Molecular Phylogenetics and Evolution 114 (2017) 153–165

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Effects of tectonics and large scale climatic changes on the evolutionary history of *Hyalomma* ticks

Arthur F. Sands [a,1], Dmitry A. Apanaskevich [b], Sonja Matthee [c], Ivan G. Horak [d], Alan Harrison [e,f], Shahid Karim [g], Mohammad K. Mohammad [h], Kosta Y. Mumcuoglu [i], Rupika S. Rajakaruna [j], Maria M. Santos-Silva [k], Conrad A. Matthee [a,*]

[a] *Evolutionary Genomics Group, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa*
[b] *United States National Tick Collection, The James H. Oliver, Jr. Institute for Coastal Plain Science, Georgia Southern University, Statesboro, GA, United States*
[c] *Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland, South Africa*
[d] *Department of Veterinary Tropical Diseases, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, South Africa*
[e] *Department of Zoology and Entomology, University of Pretoria, Hatfield, Pretoria, South Africa*
[f] *Department of Zoology, King Saud University, Riyadh, Saudi Arabia*
[g] *Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, MS, United States*
[h] *Iraq Natural History Research Centre and Museum, University of Baghdad, Bab Al-Muadham, Baghdad, Iraq*
[i] *Parasitology Unit, Department of Microbiology and Molecular Genetics, The Kuvin Centre for the Study of Infectious and Tropical Diseases, The Hebrew University-Hadassah Medical School, Jerusalem, Israel*
[j] *Department of Zoology, University of Peradeniya, Peradeniya, Sri Lanka*
[k] *Centro de Estudos de Vectores e Doenças Infecciosas Doutor Francisco Cambournac, Instituto Nacional de Saúde Doutor Ricardo Jorge, Aguas de Moura, Portugal*

ARTICLE INFO

Article history:
Received 28 February 2017
Revised 6 June 2017
Accepted 6 June 2017
Available online 15 June 2017

Keywords:
Hyalomma
Phylogenetics
Systematics
Tick evolution
Dispersal
Ixodidae

ABSTRACT

Hyalomma Koch, 1844 are ixodid ticks that infest mammals, birds and reptiles, to which 27 recognized species occur across the Afrotropical, Palearctic and Oriental regions. Despite their medical and veterinary importance, the evolutionary history of the group is enigmatic. To investigate various taxonomic hypotheses based on morphology, and also some of the mechanisms involved in the diversification of the genus, we sequenced and analysed data derived from two mtDNA fragments, three nuclear DNA genes and 47 morphological characters. Bayesian and Parsimony analyses based on the combined data (2242 characters for 84 taxa) provided maximum resolution and strongly supported the monophyly of *Hyalomma* and the subgenus *Euhyalomma* Filippova, 1984 (including *H. punt* Hoogstraal, Kaiser and Pedersen, 1969). A predicted close evolutionary association was found between morphologically similar *H. dromedarii* Koch, 1844, *H. somalicum* Tonelli Rondelli, 1935, *H. impeltatum* Schulze and Schlottke, 1929 and *H. punt*, and together they form a sister lineage to *H. asiaticum* Schulze and Schlottke, 1929, *H. schulzei* Olenev, 1931 and *H. scupense* Schulze, 1919. Congruent with morphological suggestions, *H. anatolicum* Koch, 1844, *H. excavatum* Koch, 1844 and *H. lusitanicum* Koch, 1844 form a clade and so also *H. glabrum* Delpy, 1949, *H. marginatum* Koch, 1844, *H. turanicum* Pomerantzev, 1946 and *H. rufipes* Koch, 1844. Wide scale continental sampling revealed cryptic divergences within African *H. truncatum* Koch, 1844 and *H. rufipes* and suggested that the taxonomy of these lineages is in need of a revision. The most basal lineages in *Hyalomma* represent taxa currently confined to Eurasia and molecular clock estimates suggest that members of the genus started to diverge approximately 36.25 million years ago (Mya). The early diversification event coincides well with the collision of the Indian and Eurasian Plates, an event that was also characterized by large scale faunal turnover in the region. Using S-Diva, we also propose that the closure of the Tethyan seaway allowed for the genus to first enter Africa approximately 17.73 Mya. In concert, our data supports the notion that tectonic events and large scale global changes in the environment contributed significantly to produce the rich species diversity currently found in the genus *Hyalomma*.

