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Original article

Hyalomma aegyptium: Observed global distribution, imported specimens, preferred hosts and vector competence

Franz Rubel

Climate Change & Infectious Disesases Group, University of Veterinary Medicine Vienna, Veterinaerplatz 1, Vienna, 1210, Austria

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ABSTRACT

The tortoise tick *Hyalomma aegyptium* (Linnaeus, 1758) is a three-host tick, predominantly infesting land tortoises of the genus *Testudo*. A database was compiled, resulting in 557 *H. aegyptium* georeferenced locations in the Palearctic. This dataset covers the entire range of *H. aegyptium* for the first time. Thus, the natural distribution area of *H. aegyptium* extends from Morocco in northwestern Africa to Kyrgyzstan in Central Asia between 10° W–73° E and 28–46° N, which is shown in an overview map and four detailed maps covering North Africa, the Balkans, the Near East, and the Middle East. In addition, documented findings on land tortoises that have been exported worldwide as popular pets give an impression of the occurrence of *H. aegyptium* outside its natural distribution. The host species is known from 424 mapped *H. aegyptium* locations, which can be ranked as follows: 92.9% *Testudo* spp., 4.0% mammals (mainly hedgehogs and hares), 1.7% humans, 0.9% lizards and 0.5% birds. If only tortoise hosts are considered, these are 92.6% *Testudo graeca*, 3.8% *Testudo hermanni*, 2.8% *Testudo horsfieldii* and 0.8% *Testudo marginata*. It is striking that no infestation with *H. aegyptium* has been detected on *Testudo kleinmanni* in their natural habitat, but it was detected on imported specimens in Malta and the USA. Although numerous tick-borne pathogens have been detected in *H. aegyptium*, vector competence, i.e. the experimentally proved transmission of pathogens from the vector to the host, could only be demonstrated for three pathogens. These are the two blood parasites *Hemolivia mauritanica* and *Hepatozoon kisrae* as well as *Coxiella burnetii*, the causative agent of Q fever.

1. Introduction

The geographical distribution of the tortoise tick *Hyalomma aegyptium* (Linnaeus, 1758) is relatively well known, but has not yet been published in detail. So far, two maps have been published showing georeferenced locations of *H. aegyptium*. The first map by Feider (1965) shows an idealized representation of 22 locations between Tunisia in the west and Turkmenistan and Uzbekistan, the region south of the Aral Sea, in the east. This map lacks the now well-documented sites in the western Mediterranean, especially in Algeria and Morocco. The second, more up-to-date map by Mihalca et al. (2017) shows significantly more proved locations, but goes only as far as to the Russian Black Sea coast and Türkiye in the east. A further map, published online by Kolonin (2009), did not contain any georeferenced tick locations but estimated the full range of *H. aegyptium* (Fig. 1). In summary, there is no map that covers the entire known distribution area of *H. aegyptium* based on georeferenced findings. However, there is a current list on the geographic distribution of *H. aegyptium* by countries and territories (Guglielmone et al., 2023).

Hyalomma aegyptium is a three-host tick (Široký et al., 2006), with all postembryonic life stages predominantly infesting land tortoises of the genus *Testudo*. It has been found in the same habitats as its tortoise hosts in Mediterranean and steppe climates, as well as on the edges of hot deserts. Infested tortoises are the Greek tortoise, also commonly known as the spur-thighed tortoise *Testudo graeca*, the Hermann's tortoise *Testudo hermanni*, the Horsfield's tortoise, also known as Russian tortoise, Afghan tortoise or four-clawed tortoise *Testudo horsfieldii*, the Kleinmann's tortoise, also called the Egyptian tortoise *Testudo kleinmanni*, and the marginated tortoise *Testudo marginata*. Their current natural distributions have been documented by Rhodin et al. (2021). Tortoises of the genus *Testudo* have long been exported into many countries around the world to be kept as pets. In climatically suitable regions they are often kept in gardens or released into the wild, for example, *T. graeca* in Spain (Brotóns and Estrada-Peña, 2004; Estrada-Peña, 2024). Schulze (1930) already noted that *H. aegyptium* can be found worldwide on imported *T. graeca*, especially the males, as they attach themselves to the host's shell and often remain on the tortoises for months. Field observations of *T. graeca* in Jordan revealed that the usual sites of *H. aegyptium* attachment were around the back legs and tail of the host. Of the ticks found on damaged tortoises one third was attached to fractures in the carapace

E-mail address: franz.rubel@vetmeduni.ac.at.

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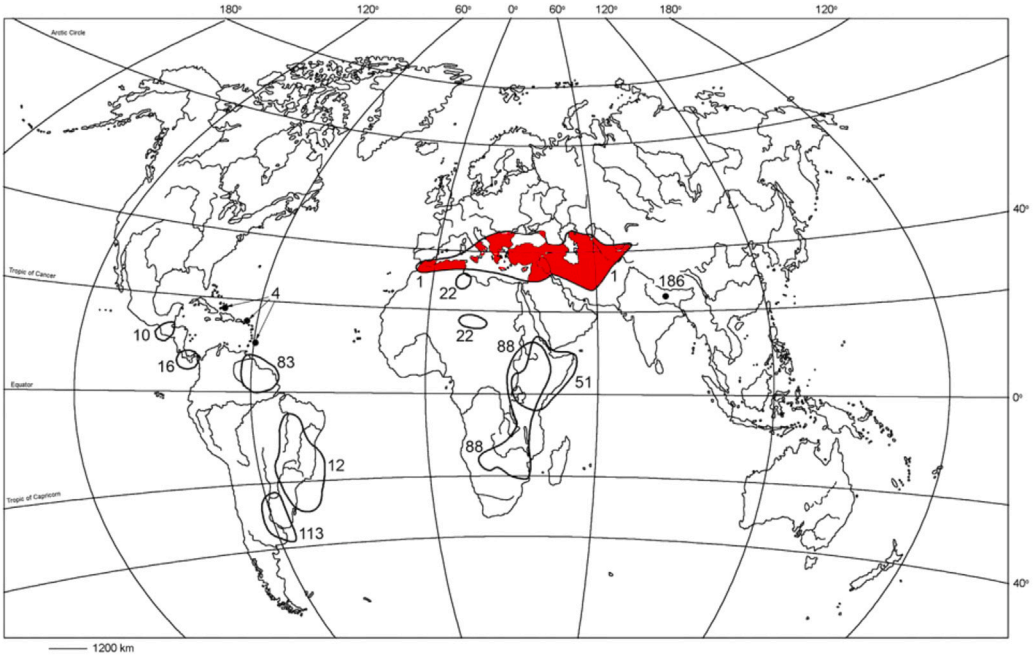

Fig. 1. Global geographical distribution of *Hyalomma aegyptium* (red area, 1), adapted and coloured from the no longer available online tick atlas by Kolonin (2009). Contour lines and dots provided with different numbers indicate the distribution of other tick species not used here.

or plastron, nearly two thirds attached to the rear and only a few to the front (Petney and Al-Yaman, 1985). Besides tortoises, lizards, hedgehogs and hares are the second most mentioned hosts of all active life stages (Schulze, 1930; Pomerantzev et al., 1940; Hoogstraal, 1956; Sweatman, 1968). In addition to the hosts mentioned above, larvae also infest rodents and birds, giving them the widest host range of all parasitic life stages (Apanaskevich, 2003). However, long lists of hosts have also been published in the past, all of which were incorrect (Hoogstraal, 1956). They come from historical records in which various *Hyalomma* species were grouped under the name *H. aegyptium*, while for the tortoise tick the synonym *Hyalomma syriacum* Schulze 1920 was used for a time. These confusions are still present in some current publications.

Illustrations and morphological characteristics of *H. aegyptium* were described by Apanaskevich (2003). A molecular characterization of *H. aegyptium* in comparison to five other *Hyalomma* species was recently presented by Roth et al. (2019).

