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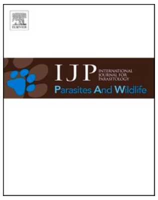

The journey into the ecology and distribution of the genus *Amblyomma* in southern Africa

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ABSTRACT

The genus *Amblyomma* represents a fascinating and ecologically diverse group of hard ticks, widely distributed across southern Africa. Despite their importance as vectors of numerous pathogens, many species remain poorly studied, with limited ecological, seasonal, and distributional records. In this review we discuss observed patterns of sympatry and parapatry, noting that reproductive interference mediated by species-specific attraction-aggregation-attachment (AAA) pheromones may play a key role in shaping species boundaries. Molecular analyses using mitochondrial markers (12S rRNA, 16S rRNA, *coi*, and *cytb*) reveal high intraspecific variation within *A. variegatum*. The limited differentiation between *A. pomposum* and *A. variegatum* suggests recent divergence, motivating further genome-wide investigations. Additionally, we document the introduction of *A. hebraeum* and *A. lepidum* into established ranges of other species, emphasising the need for ongoing surveillance to assess the ecological consequences of such events. Finally, we outline an integrated, multi-pronged approach for advancing the understanding of *Amblyomma* ecology, species boundaries, and distribution, combining extensive field sampling, genome-wide molecular tools, pheromone studies, biological compatibility experiments, and curated voucher-linked data. This holistic framework aims to resolve taxonomic ambiguities, clarify evolutionary relationships, and guide future research on this medically and veterinary significant genus.

1. Background

Like all true journeys, this one asks us to return to the place where its earliest echoes first whispered into being – the late Carboniferous period (an estimated 300 MYA) – where Gondwanaland was still intact and the earliest of tick ancestries have been recorded (Nava et al., 2009; Spickett, 2013). *Nuttalliella namaqua* has been described as an “evolutionary missing link” among ticks due to its early diverging phylogenetic position and combination of morphological features shared with both Argasidae and Ixodidae (Mans et al., 2011). Although no extant tick species represents a direct ancestor, *N. namaqua* is considered to have diverged early in tick evolution, providing insights into the characteristics of early tick lineages (Oliver, 1989; Nava et al., 2009). Ticks are classified in the class Arachnida, order Ixodida, and divided into three families: Argasidae (soft ticks), Ixodidae (hard ticks) and Nuttalliellidae (a monotypic family represented by *Nuttalliella namaqua*) (Oliver, 1989). Ticks are non-permanent haematophagous ectoparasites of vertebrates, ranked second as vectors of pathogenic organisms (Klompen et al., 1996). Of these families, Ixodidae is the largest with 786 tick species (Robbins et al., 2025). The genus *Amblyomma* is the third largest within the Ixodidae, recognised for their ornate scutums, aggressive hunting behaviour, wide host range and diverse vector competence. The work conducted Uribe et al. (2024)proposed that *Amblyomma* originated roughly 47.8 MYA within the southern Hemisphere, with Australian endemic and southern South American species forming a sister group to the remaining *Amblyomma* occurring world-wide. It is postulated that the current *Amblyomma* species in Africa reached their present distribution following the closure of the Tethys Sea and the end of the Antarctic bridge connection (between 24.6 and 23.3 MYA) (Uribe et al., 2024). To date an estimated 136 *Amblyomma* species have been identified (Robbins et al., 2025), of which 26 are documented to occur in Africa.

In southern Africa (Angola, Botswana, eSwatini, Lesotho, Mozambique, Namibia, South Africa, Zambia and Zimbabwe) 14 of these *Amblyomma* have been noted including: *A. astrion*, *A. compressum*, *A. eburneum*, *A. hebraeum*, *A. marmoreum*, *A. nuttalli*, *A. paulopunctatum*,

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A. pomposum, *A. rhinocerotis*, *A. sparsum*, *A. splendidum*, *A. sylvaticum*, *A. tholloni* and *A. variegatum* (Voltzit and Keirans, 2003) (Table 1). We have excluded *Amblyomma arcanum*, *Amblyomma exornatum*, *Amblyomma flavomaculatum*, *Amblyomma flavum*, *Amblyomma inopinatum*, *Amblyomma latum* and *Amblyomma* transversale from this review.

Table 1
Selected *Amblyomma* species from southern Africa; their adult preferred hosts, seasonality and ecology. The table was constructed using information from Robinson (1926), Petney et al. (1987), Voltzit and Keirans (2003) and Horak et al. (2018).

