



The possible region of the Late Miocene split of the sandfly subgenus *Transphlebotomus* Artemiev and the early late Neogene to late Quaternary dispersal of the ancestor of *Phlebotomus mascittii* Grassi

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Abstract

The distribution of the Mediterranean *Transphlebotomus* species shows a marked zoogeographical dichotomy in the sense that *Phlebotomus mascittii* has a wide range in Europe, and the other species are restricted to the East Mediterranean region. The study aimed to investigate how the Neogene to late Quaternary climatic-geographical alterations could influence the split of the sandfly subgenus *Transphlebotomus* and the speciation of *Phlebotomus mascitti*. For this purpose, the climatic suitability patterns of the species were modelled for seven Neogene and Quaternary periods and the divergence times of *Transphlebotomus* clades were estimated. The model results suggest that the common ancestor of the extant Mediterranean-European *Transphlebotomus* species could be adapted to the Late Miocene climate of Western and Central Europe. Phylogenetic results suggest that the speciation of *Ph. mascittii* started in the Tortonian period, plausibly related to the rise of the Dinaric land bridge. The Central and Eastern Paratethys Seas could have played an important role in the split of the ancestral *Phlebotomus mascittii* populations and other *Transphlebotomus* populations. These other species can be the descendants of ancient *Transphlebotomus* populations adapted to the hotter and drier climate of the areas south of the Central and Eastern Paratethys. Their divergence could be strongly linked to the formation of the Aegean trench and, later, the Messinian salinity crisis. The Pliocene climatic fluctuations could result in habitat loss of *Transphlebotomus* populations in Europe which was particularly significant during glacial maxima such as the Last Glacial Maximum.

Keywords Speciation · Drivers of diversification · Palaeogeographic events · Aegean area · Divergence time

Introduction

Phlebotomine sandflies (Diptera: Psychodidae: Phlebotominae) are vectors of arboviruses and are the principal, if not the sole vectors of *Bartonella bacilliformis* (Strong et al. 1913) causing human bartonellosis in Latin America (Herrer and Christensen 1975). Most importantly, however, sandflies are the principal vectors of the protozoan parasites *Leishmania* spp. (Kinetoplastida: Trypanosomatidae),

the causative agents of leishmaniasis (Akhoundi et al. 2016). The disease is endemic in 98 countries in Europe, Africa, Asia, and the Americas. Worldwide, around 12 million people are infected with *Leishmania* spp. and 50,000 to 90,000 cases of visceral leishmaniasis and 700,000 to 1 million new cases of cutaneous leishmaniasis are estimated to occur annually, with more than 1 billion people living in endemic areas. Leishmaniasis is particularly prevalent in the world's wet and semi-arid tropical regions (WHO 2021). Globally, the most affected regions are the tropical areas of Brazil, North and Northeast Africa, the Middle East, and South and East Asia (Burza et al. 2019). The New World and Old World-dwelling sandfly species have different climatic and breeding site preferences (Azar and Nel 2003).

In the Old World, several sandflies occur in arid, semi-arid, (sub-) tropical and temperate areas in which they breed in a large variety of domestic, peri-domestic, and sylvatic

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sites such wet cracks (Orshan et al. 2016), burrows of mammals or termite hills, animal barns close to human dwellings, and even tree holes or leaf litter (Feliciangeli 2004). It is worth mentioning that *Phlebotomus* species also occur in humid environments in Afro-Eurasia. For example, in Ethiopia, *Phlebotomus* (*Synphlebotomus*) *martini* Parrot, 1936 also inhabits the border zone of savanna and subtropical highland climate regions (Gadisa et al. 2015), where the annual mean precipitation reaches the 800–1000 mm value (Asefa et al. 2020). In Southwest Hungary, *Phlebotomus* (*Larroussius*) *major* subsp. *neglectus* Tonnoir, 1921 occurs in Nagyarsány (Tánczos 2012; Trájer et al. 2018a), where the annual rainfall is 572 mm (Trájer 2017). In the Americas, *Lutzomyia* França, 1924 (genus as proposed by Young and Duncan 1994) species occur mainly in tropical forests and savannas and breed predominantly in leaf litter (Dutari and Loaiza 2014) or within the tabular roots and bases of trees (Vivero et al. 2015). Female sandflies take blood on various vertebrate species, including mammals (e.g. lagomorphs; González et al. 2021) and birds (e.g. chickens; Sant’Anna et al. 2008), but the extant sandfly fauna also includes herpetophilic species, which predominantly feed on lizards (Pombi et al. 2020). In the case of mammals, burrowing species such as rodents (Yaghoobi-Ershadi and Javadian 1996), rabbits (Sáez et al. 2018) and hyraxes (Bsrat et al. 2015) play the most important role in sandfly ecology and the maintenance of local transmission cycles of leishmaniasis in the Old World.

Evolutionary hypotheses suggest a relationship between leishmaniasis’ landscape epidemiology and sandflies’ coevolution with *Leishmania* species of tropical and subtropical mammals and lizards (Ready 2013). Sandflies are a subfamily of the order Diptera L, whose members appear first in the geological record with ancient Nematoceran species in the early Middle Triassic epoch (Lukashevich et al. 2010). They emerged about the same time as the first lepidosauromorph reptiles, the ancestors of the extant lizards, appeared (Renesto and Posenato 2003). The first appearance of Psychodidae Newman, 1834, the family of the sandfly-related insect taxa is dated to the Upper Triassic period (Blagoderov et al. 2007), which coincides with the emergence of the modern ecosystems (Andrade Filho and Brazil 2003). The Late Triassic was also when mammals evolved from small, advanced cynodonts, the mammal-like reptile ancestors of the Mammaliaformes clade (Wallace et al. 2019). The parallel success of dinosaurs and other archosaur clades resulted in the extinction of most of the non-mammalian mammal-like reptiles at the end of the period (Benton 1983). Possibly, the earliest mammals hid from agile carnivorous reptiles in burrows since it is known that burrowing could have been common already among the end-Permian cynodonts (McLoughlin et al. 2020) and Late Triassic cynodonts created complex burrow systems (Benton 2021). These facts

can be related to the evolution of sandflies, and *Leishmania* parasites, as several Old-World sandfly species are known to breed in burrows of rodents and hyraxes and feed on mammalian blood. The Jurassic, parallel to the break-up of the supercontinent of Pangea, could have been the time of the speciation of Psychodidae, including the differentiation of the tribes Hertigiini and Phlebotomini (Andrade Filho and Brazil 2003). Furthermore, based on fossil records, the early members of the *Phlebotomus* genus appeared in the middle part of the Cretaceous period (Kaddumi 2007; Stebner et al. 2015). The geological and climatic changes of the Tertiary period led to the rise of the ancestors of the present-day clades. The radiation of the oriental phlebotomine sandflies could have started about 50 mya in the Eocene (Ilango 2011). The rapid Oligo-Miocene climatic changes and the collision of Eurasia and the terranes of the former Neo-Tethys Ocean could have played a crucial role in determining the climatic requirements and the range of the emerging Mediterranean sandfly taxa. Among them, the late Neogene aridification of the Mediterranean and peri-Mediterranean region (Esseghir et al. 2000; Cruaud et al. 2021; Trájer et al. 2022a), the permanently changing coastlines of the former Paratethys Sea (Depaquit et al. 2002; Trájer 2022b), as well as the Messinian Salinity Crisis (Kasap et al. 2015; Trájer et al. 2021) are worth mentioning.

The members of the sandfly genus *Transphlebotomus* occupy large regions of the Mediterranean area in Europe, Northern Africa, and Western Asia. Among them, *Phlebotomus* (*Transphlebotomus*) *mascitii* Grassi, 1908, occurs in oceanic and continental climate regions of Central Europe such as Belgium (Depaquit et al. 2005), Germany (Naucke and Pesson 2000), Austria (Kniha et al. 2020) and Hungary (Farkas et al. 2011), but also the subtropical and Mediterranean climate regions of France, Italy, or Slovenia (Veronesi et al. 2007; Prudhomme et al. 2015; Praprotnik et al. 2019). Therefore, it is plausible that *Ph. mascitii* is the northernmost sandfly species in Europe and it is an assumed but unproven vector of *Leishmania infantum* Nicolle, 1908 (Zanet et al. 2014; Obwaller et al. 2016). Surprisingly, the range of the other thermophilic *Transphlebotomus* species, *Phlebotomus* (*Transphlebotomus*) *anatolicus* Erisoz Kasap, Depaquit and Alten, 2015, *Phlebotomus* (*Transphlebotomus*) *canaaniticus* Adler and Theodor, 1931, *Phlebotomus* (*Transphlebotomus*) *economidesi* Léger, Depaquit, and Ferté, 2000a, b, *Phlebotomus killicki* Dvořák, Votýpka and Volf, 2015, and *Phlebotomus* (*Transphlebotomus*) *simonahalepae* Cazan, Erisoz Kasap and Mihalca, 2021, are restricted to the relatively mild winter and hot summer climate regions of Southeast Europe (Ivović, et al. 2007), Asia Minor (e.g. Arserim et al. 2022), and the Levantine (e.g. Maroli et al. 2009) and do not occur in the oceanic and continental regions of Europe. Kasap et al. (2015) found that the first split of

Transphlebotomus occurred around 10 million years ago. The authors suggested that the present-day occurrence and the climatic needs of species of the subgenus can be explained by the post-Miocene geographical climatic and geographical changes of the Aegean region. However, the main drivers of the diversification of the subgenus were not investigated in model environments.

The study aimed to test the Eastern Mediterranean speciation theory of the Mediterranean sandfly species using modelling tools. A special focus was given to the possible role of the Central Paratethys in the early split of these subgenera and the late Neogene-early Pleistocene zoogeographical changes of the ancestor of *Phlebotomus mascittii* and the other, non-*Ph. mascittii* *Transphlebotomus* species in Europe, Asia Minor, Levant, and North Africa.

Materials and methods

Outline of the study

To investigate the speciation drivers of the sandfly subgenus *Transphlebotomus* in the Mediterranean region, the following tasks were performed:

- 1) The known occurrences of *Ph. mascittii* and the united distribution area of the other *Transphlebotomus* taxa of the eastern Mediterranean Basin were georeferenced.
- 2) Based on the georeferenced occurrence data and climate models, the climatic limits of the species were determined. The determined number and type of climatic constraints depended on the nature of the available palaeoclimatic data. For the heterogenic nature of the climatic data used in the study, the products of all model environments were presented in different subsections in the Results.
- 3) Tortonian and Messinian climatic models were created based on existing, site-like palaeoclimatic reconstructions.
- 4) Three model environments were established: two different Late Miocene – Tortonian and Messinian – model environments and a mid-Pliocene interglacial (MIS19), Last Interglacial Period and Last Glacial Maximum age-related model environment.
- 5) Divergence time estimates of *Transphlebotomus* species were calculated to compare climatic models with potential diversification events of the member species.

