.* cf. *tugenensis*. Coombs & Cote (ref.[175]) conclude that the material is insufficient for a reliable taxonomic determination at the genus level and further suggest that the trivial nomen "*tugenense"* should refer to another African genus *Chemositia*, although the status of the latter remains unclear.

Rhinocerotidae

***Ceratotherium*.** The statements on the evolution of the genus *Ceratotherium* as well as of African Dicerotini are controversial. According to Giaourtsakis (ref.[177]) *Ceratotherium neumayeri* could be an African immigrant in Southeastern Europe and the Middle East, but this statement contradicts the biochronological data. It is a common species of the Turolian Balkan-Iranian zoogeographic province (ref.[71]) with a probable first appearance at the end of Vallesian (ref.[178]). Despite several disagreements (see ref.[179]) it seems that this taxon (C. *neumayeri* or "C." *neumayeri*, regardless of its taxonomic status) was the likely ancestor of both living African forms (ref.[60]). The oldest African species of the genus is the Pliocene and Pleistocene *C. mauritanicus* and the genus *Ceratotherium* appears on the African continent most probably in the latest Miocene (refs.[60,180]) as an immigrant from the Pikermian biome. Despite the often opposing hypotheses about the origin of *Ceratotherium* and *Diceros* (ref.[181] and references herein) it could be supposed, based on Geraads (ref.[180]), that "*Diceros*" *douariensis* from the ?Late Messinian of Douaria, Tunisia could represent the first appearance of *C. neumayri* in Africa.

Camelidae

Paracamelus**.** The genus *Paracamelus* enters Eastern Europe during the Messinian from Central Asia. Its oldest Eurasian occurrence, from Kazakhstan locality of Pavlodar 1A (=Gusiniy Perelet; ref.[182]), is dated to ca. 7.2 Ma (ref.[183]). It is known in the northern peri-Pontic region from lower Pontian (Novorossian) deposits in the Ukraine (ref.[184]), which is dated to ~6.1-5.8 Ma (ref.[185]). The same wave of dispersal probably led to the penetration of this taxon into southwestern Europe. Finds are known in the late Messinian from Spain (ref.[81]), where it is recorded at Venta del Moro (6.23 Ma) and Librilla (6.19 Ma; ref.[165]). Pickford et al.[81] suggest that camelids penetrate Spain via North Africa, but the discovery of camelids at Verduno, Italy, at ca. 5.4 Ma (ref.[140]) and the aforementioned record from the lower Pontian points to another possibility, a dispersal from Central Asia/Eastern Europe through southern Europe. In any case, it is clear that *Paracamelus* entered Africa from Central Asia during the late Messinian. The oldest African camelid record (*Paracamelus* sp) is from Kossom Bougoudi (Chad) with an age of ~6 Ma (refs.[186,187]). In summary, the first occurrence of camelids (*Paracamelus*) in western Eurasia and Africa seems to have occurred just after 6.25 Ma.

Bovidae

Cf. Caprini. The cf. Caprini (sensu ref.[142]) from the Kuseralee Member of the Sagantole Formation (≥5.2 Ma) resembles according to ref.[142] *Skoufotragus laticeps* (a member of the *Pachytragus/Protoryx* group according ref.[73,188]) from Samos and West Asia (dominant mammal assemblage of Samos, ?early Messinian, ref.[189]). This taxon is also known from the latest Tortonian of Gorna Sushitsa in Bulgaria (7.44 Ma, refs[73,74]) and may indicate another (see Caprini in the previous chapter), second dispersal of this group from Western Eurasia during the late Messinian to Miocene/Pliocene boundary (ref.[142]).

5.3.4. Late early Pliocene faunal exchange between Eurasia and Africa

Felidae

Dinofelis**.** The palaeontological data show an African origin of the genus during the late Miocene. The oldest *Dinofelis* remains are from Lothagam, where the genus is found in all members (refs.[118,190,191]). It is not impossible that it occurred in the Messinian of Venta Del Moro, Spain, but the preserved material is not reliable (ref.[190]). The first reliable occurrences outside Africa are from the early Pliocene (late Ruscinian, MN15, 4.2-3.6 Ma) of Perpignan, France (*D. diastemata*) and represent therefore a probable African immigrant into Europe during the late early Pliocene. A potentially different species of *Dinofelis* is present in the early Villafranchian (MN16) of France (Belaruc II: ref.[190]) and the middle Villafranchian (MN17) of Moldova (Novaya Etulia 2) more similar according ref.[192] to the African species *D. barlowi* and *D. piveteaui*, which may indicate subsequent dispersal(s) from Africa during the mid-Piacenzian and/or late Piacenzian.