Tick species	Adults host	Seasonality	Ecology
A. astrion	African buffalo and other ruminants	Peak in rainy season; larvae/nymphs in early wet season	Wooded savannas; altitude: 0 - 1000 m; rainfall: 500 - 1700 mm p.a.
A. compressum	Exclusively: pangolins	Adults most active in warm, wet months; immature stages throughout wet season	Forest-dwelling; ground-level vegetation for questing
A. eburneum	African buffalo and other ruminants	Peaks during rainy season	Prefers savanna and woodland habitats
A. hebraeum	Ruminants and other wild ungulates	Adults peak in summer (Nov–Mar); nymphs/larvae in early summer	Tall grass savanna and bushveld; altitude: 0 – 1525 m; rainfall: 300 – 800 mm p.a.
A. marmoreum	Tortoises and other reptiles	Adults active in summer; larval/nymphal activity peaks earlier in wet season	Often found in bushveld and savanna; ground-level questing; altitude: 0 - 1500 m; rainfall: 250 - 900 mm p.a.
A. nuttalli	Reptiles	Adults and immatures active during warm wet season	Mainly forest and savanna habitats
A. paulopunctatum	Suidae	Peaks in wet season	Bush and forest habitats
A. pomposum	Cattle, mules and African buffalo	Adults peak in summer months; larvae/nymphs early wet season	Savanna and mixed woodland; altitude: 1200 – 1700 m; rainfall: 800 – 2000 mm p.a.
A. rhinocerotis	Rhinoceros	Adults mainly in wet season; low abundance otherwise	Endangered
A. sparsum	Black rhinoceros, African buffalo and reptiles	Adult activity in summer/rainy season; immatures follow rainfall peaks	Found in savanna and semi-arid areas; altitude: 0 - 1830 m; rainfall: 250 – 1250 mm p.a.
A. splendidum	African forest buffalo and cattle	Peaks during wet season	Forest and savanna habitats
A. sylvaticum	Tortoises	Adults active in spring-summer; immatures in early summer	Life cycle takes 1-2 years to complete; bushveld and dry fynbos habitats; questing at ground level;
A. tholloni	African elephant	Adults peak in wet season	Often in savanna/forest edges but can exist in arid zones to subhumid and humid areas; altitude: 0 - 1525 m; rainfall: 1250 – 1750 mm p.a.
A. variegatum	Cattle and large artiodactyla	Adult activity peaks in summer; larvae/nymphs early wet season	Savanna and bushveld; altitude: 0 - 2590 m; rainfall: 400 – 2800 mm p.a.

Distribution records of the listed species are illustrated in Fig. 1, however, these distribution patterns should be critically evaluated as the records are old and tick populations have shifted due to anthropogenic factors including climate change, movement of infested hosts, and others (Léger et al., 2013). The need for re-evaluation can be highlighted in the conflicting distribution records of *A. pomposum* in Angola. Gomes (1993) and Smit et al. (2024) describe the distribution as limited to central western Angola, while other authors such as Dönitz (1909), Petney et al. (1987), Voltzit and Keirans (2003) and Walker et al. (2003) all describe the distribution of *A. pomposum* to span from Angola into Mozambique and northwards to Kenya (Fig. 1h). This emphasises the need for more accurate and recent distribution records as the majority of these ticks are understudied, therefore distribution, seasonal and ecological records are limited.

It is noted that all *Amblyomma* species have a three-host life cycle (Horak et al., 2018). Most of the species prefer the wet seasons with peak activity of larvae and adult stages, usually occurring after the first rains (Horak et al., 2018). Distribution of *Amblyomma* ticks are influenced by a variety of factors such as host availability and movement patterns, habitat composition, climate, physiology and anthropogenic impact (Bull, 1991; Cumming, 1999; Hassan and Salih, 2013; Léger et al., 2013).

Herewith we would like to highlight current gaps in knowledge surrounding the phylogenetic classification and physiological impact of pheromones on the distribution of southern African *Amblyomma*. We will discuss some hypotheses, raising several topics requiring further investigation, and provided suggestions to achieve more comprehensive understandings of the framework behind the distribution of *Amblyomma* species across southern Africa.

2. Distribution and phylogeny

Tick classification and taxonomy were previously reliant on three main aspects; morphology, biology and ecology (Hoogstraal and Aeschlimann, 1982). With the development and incorporation of molecular markers and phylogenetics, taxonomic paradigms have evolved at a rapid pace. Unlike the evolutionary relationship within the Argasidae, which is poorly resolved (Nava et al., 2009; Mans, 2023), the evolutionary relationships within the Ixodidae are more defined with two main clusters. The first is the early diverging Prostriata, represented by the genus *Ixodes* in the subfamily Ixodinae; the second are the Metastriata, which comprise all the remaining genera (Hoogstraal and Aeschlimann, 1982; Nava et al., 2009). The traditional classification scheme proposed by Hoogstraal and Aeschlimann (1982), divided the Metastriata into Amblyomminae, Haemaphysalinae, Hyalomminae and Rhipicephalinae, however, modern systematics has brought on some considerable shifts to this scheme. Among these shifts it is worth noting the supporting evidence for the taxonomic reassignment of the genus *Aponomma*, of which the majority of the species are now placed within Amblyomminae. However, some species were assigned to the early diverging Metastriata in the new subfamily Bothriocrotinae, genus *Bothriocroton* (Klompen et al., 2002). Furthermore, several species of the previous *Aponomma* were also observed to form independent lineages, which were raised to genus level, such as *Africaniella*, *Archaeocroton*, and *Robertsicus*, all of which display early branching in the phylogenetic tree (Barker and Burger, 2018; Hornok et al., 2020; Uribe et al., 2024). Another major taxonomic revision was the dissolution of the Hyalomminae, with its members reassigned to the Rhipicephalinae (Mans, 2023). In addition, the former genus *Boophilus* is now considered *Rhipicephalus*, a change that was met with much resistance, however, the move has been sufficiently supported with the increase in molecular information (Bakkes et al., 2022; Mans, 2023).