The QGIS free and open-source geographic information system was used for data processing and modelling purposes (Lacaze et al. 2018).

Sandfly data sources

A total of 184 *Transphlebotomus* occurrences were involved in the study in Europe, Asia Minor, and the Levant. The occurrence data of *Ph. mascittii* ($n_{\text{sites}}=157$) and the other non-*Ph. mascittii* *Transphlebotomus* occurrences ($\Sigma n_{\text{sites}}=29$) were based on the available data in the literature (Fig. 1; red points). The other, non-*Ph. mascittii* species were *Ph. anatolicus* ($n_{\text{site}}=2$), *Ph. canaaniticus* ($n_{\text{site}}=6$), *Ph. economidesi* ($n_{\text{site}}=5$), *Ph. killicki* ($n_{\text{site}}=8$), and *Ph. simonahalepae* ($n_{\text{site}}=1$). Furthermore, five additional non-*Ph. mascittii* *Transphlebotomus* occurrences from Asia Minor were also georeferenced (Fig. 1; yellow points). Table 1 shows the occurrence data sources of the studied *Transphlebotomus* species.

In 72% of the occurrences, the exact coordinates were known. In the remaining cases, heterogeneous methods were used to identify the location of the original trappings as accurately as possible. In some cases, the exact coordinates of the catch sites could be reconstructed. For example, the coordinate determination of the occurrence of *Ph. economidesi* in Mandria cave, Cyprus, was based on the coordinates of the entrance of the cave (Kasap et al. 2015); in Monteggio and Sessa, southern Switzerland, Grimm et al. (1993) provided occurrence data on a small-scale schematic map with the pattern of respective streets and even houses. By identifying the geographical position of the streets and individual houses within the small settlements, the coordinates extraction was possible within a resolution accuracy of ten meters. In the case of other small settlements, where a schematic map was not provided, the centre coordinates of the villages were considered in georeferencing. For example, Mazeris et al. (2010) collected *Ph. economidesi* in Dora, Cyprus, a village smaller than 1x1 km.

Sometimes, the resolution was between $1 \times 1 < \text{to} \leq 10 \times 10$ km. For example, Léger et al. (2000a) found *Ph. economidesi* in Armenochori, Cyprus. It is also a very small village, with a maximum extension of 5x2 km. Therefore, it can be concluded that the used coordinates were accurate or sufficiently accurate. For example, in the case of *Ph. mascittii* occurrence sites, it means that of all occurrence data points, 102 were exact point coordinates, 44 were at a scale of 1x1 km or lower, and eleven were at a scale of 10x10 km or lower. From the point of view of distribution modelling, even the accuracy of $\leq 10 \times 10$ km resolution is generally acceptable because these model experiments aim to predict large-scale occurrence patterns and not local habitats. Furthermore, the cut of 2-2 percentiles from the sampled climatic data was utilised to filter the possibly appearing non-relevant climatic values. Finally, it is worth mentioning that the resolution of the used current period's climate models, which were utilised for climatic data extraction, is 2.5 arc-minutes. This resolution in the mid-latitudes is equal

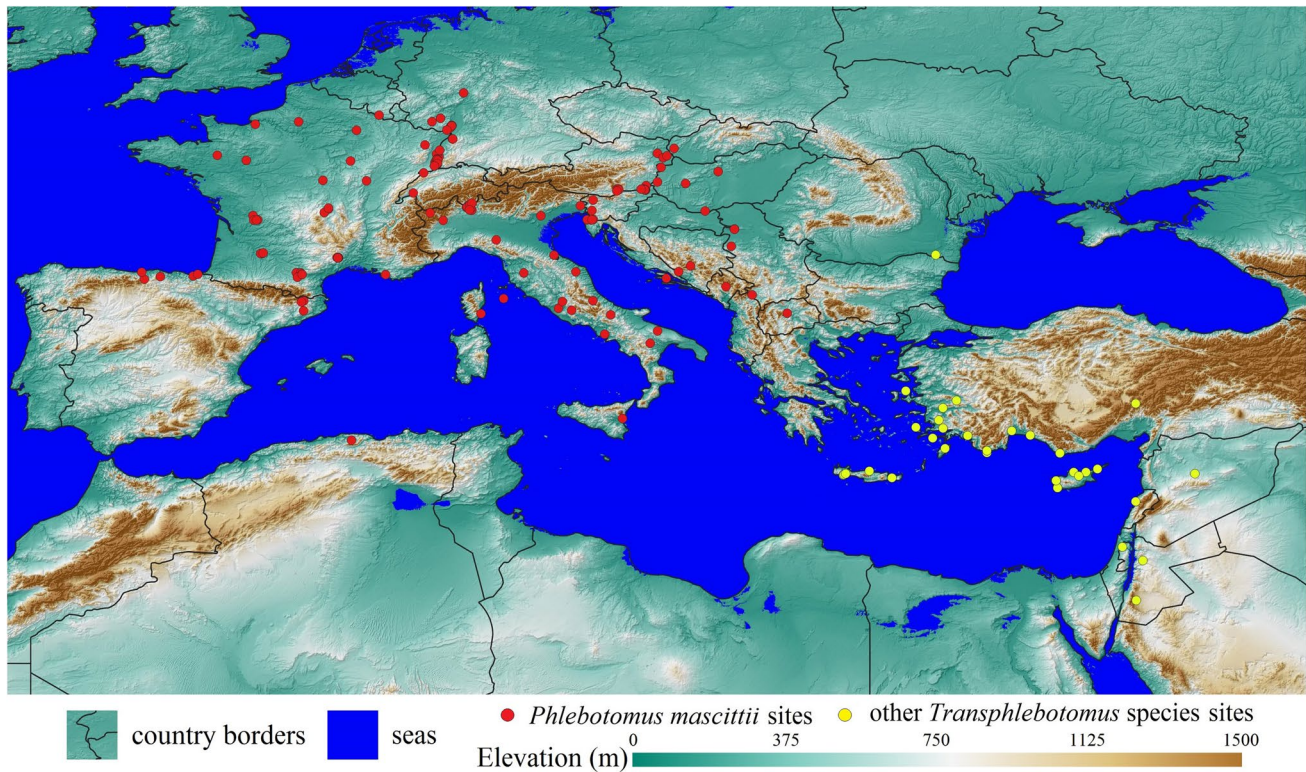


Fig. 1 The occurrence points of *Phlebotomus mascittii* and other *Transphlebotomus* species

to ~5x5 km. Therefore, it means that the accuracy of the site coordinates fits the resolution of the reference period's climatic models used in the study.

Climatic and topographic data sources

The Tortonian and the Messinian climate data were based on the palaeoclimatic reconstructions of Bruch et al. (2006, 2011). The authors applied the Coexistence Approach of Mosbrugger and Utescher (1997) using the fossil plant assemblages to estimate the former palaeoclimatic conditions of the former West and Central Paratethys, as well as the Aegean area and Asia Minor. The Coexistence Approach method or concept is based on the current distribution area-limiting values of the closest extant relatives of the fossil plant species. This method can be used mainly for the Cenozoic period, but due to the uncertainties of the similarity between the living and the extinct floral elements, the method requires robust statistical tools (e.g. Mosbrugger and Utescher 1997; Erdei et al. 2007). Bruch et al. (2006) produced the values of four bioclimatic variables. Table 2 shows the modelled periods and the related data sources.

To create continuous, georeferenced climatic data of the Mediterranean region in the wider sense, the method of Trájer (2022a, b, c) was used who utilised the following steps to produce the palaeoclimatic maps:

- 1) The sites of the palaeoclimatic reconstructions were georeferenced in QGIS software, and the site-related values were added to the sites in the attribute table. Not the absolute values, but the differences between the palaeoclimatic and the modern values were applied.
- 2) The differences between the palaeoclimatic and the modern values were interpolated using the IDW interpolation function of the QGIS software.
- 3) The modern climatic values were modified by the interpolated difference values.
- 4) Finally, the former sea level was reconstructed. It should be noted that this study did not aim to create exact geological or palaeogeographical reconstructions.

Figure 2 shows the interpolated difference values compared to the reference periods of the Tortonian annual precipitation sum (bio12), annual mean temperature (bio1), January T_m 01), and July mean temperature (T_m 07) values. The Tortonian values were produced by modifying the present-day values by the IDW interpolated differences.

Figure 3 shows the interpolated difference values compared to the reference periods of the Messinian temperature annual range (bio5-bio6; bio7), annual precipitation (bio12) and July precipitation sum (P07) values. The Messinian values were produced by modifying the present-day values by the IDW interpolated differences.

Table 1 The sources of the occurrence data of the studied *Transphlebotomus* species