Homotherium. The earliest fossils attributed to *Homotherium* are close to 4 Ma and have an African origin in the Lonyumun member (4.3-4.1 Ma), Koobi Fora Formation of Kenya

(Werdelin and Sardella, 2006) and at Kanapoi (the early Pliocene levels, ref.[191]). The earliest appearance of the genus in Eurasia is in Odessa Catacombs (Ukraine) ([193-195]). The magneto-biochronologic age of the Odessa Catacombs is referred to the end of Ruscinian or Ruscinian-Villafranchian transition (latest MN15 or MN15/MN16, refs.[196-198]) at ~3.6 Ma (ref.[199]). On the basis of previous notions for a slightly older Pliocene age of Odessa Catacombs, Antón et al. (ref.[195]) believe that it is not currently possible to determine if the geographical origin of the genus is African or Asian. Given that the Ukrainian locality may be ~0.5 Ma younger than the oldest African occurrences, we regard *Homotherium* as the second possible late early Pliocene African immigrant into Eurasia.

5.3.5. Mid-Piacenzian faunal exchange between Eurasia and Africa

Canidae

Canis. The genus *Canis* is a North American immigrant in the Old World and the *Canis* event in Asia (China) is dated to ca 3.4 Ma (ref.[164]). Following Lacombat et al. (ref.[200]) it was accepted that the first *Canis* entered in Europe is at ca 3 Ma (Vialette, France), but the *Canis* from Vialette is actually an *Eucyon* (N. Spassov, pers. opinion, this paper). The first *Canis* record from Europe could be represented by a mandible labelled as C. *neschersensis* from Perrier (Les Etouaires), stored in the MNHN (Paris) (2.78 Ma, ref.[201]; N. Spassov, pers. opinion, this paper). The first occurrence of the genus in Africa seems to be older than in Europe. *Canis* nov. sp. is mentioned from South Turkwel, Kenya (ref.[202]). The chronology of the fossiliferous level of the South Turkwel fauna is neither constrained by datable tuffs nor magnetostratigraphy and Ward et al. (ref.[203]) estimate an age between 3.6 and 3.2 Ma based on regional correlation and sedimentation rates. These data suggest perhaps a very fast dispersal event of the genus after its entering from North America through Asia into Africa at the beginning, or just before the mid-Piacenzian.

Nyctereutes**.** The origin of the genus is uncertain. In the Plio-Pleistocene *Nyctereutes* is widespread in Eurasia and Africa. Morales and Aguirre (ref.[204]) described remains of *Nyctereutes* as *N.* cf. *donnezani* from the Messinian of Venta del Moro. After several revisions, these remains were identified as a new species of *Eucyon* (ref.[205] and references herein). The earliest secure occurrence of the genus is *N. tingi* from the Pliocene localities of the Yushe Basin, China (approximately at ca. 4.4 Ma; refs.[206,207]). *Nyctereutes* appears in both Asia Minor and in Europe during the Pliocene (first occurrence in Europe probably at La Gloria 4, at 4.19 Ma; ref.[208]). Its first occurrence in Africa is obscure. A mandible from Lissasfa, Morocco, with a probable age of 6.0 – 5.5 Ma. was referred by Geraads (ref.[209]) to *Nyctereutes,* albeit tentatively. Given the data on the time and place of origin of the genus, this determination seems unreliable. The species ?*N. barryi* from Laetoli (Upper Laetolil beds), Tanzania, (3.60–3.85 Ma) (refs.[96,210]) is only tentatively referred to that genus. In contrast, *Nyctereutes lockwoodi* from Dikika (Lower Awash, Ethiopia, ~3.35 Ma; ref.[211]) is more closely related to the Chinese species *N. tingi* and Geraads et al. (ref.[211]) suggest an immigration of that species into Africa over South Asia.