Improved understanding of tick systematics impacts species distribution records. This is particularly true when species have been synonymised and combined such as *Amblyomma aureum* found in Tanzania

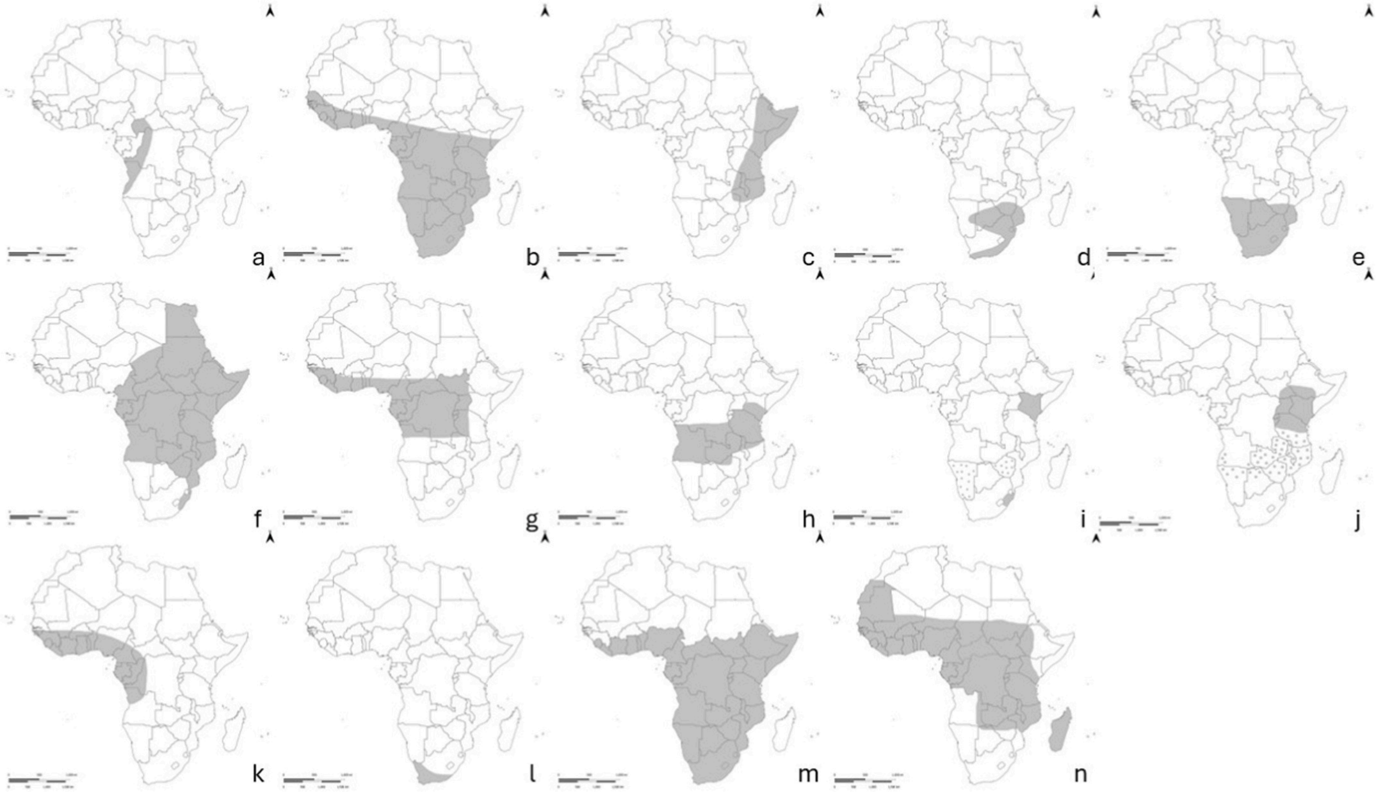

Fig. 1. Distribution of ticks occurring in southern Africa based on Voltzit and Keirans (2003) with updates from Uribe et al. (2024), including: (a) *A. astrion*, (b) *A. compressum*, (c) *A. eburneum*, (d) *A. hebraeum*, (e) *A. marmoreum*, (f) *A. nuttalli*, (g) *A. paulopunctatum*, (h) *A. pomposum*, (i) *A. rhinocerotis*, (j) *A. sparsum*, (k) *A. splendidum*, (l) *A. sylvaticum*, (m) *A. tholloni* and (n) *A. variegatum*. Grey shading indicates areas with confirmed distributions while dotted areas indicate areas of scattered distribution.