Species	Country	References
<i>Phlebotomus (Transphlebotomus) anatolicus</i> Erisoz Kasap, Depaquit and Alten, 2015	Turkey	Kasap et al. (2015, 2019); Pekağırbaş et al. (2021)
<i>Phlebotomus (Transphlebotomus) canaaniticus</i> Adler and Theodor, 1931	Jordan	Kanani et al. (2015); Léger et al. (2000a); Saliba et al. (1997)
	Lebanon	Depaquit et al. (2005)
	Palestine	Sawalha et al. (2017)
	Syria	Léger et al. (2000a); Maroli et al. (2009)
<i>Phlebotomus (Transphlebotomus) economidesi</i> Léger, Depaquit, and Ferté, 2000a, b	Cyprus	Demir et al. (2010); Depaquit et al. (2005); Mazeris et al. (2010); Léger et al. (2000b); Dokianakis et al. (2018)
	Greece	Kasap et al. (2015); Léger et al. (2000a, b)
	Turkey	Kasap et al. (2015)
<i>Phlebotomus (Transphlebotomus) killicki</i> Dvořák, Votýpka and Volf, 2015	Cyprus	Dokianakis et al. (2018)
	Greece	Kasap et al. (2015); Léger et al. (2000a)
	Turkey	Kasap et al. (2015, 2019); Pekağırbaş et al. (2021)
<i>Phlebotomus (Transphlebotomus) mascittii</i> Grassi, 1908	Algeria	Berdjane-Brouk et al. (2011)
	Austria	Naucke et al. (2011); Poepl et al. (2013); Kniha et al. (2020)
	Belgium	Depaquit et al. (2005)
	Bosnia and Herzegovina	Dvořák et al. (2020)
	Croatia	Bosnic et al. (2006)
	France (including Corsica)	Larrousse (1923); Young et al. (1980); Léger et al. (1985); Pesson et al. (1985); Guilvard et al. (1980); Depaquit et al. (2005); Naucke et al. (2008); Mahamdallie et al. (2011); Kasbari et al. (2012); Kasap et al. (2015); Prudhomme et al. (2015)
	Germany	Naucke and Pesson (2000); Naucke and Schmitt (2004); Melaun et al. (2014); Oerther et al. (2020)
	Hungary	Farkas et al. (2011)
	Italy (including Montecristo, Sardinia, and Sicily)	Biocca et al. (1977); Lewis (1982); Houry et al. (1992); Bongiorno et al. (2003); Maroli et al. (1994, 2002, 2006); Veronesi et al. (2007); Rossi et al. (2008); Dantas-Torres et al. (2014); Lisi et al. (2014); Zanet et al. (2014); Michelutti et al. (2021)
	Kosovo	Vaselek et al. (2020)
	Montenegro	Anonymous (1993)
	North Macedonia	Anonymous (1993)
	Serbia	Vaselek et al. (2017, 2019)
	Slovakia	Dvořák et al. (2016)
	Slovenia	Ivočić et al. (2015); Praprotnik et al. (2019);
	Spain	Rioux et al. (1984); Alarcón-Elbal et al. (2021)
	Switzerland	Gaschen (1956); Knechtli and Jenni (1989); Grimm et al. (1993); Kasbari et al. (2012)
<i>Phlebotomus (Transphlebotomus) simonahalepae</i> Cazan, Erisoz Kasap & Mihalca, 2021	Romania	Cazan et al. (2021)
' <i>Transphlebotomus</i> '	Turkey	Karakuş et al. (2017, 2019) Arserim et al. (2022) Omondi et al. (2020)

As the potential Messinian range of the non-*Ph. mascittii* *Transphlebotomus* species were observed to cover former coastal regions, and the palaeoclimatic conditions of the formerly desiccated Mediterranean Basin's floor were also reconstructed following the method of Trájer et al. (2021).

In this process, the steps were as follows in the case of July and the Annual Precipitation Sum values:

- 1) Several coastal points were designated along the entire Mediterranean basin.

Table 2 The sources of the used climatic models and data (* it was used for the derivation of the range-limiting climatic extrema of sandflies)

Model period	Age	Reference
Current/reference period (Anthropocene)*	1979–2013	Karger et al. (2017)
Last Glacial Maximum	21 ka	Karger et al. (2021)
Last Interglacial Period	130 ka	Otto-Bliesner et al. (2006)
Pleistocene MIS19 period	787 ka	Brown et al. (2018)
mid-Pliocene warm period	3.205 Ma	Hill (2015)
mid-Pliocene (M2) cold period	3.3 Ma	Dolan et al. (2015)
Messinian period	7.246–5.333 Ma	Bruch et al. (2011)
Tortonian period	11.608–7.246 Ma	Bruch et al. (2006)

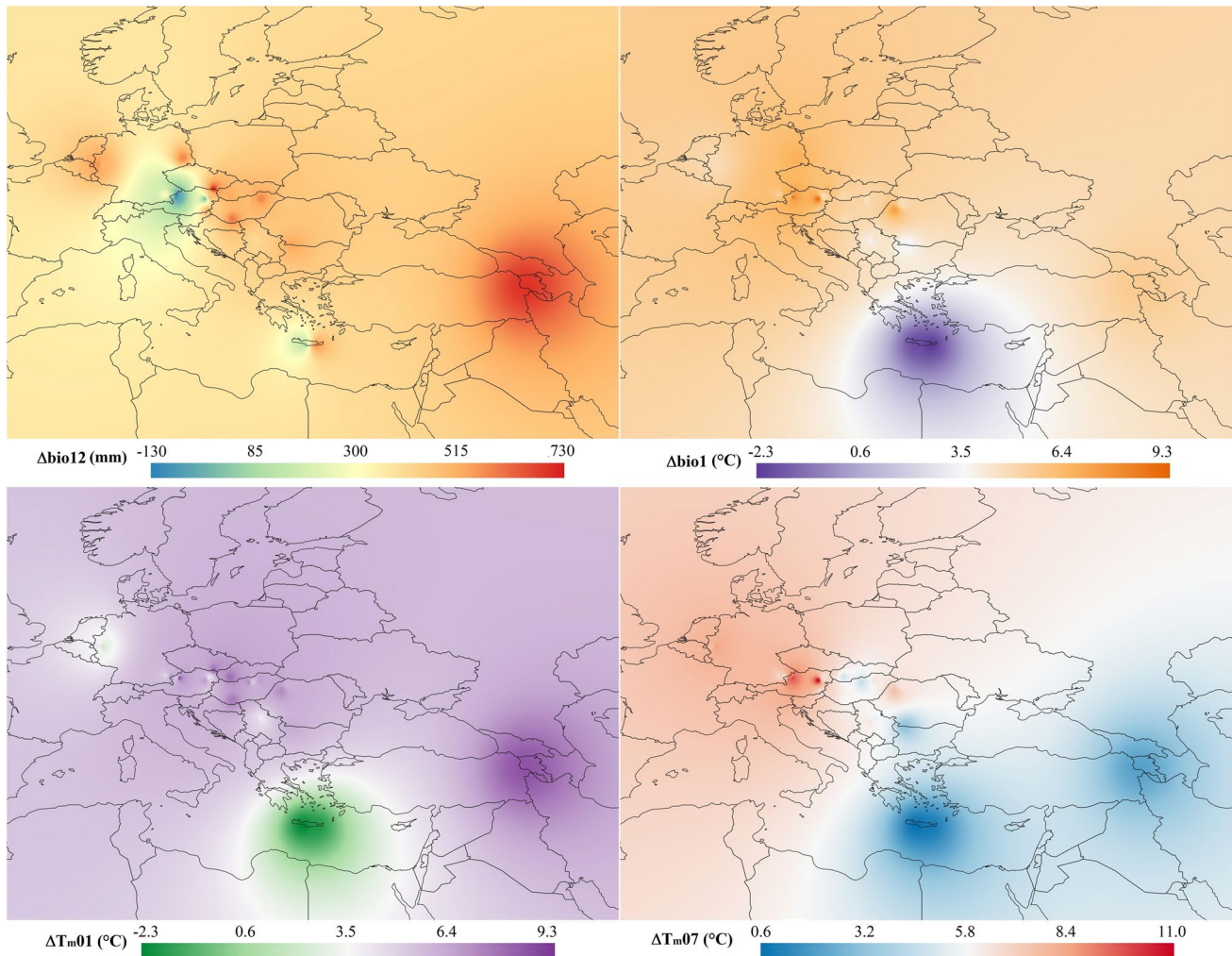


Fig. 2 The interpolated difference values compared to the reference periods of the Tortonian annual precipitation sum, annual mean temperature, January, and July mean temperature values

- 2) The reconstructed coastal precipitation sum values were determined with the sampling tool of the QGIS program.
- 3) The determined, reconstructed values were interpolated using the IDW (Inverse Distance Weighting) interpolation method. The values obtained represent July and the

Annual Precipitation Sum precipitation values of the former, desiccated Mediterranean Basin.

The sea surface temperature on the formerly desiccated abyssal plain of the Mediterranean Sea was calculated

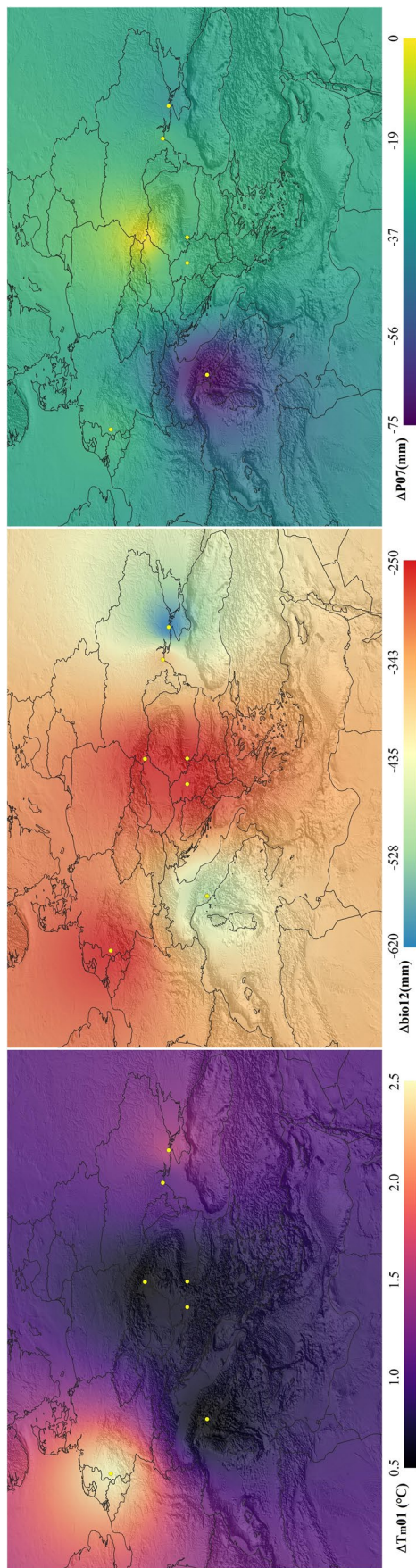


Fig. 3 The interpolated difference values of the climatic factors, compared to the reference periods of the Messinian temperature annual range, annual precipitation and July precipitation sum values

according to the dry adiabatic lapse rate. The global sea level was 25 m higher than today (Dwyer and Chandler 2009). The thermal patterns of the Mediterranean Basin can be calculated according to the following formula during the Messinian Salinity Crisis and the dry adiabatic lapse rate (Ritter 2006):

$$T_{agl} = (6.5 \times 10^3 \times (\Delta h + 25)) + T_{srl}$$

where T_{agl} is the abyssal ground-level temperature (°C) of the Messinian seafloor, Δh is the altitude below sea level (m), and T_{srl} is the reconstructed Messinian temperature at sea level. Figure 4. shows the thermal surplus of the desiccated Mediterranean seafloor in the Messinian period.

As the topographic model, the ETOPO1 1 Arc-Minute Global Relief Model of the Earth's surface was utilised, integrating land topography and ocean bathymetry (Amante and Eakins 2009). In the case of the mid-Pliocene and the MIS19 Quaternary period's model, existing palaeoclimatic models were used.