The temperature-dependent development of *H. aegyptium* was investigated in detail by Sweatman (1968), Sweatman and Gregson (1970). They found that oviposition is most successful between 20 and 35° C, and nymphs being able to engorge only at temperatures above 20° C. The life cycle of *H. aegyptium* may be completed within five months (Široký et al., 2011), whereby adult ticks are active from April to July, and larvae from June to August (Pomerantzev et al., 1940). In the Turkish region of Thrace, the highest bite rates in hospitalized human patients were recorded by adult *H. aegyptium* in June and by nymphal *H. aegyptium* from August to September (Gargili et al., 2010).

Although several pathogens have been detected in *H. aegyptium* (Bonnet et al., 2023), vector competence, i.e. the experimentally proved transmission of pathogens from the vector to the host, is incompletely listed in that review. Conversely, the list of pathogens detected in *H. aegyptium* provided by Mihalca et al. (2017) requires critical revision, not least because of the confusion regarding the identification of *H. aegyptium* discussed above. Therefore, revised tables on detected pathogens and the vector competence of *H. aegyptium* are compiled here. Essentially, however, this article presents new maps that show the complete geographical distribution of *H. aegyptium* as far as it is known to date.

2. Materials and methods

To determine the entire distribution area of *H. aegyptium* from the Atlantic coast of northwestern Africa to the western foothills of the Himalayas in Central Asia (Fig. 1), a comprehensive literature search without language restrictions was carried out. Articles with documented localities of *H. aegyptium* were searched in PubMed, Scopus and Cyber Leninka, which allows searching in Russian, but also using the Google search engine. In addition, historical works published in German language were also taken into account, such as the description of the genus *Hyalomma* by Schulze (1930) or the results of Austrian excursions to Iran (Nemenz, 1953), Türkiye and Karakorum (Nemenz, 1962), as well as Rhodes (Nemenz, 1966). The results of the German excursion to Afghanistan in 1952/53 were described by Anastos (1956). According to the following numbers of *H. aegyptium* locations were included: 4 Afghanistan, 4 Albania, 39 Algeria, 3 Armenia, 12 Azerbaijan, 8 Bulgaria, 1 Croatia, 2 France, 12 Georgia, 11 Greece, 53 Iran, 6 Iraq, 2 Israel, 9 Italy, 3 Jordan, 2 Kazakhstan, 2 Kyrgyzstan, 6 Lebanon, 1 Libya, 1 Malta, 47 Morocco, 1 North Macedonia, 1 Pakistan, 3 Palestine, 28 Romania, 13 Russia, 22 Syria, 3 Tajikistan, 56 Tunisia, 127 Türkiye, 16 Turkmenistan, 1 Ukraine, and 2 Uzbekistan.

In addition to the country from which the ticks originate, also indicates the host from which the ticks were collected. Since tortoises of the genus *Testudo* are the predominant hosts of *H. aegyptium* (Hoogstraal, 1956), this information can be used to assess the reliability of findings. In one case, *H. aegyptium* was found on the ground and in a cave. Four specimens were caught with a CO_2 trap (Aydin et al., 2020), a suitable method for collecting host-seeking hunter ticks (Orkun and Emir, 2020). Table 2 lists *H. aegyptium* that were collected from imported and often confiscated tortoises of the genus *Testudo*. Accordingly, there are documented locations outside the natural distribution area of *H. aegyptium* in Austria, Belgium, Denmark, England, Egypt, France, Germany, Italy, Japan, Malta, the Netherlands, Poland, Qatar, Slovenia, Spain, and the United States of America.

Tick findings for which no geographical coordinates are available were digitized based on text information on the locations or printed maps. These digitized locations, of course, are generally of lower accuracy than locations described by geographical coordinates determined

Table 1
Number, accuracy (very low, low, medium and high), country, and host species of georeferenced *Hyalomma aegyptium* sampling sites compiled in this study.

No.	Acc.	Country	Host	References
1	l	Afghanistan	*T. horsfieldii*	Sharif (1928)
1	l	Afghanistan	Unspecified	Anastos (1956)
1	l	Afghanistan	*T. horsfieldii*	Kaiser and Hoogstraal (1963)
1	l	Afghanistan	Mammal	Kaiser and Hoogstraal (1963)
4	l	Albania	*T. hermanni*	Bizhga et al. (2022)
1	m	Algeria	*T. graeca*	Široký et al. (2009)
15	m	Algeria	*T. graeca*	Harris et al. (2013)
4	l	Algeria	*T. graeca*	Tiar et al. (2016)
2	m	Algeria	*T. graeca*	Lakehal et al. (2020)
10	u	Algeria	*T. graeca*	Mechouk et al. (2022)
7	l	Algeria	*T. graeca*	Norte et al. (2022)
2	l	Armenia	*T. graeca*	Apanaskevich (2003)
1	l	Armenia	Unspecified	Apanaskevich (2003)
12	l	Azerbaijan	*T. graeca*	Apanaskevich (2003)
2	l	Bulgaria	*T. graeca*	Široký et al. (2006)
2	l	Bulgaria	*T. hermanni*	Široký et al. (2006)
2	l	Bulgaria	*T. graeca*	Nader et al. (2018)
1	l	Bulgaria	*T. graeca*	Panayotova et al. (2023)
1	h	Bulgaria	Ground	Kolarova et al. (2024)
1	l	Croatia	*T. hermanni*	Široký et al. (2006)
1	v	France	Unspecified	Ronsisvalle (1891)
1	l	France	*T. hermanni*	Matsumoto et al. (2004)
2	l	Georgia	*T. graeca*	Apanaskevich (2003)
1	l	Georgia	Unspecified	Apanaskevich (2003)
1	v	Georgia	Unspecified	Kerbabaev and Tsushba (2011)
6	h	Georgia	Unspecified	USAMRD-G (2024)
2	h	Georgia	*T. graeca*[a]	USAMRD-G (2024)
1	l	Greece	Unspecified	Sharif (1928)
1	l	Greece	*T. graeca*	Schulze (1930)
1	h	Greece	Lizard	Nemenz (1966)
1	l	Greece	Unspecified	Apanaskevich (2003)
3	l	Greece	*T. hermanni*	Široký et al. (2006)
3	l	Greece	*T. marginata*	Široký et al. (2006)
1	l	Greece	*T. graeca*	Hepner et al. (2020)
1	l	Iran	*T. graeca*	Nemenz (1953)
4	l	Iran	Unspecified	Abbassian-Lintzen (1960)
3	l	Iran	Unspecified	Apanaskevich (2003)
1	l	Iran	*T. horsfieldii*[c]	Apanaskevich (2003)
3	l	Iran	Mammal	Apanaskevich (2003)
1	l	Iran	Mammal	Telmadarraiy et al. (2004)
1	l	Iran	*T. graeca*	Tavassoli et al. (2007)
3	m	Iran	*T. graeca*	Široký et al. (2009)
1	v	Iran	*T. graeca*	Bahrami et al. (2013)
1	l	Iran	*T. graeca*	Kheirabadi et al. (2013)
27	m	Iran	*T. graeca*	Javanbakht et al. (2015)
1	l	Iran	*T. graeca*[a]	Banafshi et al. (2018)
4	h	Iran	Unspecified	Hosseini-Chegeni et al. (2019)
1	m	Iran	*T. graeca*	Adeli-Sardou et al. (2019)
1	l	Iran	*T. graeca*	Khademi et al. (2023)
1	l	Iraq	*T. graeca*	Reed and Marx (1959)
1	l	Iraq	*T. graeca*	Shamsuddin and Mohammad (1988)
4	l	Iraq	*T. graeca*	Koyee (2011)
2	l	Israel	*T. graeca*	Mumcuoglu et al. (2022)
2	l	Israel	*T. graeca*	Azagi et al. (2017)
6	l	Italy	Unspecified	Ronsisvalle (1891)
1	m	Italy	Bird	Manilla (1990)
2	v	Italy	Unspecified	Brianti et al. (2010)
3	l	Jordan	*T. graeca*	Petney and Al-Yaman (1985)
1	l	Kazakhstan	*T.horsfieldii*[c]	Apanaskevich (2003)
1	l	Kazakhstan	Unspecified	Apanaskevich (2003)
1	l	Kyrgyzstan	*T. horsfieldii*	Apanaskevich (2003)
1	l	Kyrgyzstan	Unspecified	Apanaskevich (2003)
1	v	Lebanon	*T. graeca*[b]	Sweatman (1968)
5	m	Lebanon	*T. graeca*	Široký et al. (2009)
1	v	Lybia	*T. graeca*	Široký et al. (2009)
1	l	Malta	Unspecified	Schulze (1930)
11	v	Morocco	*T. graeca*	Bailly-Choumara et al. (1976)
4	l	Morocco	*T. graeca*	Gemel and Hörweg (2011)
3	m	Morocco	*T. graeca*	Široký et al. (2009)
1	l	Morocco	*T. graeca*	Segura et al. (2019)
7	l	Morocco	*T. graeca*	Laghzaoui et al. (2022)
20	l	Morocco	*T. graeca*	Norte et al. (2022, 2024)
1	l	Morocco	Lizard	Norte et al. (2024)