which has been synonymised with the endangered *Amblyomma rhinocerotis* (Camicas et al., 1998; Robbins et al., 2025). With these continuous shifts, the genus *Amblyomma* has preserved plesiomorphic characteristics which blurs taxonomic boundaries. This remains an ongoing challenge, as the existing evolutionary framework for these lineages - largely derived from mitochondrial genome data - is still too incomplete to pinpoint possible diversification events. Currently, 39 mitochondrial genomes are available for the genus *Amblyomma* and have proven to provide a robust and stable evolutionary framework (Uribe et al., 2024). Uribe et al. (2024) reinforced the findings that most traditional subgenera (*Cernyomma*, *Anastosiella*, *Xiphiastor*, *Adenopleura*, *Aponomma*, *Dermiomma*) were not monophyletic, emphasising that only the subgenera *Amblyomma* and *Walkeriana* were consistently recovered as monophyletic. Furthermore, Santodomingo et al. (2021) performed phylogenetic analysis of the Neotropic *Amblyomma* using concatenation of *12S*, *16S*, *18S*, *cox1* and *cox2* genetic markers and documented that their phylogenetic topologies may suggest that the diversification of the genus *Amblyomma* may have arisen from species with Australian and American distributions. This was strongly supported by Uribe et al. (2024), who demonstrated, with high probability, that *Amblyomma* diversification is no longer interpreted as “Neotropical-first” with later dispersal, but as a Southern Hemisphere radiation shaped by Gondwanan connections, especially the Antarctic land bridge. Both Santodomingo et al. (2021) and Uribe et al. (2024) highlight that the African *Amblyomma* species are not among the earliest-diverging lineages of the genus, but rather they are nested within more derived clades that diversified after the initial Gondwanan radiation, with a recent migration event from America and the Indo-Pacific region. Furthermore, Uribe et al. (2024) noted that African tick species assigned to subgenera such as *Aponomma*, *Adenopleura*, and *Cernyomma* do not form monophyletic groups, with the African taxa observed to be scattered across the phylogeny, revealing extensive homoplasy. Therefore, emphasising the need for a taxonomic revision based on genomic data for this region.

Several *Amblyomma* species complexes have been documented in Africa, such as the *A. marmoreum* complex and the *A. variegatum* complex (Theiler and Salisbury, 1959). The *Amblyomma marmoreum* complex consists of five species: *A. marmoreum* sensu stricto, *A. sparsum*, *Amblyomma falsomarmoreum*, *A. nuttalli*, and *A. paulopunctatum*. While *A. marmoreum* has been well studied, there is a lack in morphological, genetic, and ecological data for the remaining four species (Cotes-Perdomo et al., 2024). Adults of the *A. marmoreum* complex are primarily associated with large reptiles and occasionally birds and large mammals, while the immature stages favour small mammals and birds (Theiler and Salisbury, 1959). Species within the *A. marmoreum* complex are frequently confused due to overlapping morphological characters (Hoogstraal, 1956). A resent example of such misidentification has been noted between *A. marmoreum* and *A. sparsum*, where specimens initially identified morphologically as *A. marmoreum* on migratory birds were later molecularly confirmed to be *A. sparsum* (Menegon et al., 2024). This association with avian hosts has allowed for long-distance dispersal, as demonstrated by the collection of *A. sparsum* from migratory birds in Italy (Menegon et al., 2024). The increase in reptile trade and translocation has also affected the distribution range as can be seen with the collection of four *A. sparsum* males collected from a puff adder (*Bitis arietans*) in Senegal (Cotes-Perdomo et al., 2024). Overlapping distributions can be seen between the species of the *A. marmoreum* complex (Fig. 1) and has resulted in common misidentifications which may have led to inaccurate distribution records. Furthermore, few phylogenetic studies are available on these species and their marker selection are rarely the same, making phylogenetic comparisons nearly impossible (Cotes-Perdomo et al., 2024). Cotes-Perdomo et al. (2024) provided the first complete mitochondrial genome of *A. sparsum*, which greatly resembled that of *A. nuttalli*. The *A. sparsum* and *A. nuttalli* clade formed a sister clade to that of the *A. marmoreum* sensu stricto, confirming the monophyly of the core *A. marmoreum* complex. Theiler and Salisbury (1959) highlights the usefulness of whole mitogenomic data for resolving deeper nodes within the complex and underscores that morphological variability reflects intraspecific plasticity, not necessarily cryptic species.

Another clear example of the lack of genetic and genomic data for *Amblyomma* species and the impact on distribution records can be found in the controversy between *A. pomposum* and *A. variegatum* highlighted by Dias (1953, 1958) and revisited by Smit et al. (2024).