Model environments and the determination of the extrema

As mentioned, the available data sources made different numbers and types of climatic extrema possible. Model 1 environment was attributed to the creation of the Tortonian models; the mid-Pliocene models and three different, MIS19, Last Interglacial Period and Last Glacial Maximum's Quaternary period-related models were performed in model environment 2, and model environment 3 was the source of the Messinian period's models. The climatic values used in the different model environments and determined climatic extrema can be seen in Table 3.

For acquiring the range-limiting extrema of *Ph. masicittii* and the united group of the other East Mediterranean *Transphlebotomus* species, the 2.5 arcmin resolution model of Karger et al. (2017) related to the reference period of 1979–2013 was used. As was previously mentioned, 2–2 percentiles were cut from the absolute maximum and minimum values of the factors to avoid the involvement of unrealistic climatic contracts according to the generally applied considerations of environmental modelling (Trájer et al. 2013). Table 4 shows the determined climatic distribution-limiting extrema.

Modelling the former sandfly ranges

The modelling of the former distribution areas followed the logic of Boolean algebra. The area of all range areas was modelled according to the following general equations:

$$1(v_n) = \begin{cases} 0 & \text{if } v_{n_limit_min} > v_n \text{ and } v_n > v_{n_limit_max} \\ 1 & \text{if } v_{n_limit_min} \leq v_n \text{ and } v_n \leq v_{n_limit_max} \end{cases}$$

Where v_n represents the n^{th} climatic constraint of the distribution area of a species, $v_{n_limit_min}$ and $v_{n_limit_max}$ are the

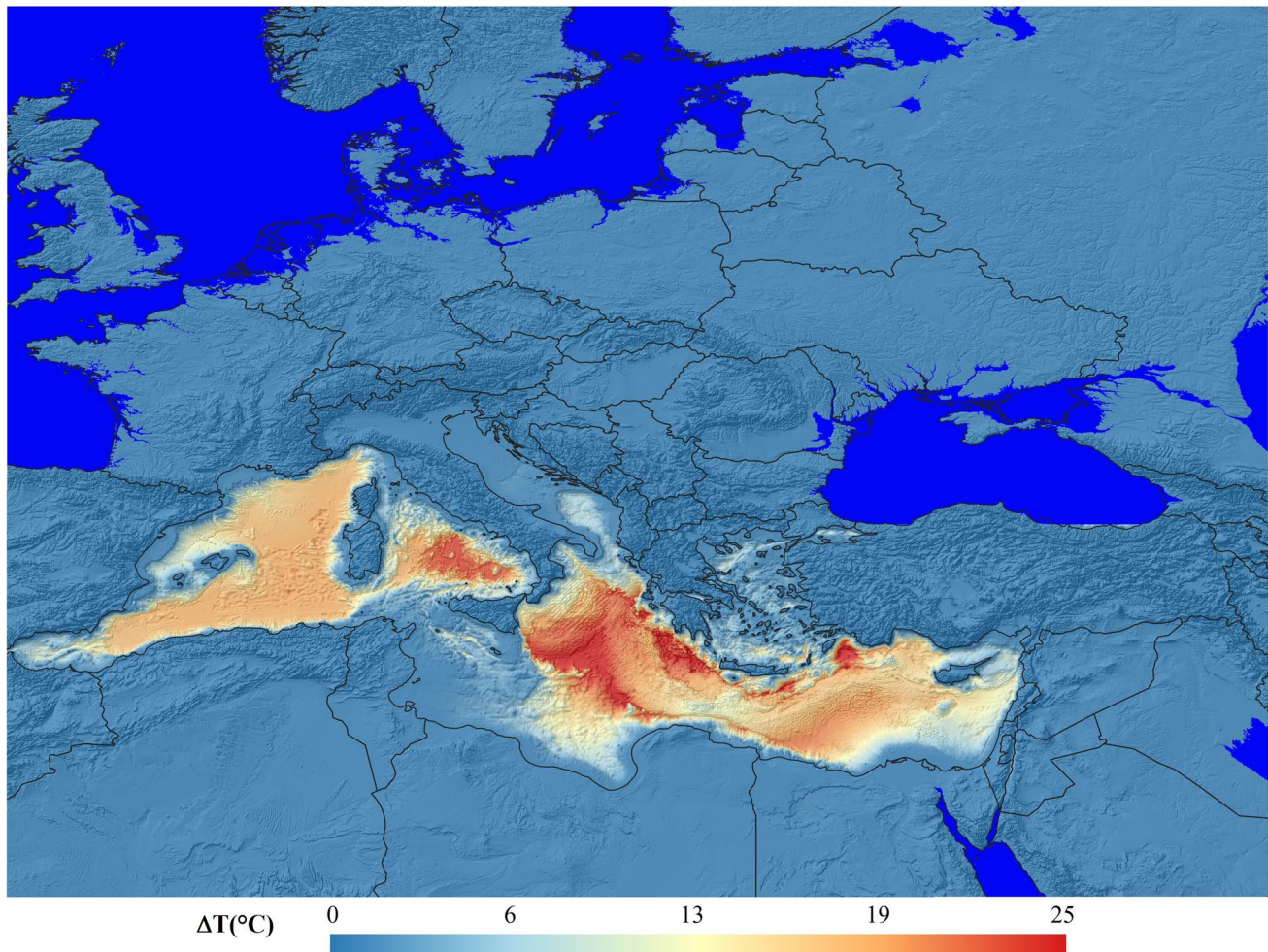


Fig. 4 The calculated difference between the Messinian sea-level temperature and the thermal conditions of the desiccated basin of the present-day Mediterranean Sea

lower and upper distribution-limiting values related to the climatic constraint.

The potential area-based suitability patterns were determined according to the following mathematical formalism:

$$A(v_1; v_2; \dots; v_n) = 1(v_1) - v_1 \cap 1(v_2) - v_2 \cap \dots \cap 1(v_n) - v_n$$

where $A(v_1; v_2 \dots v_n)$ shows the potential distribution area of the given species, which contains the remaining areas after taking into consideration the factor-related limitations.

Then, the modelled values were transformed into percentage (%) values and were colourized.

Phylogenetic analysis and divergence times estimates

Available *Transphlebotomus* cytochrome b (cytb) sequences were downloaded from GenBank. Altogether, eleven *Transphlebotomus* cytb sequences (332 basepairs) and one *Phlebotomus chinensis* Newstead, 1916 sequence

functioning as an outgroup were included. Sequences were aligned with ClustalX 2.1 for multiple alignments and GeneDoc 2.7.0. was used for manual editing and data analysis. Maximum likelihood (ML) analysis was performed with MEGAX (Kumar et al. 2018) to compare ML tree topology to previous studies (Kasap et al. 2015; Cazan et al. 2021). Based on the best-fit evolutionary model selection, a Hasegawa-Kishino-Yano + G model with bootstrap support of 1000 replications was applied. Divergence time estimates were conducted using BEAUti v1.10.4 and BEAST v1.10.4 (Suchard et al. 2018) under the multiple species' coalescent models. MEGAX was used to test for the molecular clock hypothesis (Thorpe 1982). The MCMC was run in BEAST under the Yule speciation process (Gernhard 2008) for 10 million generations sampling every 1000th generation; the first 25% were discarded as burn-in. The molecular clock was calibrated to 2.4% per myr based on the estimated divergence rates of mtDNA (without partitions) in BEAST

Table 3 The used climatic variables in modelling (me1=model environment 1: Tortonian models; me2=model environment 2: mid-Pliocene (M2) cold and warm and the Pleistocene MIS19, Last Interglacial and Last Glacial Maximum periods; me3=model environment 3: Messinian period’s models)

Variable	Description	Unit	Model environment
T_{m01}	Mean January Monthly Temperature	(°C)	me1, me3
T_{m07}	Mean July Monthly Temperature	(°C)	me1
$P07$	July Precipitation Sum	mm	me3
bio1	Mean Annual Temperature	(°C)	me1, me2
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	(°C)	me1
bio4	Temperature Seasonality (standard deviation ×100)	(°C)	me2,
bio8	Mean Temperature of Wettest Quarter	(°C)	me2
bio9	Mean Temperature of Driest Quarter	(°C)	me2
bio10	Mean Temperature of Warmest Quarter	(°C)	me2
bio11	Mean Temperature of Coldest Quarter	(°C)	me2
bio12	Annual Precipitation Sum	mm	me2, me3
bio13	Precipitation of Wettest Month	mm	me2
bio14	Precipitation of Driest Month	mm	me2
bio15	Precipitation Seasonality (Coefficient of Variation)	mm	me2
bio16	Precipitation of Wettest Quarter	mm	me2
bio17	Precipitation of Driest Quarter	mm	me2
bio18	Precipitation of Warmest Quarter	mm	me2
bio19	Precipitation of Coldest Quarter	mm	me2

Table 4 The distribution-limiting extrema of *Phlebotomus mascittii* and the union of the other *Transphlebotomus* species used in the different model environments (**Variable Ph masc**: the climatic distribution-limiting extrema of *Phlebotomus mascittii*; **Variable other-TransPhleb**: the climatic distribution-limiting extrema of the union of other *Transphlebotomus* species).

Variable Ph masc	min	max	Variable other-TransPhleb	min	max
T_{m01}	-3.3	8.9	T_{m01}	-3.0	12.9
T_{m07}	16.3	24.1	T_{m07}	18.7	28.0
$P07$	0	126	$P07$	0	47
bio1	8.0	16.0	bio1	8.4	20.0
bio2	7.0	10.5	bio2	6.1	13.4
bio9	-0.9	23.9	bio9	2.2	28.1
bio10	16.1	23.9	bio10	17.0	28.3
bio11	-1.4	9.9	bio11	-1.6	12.9
bio12	536	1463	bio12	343	1052
bio13	63	172	bio13	57	231
bio14	9	82	bio14	0	27
bio15	11.2	47.8	bio15	21	115
bio16	181	475	bio16	146	6410
bio17	45	290	bio17	0	89
bio18	70	419	bio18	0	140
bio19	103	335	bio19	89	610

by Papadopoulou et al. (2010). The output of BEAST was analysed in TRACER v1.7.1. A maximum clade credibility tree (based on the maximum clade credibility consensus tree method; O’Reilly and Donoghue 2018) was estimated

with TREEANNOTATOR v1.10.4 (Drummond and Rambaut 2007) and visualized with FIGTREE v1.4.4 free online software (<http://tree.bio.ed.ac.uk/software/figtree/>) showing divergence times (% per myr) and 95% highest posterior densities (HPDs).