(*continued on next page*)

Table 1 (*continued*).

1	l	North Macedonia	*T. graeca*	Schulze (1918, 1930)
1	l	Palestine	Lizard	Paperna et al. (2002)
1	l	Palestine	*T. graeca*	Azagi et al. (2017)
1	v	Palestine	*T. graeca*	Mumcuoglu et al. (2022)
1	l	Pakistan	*T. horsfieldii*[c]	Sharif (1928)
2	l	Romania	*T. graeca*	Široký et al. (2006)
1	m	Romania	*T. graeca*	Široký et al. (2009)
2	v	Romania	*T. graeca*	Coipan et al. (2011)
23	l	Romania	*T. graeca*	Mihalca et al. (2012)
4	l	Russia	*T. graeca*	Robbins et al. (1998)
7	l	Russia	*T. graeca*	Apanaskevich (2003)
2	l	Russia	*T. graeca*	Filippova and Stekolnikov (2007)
2	l	Syria	*T. graeca*	Sharif (1928)
2	l	Syria	*T. graeca*	Paperna (2006)
16	m	Syria	*T. graeca*	Široký et al. (2009, 2014)
2	l	Tajikistan	*T. horsfieldii*	Apanaskevich (2003)
1	l	Tajikistan	Unspecified	Apanaskevich (2003)
1	l	Tunisia	Unspecified	Apanaskevich (2003)
54	l	Tunisia	*T. graeca*	Najjar et al. (2020)
1	l	Tunisia	*T. graeca*	Norte et al. (2022)
4	m	Türkiye	*T. graeca*[a]	Nemenz (1962)
5	l	Türkiye	*T. graeca*	Hoogstraal and Kaiser (1960b)
1	l	Türkiye	Lizard	Hoogstraal and Kaiser (1960b)
6	l	Türkiye	Mammal	Hoogstraal and Kaiser (1960b)
1	l	Türkiye	Bird	Hoogstraal and Kaiser (1960b)
1	l	Türkiye	Human	Hoogstraal and Kaiser (1960b)
2	l	Türkiye	*T. graeca*[a]	Apanaskevich (2003)
10	m	Türkiye	*T. graeca*	Široký et al. (2009)
1	m	Türkiye	Mammal	Gazyağci et al. (2010)
5	v	Türkiye	Human	Bursali et al. (2011)
2	h	Türkiye	Unspecified	Hekimoglu et al. (2012)
2	v	Türkiye	Unspecified	Bursali et al. (2013)
1	m	Türkiye	*T. graeca*	Kirecci et al. (2013)
4	m	Türkiye	*T. graeca*	Yilmaz et al. (2013, 2018)
3	m	Türkiye	*T. graeca*	Široký et al. (2014)
3	h	Türkiye	*T. graeca*	Heikimoğlu and Özer (2015)
9	l	Türkiye	Unspecified	Keskin et al. (2015)
5	l	Türkiye	*T. graeca*[a]	Koc et al. (2015)
6	l	Türkiye	*T. graeca*	Bakirci (2016)
1	v	Türkiye	Human	Kar et al. (2017)
1	l	Türkiye	Mammal	Orkun et al. (2019)
1	l	Türkiye	Mammal	Keskin et al. (2019)
1	l	Türkiye	*T. graeca*	Orkun and Emir (2020)
1	l	Türkiye	*T. graeca*	Ergünay et al. (2020)
1	l	Türkiye	*T. graeca*	Demir et al. (2020)
20	m	Türkiye	*T. graeca*	Kar et al. (2020)
4	m	Türkiye	*T. hermanni*	Kar et al. (2020)
8	m	Türkiye	Unspecified	Kar et al. (2020)
4	m	Türkiye	CO_2 trap	Aydin et al. (2020)
1	m	Türkiye	*T. graeca*	Akveran et al. (2020)
1	l	Türkiye	*T. graeca*	Hepner et al. (2020)
6	h	Türkiye	*T. graeca*[a]	Hekimoglu et al. (2021)
1	l	Türkiye	*T. graeca*[a]	Polat et al. (2021)
1	h	Türkiye	Cave	Hekimoglu et al. (2022)
3	l	Türkiye	*T. graeca*	Norte et al. (2022)
1	h	Türkiye	*T. graeca*	Dincer et al. (2023)
10	l	Turkmenistan	Unspecified	Berdyyev and Annayev (1997)
1	l	Turkmenistan	Unspecified	Apanaskevich (2003)
3	l	Turkmenistan	Mammal	Apanaskevich (2003)
2	l	Turkmenistan	*T. horsfieldii*	Apanaskevich (2003)
1	v	Ukraine	Unspecified	Hoogstraal (1956)
1	l	Uzbekistan	*T. horsfieldii*	Apanaskevich (2003)
1	l	Uzbekistan	Unspecified	Apanaskevich (2003)
501	**Total**			

[a] Tortoise specified as *T. graeca*.

[b] *T. kleinmanni* corrected to *T. graeca*.

[c] Tortoise specified as *T. horsfieldii* (for details see text).

by GPS in the field. To provide evidence of this, accuracy measures were given for all data referenced in in accordance with a scheme established in previous studies (Rubel and Kahl, 2023; Rubel, 2024), in which accuracy is classified as high (h ≈ ±0.1 km), medium (m ≈ ±1 km), low (l ≈ ±10 km) and very low (v). The latter identifies all reports that relate only to political districts, mountain ranges or river sections. Such information is obligatory in Russian literature and was used in the absence of more precise location information.

Data from the scientific literature () were supplemented by *H. aegyptium* locations retrieved from the Global Biodiversity Information Facility (GBIF.org, 2024). More than 76% of these relate to the period 2020–2024. From the original 67 GBIF locations, duplicates and locations already described in the scientific literature were removed, leaving 56 *H. aegyptium* locations that were used here (Fig. S1). These are distributed across 15 countries as follows: 1 Albania, 1 Algeria, 2 Bulgaria, 3 Georgia, 24 Greece, 1 Iran, 3 Israel, 4 Morocco, 2

Table 2
Number, country, and host species of georeferenced *Hyalomma aegyptium* sampling sites collected mainly from imported/confiscated tortoises of the genus *Testudo*.