Amblyomma variegatum, as described by Fabricius (1794), is a large dark tick with metallic ivory, green and red patterning, uniformly dark festoons, mild punctations and convex eyes. Its distribution range is extensive in Africa, making it one of the most economically important tick species in the continent (Theiler and Salisbury, 1959; Petney et al., 1987; Walker and Olwage, 1987). *Amblyomma pomposum* was first described by Dönitz (1909) just south of lake Tanganyika, Zambia. This specimen greatly resembled *A. variegatum*, however was adorned with coarser punctations, more vibrant ornamentation and prominent lateral patches. Two years later, Robinson (1911), described two male ticks from southern Rhodesia (now Zimbabwe) as *Amblyomma variegatum* var. *nocens*. He reported the distribution of *A. variegatum* var. *nocens* to span from eastern Zimbabwe (Makoni, Umtali/Mutare, Melsetter) into the Manica province, Mozambique, occurring in bushveld at an altitude of 609.6– 914.4 m. He distinguished *A. variegatum* var. *nocens* by coarser punctations and more vibrant coloration but later treated it as synonymous with *A. pomposum*, after reviewing the description by Dönitz (1909). Subsequently, Dias (1950) described *A. variegatum* var. *Govurensis* from Govuro, Mozambique, noting similar coarse punctations and intense patterns. After comparing with Robinson's material, Dias (1953) concluded that *A. variegatum* var. *Govurensis* equalled to *A. variegatum* var. *nocens* and was therefore synonymous with *A. pomposum*. To confirm this description Dias examined the voucher species of Dönitz (1909) for *A. pomposum* and confirmed that the samples he observed were indeed *A. pomposum*. As *A. pomposum* is described as an eastern *Amblyomma* species, Dias investigated the Angolan *A. pomposum*. From his observations, the *A. pomposum* located in Angola did not match the specimens that he collected in Mozambique, nor did it match the voucher specimens described by Dönitz (1909). Dias (1953) then redescribed the *A. pomposum* occurring in western Africa (mainly Angola) as *Amblyomma superbum*. This controversy was re-examined by Theiler and Salisbury (1959), and the proposed species name *Amblyomma superbum* was rejected by these authors and subsequently not used by tick taxonomists. This highlights taxonomic difficulties at species boundaries, which in turn influence species boundary descriptions.

Molecular tools have allowed for a more in-depth analysis of *Amblyomma* species. One such analysis was conducted by Beati et al. (2012) on *A. variegatum* intraspecific diversity. Beati et al. (2012) investigated the genetic diversity of *A. variegatum* from four Caribbean islands and five African countries using the mitochondrial 12S rRNA and D-Loop-DL, and the intergenic transcribed spacer 2. In spite of the low variation between the widely distributed *A. variegatum,* the formation of two main clusters, East African and West African, were observed (Beati et al., 2012). The East African clade displayed a greater haplotype diversity with more stable lineages. In contrast, the West African clade formed a star-like pattern, consistent with recent population expansion (Beati et al., 2012). *Amblyomma variegatum* sequences from the Caribbean clustered consistently within the West African clade, indicative of their origin. Several haplotypes of *A. variegatum* from the Caribbean also displayed local variation, which is to be expected with the interrupted gene flow (Beati et al., 2012). Lastly, Beati et al. (2012) noted an intermediate Zambian lineage haplotype, bridging the eastern and western clades. This transitioning from diverse but genetically conserved lineages in East Africa to the diverse and rapidly evolving lineages in West Africa, suggest a progressive east-to-west spread of the species. Overall, the phylogenetic and haplotype analyses support an origin of *A. variegatum* in East Africa followed by relatively recent westward expansion and subsequent introduction to the Caribbean, with diversification occurring in Zambia. We hypothesise that *A. pomposum* could be a result of this westward expansion of *A. variegatum*, with a possible speciation event occurring in west Zambia, south DRC and Angola. This hypothesis would account for the morphological similarities between the species and explain the distribution patterns observed (Smit et al., 2024).

While *A. variegatum* is well studied both morphologically and molecularly, *A. pomposum* has received much less attention. Recently, Smit et al. (2024) readdressed the controversy between *A. pomposum* and *A. variegatum* using the mitochondrial 12S rRNA, 16S rRNA, cytochrome oxidase 1 (*coi*) and cytochrome *b* (*cytb*) markers. This was a challenging task as no sequence data was available for *A. pomposum* on any public repository to compare the results with. Ultimately, Smit et al. (2024) were unable to differentiate between *A. pomposum* collected in Angola and *A. variegatum* collected in Angola, Mozambique, Zambia, or Zimbabwe. Smit et al. (2024) also observed varying subclades forming within the *A. variegatum* itself. This may be indicative of high intra species variation. The observed variation on *A. variegatum* was much greater than other *Amblyomma* species investigated. This is to be expected with the wide distribution range of *A. variegatum* in the African continent. Such a large distribution range will allow for limited gene flow between separated populations, increasing the probability of speciation by isolation. Interestingly, Smit et al. (2024) documented *A. pomposum* as being restricted to the central-western parts of Angola, unlike previous records by Hoogstraal (1956), Petney et al. (1987), Walker and Olwage (1987), Voltzit and Keirans (2003), and Walker et al. (2003). The high intraspecific variation observed in *A. variegatum*, coupled with morphological similarities and the inability of molecular tools to distinguish it from *A. pomposum*, supports Hoogstraal (1956) proposal that they are a subspecies rather than a distinct species. It may also suggest that the classification proposed by Dias (1953) might require a more in-depth investigation.

Thus, unresolved complexes such as this one raises the question on the accuracy of the current distribution records.

3. Distribution and pheromones

Several key observations of *Amblyomma* distribution patterns within southern Africa have been made by Bournez et al. (2015), Smit et al. (2023, 2024) and Smit et al. (2025). Some species occur in a sympatric manner (Smit et al., 2023) while others appear to form clear parapatric borders (Bournez et al., 2012; Smit et al., 2024). According to Chilton and Andrews (1988), the observed distribution patterns may result from disrupted female sex-pheromone signalling, non-specific sexual attraction between species, or physical interference with mating by heterospecific males, although experimental evidence supporting these hypotheses is still lacking.