Results

The modelled Tortonian ranges

The model results suggest that a *Ph. mascittii*-like species could have inhabited wide regions of Central and East Europe, the southern regions of Northern Europe and the mountainous regions of the Balkans and Asia Minor in the Tortonian stage. The potential Tortonian range of the species, which had similar climatic requirements to the present-day *Ph. mascittii*, could have formed a continuous area in the present-day continental regions of Europe, and the potential former lowland and mid-elevation occurrences can be seen north of the Central and East Paratethys. The potential area of such sandfly species which had similar climatic requirements like the union of the present-day *Ph. anatolicus*, *Ph. canaaniticus*, *Ph. economidesi*, *Ph. killicki*, and *Ph. simonahalepae* (hence: ‘non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa’) seem to be quite fragmented and predominantly restricted to some regions of Central Europe, the former northern coastline of the East Paratethys region, Anatolia, and the Zagros Mts. (Fig. 5).

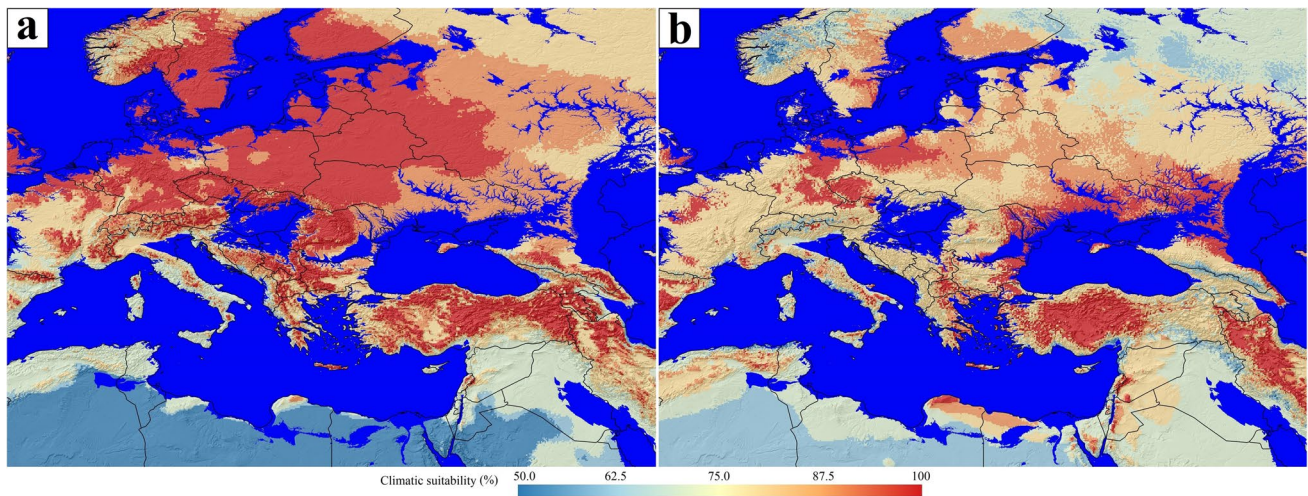


Fig. 5 The modelled climatic suitability values of *Phlebotomus mascittii*-like (a) and ‘non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa’ (b) in the Tortonian period

Messinian climatic suitability values

The models suggest that in the Messinian period, a sandfly species with the climatic needs of the extant *Ph. mascittii* could have occupied large regions of East, Central and South Europe, excluding the Mediterranean coastlines, as well as Asia Minor. The range of an ancestral sandfly species had similar climatic requirements as the present-day ‘non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa’ and could have been restricted to the coastline of the East Mediterranean Basin, including the Aegean area, Asia Minor, and the Levant. The model results indicate that the ancestors of ‘non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa’

could occur in the desiccated Aegean seafloor, but it is not probable that they would have inhabited the deeper parts of the desiccated Mediterranean Basin (Figs. 6 and 7).

The potential mid-Pliocene distribution areas

The potential mid-Pliocene cold period’s range of a *Ph. mascittii*-like species based on the former climatic suitability values is focused predominantly on Western Europe, including, e.g. the territory of the present-day British Islands, the Dogger Bank region, and South France. The potential mid-Pliocene cold period’s range of a non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa could have

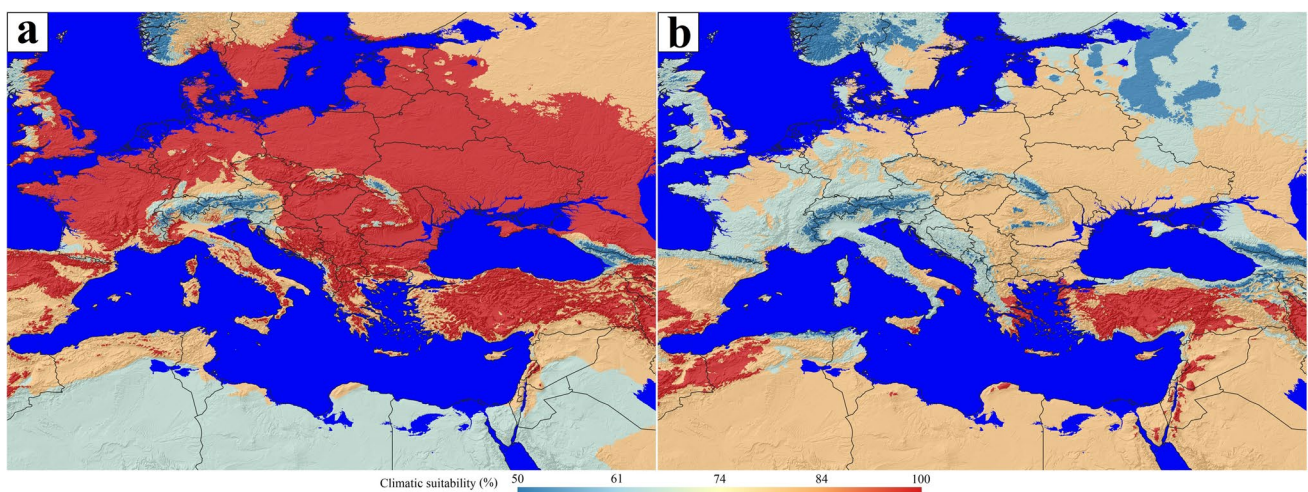


Fig. 6 The modelled climatic suitability values of *Phlebotomus mascittii*-like (a) and ‘non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa’ (b) in the Messinian period in the case of a flooded Mediterranean Basin

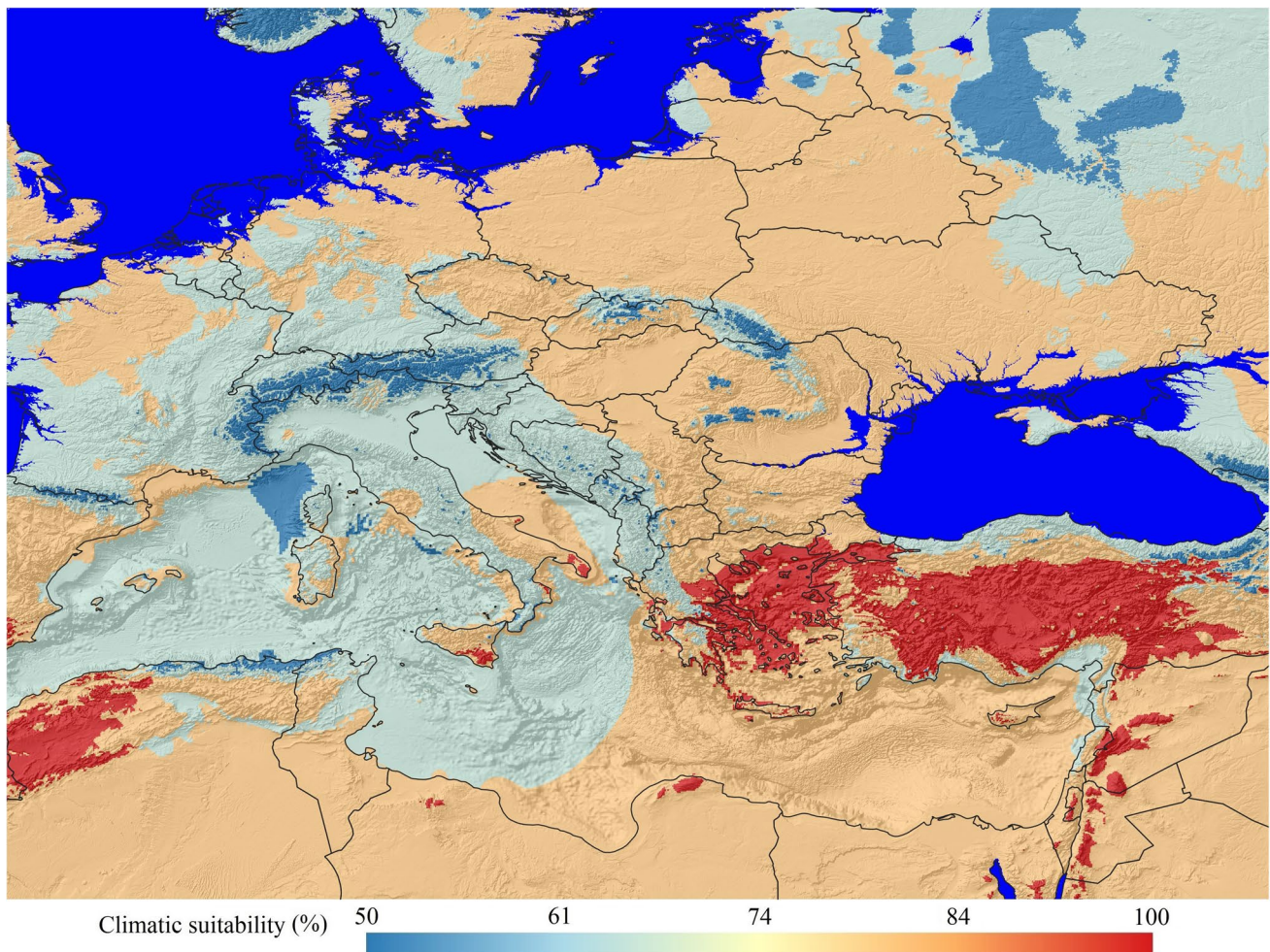


Fig. 7 The modelled climatic suitability values of ‘non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa’ in the Messinian period in the case of a desiccated Mediterranean Basin

shown the highest affinity to the area of present-day Eastern England, France, the Iberian Peninsula, Asia Minor, the South Apennine Peninsula, and certain regions of North Africa (Fig. 8).