No.	Country	Host	References
1	Austria	*T. hermanni*	Sixl (1971)
3	Belgium	*T. graeca*	Obsomer et al. (2013)
1	Denmark	*T. graeca*	Johnsen (1943)
1	Denmark	*Testudo* sp.	Arthur (1955)
1	England	*Testudo* sp.	Pocock (1900)
1	England	*Testudo* sp.	Nuttall (1915)
1	England	*Testudo* sp.	Browning (1950)
1	Egypt	*Testudo* sp.	Apanaskevich (2003)
1	France	*T. graeca*	Lamontellerie (1965)
1	France	*T. graeca*	Rageau (1972)
1	Germany	*T. graeca*	Weidner (1954)
1	Germany	*Testudo* sp.	Negrobov and Borodin (1964)
1	Iceland	Human	Richter et al. (2013)
1	Italy	*T. graeca*	Brianti et al. (2010)
1	Japan	*T. graeca*	Andoh et al. (2015)
1	Japan	*T. horsfieldii*	Andoh et al. (2015)
1	Malta	*T. graeca*	Sultana Loporto et al. (2018)
1	Malta	*T. kleinmanni*	Sultana Loporto et al. (2018)
1	Netherlands	*Testudo* sp.	Bronswijk et al. (1979)
2	Poland	*Testudo* sp.	Nowak (2010)
1	Poland	*T. graeca*	Nowak (2010)
1	Poland	*T. marginata*	Nowak (2010)
1	Qatar	*T. graeca*	Barradas et al. (2021)
1	Slovenia	*T. graeca*	Rataj et al. (2011)
1	Spain	*T. graeca*	Brotóns and Estrada-Peña (2004)
1	USA	*T. graeca*	Eglis (1959)
1	USA	*T. graeca*	Clark and Doten (1995)
1	USA	*T. kleinmanni*	Clark and Doten (1995)
3	USA	*Testudo* sp.	Keirans and Durden (2001)
34	**Total**		

Palestine, 2 Romania, 3 Russia, 1 Spain, 1 Syria, 1 Tunisia, and 7 Türkiye. GBIF.org (2024) also contains five historical records of ticks introduced into the Netherlands (syn. *Hyalomma testudinis* Hasselquist 1762) and 53 records of ticks on *Testudo* sp. introduced into Great Britain and Ireland, the latter from the Biological Records Centre of the UK National Biodiversity Network.

To visualize the geographical distribution of *H. aegyptium*, the georeferenced locations were plotted on terrain maps (OpenStreetMap contributors, 2017) using R, a language and environment for statistical computing (R. Development Core Team, 2023). Artificial data clusters caused by single studies were reduced using a random selection and a thinning algorithm (Aiello-Lammens et al., 2019). For example, for the overview map (Fig. 2) a minimum distance of 40 km between the mapped locations was chosen to avoid overlaps. For the other maps this distance was reduced to 0.5–10.0 km to show more details.

3. Results and discussion

Fig. 2 (orange dots) depicts the entire natural distribution of *H. aegyptium* locations around the Mediterranean Sea, the Black Sea and the Caspian Sea up to the eastern border of China. A total of 557 *H. aegyptium* locations was mapped, including 501 locations from the literature study and 56 locations from the GBIF database. In addition, *H. aegyptium* locations of imported ticks, attached to tortoises and in one case to a human (Richter et al., 2013), are shown (Fig. 2, green dots).

The westernmost locality is in North Africa, Morocco, at 9.7° W, where *H. aegyptium* was found on *T. graeca* (Laghzaoui et al., 2022). Further records of *H. aegyptium* in North Africa are known from Algeria (Harris et al., 2013; Mechouk et al., 2022) and Tunisia (Najjar et al., 2020) (Fig. 3), while only isolated findings of *H. aegyptium* are documented on the European coasts and islands of the western Mediterranean. One of these records is in the French island of Corsica (Matsumoto et al., 2004), further six in Italy (Ronsisvalle, 1891; Brianti et al., 2010) and one in Malta (Schulze, 1930). Exceptions to this are *H. aegyptium* imported on tortoises (Fig. 2, green dots), which will be discussed below. In the eastern Mediterranean, *H. aegyptium* is documented in the Balkan countries Bulgaria, Croatia, Greece, North Macedonia, Romania, Türkiye (Fig. 4) and in countries of the Near East. The latter include Lebanon, Jordan, Israel, Palestine (West Bank), Syria and Türkiye (Fig. 5). The easternmost locality is in Kyrgyzstan at 72.8° E, where *H. aegyptium* usually parasitizes *T. horsfieldii*. Apanaskevich (2003). While the western distribution of *H. aegyptium* in Morocco is naturally bordered by the Atlantic Ocean, the eastern distribution limit must be considered as provisional, since only sparse information is available from Kyrgyzstan and neighbouring Kazakhstan.

The northern distribution limit is on the western Black Sea coast of Romania at 45.3° N, where *H. aegyptium* was found on *T. graeca* (Mihalca et al., 2012). At a similar geographical latitude, *H. aegyptium* has also been found on the north-eastern Black Sea coast of Russia, also on *T. graeca* (Apanaskevich, 2003). In between lies the Crimean peninsula, where an introduced or possibly historically relict population of *T. graeca* has been mapped (Rhodin et al., 2021). This location in the south of the Crimea is also marked in the map of Feider (1965) and refers to the occurrence of *H. aegyptium* mentioned by Hoogstraal (1956). On the southern Black Sea coast, namely in Türkiye, a total of 126 findings were documented in the scientific literature, placing Türkiye at the top of the country ranking of *H. aegyptium* reports. The southern limit is in Iran at 28.8° N (Javanbakht et al., 2015), where *H. aegyptium* was also collected from *T. graeca*. The map of the Middle East (Fig. 6) shows that *H. aegyptium* has been distributed throughout the north and west of Iran up to the border regions of northern Iraq. North of Iran, the distribution area includes all countries of the southern Caucasus, namely Armenia, Azerbaijan, Georgia, Türkiye and Russia, as well as Turkmenistan in the east of the Caspian Sea. Also in Afghanistan *H. aegyptium* has been found. In addition, *H. aegyptium* were collected in Quetta, Pakistan, from unspecified tortoise species (Sharif, 1928), most likely from the only land tortoise species endemic to this region, *T. horsfieldii*. Further descriptions of *H. aegyptium* from Pakistan are to be considered misclassifications and were not used here. See the brief note on the confusion of *H. aegyptium* with other tick species in the Supplement.

The natural distribution area of *H. aegyptium* extends from Morocco in northwestern Africa to Kyrgyzstan in Central Asia between 10° W–73° E and 28–46° N. In total, *H. aegyptium* locations were mapped from 33 countries (), which largely corresponds to the country list from Guglielmone et al. (2023). There are only marginal differences at the edges of the distribution area. In particular, the present study could not confirm *H. aegyptium* locations in Serbia. Conversely, locations in France (southern France and the Mediterranean islands of Corsica), in Malta as well as in Libya, were mapped, although these countries were not mentioned by Guglielmone et al. (2023). Corsica can be assigned to the natural distribution area of *T. hermanni* and *H. aegyptium*, which also applies to Malta. In Malta, however, *H. aegyptium* was also found on *T. graeca* and *T. kleinmanni*, which were illegally imported, wild caught specimens from northern Africa. According to Sultana Loporto et al. (2018), this was the first record of *H. aegyptium* in Malta and also the first record of *T. kleinmanni* as a host for *H. aegyptium*. However, *H. aegyptium* was already described in Malta by Schulze (1930) and already found on *T. kleinmanni* imported to the USA (Clark and Doten, 1995). It is noteworthy, however, that they were found on *T. kleinmanni* that were imported together with other *Testudo* species. No documented locations concerning *H. aegyptium* on tortoises are available from Libya, but this tick might be widely distributed in Libya (Hoogstraal and Kaiser, 1960a; Široký et al., 2009). Therefore, in accordance with the map from Feider (1965) and using the qualitative information from Široký et al. (2009), an occurrence was mapped on the Cyrenaica peninsula (Fig. 2).