During field expeditions for tick collections to the Zambezi valley in central Mozambique, *A. eburneum* and *A. variegatum* were observed occurring on the same host (African buffalo mainly in forest habitats) (Smit et al., 2023). Not only did they share the same host, but also the same predilection sites and fed in the same clusters. In all inspected animals *A. variegatum* had higher tick infestations than that of *A. eburneum*, approximately 4:1 (Smit et al., 2023). In contrast, two clear parapatric boundaries were observed. The first between *A. hebraeum* and *A. variegatum* in Mozambique and Zimbabwe (Bournez et al., 2015; Smit et al., 2024), the second between *A. pomposum* and *A. variegatum* in Angola (Smit et al., 2024). At the border between the species, ticks would rarely share the same host. In both cases, environmental landscapes and host densities are identical on both sides of the boundary, thus they are unlikely to be contributing factors. The main hypothesis for the observation of parapatric boundaries, when excluding ecotonal and host factors, is sexual competition or reproductive interference

(Bull, 1991).

The reproductive behaviour of ticks is predominantly mediated by pheromones (Kiszewski et al., 2001). Although broad similarities exist in courtship and mating behaviours within the Ixodidae, distinct differences are evident between metastriate and prostriate species (Carr et al., 2016). Species within the genus *Ixodes* (prostriate) are divided into two broad ecological categories; nidicolous species and non-nidicolous species (Kiszewski et al., 2001). Nidicolous species typically engage in nest-based mating strategies, whereas non-nidicolous species often mate during host-seeking behaviour, prior to host attachment (Kiszewski et al., 2001).

In contrast, metastriate species (such as ticks within the genera *Amblyomma*, *Dermacentor*, and *Rhipicephalus*), employ obligated on-host mating strategies characterised by aggregation and feeding sites (Kiszewski et al., 2001). A fundamental distinction between prostriate and metastriate mating systems is that the metastriate species require blood feeding to initiate mating, whereas prostriate species employ an autogenous mating physiology in which mating can occur independently of blood feeding (Kiszewski et al., 2001; Carr et al., 2016). This dependence on host association has driven the evolution of complex pheromone-mediated mechanisms in metastriate ticks that regulate aggregation, mate attraction, and species recognition directly on the host.

Gothe (1987) provided seven categories based on pheromones activity profile: "assembly, aggregation/attachment, pre-attachment or pre-feeding, attractant sex, contact sex, fecundity-reducing and various ungrouped". Of these pheromones, the attraction-aggregation-attachment (AAA) pheromone has been well studied in its role in tick mating, reproductive isolation and control measures (Norval et al., 1994, 1996; Kiszewski et al., 2001; Sonenshine, 2004). AAA pheromones are produced by males after spermatogenesis and it assists in the regulation of tick attachment to the host and the aggregation of other unfed males, females and nymphs to the site of attachment (Gothe, 1987). Within the metastriate ticks, pheromonal communication coordinates a tightly ordered sequence of events from host location and attachment through to mate recognition and copulation. During host-seeking and early attachment, long-range volatile AAA pheromones play a prominent role in certain genera. These pheromones are a defining feature of *Amblyomma*, where they are produced by feeding males in Type II dermal glands and can attract conspecifics over distances of up to 10 m, resulting in dense aggregations on the host (Price Jr et al., 1994; Sonenshine, 2006). Similar activity has been documented in *Rhipicephalus evertsi evertsi*,(Gothe, 1987; Sonenshine, 2004), whereas AAA pheromones are absent in *Dermacentor* species, whose chemical communication is largely restricted to short-range, sex-specific courtship cues rather than long-range aggregation (Sonenshine, 2004). Furthermore, in *Amblyomma*, AAA pheromones also contribute to male–male interactions by increasing local male density at feeding sites, thereby, shaping mating opportunities and competition.

Following attachment and initiation of feeding, genus-specific differences in mating initiation become apparent. In *Amblyomma,* mating is typically initiated by feeding males, with pheromone production tightly coupled to feeding-induced sexual maturation, ensuring that only sexually competent males signal (Gothe, 1987). In contrast, *Dermacentor* species exhibit a highly structured courtship process consisting of a strict nine-phase behavioural sequence that is triggered by feeding females (Sonenshine, 2004). *Rhipicephalus appendiculatus* displays a further variation, as females readily attach to the host in the absence of males and, after approximately four days of feeding, produce phenolic compounds that attract both sexually mature and unfed males to the feeding site (Bramuel, 2017).

Across all three genera, feeding females produce the attractant sex pheromone 2,6-dichlorophenol (2,6-DCP), which functions as a primary volatile cue drawing males towards the attached females and facilitating mate location on the host (Price Jr et al., 1994; Gowrishankar et al., 2019). In *Amblyomma*, the activity of 2,6-DCP is feeding-stage dependent and operates synergistically with host-derived cues such as carbon dioxide and heat, facilitating orientation rather than acting as a stand-alone long-range attractant. In addition to on-host signalling, *Amblyomma* and *Rhipicephalus* species utilise purine-based assembly pheromones, primarily guanine and xanthine excreted in faeces, to form off-host clusters in the environment that reduce desiccation risk prior to host contact (Gothe, 1987). Such assembly pheromones are absent in *Dermacentor* species (Sonenshine, 2004).