In the mid-Pliocene warm period, the potential range of a *Ph. mascittii*-like species could have covered large regions of West and Central Europe, including, e.g. the northern and central regions of present-day France, Central Germany, the southwest part of Scandinavia, the Transdanubian part of Hungary and Transylvania. In contrast, the potential mid-Pliocene warm period’s climatic suitability values of a non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa show a markedly different picture, being restricted to certain Mediterranean regions of Europe, including certain parts of the Iberian, the Apennine and the Balkan Peninsulas, Asia Minor, the Mediterranean islands like Corsica, Sardinia and Sicily and certain smaller Northwest African and Levantine regions (Fig. 9).

The potential Pleistocene distribution ranges

The modelled MIS19 period’s potential range of a *Ph. mascittii*-like species is somewhat like the present-day occurrence of the species, which covers large regions of West and Central Europe (Fig. 10a). However, the model suggests that in this period, the climatic suitability of the Mediterranean peninsulas could be lower for the species than today. In the Last Interglacial Period, a *Ph. mascittii*-like species could occur in Western Europe, including the wider coastal regions of the Bay of Biscay, North France and the southern area of the Benelux states, the milder regions of the British Isles and maybe some mountainous regions of the Apennine Peninsula (Fig. 10b). During the Last Glacial Maximum, the climatically suitable areas for a *Ph. mascittii*-like species could be restricted to the narrow, currently partly submerged shelf and coastal regions of the Mediterranean Sea including the territories around

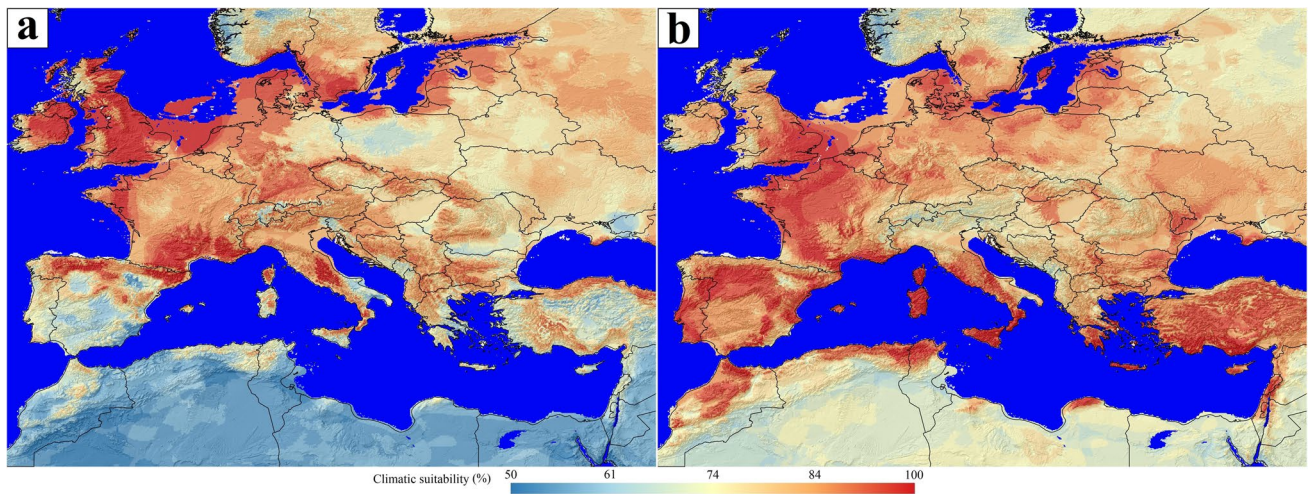


Fig. 8 The modelled climatic suitability values of a *Phlebotomus mascittii*-like species (a) and a non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa (b) in the mid-Pliocene cold period

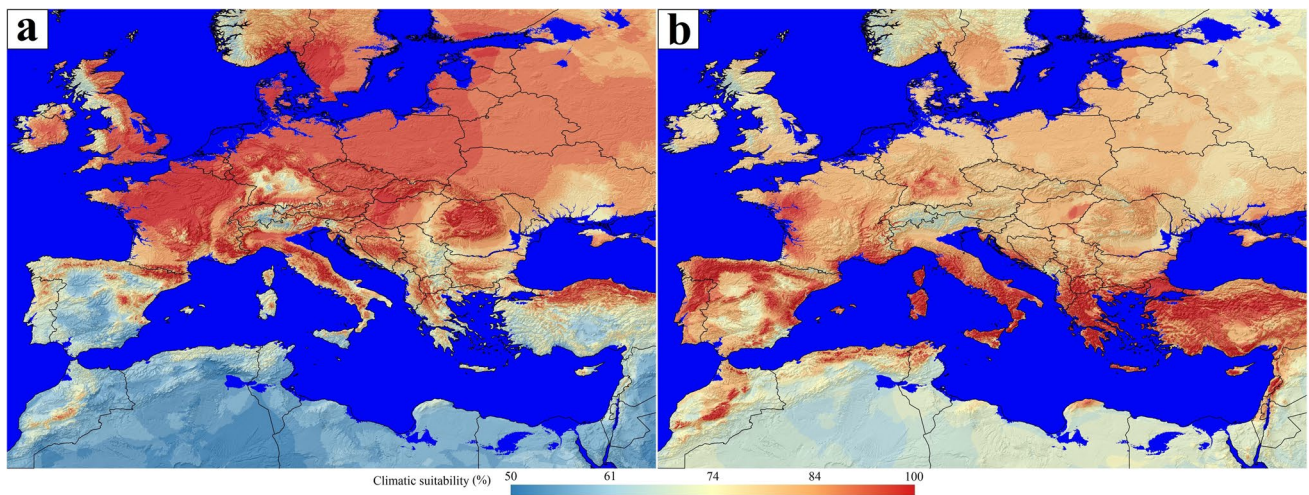


Fig. 9 The modelled climatic suitability values of *Phlebotomus mascittii*-like species (a) and a non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa (b) in the mid-Pliocene warm period

the Gulf of Lyon or the currently submerged Adriatic Plain and other shelves of the Apennine Peninsula (Fig. 10c).

As of today, in the MIS19 period, the potential range of a non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa could cover the Mediterranean territories, including large regions of the South Balkan, the Apennine, and the Iberian Peninsulas, as well as some North African and Levantine territories and the western and central part of present-day France (Fig. 10d). In the Last Interglacial Period, a non-*Ph. mascittii*-like *Transphlebotomus* species could inhabit large regions of present-day southern Europe and Western Europe (Fig. 10e). For the Last Glacial Maximum, the potential area of a non-*Ph. mascittii*-like *Transphlebotomus* species could be restricted to South Europe (Fig. 10f).

Divergence time estimates

Based on the rejection of the null hypothesis of the equal evolutionary rate at a 5% significance level ($p < 0.0001$), BEAST analysis was conducted under a lognormal, uncorrelated relaxed clock model. The determined tree topology divides the studied *Transphlebotomus* species into two major clades. The first clade consists of *Ph. anatolicus* and *Ph. canaaniticus*. *Phlebotomus mascittii*, *Ph. killicki*, *Ph. economidesi* and *Ph. simonahalepae* form the second clade. In the second clade, *Ph. mascittii* is the sister taxon of the other sandfly species. Divergence time estimates of the six *Transphlebotomus* species ranged from 5.4 to 10.9 mya. The divergence between clade I and clade II could happen ca.

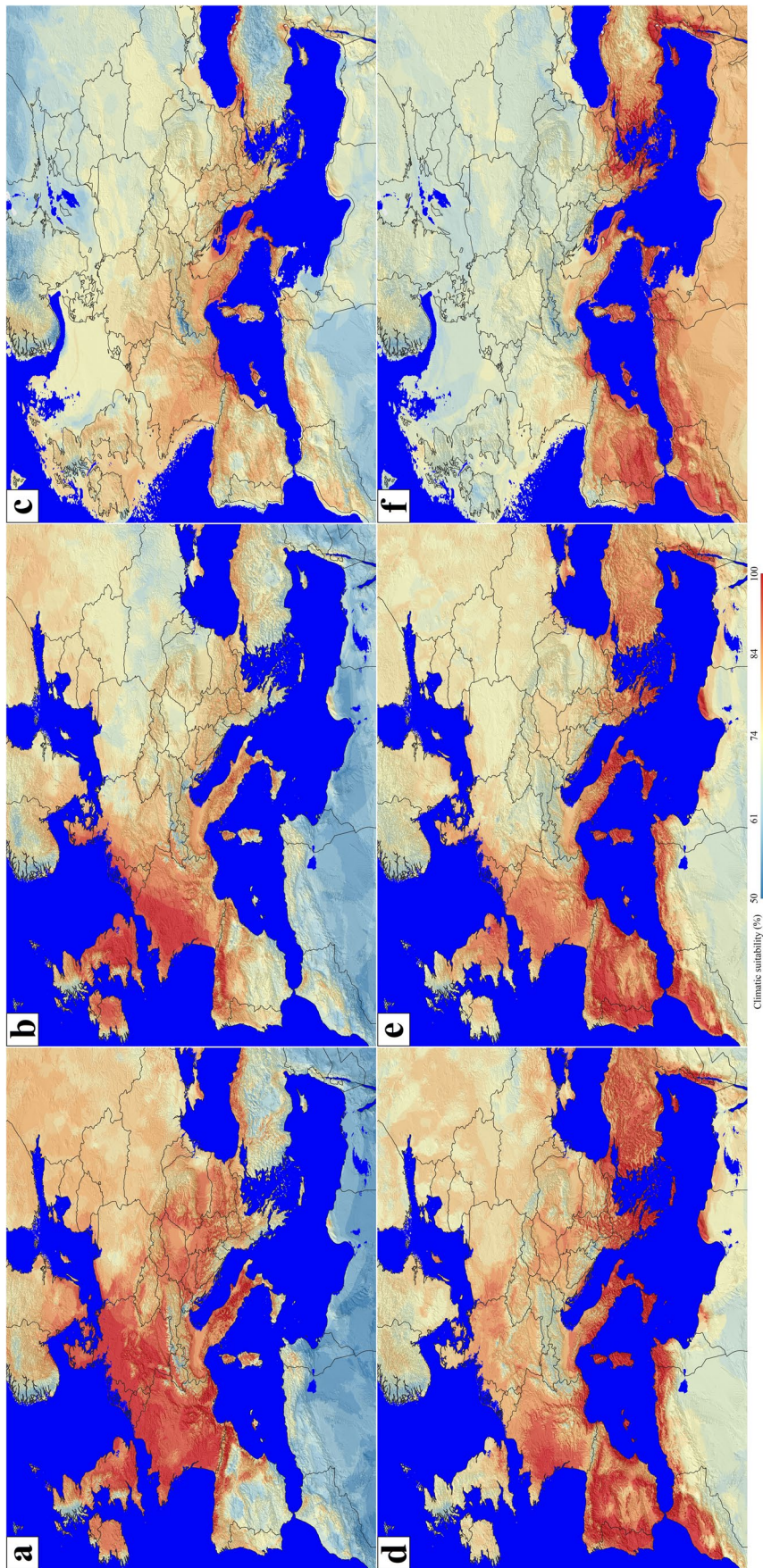


Fig. 10 The modelled climatic suitability values of a *Phlebotomus mascittii*-like species in the MIS19 Pleistocene interglacial (a), the Last Interglacial (b) and the Last Glacial Maximum period (c). The similar values of a non-*Ph. mascittii*-like *Transphlebotomus* sandfly taxa in the MIS19 Pleistocene interglacial (d), the Last Interglacial (e) and the Last Glacial Maximum Period (f)

10.9 mya (95% HPD interval = 7–16). Within clade I, the estimated split of *Ph. anatolicus* and *Ph. canaaniticus* happened 5.6 mya (95% HPD interval=3.2–8.8). Within clade II, the first split between *Ph. mascittii* and the other lineages (*Ph. killicki*, *Ph. economidesi*, and *Ph. simonahalepae*) was estimated at approximately 9.5 mya (95% HPD interval = 5.9–14.3), the second split between *Ph. killicki* and *Ph. economidesi* + *Ph. simonahalepae* at around 7.4 mya (95% HPD interval = 4.4–11.2), and the last split between *Ph. economidesi* and *Ph. simonahalepae* at approximately 5.4 mya (95% HPD interval = 3.1–8.3) (Fig. 11).