Hyaenidae

Pachycrocuta (*P. brevirostris*). The timing of the appearance of this, the largest hyaenid in Africa, is not entirely clear. In South Africa the oldest records are from the M3 deposits of Makapansgat with an age of ca. 3 Ma (refs.[212,213]). Werdelin (1999) identifies a relatively small *P. brevirostris* from Turkana Basin, Kenya with an age in the time span of 3.44-3.2 Ma (Tulu Bor and lower Lomekwi Mbs). *Pachycrocuta* sp. (also smaller in size) is known from South

Turkwel Kenya (3.6-3.2 Ma; ref.[202]), but most probably this is a different species. Werdelin and Dehghani (ref.[210]) ascribe a tooth fragment from the upper unit of Laetolil Beds tentatively to ?*Pachycrocuta* sp. In the Siwalik the first occurrence of the species is probably at ca 2.6 Ma (Pinjor Fm, Patnaik & Nanda 2010) and in China, Nihevan, at ca 3 Ma (ref.[213]). In Europe it is known from the late Villafranchian to the Middle Pleistocene (ref.[214]) and its first occurrence is in Gerakarou (MNQ18-a2/MNQ l8-b boundary, at ca. 1.9-1.8 Ma; ref.[215]). Werdelin (ref.[216]) hypothesized that *P. brevirostris* originates in Asia and migrated from there to Africa ca. 3.4 Ma and later to Europe during the late Villafranchian. The palaeoecological arguments of this hypothesis seem logical, suggesting a possible dispersion from there to Asia in mid-Piacenzian.

Suidae

Metridiochoerus. The African FOD of *Metridiochoerus* (*M*. sp. and *M*. cf. *shawi*) is during mid-Piacenzian (3.33-3.20 Ma Usno 12; ~3.0 Ma Shungura B11, ref.[217]). The genus *Metridiochoerus* may derive from south Asian ancestors (refs.[217,218]), probably related to the hypsodont suid *Hippohyus* from the Pliocene Siwaliks (ref. [219]).

Giraffidae

Giraffa. Hooijer (ref.[220]) originally described *Giraffa* cf. *G. camelopardalis* from the Bethlehem conglomerate (early Villafranchian, 3.5-3.0 Ma after ref.[221]). The scarce and fragmented materials were later be assigned to *Giraffa* sp. (ref.[222]). Nevertheless, because the genus *Giraffa* is known since the early Pliocene of Africa (ref.[126], see above), the Bethlehem record has been discussed as African immigrant in the Levant in several publications (e.g. [222,223]). This seems plausible since this site also yields the first record of *Mammuthus* outside Africa (see below, ref.[221]). In contrast to Belmaker (ref.[224]), who discuss “several Pliocene *Giraffa* ssp. dated back to 4.0 Ma” in Eurasia, we are not aware of any pre-mid-Piazenzian *Giraffa sensu strictu* fossils there.

Bovidae

Hippotragus. Hippotragini is a tribe of African bovids known since the Late Miocene (ref.[148]). The antelope *Hippotragus brevicornis* was described from Pilgrim (ref.[149]) from the Tatrot Fm of the Siwaliks (3.5-3.3 Ma, ref.[68]). This species is viewed as an African immigrant in South Asia during the mid-Piacenzian (refs.[225,226]).

Budorcas. The African ovibovine species *Budorcas churcheri* was described by Gentry (ref.[227]) from the mid-Piacenzian Denem Dora Mb (Hadar Fm, 3.26-3.22 Ma). This fossil takin is regarded as an Eurasian immigrant into Africa (ref.[228]).

Elephantini

Elephas. The elephant subfamily originated in Africa during the latest Miocene. The first *Elephas* species are known in Africa. Their oldest remains are from Kenya, Ethiopia and South Africa and have an early Pliocene age (ca. 5-4.2 Ma, ref.[78]). The first Asian elephantine, *Elephas planifrons,* is recorded from the Upper Siwaliks (refs.[221,229-231]) and characterize the Tatrot fauna (*E. planifrons* interval-zone of Barry et al., ref.[232]). Magnetostratigraphy places its FO in the lower half of the lower Gauss chron (C2An.3n, 3.569-3.330 Ma, ref.[229]), indicating an age of 3.5 Ma (ref.[233]). Possibly, an early *Elephas* is also recorded, besides *Mammuthus* (see below), in the elephantine remains from Bethlehem (refs.[221,234]).