If the 501 *H. aegyptium* locations extracted from the literature are broken down according to which host species the ticks originate from (), the following host species-related location numbers result: 365 *T.*

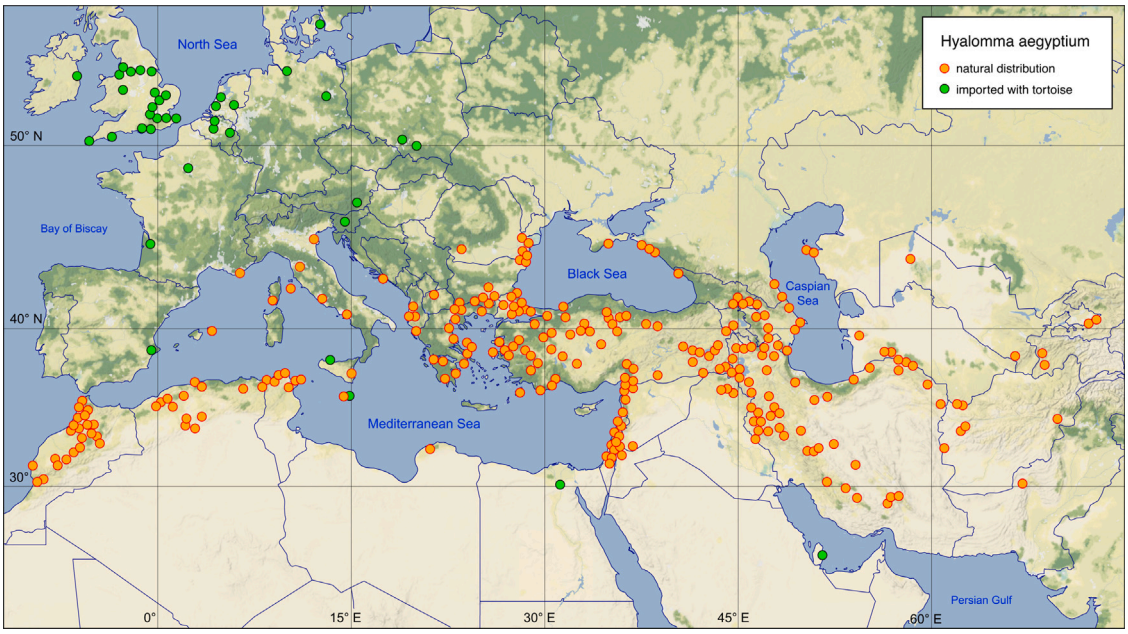

Fig. 2. Global distribution of *Hyalomma aegyptium*.

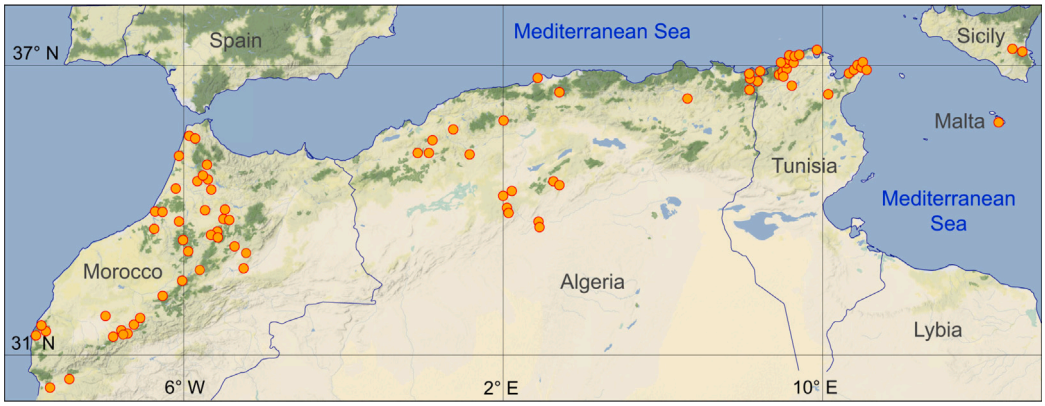

Fig. 3. Distribution of *Hyalomma aegyptium* in North Africa (Algeria, Morocco, Tunisia), the island-state of Malta, and Sicily (Italy).

graeca, 15 *T. hermanni*, 11 *T. horsfieldii*, 3 *T. marginata*, 17 mammal, 7 human, 4 lizard, 2 bird, and 71 unspecified. In addition, 6 locations were mapped where ticks were not collected from a host. In summary, the host species is known from 424 mapped *H. aegyptium* locations, which can be ranked as follows: 92.9% *Testudo* spp., 4.0% mammals, 1.7% humans, 0.9% lizards and 0.5% birds. If only the tortoise hosts infested with *H. aegyptium* are considered, these are 92.6% *T. graeca*, 3.8% *T. hermanni*, 2.8% *T. horsfieldii* and 0.8% *T. marginata*. Since some authors simplify the description of the host animals as tortoises, the species names have been added when this was clearly evident from the geographical distribution of the five *Testudo* species according to Rhodin et al. (2021). A total of 21 tortoises without species information was specified as *T. graeca* and three as *T. horsfieldii* (). Sweatman (1968) suggested *T. kleinmanni* as the most important host species of *H. aegyptium* in Lebanon, although it does not occur there. Therefore, one location of *T. kleinmanni* was corrected to the only endemic *Testudo* species in Lebanon, *T. graeca*, as Široký et al. (2011) already proposed. Another confusion of tick species was found in Polat et al. (2021). Reported specimens of *Hyalomma marginatum* collected from tortoises were interpreted as *H. aegyptium* collected from *T. graeca* ().

At 17 locations where mammals were reported as hosts, these hosts were mainly hedgehogs (*Erinaceus concolor, Erinaceus europaeus*) and hares (*Lepus europaeus*). These include the first documentation of *H. aegyptium* (syn. *H. syriacum*) on a warm-blooded animal by Schulze (1918), who found two ticks on a hedgehog and also on *T. graeca* in today's North Macedonia. Four locations were mapped where the tick was found on lizards, roughtail rock agama (*Stellagama stellio*) and common wall gecko (*Tarentola mauritanica*). Two locations were also mapped where the tick was found on birds. The first location is in Türkiye, where *H. aegyptium* was found on small game, partridges (*Perdix perdix*) and hares (*L. europaeus*), according to Hoogstraal and Kaiser (1960b). The second location is the Italian island of Montecristo, where nymphal *H. aegyptium* were collected from migratory birds (*Anthus trivialis*, *Lanius senator*, *Phoenicurus phoenicurus*, *Saxicola rubetra*) and also a native population of *T. hermanni* does occur (Manilla, 1990). Additional immature *H. aegyptium* have been found sporadically on migratory birds in Tuscany, Calabria and Sicily (Italy), but could not be mapped due to a lack of location information.

As mentioned above, *H. aegyptium* have often been introduced with tortoises, which were traded in large quantities worldwide as popular pets, especially in the 20th century (Table 2). The earliest *H. aegyptium* (syn. *Hyalomma affine*, Neumann) documented here was found in England in 1900 (Pocock, 1900). In 1913, another specimen of *H. aegyptium* (syn. *H. syriacum*) was described from a tortoise in England (Nuttall, 1915). Further descriptions can be found in the Illustrated London News of August 26, 1950, according to which a