1. Introduction

Bont-legged ticks belonging to the genus *Hyalomma* Koch, 1844 are obligate haematophagous ectoparasites of mammals, birds and

---

* Corresponding author.
E-mail address: cam@sun.ac.za (C.A. Matthee).

[1] Current address: Department of Animal Ecology and Systematics, Justus Liebig University, Giessen, Germany.

http://dx.doi.org/10.1016/j.ympev.2017.06.002
1055-7903/© 2017 Elsevier Inc. All rights reserved.

reptiles. They occur widespread across the Afrotropical, Palearctic and Oriental zoogeographic regions (Guglielmone et al., 2014) and the oldest fossil remains resembling *Hyalomma* were found in the Baltic region (dating back to 35–50 million years ago (Mya): de la Fuente, 2003). *Hyalomma* are important ectoparasites from a medical and veterinary perspective (Aktas et al., 2004; Bente et al., 2013; Formosinho and Santos-Silva, 2006; Heisch et al., 1962; Norval and Horak, 2004; Taboada and Merchant, 1991; Shyma et al., 2012) and are known vectors for various pathogens such as *Nairovirus (*the agent of Crimean-Congo haemorrhagic fever in humans: Bente et al., 2013; Swanepoel and Burt, 2004) and *Theileria annulata* (causative agent of bovine tropical theileriosis in cattle: Morrison, 2015). Despite the fact that they are one of the most common ectoparasites on domesticated animals, the most comprehensive molecular comparisons among members of the genus merely includes five of the 27 recognized species (Bakheit et al., 2012; Barker and Murrell, 2004; Guglielmone and Nava, 2014; Zhang and Zhang, 2014). In addition, the difficulties of sampling throughout their wide range, identifying all the life stages of each species correctly, the clear-cut sexual dimorphism in adults, and the preponderance of intraspecific morphological variation in *Hyalomma* have made it nearly impossible to create an accurate and well resolved morphological phylogeny for extant members of the genus (Apanaskevich and Horak, 2008a, 2008b, 2005).

At the subgeneric level, Schulze (1930) recognized three assemblages: (1) *Hyalommasta* Schulze, 1930 with a single species *H. aegyptium* (Linnaeus, 1758); (2) *Hyalommina* Schulze, 1919 with *H. brevipunctatum* Sharif, 1928, *H. kumari* Sharif, 1928 and *H. hussaini* Sharif, 1928 from the Indian subcontinent, and the extralimital Near Eastern/North African *H. rhipicephaloides* Neumann, 1901; (3) *Hyalomma* s. str. with all the remaining species known at that time. Later, the subgeneric nomenclature was revised by Filippova (1984), who synonymized the monotypic subgenus *Hyalommasta* with *Hyalomma* s. str. and proposed the subgenus *Euhyalomma* Filippova, 1984. Since this revision the taxonomic content of subgenera has not changed, except that more species of *Hyalommina* and *Euhyalomma* were recognized and added over time.

At the species level the taxonomy is equally obscured: *Hyalomma excavatum* Koch, 1844 has been considered either a synonym or a subspecies of *H. anatolicum* Koch, 1844 (Delpy, 1949; Hoogstraal, 1956; Hoogstraal and Kaiser, 1959) but Apanaskevich (2003) and Apanaskevich and Horak (2005) afforded *H. excavatum* a full species status closely related to *H. anatolicum*. Similarly, *H. isaaci* Sharif, 1928, *H. rufipes* Koch, 1844 and *H. turanicum* Pomerantzev, 1946 were treated as subspecies of *H. marginatum* Koch, 1844 (Hoogstraal and Kaiser, 1960; Kaiser and Hoogstraal, 1963; Pomerantzev, 1946). After a thorough morphological revision, Apanaskevich and Horak (2008a) recognized *H. isaaci*, *H. rufipes* and *H. turanicum* as full species. Moreover, Apanaskevich and Horak (2006) also re-established *H. glabrum* Delpy, 1949 that was then considered a synonym of *H. turanicum* (Hoogstraal, 1956). The full species status of morphologically near similar *H. albiparmatum* Schulze, 1919 from central-East Africa (that has an ivory-coloured parma in males), *H. nitidum* Schulze, 1919 from West Africa (that shows a reduction in clarity of ivory-coloured bands on the segments of the legs in both sexes and the external cuticular preatrial fold of the genital aperture of females are convex) and the widely distributed *H. truncatum* Koch, 1844 have also been a subject of much debate (see Apanaskevich and Horak, 2008b; Camicas et al., 1998; Feldman-Muhsam, 1962; Hoogstraal, 1979, 1956; Tomassone et al., 2005; Walker, 1974). Finally, at the intraspecific level, evidence also exists that species occupying wide geographic ranges such as *H. truncatum* and *H. rufipes* show cryptic speciation (Cangi et al., 2013; Sands et al., 2017).