Once physical contact is established, close-range pheromones regulate species recognition and copulatory progression. All three genera employ cholesteryl esters as mounting sex pheromones on the female cuticle. *Dermacentor variabilis* relies predominantly on a single compound, cholesteryl oleate, (Sonenshine, 2004), while *Amblyomma* and *Rhipicephalus* species typically utilise more complex blends in which species specificity is determined largely by relative ester ratios rather than unique compounds (Sonenshine, 2004). This redundancy permits occasional heterospecific mounting while maintaining effective reproductive isolation. In *Dermacentor*, mating culminates in the action of a well-characterised genital sex pheromone consisting of C14–C22 saturated fatty acids and ecdysteroids, including 20-hydroxyecdysone, which functions as a final species-recognition filter prior to insemination (Taylor et al., 1991), In contrast, evidence for a comparable genital sex pheromone is weak or absent in many *Amblyomma* species, suggesting that species recognition is resolved earlier in the mating sequence through AAA and mounting pheromones rather than late-stage chemical gating (Sonenshine, 2004).

Importantly, AAA pheromones are highly species-specific, contributing to reproductive isolation by limiting non-specific aggregation and reducing the likelihood of interspecific mating. This specificity, together with their central role in host-associated mating, underpins the value of AAA pheromones as focal targets for both evolutionary investigations and pheromone-based tick control technologies.

Given the central role of the AAA pheromone in species-specific mating, it can be hypothesised that the chemical composition similarity between AAA pheromones reflects the recency of evolutionary divergence between tick species. Species that have diverged more recently are therefore expected to possess more similar AAA pheromone profiles, increasing the likelihood of interspecific attraction and mating. Conversely, where a substantial period has elapsed since divergence, AAA pheromones are expected to have diverged accordingly, reducing the probability of interspecific mating.

Within *Amblyomma*, AAA pheromones have been well characterised in *A. hebraeum* and *A. variegatum* (Norval et al., 1994, 1996; Sonenshine, 2004), whereas other *Amblyomma* species, such as *A. eburneum* and *A. pomposum,* remain comparatively understudied. Notably, the AAA pheromones of *A. hebraeum* and *A. variegatum* are highly similar in terms of chemical composition (Rechav et al., 1982; Gothe, 1987; Price Jr et al., 1994), resulting in pronounced interspecific attraction. This chemical similarity is reflected behaviourally, as both laboratory and field studies have documented cross-mating between these two species (Rechav et al., 1982; Price Jr et al., 1994; Clarke and Pretorius, 2005; Bournez et al., 2015). Although cross-mating occurs and egg masses are produced, hatching success is extremely low (0–1%), yielding progeny numbers insufficient to sustain a population. This post-mating reproductive incompatibility likely contributes to the maintenance of the parapatric boundary observed between *A. hebraeum* and *A. variegatum.* Moreover, Smit et al. (2023, 2024) noted that *A. eburneum* occurs sympatrically with *A. variegatum,* suggesting a different reproductive dynamic. Based on the above hypothesis, it is plausible that *A. eburneum* diverged from *A. variegatum* earlier than did either *A. hebraeum* or *A. pomposum*, allowing sufficient time for AAA pheromone divergence and increased species specificity. Such divergence would minimise interspecific attraction and sexual competition, thereby facilitating stable sympatric coexistence. However, in the work of Smit et al. (2024), *A. eburneum* and *A. hebraeum* clades were sister to that of the *A. pomposum/A. variegatum* clade when using the *coi*, 12S rRNA and 16S rRNA mitochondrial markers. Although Smit et al. (2024) did not incorporate an evolutionary time framework, it might suggest that both *A. eburneum* and *A. hebraeum* have similar evolutionary divergence time from *A. variegatum*. It is key to note that the markers used are not responsible for pheromone production and *A. eburneum* pheromone composition has not been evaluated, Although, co-occurrence is evident, the reasons for it have not yet been experimentally proven. Furthermore, no interspecific mating trials have been conducted between *A. pomposum* and *A. variegatum*, precluding definitive conclusions regarding the role of sexual competition or reproductive interference in shaping their parapatric distributions. However, given that their spatial distribution closely parallels that of *A. hebraeum* and *A. variegatum*, it is reasonable to hypothesise that similar pheromone-mediated mechanisms contribute to the establishment and maintenance of parapatric boundaries in this species pair as well.

A comparable situation may exist in East Africa involving *Amblyomma lepidum* and *Amblyomma gemma*, which have been reported to occur both sympatrically and parapatrically (Walker and Olwage, 1987). Their sympatric distributions may result from the introduction of a high number of ticks into the other species' "territory" along parapatric borders. Such introductions could facilitate successful establishment, thereby overwhelming the effects of sexual competition that are thought to maintain parapatric boundaries. *Amblyomma lepidum* has been documented to have a growing distribution, with new introductions (Piazak, 2005; Okely et al., 2022; Smit et al., 2025) Consequently, these taxa represent important targets for future comparative and experimental studies.