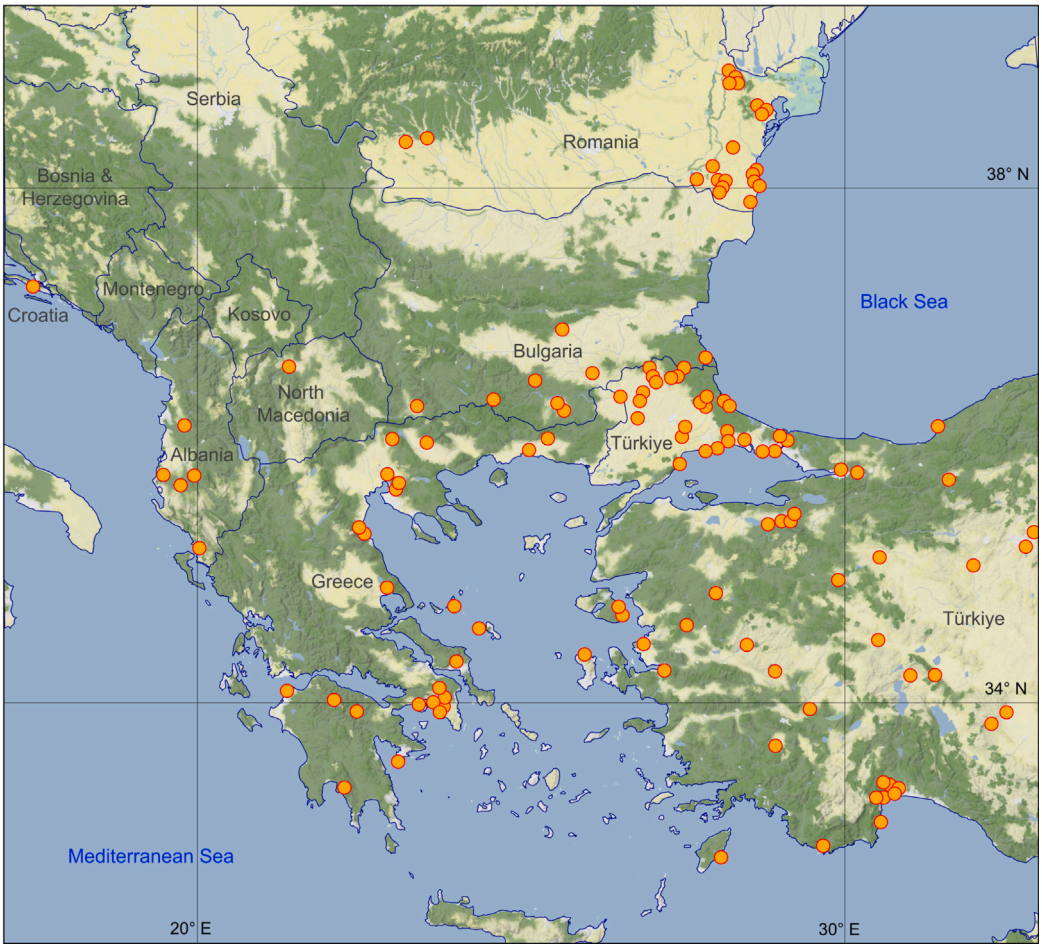

Fig. 4. Distribution of *Hyalomma aegyptium* in the Balkans (Albania, Bulgaria, Croatia, Greece, North Macedonia, Romania, Türkiye).

large number of ticks were sent by the public to the British Museum of Natural History for identification. Many concerned citizens thought that the *H. aegyptium* attached to *Testudo* were baby tortoises (Browning, 1950). Early findings on *T. graeca* are also known from Denmark (Johnsen, 1943), Germany (Weidner, 1954), USA (Eglis, 1959) and France (Lamontellerie, 1965). Fig. 2 (green dots) shows these *H. aegyptium* localities together with more recent findings, for example from Qatar (Barradas et al., 2021). Outside the map section, findings from the USA, more specifically from Florida, New York and North Carolina, on *T. graeca* and *T. kleinmanni* are documented (Clark and Doten, 1995; Keirans and Durden, 2001). Further imported *H. aegyptium* outside the map section originate from Japan, where ticks have been reported on *T. graeca* from Jordan and on *T. horsfieldii* from Russia and Uzbekistan (Andoh et al., 2015). The 34 locations of *H. aegyptium* ticks on imported tortoises documented here (Table 2) represent only a tiny fraction of the ticks actually transported by traded tortoises. They are found on practically all imported *Testudo* species caught in the wild or reintroduced from breeding programmes (Schulze, 1930; Estrada-Peña, 2024). A better impression of the number of imported *H. aegyptium* is provided by the detailed map in Fig. 7, which also shows unpublished tick findings from Great Britain and Ireland from the period 1904–1982 and the Netherlands from the period 1902–1930 (GBIF.org, 2024). In the Atlas of Ticks (Ixodidea) of the British Isles, Martyn (1988) wrote that this species was introduced on tortoises intended for the pet trade, that there are no records of established populations, and that *H. aegyptium* is unlikely to survive the winter months. With the ban on importing live tortoises, *H. aegyptium* may now have disappeared from Great Britain.

Today, humans are rarely infested by tortoise ticks, with the exception of Türkiye, where *H. aegyptium* was the most common tick species removed from patients by hospital medical staff (Vatansever et al., 2008; Gargili et al., 2010). Interestingly, nymphs of *H. aegyptium* rather than adults and larvae often prefer humans as hosts (Gargili et al., 2012; Orkun et al., 2014). In particular, *Hyalomma* nymphs infesting humans in both rural and urban areas of Türkiye have been reported to be predominantly *H. aegyptium*. In the past, human infestation was also observed more frequently in Europe, as (Bertkau, 1892) reports. A time when the main hosts of *H. aegyptium*, reptiles and especially land tortoises, were present in much greater numbers than today and the human population engaged in traditional agriculture was much more exposed to *Hyalomma* infestation. Accordingly, Ronsisvalle (1891) investigated the clinical importance of *H. aegyptium* in Sicily (Lentini, Carlentini, Palagonia, Scordia), Tuscany and Veneto, as well as in neighbouring southern France, where it not infrequently infested humans. As a consequence of *H. aegyptium* bites and the saliva entering the wound, he described local inflammation of the skin in the form of erysipelas, but also high fever and loss of strength, sometimes even delirium. Today, these observations can be interpreted as early evidence of the vectorial capacity of *H. aegyptium*.

Numerous tick-borne pathogens or their DNA/RNA have been detected in *H. aegyptium*. These are listed in the Table 3 together with the countries in which they were found, with only the earliest reference

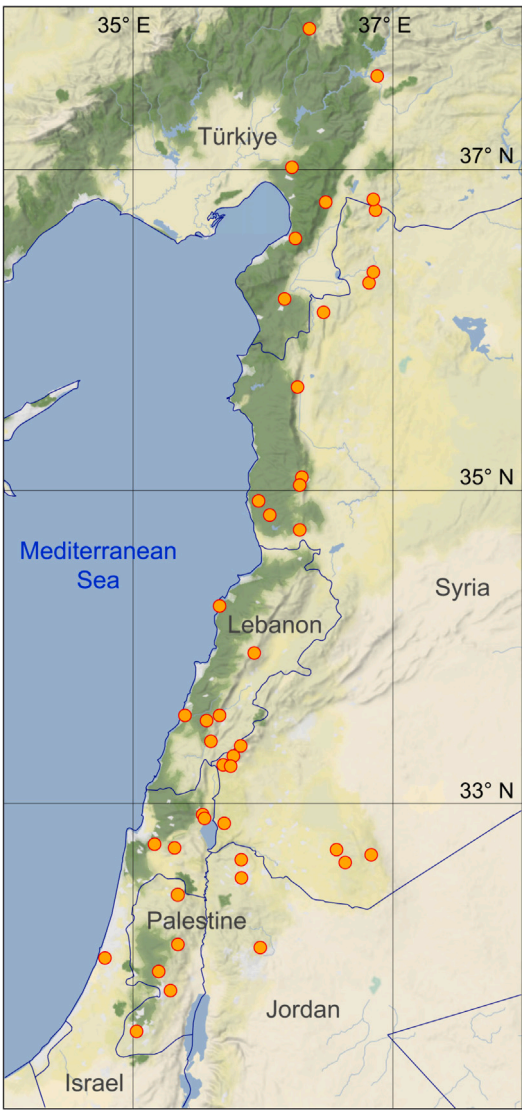

Fig. 5. Distribution of *Hyalomma aegyptium* in the Near East (Israel, Jordan, Lebanon, Palestine–West Bank, Syria, Türkiye).