Mammuthus. The origins of the genus are known to be African.The first known member of the genus *Mammuthus, M. subplanifrons* (which likely is a wastebasket taxon), appears in Eastern and Southern Africa at the very end of the Miocene and the beginning of the Pliocene (ref.[78]). The oldest *Mammuthus* remains in Eurasia are known from Tuluceşti and Cernãteşti (Romania, ref.[235]) and the Skortselkian fauna (Moldova, ref.[236]) and represent the first *Mammuthus* species from Eurasia: *M. rumanus* (refs.[234,237-239]). This oldest Eurasian *Mammuthus* is early Villafranchian. The localities have been palaeomagnetically correlated to the mid-Gauss subchron (C2An2n, 3.207-3.116 Ma) in Ripa Skortsel'skaya (Tulucesti Fm, Skortselslian horizon, ref.[240]) and Podari (nearby and in the same stratigraphic position as Cernatesti, refs.[235,241]). Tuluceşti, the type-locality of *M. rumanus,* is lithostratigraphically (by the Tuluceşti Fm) correlated to Ripa Skortsel'skaya (refs.[235,241]). Thus, the FO of *M. rumanus* in Eastern Europe is confined to 3.2 Ma (ref.[235]) correlating to the Plescoi flooding event (3.20 to ~2.95 Ma, middle-upper Romanian boundary), a transgression of the Black Sea (see Fig. 5F in the main text) into the Dacian Basin during the mid-Piacenzian (ref.[242]). Probably close in age are the remains from Bethlehem (Israel-Palestine), representing perhaps an early stage of *M. rumanus* (ref.[221]). It seems plausible that *M. rumanus* originated in Africa around 3.5 Ma and migrated to Eurasia via the Levant (ref.[234]). Undoubtedly, in Eurasia *Mammuthus* was a newcomer from Africa during the mid-Piacenzian, which had its European FO at 3.2 Ma.

5.3.6. Ibero-Maghrebian and Afro-Calabrian exchanges

Faunal interchange between North Africa and southern Europe during the latest Miocene has been documented for several decades (refs.[243-245]). It comprises mainly small mammals like rodents (gerbils, hamsters, murids) and lagomorphs (pikas) and is restricted both temporary and spatially. Jaeger & Hartenberger (ref.[246]) state that „some limited terrestrial faunal exchanges … occur during the Messinian between southwestern Europe and northwestern Africa [that] do not deeply affect the general faunal dynamics. Both allochthonous cohorts of immigrants become rapidly extinct". Based on significant improvements of chronologies and larger data-sets since then several biogeographic scenarios have been proposed (refs.[165,247,248]), all invoking narrowing or closing of Mediterranean gateways toward the Atlantic during the Messinian Salinity Crisis. Gibert et al. (ref.[165]) conclude that three dispersal events occurred: the 1st Africa-Iberian Mammal Dispersal (AFID) at 6.3 Ma with the emigration of the African hippopotamid *Hexaprotodon,* without landbridge involvement because of the swimming capabilities of hippos; the 2nd AFID at 6.24 Ma with a bi-directional dispersal (Eurasian pika *Prolagus* and murid *Apodemus*; African murid *Paraethomys*) and the 3rd AFID between 5.5 and 5.3 Ma with bi-directional exchange Eurasian murids and African gerbils and hamsters. Except for the African murid *Paraethomys*, no other migrant reaches significant distribution in the regions into which it dispersed (ref.[248]).

However, it has to be stressed that latest research has shown that Mediterranean-Atlantic gateway closure in the Rifian and Betic regions significantly precede these dispersal events and was finished already during late Tortonian-early Messinian (refs.[249,250]). An exception is the (hypothetical for the Miocene, ref.[250]) Gibraltar Straight, which had to remain open at least until Messinian stage 2 (5.6 Ma) to deliver the Messinian salts. So, it is highly questionable if gateway closure is involved in any of the observed dispersals or if instead climatic events should account for these restricted phenomena.

Very few non-swimming large mammals have been observed to be involved in these Messinian faunal exchanges in the western Mediterranean. As we have argued above, the occurrence of the camel *Paracamelus* in eastern Spain at 6.23 Ma could be better explained by a dispersal from Central Asia, via Eastern and Southern Europe, instead via Africa. Two other cases, the African elephantid *Stegotetrabelodon* in Calabria (Italy) and the African monkey *Macaca* in southern Europe will be briefly discussed here.