A better understanding of the mechanisms involved in the diversification of tick species can facilitate a more stable taxonomic framework for *Hyalomma*. In general, host association and host movement are regarded as important facilitators of tick dispersal across the landscape (Araya-Anchetta et al., 2015; Blouin et al., 1995; Engelbrecht et al., 2016; Sands et al., 2017). Life history, ecology and environmental factors off the host are however equally important (Araya-Anchetta et al., 2015; Johnson et al., 2010; Maze-Guilmo et al., 2016). In ticks, deciphering the mechanisms responsible for speciation is particularly complex since members of the group are characterized by complex life cycles (Sonenshine, 1991; Walker et al., 2014). They are often dependent on various hosts for part of their life cycle (Sonenshine, 1991; Walker et al., 2014), and they are also sensitive to environmental influences that can severely affect the survival of free-living stages off the host (Walker et al., 2014). Since tick species also differ in time spent off the host, it is to be expected that the effect of external environmental conditions will be more important for tick species that spend a larger portion of the life cycle off the host (two- and three-host ticks) compared to those that spend less (one-host ticks) (Sonenshine, 1991).

Because the majority of *Hyalomma* species are multi-host parasites with wide host ranges (Apanaskevich, 2004), we predict that host association and host diversification *per se* will play a less important role in the speciation process of *Hyalomma* (Cumming, 1999; McCoy et al., 2013). It is more likely that the majority of the recent diversifications of *Hyalomma* species are driven by a combination of ecological interactions between the parasites and their hosts (Cangi et al., 2013) and the abiotic biogeographic conditions in the environment (Klompen et al., 1996; McCoy et al., 2013). The latter also specifically includes the effects that biogeography can have on host movement and distribution (Sands et al., 2017).

Based on fossil evidence, the origin of *Hyalomma* potentially dates back to 50 Mya (de la Fuente, 2003). Since members of the genus are distributed across continents, it is possible that deeper divergences among lineages may coincide with tectonic events and large scale climatic changes that were responsible for the formation and disappearances of land bridges throughout geological time periods (Rögl, 1999). In particular, restricted dispersal imposed on multiple hosts (vicariance) could have resulted in allopatric speciation processes within the genus (Sands et al., 2017). The formation of land bridges in turn could have facilitated intercontinental exchanges of host species between the Afrotropics and Paleartic/Oriental regions (Popov et al., 2004; Portik and Papenfuss, 2015; Rögl, 1999). Particularly pertinent to this study, the Arabian plate separated from Africa approximately 30 Mya and this was followed by rifting in the southern Red Sea at approximately 27 Mya (Bohannon, 1986; Bosworth et al., 2005; Jolivet and Faccenna, 2000). This resulted in the formation of the Tethyan seaway which only temporarily closed again at approximately 19 Mya (forming of the so-called *Gomphotherium* land bridge: Cox, 2000; Popov et al., 2004; Rögl, 1999). At 15 Mya, a more permanent land bridge was formed between Africa and Arabia when the Arabian plate fused with Eurasia (Bosworth et al., 2005). These geologic activities had severe effects on the faunal biogeography in the region (Fernendes et al., 2006; Portik and Papenfuss, 2015) and we predict that it may have also affected the evolution of *Hyalomma* in a similar way.

The aim of this study was to investigate some of the mechanisms involved in the diversification of *Hyalomma*, by constructing a dated phylogeny based on molecular data sets. In addition, we aimed to test some of the numerous taxonomic hypotheses by generating various phylogenetic trees based on mtDNA, nuclear DNA and morphological data. The geographic variation present in some of the more widespread taxa was addressed by using