Discussion

The model results suggest that if the ancient *Transphlebotomus* populations had similar climatic tolerance to their extant offspring, their Late Miocene range could have covered both the North and the South sides of the Central and east Paratethys Seas. Several authors claimed that the Paratethys realm played a very important role in the Neogene evolution of the Mediterranean sandfly species and the speciation of the present-day clades (Steininger and Rogl 1984; Léger and Pesson 1987; Marchais 1992; Essegir et al. 1997; Depaquit et al. 1998, 2002; Trájer 2022a, b). The Paratethys Sea became a semi-locked sea approximately 30–35 Ma during the lower Oligocene epoch when it had several narrow connections to the Atlantic and the Mediterranean Seas via, e.g.

the Rhine Graben, the Rhone Strait, and the Slovenian Strait (Palcu 2018). Later, due to the rise of the Alpine and Dinaric Mountain systems, the Paratethys lost its direct connections to the epicontinental seas. After the close of the Slovenian Strait in the early Serravallian, it became an intermittently isolated or semi-isolated sea (Palcu et al. 2015). The connection between the Paratethys Sea and the global seas was re-established due to the formation of the Mid-Aegean trench ca. 12 mya (Popov et al. 2006), which also formed a significant barrier against the migration of invertebrate species (Simaiakis and Mylonas 2008; Papadopoulou et al. 2010). From this era, the Central and the East Paratethys partly divided the Eastern European and Southwest Asian fauna.

However, at the turn of the late Middle – early Late Miocene epochs, the isolation only became partial in the westernmost part of the Central Paratethys area since a narrow land bridge was formed between the Balkans and the Alps due to the rise of the mountain systems (Kováč et al. 2017). Based on the phylogenetic results of this study, it is very plausible that this geographical change led to the north-westward spread of ancient *Transphlebotomus* populations and the speciation of *Ph. mascittii*. With the formation of the Aegean trench, these large-scale geographical processes could also explain the appearance of the *Ph. killicki*-*Ph. economidesi*-*Ph. simonahalepae* clade in the Aegean area. It should be noted that the phylogenetic results of the study are following the ML analysis-supported previously published cytb tree topologies (Kasap et al. 2015; Cazan

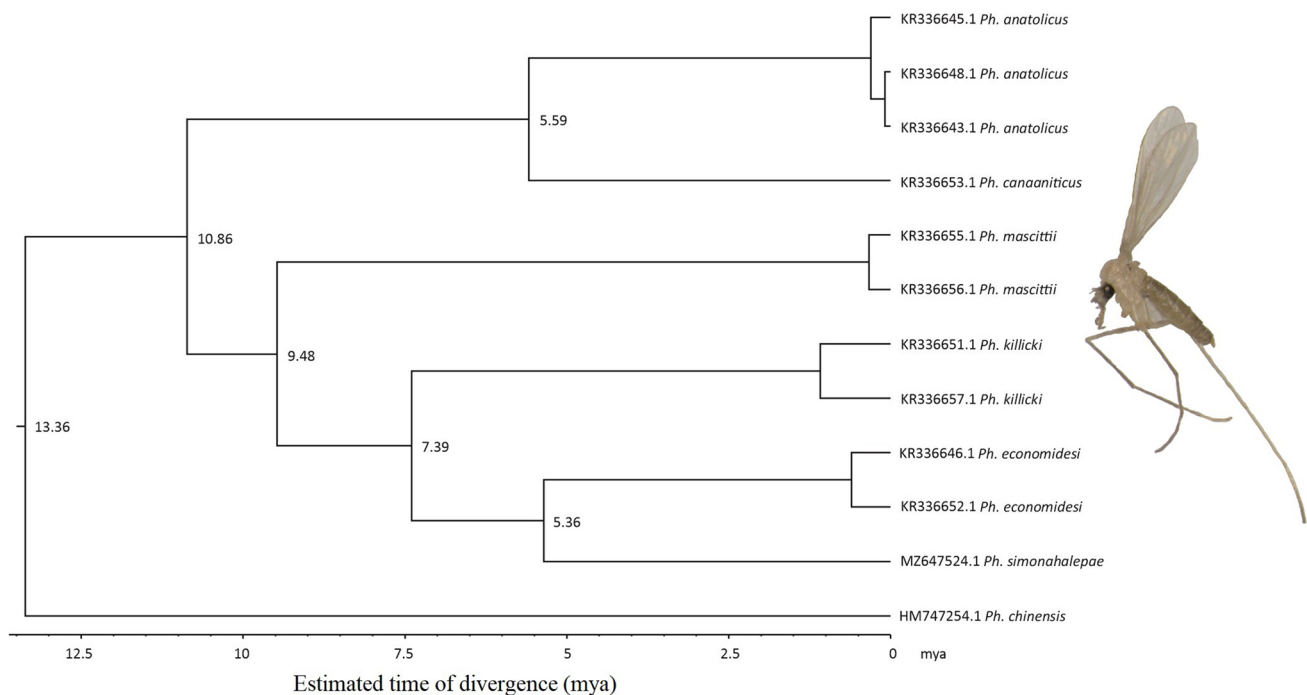


Fig. 11 Phylogenetic analysis of cytb from *Ph. anatolicus*, *Ph. canaaniticus*, *Ph. economidesi*, *Ph. killicki*, *Ph. mascittii*, *Ph. simonahalepae*, and *Ph. chinensis* as outgroup with the estimated divergence times

et al. 2021), which divided *Transphlebotomus* species into two major clades. While clade I consisted of *Ph. anatolicus* + *Ph. canaaniticus*, clade II comprised all other *Transphlebotomus* species (*Ph. mascittii*, *Ph. killicki*, *Ph. economidesi*, and *Ph. simonahalepae*). *Ph. economidesi* and *Ph. simonahalepae* were confirmed as sister species.

The calculated appearance times suggest that both the divergences of the *Ph. anatolicus*–*Ph. canaaniticus* (5.59 mya) and the *Ph. economidesi*–*Ph. simonahalepae* (5.36 mya) approximately coincides with the Messinian Salinity Crisis (~5.96 to 5.33 mya; Gautier et al. 1994). The possible role of the Messinian Salinity Crisis on the speciation of sandfly species was suggested by many authors (Kasap et al. 2015; Cruaud et al. 2021; Trájer et al. 2021; Pavlou et al. 2022).

The distribution of terrestrial mammals strongly supports zoogeographical and land connections in the Mediterranean between the mainland areas and the Mediterranean islands (Azzaroli and Guazzone 1979). It is known that after backstripping the Pliocene–Quaternary and the evaporite layer, the Pre-Messinian seafloor was generally 1800–1900 m deep (Netzeband et al. 2006) However, notably deeper areas also could have existed, e.g. in the Hellenic Trench (the current deepest point: Calypso Deep, 5,110 m u.s.l.). Considering the physiological-thermal tolerance of sandflies, it seems problematic because it is hard to explain how the relatively sensitive sandflies survived and spread in the bottom of the extremely hot Mediterranean basin (Trájer et al. 2021). For comparison, on the coast of the present-day Dead Sea, the mean annual temperature is 24°C, the average temperature of the warmest quarter is 32°C, and the annual precipitation is about 300 mm (Harris et al. 2014). On the Gaza coasts, around 100 km to the west of the Dead Sea coasts, at sea level, these values are about 21°C, 27°C and 480 mm. Differences in the climatic conditions exist at the approximately -435 meters elevation difference between the sea-level elevation sites of the Eastern Mediterranean Sea at Gaza and the coastal regions of the salt lake.

The desiccated Mediterranean Basin generally could have been more than four times deeper than the present-day Dead Sea or even deeper. Since – as was mentioned – the adiabatic temperature change is 0.65°C per 100 m (Ritter 2006), it can be calculated that the annual mean temperature of the Mediterranean seafloor could have been at least 12°C higher than the former 0 m level territories which were 25 m higher than today (Dwyer and Chandler 2009). These harsh conditions could have posed unsolvable problems for ancient sandfly species even if we know that they can live in certain hot, semi-arid regions like the Negev in Israel (Schlein et al. 1984) or Central Tunisia (Barhoumi et al. 2016). On the other hand, large areas of the seafloor – including the Algerian, the Balearic, the Ionian, and the Levantine sub-basins – could have been covered by hypersaline residual

lakes according to the occurrence of large covered evaporitic formations (Rouchy et al. 2006). The most probable free migration route could have existed between present-day Tunisia, Sicily, and Calabria.