Stegotetrabelodon. The genus could be of African origin and is not known before the Messinian (ref.[78]). *S. syrticus*, described from the early Messinian Sahabi Fm (Libya, ref.[78] and references herein) is reported also for southernmost Italy, from Cessaniti (terminal Tortonian or the Tortonian/Messinian boundary, ref.[127]). Marra et al. (ref.[127]) hypothesize a possible land connection of the Calabrian Arch to North Africa at this time, but there is no geological evidence for such connection at the end of the Tortonian. Cessaniti is the only record of this elephantid in Europe.

Macaca. The first appearance of this monkey in Europe, the first sure occurrence in Eurasia, is based on two southern European Messinian localities, Almenara-Casablanca M (Spain) , with an age of less than 5.9 Ma and Moncucco, Italy, with an age of 5.40-5.33 Ma (ref.[251] and references herein). These records represent evidence that macaques dispersed from Africa into Europe during the late Messinian. Although rare in fossil fauna European macaques (several subspecies of the extant Barbary macaque *M. sylvanus*) managed to survive until the late Pleistocene (ref.[252]).

5.3.7. Neogene biogeography of Hominidae

The Hominidae (great apes and humans) is descended from Afro-Arabian stem hominoids (*e.g. Ekembo, Afropithecus/Heliopithecus*) and first appear in Europe in the late early Miocene (refs.[253,254]). Between about ~16 and 13.5 Ma they diversify in Europe and disperse into Africa (*Griphopithecus* and *Kenyapithecus* in Europe/Western Asia and *Nacholapithecus*, *Equatorius*, and *Kenyapithecus* in Africa (refs.[255-259]). Hominids are not found in Africa between about 13.5 and 9.8 Ma while they become even more diverse and abundant in Europe, radiating into an impressive diversity of taxa (*Pierolapithecus, Anoiapithecus, Dryopitheus, Danuvius, Hispanopithecus, Rudapithecus, Ouranopithecus, Graecopithecus*, and at least one more unnamed genus (refs.[255,260,261]). In Asia there is also an impressive diversity of hominids including *Sivapithecus, Lufengpithecus, Khoratpithecus, Indopithecus* among the best-known taxa, with more diversity possible (ref.[262]). There is much debate on the evolutionary relations among European/Western Asian and African taxa, the two prevailing hypotheses being that they all represent stem hominids (ref.[261]) or that the European taxa are stem hominines (African apes and humans; refs.[255,260]). Either way, there is strong evidence of dispersals between Europe and Africa from 17 to 13.5 Ma, with at least one taxon shared between the two continents. Because derived great apes (either hominines or hominids) are found in abundance in Eurasia between 13.5 and 7.2 Ma but not in Africa, the most parsimonious explanation is that the first hominines to be found in Africa, *Sahelanthropus* and *Orrorin*, descend from taxa that dispersed there from Europe, respectively Western Eurasia (refs.[255,263]). The timing of this dispersal corresponds well with that of many other Eurasian taxa dispersing into Africa during the Messinian (see conclusions below).

A more recent interpretation of relations between European and African apes is that the individual clades of crown hominines (*Pan*, *Gorilla* and hominins) had already split in Europe before independently dispersing into Africa after about 8 Ma (refs.[260,263,264]). In this regard it is important to note that the hominine ancestral positional behavior adaptations are known for *Danuvius*, a 11.6 Ma old European ape (refs.[265,266], but see ref.[267]). This is consistent with the interpretation that *Graecopithecus* and possibly *Ouranopithecus* are hominins and that thinly enameled dryopithecins are members of the gorilla clade (refs.[260,263,264]). The concept that *Graecopithecus* is the first potential hominin is not accepted by all researchers (ref.[268]) due to the limited number of features coming from the scarce fossils, but the arguments put forward against this hypothesis do not seem stronger than the stated opinion (ref.[269]). It is noteworthy that the appearance of *Graecopithecus* in the Balkans coincides with the post-Pikermian faunal turnover (ref.[72]), related to a landscape aridification and an early Messinian dispersal of faunal elements from the east, resulting to the replacement of a part of the Pikermian fauna. This post-Pikermian turnover in the Balkans is largely contemporary with the observed penetration of Eurasian elements into the fauna of the southern Arabian Peninsula and Africa (see conclusions below).