Furthermore, Smit et al. (2024) have made some observations during field collections on newly introduced *A. hebraeum* populations in *A. variegatum* "territory" in Mozambique, as well as *A. lepidum* in *A. hebraeum* "territory" in Zimbabwe (Smit et al., 2025). These introductions are believed to be from infested cattle that were introduced into specific areas of each country without adequate tick control. Regarding the *A. hebraeum* introduction in the central province of Sofala, Mozambique, which was previously reported as *A. variegatum* territory, it would be interesting to longitudinally observe if this newly introduced population permanently establishes, redefining the borders between *A. hebraeum* and *A. variegatum* in this region of Mozambique. This is reliant on the numbers of the newly introduced *A. hebraeum*. As *A. hebraeum* and *A. variegatum* have the same host and ecological preferences, the number of newly introduced *A. hebraeum* will determine whether the population is sustainable. Additionally, Smit et al. (2025) noted the collection of both males and females (fed and unfed) in the introduced region, emphasising the possibility of establishment. With the introduction of *A. lepidum* the same observations were made; *A. hebraeum* and *A. lepidum* share the same host and ecological preferences. Both males and females of *A. lepidum* were collected in these regions, therefore Smit et al. (2025) suggests the defining factor will be whether the magnitude of this introduction was sufficient for the long-term establishment of this species. These recent introductions, alongside those discussed in Uribe et al. (2024), underscore the limitations of relying solely on static distribution maps. Together, these observations highlight the dynamic and potentially unstable nature of southern African *Amblyomma* distributions, emphasising how recent anthropogenic introductions, unresolved species boundaries, and incomplete understanding of reproductive isolation mechanisms complicate both taxonomy and biogeographic inference in the region.

4. Way forward

And so, true to the nature of all complex journeys, its road remains long, urging us onward into what comes next. To address these gaps and pitfalls we recommend an integrated, multi-pronged approach. Primarily, expand geographic sampling strategies to target field collections across the full ranges of each species, including contact zones and distant populations. This includes longitudinal field surveys which should track newly introduced species in undocumented areas to determine whether they establish sustainable populations, affect sympatric species, or shift existing parapatric boundaries. Furthermore, data pertaining to ecology and behaviour (host preference, seasonal activity, and habitat) should also be noted. This will ensure we capture the true breadth of ecological, morphological and genetic variation, to identify areas of sympatry or parapatry between species. Subsequently, to move beyond mitochondrial markers: 12S rRNA, 16S rRNA, *coi* and *cytb*. Mitochondrial markers are useful for the initial screening, however, they provide limited resolution in recently diverged lineages as they are maternally inherited (Camus et al., 2012). Whole-genome data (or genome-wide marker panels) offer much greater power to resolve recent divergence, infer gene flow, and detect hybridisation or introgression. Equally, investigating the species-specific composition and activity of AAA pheromones across both sympatric and parapatric *Amblyomma* species will clarify the role of reproductive interference in shaping distribution patterns. Likewise, the incorporation of biological compatibility data to aid in species delineation would be greatly beneficial. Controlled cross-mating and progeny viability studies can provide direct evidence of reproductive isolation. Successful mating producing fertile offspring supports conspecific status. In turn, the linking of morphological and molecular data with voucher specimens would aid in traceability and accurate identification records. Every genetic sample should be tied to a properly curated museum voucher with high-resolution images and complete collection metadata (host, life stage, GPS coordinates, habitat, date), linked with the sequence deposits (e.g., via BOLD or institutional collections). Finally, the field would benefit from a standardised, integrative species-delineation framework that combines molecular, morphological, ecological, and biological compatibility data. Such a protocol will ensure methodological and reporting consistency and comparability, allowing researchers to apply uniform criteria for species identification, thereby improving taxonomic clarity and strengthening our understanding of species boundaries within the genus *Amblyomma*.

To conclude, *Amblyomma* ticks have a complex yet still poorly understood evolutionary history, with unresolved species boundaries, incomplete molecular data and uncertain distribution patterns. The long-standing confusion around species like *A. pomposum* and *A. variegatum*, along with sympatric and parapatric patterns across southern Africa, highlights how ecological, genetic and pheromonal factors likely shape their ranges but remain understudied. As new introductions alter known distributions, it is clear that many aspects of *Amblyomma* systematics and biogeography are still unresolved, and much work remains to fully understand these ticks.

CRediT authorship contribution statement

Andeliza Smit: Writing – original draft, Visualization, Conceptualization. **Darshana Morar-Leather:** Writing – original draft, Conceptualization. **Luis Neves:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of generative AI use

During the writing of this article, the author(s) used Chatgpt and duck.ai in order to refine the written work. After using this tool, the author(s) reviewed and extensively edited the content as needed and take(s) full responsibility for the content of the published article.

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Conflict of interest

The authors declare that they have no known financial, personal, or professional conflicts of interest that could have influenced the work reported in this manuscript.

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