Based on the ideas, and results discussed above, the following hypotheses can be set related to the Late Miocene Late Pleistocene speciation and migration events of the Mediterranean *Transphlebotomus* species:

1. The first splits of *Transphlebotomus* fall into the Tortonian stage (11.608–7.246 mya) of the Late Miocene epoch. Since some species of the sister genus *Adlerius* are present in the Balkan region, a common ancestor of *Transphlebotomus* and *Adlerius* could have been present throughout Eastern Europe, the Balkan region in the wider sense and Asia Minor. Before the divergence, the ecological claims of the common ancestor could have been like those of present-day sandfly species, which occupy semi-humid subtropical, warm temperate climate regions with hot and relatively dry summers.
2. After the split of *Ph. mascittii*, the species could have already migrated all over Europe. In contrast, the other *Transphlebotomus* species remained in areas likely south of the Central and the East Paratethys seas. Under its northwest migration, *Ph. mascittii* could have adapted to the cooler but more balanced ocean-affected humid tropical climate of the Late Miocene West-central and Western Europe. This assumption is supported by the phylogenetic results, which show that *Ph. mascittii* in phylogenetical sense is wedged to those *Transphlebotomus* taxa which require relatively high annual mean temperature and tolerate the hot and rainless summers of the East Mediterranean territories.
3. The unique geographical conditions of the Messinian stage of the Late Miocene epoch might have supported the dispersal of *Ph. mascittii* via former Gibraltar or the Pantelleria land bridge. However, both the model results of the later periods call into question whether the species may have persisted between North Pliocene and Middle Pleistocene at all in North Africa. On the other hand, the results indicate that the extremely hot climate of the desiccated basin did not make possible a direct crossing to North Africa or the other Mediterranean islands.
4. The other ancient *Transphlebotomus* species colonised the coastal areas of the South Balkan and Asia Minor, the presently flooded northern Aegean seafloor and certain, also coastal Levantine territories during the Messinian stage. The split of *Ph. economidesi* and *Ph. simonahalepae*, dated to the end of Messinian can also be related to the Messinian Salinity Crisis. The ancient *Transphlebotomus* species, including the common ancestor of *Ph. economidesi* and *Ph. simonahalepae*, probably dispersed northwards only at the end of Messinian.

It must be acknowledged that apart from only one record, *Ph. simonahalepae* might be cavernicolous (Cazan et al. 2021), which means that it might have special requirements (climatically and ecologically in general). It also explains that the climate of the mid-Pliocene warm period seems unsuitable for *Transphlebotomus* in Romania and Bulgaria; however, *Ph. simonahalepae* could have survived in caves, a more stable environment. Caves can provide adequate shelter for extrazonal sandfly populations to survive in continental areas. For example, *Phlebotomus (Larrousius) perfiliewi* Parrot, 1930 from Esztergom, North Central Transdanubia, Hungary and the Gellért Hill cave, Budapest, were found in Hungary in the 1960s (Tánczos 2012; Trájer 2017) and *Ph. neglectus* uses the fissures of an abandoned quarry in Southern Transdanubia, Hungary, as shelters (Trájer et al. 2018a) plausibly to survive the cool winters of the area. As another example, *Ph. mascittii* is active year-round in Corsica as it lives in a cave-like habitat (tunnel) with stable climatic conditions all year (Naucke et al. 2008). As was mentioned, the presence of *Ph. mascittii* in Northern Africa raises questions. At first, it can be mentioned that the species is only known from one localization from the area (Berdjane-Brouk et al. 2011).

It is not surprising that Mediterranean sandflies, which occur in Southern Europe, can also be found in Northern Africa. For example, *Phlebotomus (Paraphlebotomus) alexandri* Sinton, 1928, *Phlebotomus (Larrousius) perniciosus* Newstead, 1911, *Phlebotomus (Phlebotomus) papatasi* (Scopoli, 1786), *Phlebotomus (Larrousius) ariasi* Tonnoir, 1921, *Ph. perfiliewi* and *Phlebotomus (Paraphlebotomus) sergenti* Parrot, 1917 can be found on both, the European and the African sides of the Mediterranean Sea (ECDC 2022). Among them, *Ph. perniciosus* and *Ph. ariasi* have a somewhat similar distribution in the West Mediterranean region in that sense that they are absent in the East Mediterranean Basin but occur on the West Mediterranean coastlines both in Africa and Europe. This can be a consequence of a similar evolutionary and palaeozoogeographical history. It is plausible that before the Messinian epoch, *Ph. ariasi* and *Ph. perniciosus*, which together form a so-called ‘West-Mediterranean group’ were adapted to the more humid and balanced climate of Southwestern Europe (Trájer et al. 2018b).

It is plausible that *Ph. mascittii* were also adapted to somewhat similar conditions in the Late Miocene era in the West Mediterranean Basin. The presence of the species in Corsica (Naucke et al. 2008), Sardinia (Biocca et al. 1977), Sicily (Lisi et al. 2014), and Montecristo (Zanet et al. 2014) raises the question of when and how this species dispersed to these islands. The cooler or humid climatic events of the Messinian stage might have formed a dried-up corridor for migration events; however, this was not shown in the models for average climatic conditions. In addition, the close genetic distances (cytb) of *Ph. mascittii* from Corsica and mainland

Europe suggest a more recent dispersal to the island rather than during the Messinian (Kniha et al. 2020). Model results show that during the humid and tempered climate of the Late Pliocene Glacial Event (Marine Isotope Stage M2) in Europe, *Ph. ariasi* and *Ph. perniciosus*-like ancestral sandfly species could have covered large regions of Europe ca. 3.3 mya, the large potential range area of which collapsed suddenly at the start of the warm mid-Pliocene warm period 3.205 mya (Trájer 2020). The mid-Pliocene climatic fluctuations could also have caused notable stress for ancient populations of *Ph. mascittii* which can explain why isolated populations remained in North Africa. However, it is questionable whether the later glacial-interglacial climatic fluctuations could support the survival of the North African populations. It should be noted that in the case of island populations, late anthropogenic transport also cannot be excluded from the Neolithic period. However, natural transport media like trees floating on the water surface could also have promoted the dispersal of Mediterranean sandflies (Trájer 2021).

It is striking that since *Ph. mascittii* diverged from the *Ph. killicki-Ph. economidesi-Ph. simonahalepae* clade as early as ca. 9.5 mya in the Tortonian stage of the Late Miocene, and the model results suggest that the climatic conditions of the warmer periods of the Neogene theoretically could make it possible for the eastward migration of the species to the Balkans, it has never been recorded in continental Greece. *Phlebotomus mascittii* plausibly formed from the division of the ancestral *Transphlebotomus* population due to the separation effect of geographic barriers. The barrier originally could be the Central Paratethys, and later, it was formed by the emerging Dinarids and the Alpine Mountain ranges. The investigation of the Late Miocene mammal faunas (e.g. Ataabadi et al. 2016) and palaeovegetation models (e.g. Pound et al. 2011) revealed that in the Tortonian, two major biomes existed in Western Eurasia: the zone of dense, humid, subtropical temperate forests which flourished predominantly in Central Europe and the Apennine Peninsula, and a woodland-shrubland biome zone with relatively open vegetation, which was characteristic to the South Balkan and Anatolia. At that time, temperate forests were present above 60°N, and warm-temperate mixed forests covered much of Europe and South-East Asia (Pound et al. 2011). As described above, the ancestors of *Ph. mascittii* plausibly were adapted to this environment.

In the latest Miocene, the increasing aridity caused the decline of subtropical forests thorough the mid-latitude regions of Eurasia (Nelson 2021; Habinger et al. 2022). This event could play a central role in the Late Miocene diversification of *Transphlebotomus* species, establishing the differences between the climatic requirements of the ancestors of *Ph. mascittii* and the other *Transphlebotomus* species. Although in the first part of the Pliocene period, the climate of such Central European regions like

the Carpathian Basin was still mild and humid, supporting mesophytic forest (Erdei et al. 2007), which could be a suitable habitat for a *Ph. mascitti*-like sandfly species (see Fig. 9a). However, the Late and mid-Pliocene cooling events created relatively cool and dry climatic conditions in Central Europe, which narrowed the occurrence of the ancestral *Ph. mascittii* populations to South-Eastern Europe and Anatolia; and the non-*Ph. mascittii* populations to the oceanic climate-influenced regions of Western Europe (Fig. 8b). For the MIS19 interglacial, a wide range gap could exist between the ancestors of *Ph. mascittii* and the other *Transphlebotomus* species, which became wider for the Late Pleistocene (Fig. 10). This distribution gap and the different climatic adaptation of *Ph. mascittii* and its relatives can probably explain the distribution differences seen today, including the distribution patterns of *Ph. mascittii* and other *Transphlebotomus* taxa in the Balkans.

The late Quaternary models suggest that even in such interglacial periods as the Last Interglacial, a *Ph. mascittii*-like sandfly species could not reach its current, wide European range, which covers Central Europe. Instead, the potential area of the species covered the present-day milder oceanic climate regions of Western Europe. The glacial maximums could lead primarily to the serious habitat loss of *Ph. mascittii*, the other *Transphlebotomus* populations could find relatively large refugia in South Europe and Anatolia. The more expressed vulnerability of a *Ph. mascittii*-like to the period can be explained by the fact that the extant species dominantly occupy temperate seasonal forest biome-covered regions in Europe (compare the *Ph. mascittii* occurrences in Fig. 1 with the present-day potential natural vegetation map of Hickler et al. 2012). However, the temperate mixed broad-leaved forests and thermophilous mixed broad-leaved forests were significantly shrunk and retreated to Southern Europe during the Last Glacial Maximum (Svenning et al. 2008; Trájer 2022a). The glacial retreat of the humid, mild-climate forest habitats should have caused a significant genetic bottleneck effect in the case of the ancestral *Ph. mascittii* and other *Transphlebotomus* populations. It is worth mentioning that similar glacial refugia, as shown in Fig. 10c and f can also be hypothesised in the case of other European sandfly taxa in Southern Europe, including the Iberian Peninsula, territories north of the Pyrenees, the coastal regions of the Apennine Peninsula, the South Balkan, and the Aegean islands and Western Anatolia (Aransay et al. 2003; Mahamdallie et al. 2011; Depaquit et al. 2015; Trájer and Sebestyén 2019). Finally, it can be added that further phylogenetic studies are needed to elucidate where glacial refugia existed in southern Europe and how post-glacial warming impacted the northward migration of the ancestral populations of the extant *Transphlebotomus* species.

Conclusions

Transphlebotomus species could have emerged in the Late Miocene in the Aegean-Asia Minor area. In the Tortonian stage, certain *Transphlebotomus* populations may have crossed Central Paratethys over the Dinaric land bridge, and this population became the founder of the later *Ph. mascittii* species. In parallel, the formation of the Aegean trench could have led to the emergence of other *Transphlebotomus* species. These geological processes dissected the ancestral *Transphlebotomus* populations into a European, Balkan and Asia Minor-Levantine group. Due to the desiccation of the Mediterranean Sea in the Messinian stage, the ancestors of *Ph. mascittii* perhaps could have migrated to Northern Africa during the cooler and more humid periods. However, the model results, which were based on the general climatic conditions, do not support this hypothesis. The Messinian Salinity Crisis triggered the speciation of several East Mediterranean *Transphlebotomus* taxa.

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Data availability statement The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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