5.3.8. Conclusions about Neogene Afro-Eurasian mammal dispersals

Reconstructing mammalian biogeography can be heavily biased by the range of completeness of the fossil record, by chronologic dating, and by taxonomic concepts. Therefore, our review does not claim to be final and after forthcoming research some intra-continental dispersers will be identified in addition, removed from our list, or will be even find to took the opposite direction of dispersal. However, we presented here the so far most comprehensive investigation of this topic, incorporating state-of-the-art taxonomy and chronology. We have been able to identify several new and unique patterns of Afro-Eurasian mammalian biogeography, whereby addressing some long-standing biogeographic problems.

Our review of late Neogene mammalian dispersals confirms earlier findings of Thomas (ref.[161]) and Vrba (ref.[225]) that late Miocene dispersal between Africa and Eurasia are unidirectional into-Africa (but see the case of *Brachypotherium*) and late Pliocene dispersals are bi-directional. Our study supports to a large extent and on the base of concrete examples the idea of Solounias et al. (ref.[270]) that the origin of the recent African savannah fauna must be sought in the late Miocene Pikermian biome (sensu ref.[271], corresponding to Graeco-Iranian-Afghan province of ref.[272]). We identified here 28 taxa of late Miocene immigrants into Africa.

- Early Messinian dispersal: We identify at least 21 taxa involved in a unidirectional into-Africa dispersal. The majority of them, 14 taxa, most probably derived from western Eurasian Savannas of the Pikermian biome, whereas seven taxa probably have an eastern Eurasian (South Asian) source, some being defined to mesic habitats (*Stegodon*, Suinae, *Dorcadoxa*, Reduncini, Bovini).
- Late Messinian dispersal: Seven large mammal taxa have been found to reach the African continent between 6.1 and 5.6 Ma. Again, the majority of them, five taxa, have their roots in Western Eurasia (Central Eurasia for *Paracamelus*).

Interestingly, during the Tortonian-Messinian transition a faunal dispersal from Asia is observed in the Pikermian biome (the post-Pikermian turnover of ref.[72] involving *Anancus*, *Tragoportax macedonensis*, and other taxa) as well as a dispersal from Southeast Europe and Southwestern Asia (Pikermian faunal elements) into South Asia. The latter dispersal involves according to ref.[273] large bovids, leporids, colobines, ursids, *Lycyaena*, *Plesiogulo*, *Machairodus*, and several hypsodont Pecora between 7.4-7.1 Ma (ref.[68], recalibrated into the actual polarity time scale of ref.[48]). This led us to conclude that dispersals around the Tortonian-Messinian transition occurred simultaneously in Africa, Europe and South Asia. Based on the data presented in this work we hypothesize that these dispersals have a common cause, related to the two consecutive late Tortonian transient desert events centered at 7.78 and 7.50 Ma in West Asia (see Figs. 5 and 6 in the main text).

After 5.6 Ma (corresponding to the desiccation of the Mediterranean during stage 2 of the Messinian Salinity Crisis) no mammal dispersal into-Africa is observed until the mid-Piacenzian (3.4-3.2 Ma). It is impressive that this conclusion coincides with the statement in the comprehensive study on the African land mammal ages (ref.[274]), which came out after this article was submitted, that there is no first nor last appearance of African taxa during the time span 5.3-3.6 Ma. This could be explained namely by the lack of faunal dispersals that would lead to the emergence of new taxa, but which could also cause the extinction of native species. The mid-Piacenzian dispersals involve for the first time a bi-directional exchange dominated by Eastern Eurasian immigrants into-Africa (*Canis, Nyctereutes, Metridiochoerus, Budorcas*) and African immigrants into South Asia (*Elephas, Hippotragus*, and possibly *Pachycrocuta*). This bi-directional dispersal involves at least nine taxa. In contrast to the Messinian dispersals, into-African migrants dominantly have Eastern Eurasian (South Asian) affinities. Only the genus *Mammuthus* disperses in mid-Piacenzian times out-of-Africa to Western Eurasia (Eastern Europe), whereas *Giraffa* reached the Levant. So, mid-Piacenzian mammalian dispersals can be mainly observed between the Africa and South Asia. Two taxa (*Dinofelis, Homotherium*) may have dispersed earlier, during latest Zanclean (4.0-3.6 Ma), from Africa to Western Eurasia (*Dinofelis* also to Eastern Eurasia).

Consistent with our Mesopotamian climate record, the cause of significant bi-directional African Eurasian dispersals during mid-Piacenzian may involve the warming and the global retreat of deserts during that time as is indicated by both pollen data and modelling results (refs.[275,276]).

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