being given. The pathogens found include the Crimean-Congo haemorrhagic fever virus as well as the Meram and Tamdy viruses, but also bacteria such as *Anaplasma phagocytophilum*, *Bartonella bovis*, *Borrelia* spp., *Coxiella burnetii*, *Ehrlichia* spp., *Francisella* spp., *Midichloria mitochondrii*, *Rickettsia* spp., and *Wolbachia* spp. The Piroplasmorida (Protozoa) include *Babesia* spp., *Hemolivia mauritanica*, *Hepatozoon kisrae* and *Leishmania major*. While some of the pathogens listed in Table 3 are single findings, the occurrence of other pathogens in *H. aegyptium* has been confirmed by many authors. These include, in particular, *Borrelia turcica* (Güner et al., 2004; Kalmár et al., 2015; Hepner et al., 2020; Benyahia et al., 2022), a member of the reptile-associated *Borrelia* clade, while relapsing-fever-associated *Borrelia* (Norte et al., 2022) and Lyme-disease-related *Borrelia* (Kar et al., 2011) have been documented only once. Other common pathogens are *Rickettsia aeschlimannii* (Bitam et al., 2009; Gargili et al., 2012; Orkun et al., 2019; Akveran et al., 2020; Benyahia et al., 2022) and *He. mauritanica* (Široký et al., 2005; Paperna, 2006; Harris et al., 2013; Javanbakht et al., 2015; Orkun et al., 2019; Akveran et al., 2020; Barradas et al., 2021; Norte et al., 2022). Not included in Table 3 is the study by Ray (1950a), who describes *H. aegyptium* as a vector of *Theileria annulata* in Punjab. Although Ray (1950b) himself pointed out that the tick *H. aegyptium* Neumann studied was not *H. aegyptium* (Linnaeus, 1758), his article is also miscited in recent publications such as those by Mihalca et al. (2017) and Benyahia et al. (2022). Thus, the confusion about the species *H. aegyptium*, the type species of the genus *Hyalomma*, continues up to now (see Supplements).

Although numerous tick-borne pathogens have been detected in *H. aegyptium*, vector competence, i.e. the experimentally proved transmission of pathogens from the tick to the host, could only be demonstrated for three pathogens. These are the two blood parasites *He. mauritanica* and *Hep. kisrae*, whose transmission to reptiles (*T. graeca*, *S. stellio*) through the ingestion of infected ticks has been experimentally confirmed (Brumpt, 1938; Paperna et al., 2002; Široký et al., 2004; Paperna, 2006), as well as *C. burnetii* (Široký et al., 2010), the causative agent of Q fever (Table 4). For a fourth pathogen, the reptile-associated *B. turcica*, at least transstadial survival in *H. aegyptium* could be demonstrated experimentally (Kalmár et al., 2015). A first indication that *H. aegyptium* is a putative vector for *R. aeschlimannii* and *R. sibirica mongolitimonae* is provided by the detection of these pathogens in host-seeking *H. aegyptium* (Orkun et al., 2020). Remarkably, Mihalca et al. (2017) incorrectly stated a proven vector capacity for *R. aeschlimannii*, although no transmission studies are described in the cited paper by Bitam et al. (2009) or any other reference.

4. Conclusions and outlook

An overview map and four detailed maps of North Africa, the Balkans, the Near East, and the Middle East show the known locations of the tortoise tick *H. aegyptium* between 10° W–73° E and 28–46° N. In addition, documented findings on imported land tortoises that have been exported worldwide as popular pets give an impression of the distribution of *H. aegyptium* outside its natural distribution area.

The first records of *H. aegyptium* mapped here date back to the 19th century, when (Ronsisvalle, 1891) observed the ticks in Italy and southern France. The most common hosts from which *H. aegyptium* was collected were tortoises of the genus *Testudo*, predominantly *T. graeca*. It is striking that no infestation with *H. aegyptium* has been detected on *T. kleinmanni* in their natural habitat. This suggests that *T. kleinmanni* may play a minor role as a host. However, it may also be due to the lack of data from the distribution area of *T. kleinmanni*, which includes mainly Libya, apart from isolated occurrences on the Sinai Peninsula and in the adjacent south of Israel (Rhodin et al., 2021).

Although numerous tick-borne pathogens have been detected in *H. aegyptium*, vector competence was only be demonstrated for the three pathogens *C. burnetii*, *He. mauritanica* and *Hep. kisrae*. For the reptile-associated *B. turcica*, the experimentally demonstrated transstadial survival in *H. aegyptium* is one prerequisite for vector competence.

The first map of *H. aegyptium* based on georeferenced localities and covering the entire distribution area was compiled here. Nevertheless, it is obvious that the available data only incompletely cover some regions, for example at the eastern distribution limit in Afghanistan, Pakistan, Tajikistan, Kazakhstan and Kyrgyzstan. There are also no current studies on *H. aegyptium* from Libya, where the tick presumably occurs in local populations of *T. gracea* and *T. kleinmanni*. Knowing that the distribution of *H. aegyptium* correlates with that of its predominant hosts and other hosts are generally coincidental and unable to ensure the establishment and maintenance of the *H. aegyptium* population may be helpful in this case. Therefore, a follow-up study will investigate the co-distribution of *H. aegyptium* with tortoises of the genus *Testudo* and quantify the climatic regions in which the ticks and their hosts occur. Climate adaptation can be defined by digital maps of climate classification, as has already been shown for other tick species such as *Haemaphysalis concinna* (Rubel et al., 2018) or *Ixodes trianguliceps* (Rubel and Kahl, 2023). The generated datasets on the co-distribution of *H. aegyptium* with *Testudo* spp. and their climate adaptation may then be used as input data of species distribution models to better estimate the potential distribution of *H. aegyptium*.

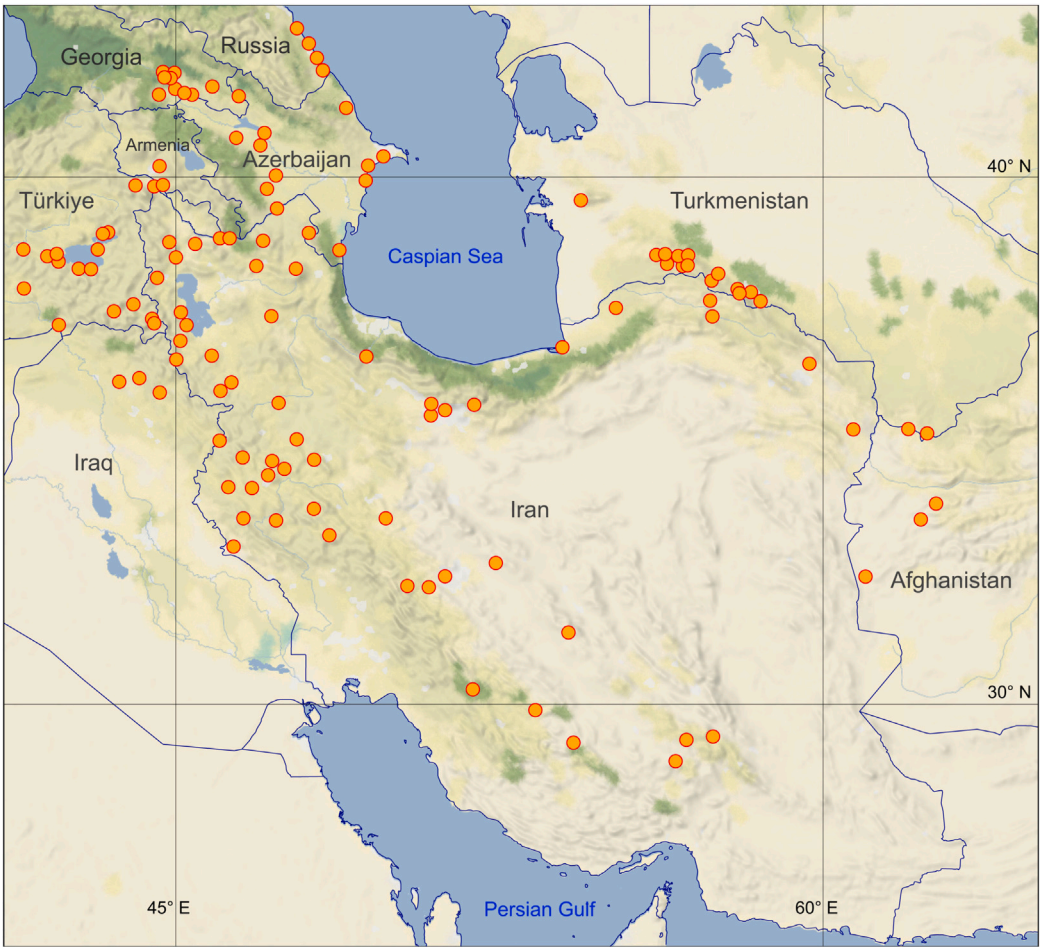

Fig. 6. Distribution of *Hyalomma aegyptium* in the Middle East (Afghanistan, Armenia, Azerbaijan, Georgia, Iran, Iraq, Russia, Türkiye, Turkmenistan).

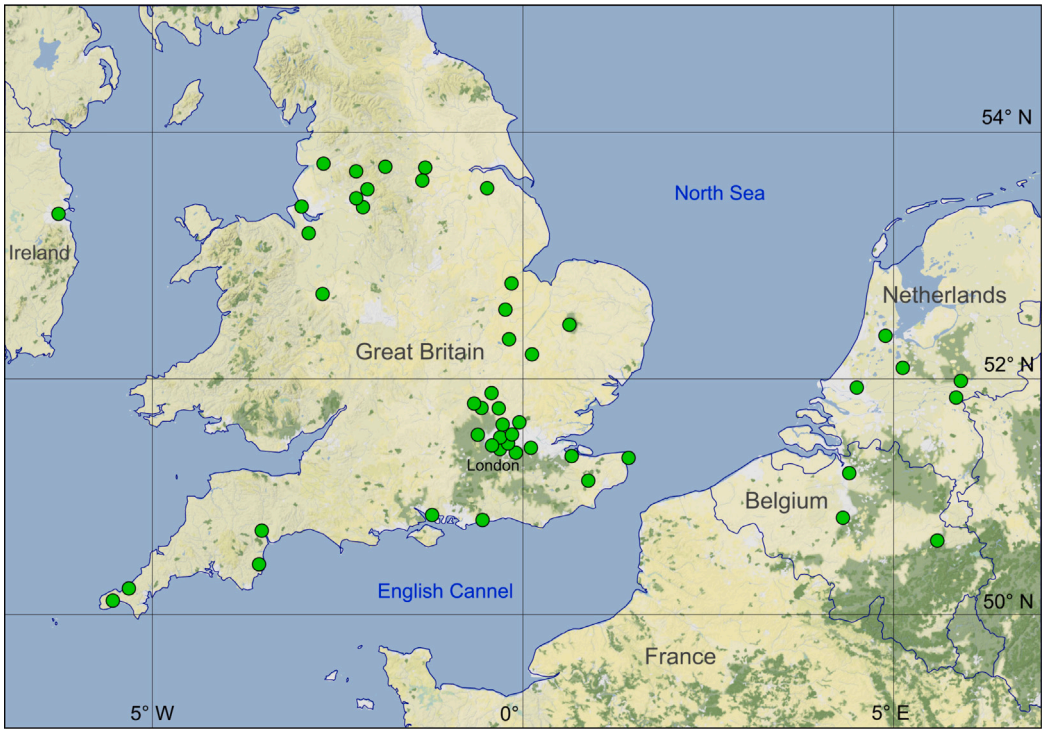

Fig. 7. Historical records of *Hyalomma aegyptium* found on tortoises imported into Belgium, Great Britain, Ireland and the Netherlands (period 1900–1982).

Table 3
Detection of tick-borne pathogens or their DNA/RNA in *Hyalomma aegyptium* removed from hosts, mainly tortoises of the genus *Testudo*.

Pathogen	Disease	Country	References
Viruses			
CCHF virus	Crimean-Congo hemorrhagic fever	Türkiye	Široký et al. (2014)
		Syria	Široký et al. (2014)
		Algeria	Kautman et al. (2016)
Meram virus		Türkiye	Ergünay et al. (2020)
Tamdy virus		Türkiye	Ergünay et al. (2020)
Bacteria			
Anaplasma phagocytophilum	Granulocytic anaplasmosis	Romania	Pastiu et al. (2012)
		Tunisia	Rjeibi et al. (2022)
Bartonella bovis		Türkiye	Akveran et al. (2020)
Borrelia spp.		Türkiye	Norte et al. (2022)
		Algeria	Norte et al. (2022)
		Morocco	Norte et al. (2022)
B. burgdoferi s.l.	Lyme borreliosis	Türkiye	Kar et al. (2011)
B. turcica		Türkiye	Güner et al. (2004)
		Romania	Kalmár et al. (2015)
		Greece	Hepner et al. (2020)
		Algeria	Benyahia et al. (2022)
		Morocco	Norte et al. (2024)
Coxiella burnetii	Q fever	Romania	Pastiu et al. (2012)
		Iran	Khademi et al. (2023)
Ehrlichia spp.	Monocytotropic ehrlichiosis	Jordan	Andoh et al. (2015)
		Algeria	Norte et al. (2022)
		Morocco	Norte et al. (2022)
		Türkiye	Akveran et al. (2020)
E. canis		Romania	Pastiu et al. (2012)
E. ewingii	Human granulocytic ehrlichiosis	Italy[a]	Manoj et al. (2021)
		Qatar[a]	Barradas et al. (2021)
Francisella spp.		Morocco	Norte et al. (2022)
F. tularensis	Tularaemia	Iran	Tukmechi et al. (2024)
Midichloria mitochondrii		Algeria	Norte et al. (2022)
		Morocco	Norte et al. (2022)
		Türkiye	Norte et al. (2022)
Rickettsia spp.	Rickettsiosis	Algeria	Norte et al. (2022)
		Jordan	Andoh et al. (2015)
		Uzbekistan	Andoh et al. (2015)
		Morocco	Norte et al. (2022)
		Türkiye	Kar et al. (2011)
R. aeschlimannii		Algeria	Bitam et al. (2009)
		Türkiye	Gargili et al. (2012)
		Morocco	Norte et al. (2024)
R. africae		Türkiye	Gargili et al. (2012)
		Algeria	Benyahia et al. (2022)
R. sibirica mongolitimonae	Siberian tick typhus	Türkiye	Orkun et al. (2019)
		Algeria	Benyahia et al. (2022)
		Morocco	Norte et al. (2024)
R. slovaca		Türkiye	Orkun et al. (2019)
Wolbachia spp.		Morocco	Norte et al. (2022)
Piroplasmorida (Protozoa)			
Babesia spp.	Babesiosis	Tunisia	Rjeibi et al. (2022)
Hemolivia mauritanica		Bulgaria	Široký et al. (2005)
		Greece	Široký et al. (2005)
		Türkiye	Široký et al. (2005)
		Syria	Paperna (2006)
		Algeria	Harris et al. (2013)
		Iran	Javanbakht et al. (2015)
		Qatar[a]	Barradas et al. (2021)
		Morocco	Norte et al. (2022)
Hepatozoon kisrae		Palestine	Paperna et al. (2002)
Leishmania major	Cutaneous leishmaniasis	Algeria	Hocine et al. (2023)

[a] *Hyalomma aegyptium* attached to imported *Testudo graece*.

Table 4
Vector competence of *Hyalomma aegyptium* based on the results of transmission studies (tick to host transmission TH, transstadial survival TS, and tick stages larva L, nymph N, adult A).

Pathogen	Transmission	Tick stage	References
Borrelia turcica	TS	N, A	Kalmár et al. (2015)
Coxiella burnetii	TH (guinea pigs), TS	L, N, A	Široký et al. (2010)
Hemolivia mauritanica	TH (ingestion of inf. ticks)	N, A	Brumpt (1938)
Hepatozoon kisrae	TH (ingestion of inf. ticks)	N, A	Paperna et al. (2002)

Declaration of competing interest

The authors declare that there are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ttbdis.2025.102438.

Data availability

Data sources are given in the paper.

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