



Succinctus

The “tropical lineage” of the brown dog tick *Rhipicephalus sanguineus* sensu lato identified as *Rhipicephalus linnaei* (Audouin, 1826)[☆]Jan Šlapeta^{a,*}, Shona Chandra^a, Bruce Halliday^b^a Sydney School of Veterinary Science, Faculty of Science, University of Sydney, Sydney, New South Wales 2006, Australia^b Australian National Insect Collection, CSIRO, GPO Box 1700, Canberra, Australian Capital Territory 2601, Australia

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ABSTRACT

The brown dog tick (*Rhipicephalus sanguineus*) parasitises dogs. Over the past decade, two distinct lineages have been recognised – *R. sanguineus* sensu lato “temperate lineage” and *R. sanguineus* sensu lato “tropical lineage”. The nominal taxon *R. sanguineus* (Latreille, 1806) was recently associated with the “temperate lineage”. We here identify the “tropical lineage” as *Rhipicephalus linnaei* (Audouin, 1826) using material from Australia, where no other *Rhipicephalus* species parasitises dogs. Whole genome sequencing of *R. linnaei* from Australia, Fiji and Laos, and assembly of their complete mitochondrial DNA (~15 kb) confirms the genetic identity and distinctness from all other known species within the brown dog tick species complex. Designation of the species *R. linnaei* is unequivocally supported by material available through the Australian National Insect Collection, Australia. Accordingly, we are formally justified in using *R. linnaei* for the “tropical lineage”.

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1. Introduction

The brown dog tick is one of the most commonly recognised ticks found on dogs (Walker et al., 2000; Dantas-Torres, 2010). It has a world-wide distribution and is the vector for a large number of canine vector-borne diseases (Jongejan and Uilenberg, 2004). It is referred to in hundreds of publications as *Rhipicephalus sanguineus* (Latreille, 1806). However, many authors have noted morphological and biological variation among brown dog ticks, and have described new species for slightly different specimens from different hosts and localities. The result is a long list of available names that are often considered as junior synonyms of *R. sanguineus* (for example, Zumpt, 1950; Camicas et al., 1998; Gray et al., 2013; Chitimia-Dobler et al., 2017; Hornok et al., 2017; Nava et al., 2015, 2018; Bakkes et al., 2020). The introduction of DNA analysis and surveys of different morphological forms and geographical specimens has now shown that the name *R. sanguineus* has been applied to several different species (Moraes-Filho et al., 2011).

The identity of *R. sanguineus* sensu stricto has recently been stabilised by the publication of detailed morphological and genetic descriptions of all instars, the deposition of reference material in reputable museum collections, and by the fixation of a neotype (Nava et al., 2018). The species defined in this way has previously been referred to as the “temperate lineage” of *R. sanguineus* sensu lato (s.l.), but also as *Rhipicephalus* sp. II, “temperate species” or “southern lineage” (Moraes-Filho et al., 2011; Chitimia-Dobler et al., 2017; Hornok et al., 2017; Nava et al., 2018), but it is now referred to more correctly as *R. sanguineus* sensu stricto (s.s.).

The name *R. sanguineus* has been unequivocally defined by linking it to extant type material, but the species it represents can still be interpreted subjectively (Nava et al., 2018). In a narrow or strict interpretation, *R. sanguineus* can only represent the genetically defined lineage supported by the neotype. In a broader sense, the name *R. sanguineus* s.l. can be applied to the entire species complex. The existence of multiple species within this complex has been recognised by the recent description of *Rhipicephalus afranicus* Bakkes et al., 2020 and the re-description of *Rhipicephalus turanicus* Pomerantzev, 1940 (in Pomerantzev et al., 1940; Bakkes et al., 2020). It is also supported by biological evidence from cross-breeding experiments involving populations of *R. sanguineus* s.l. from different geographical regions (Levin et al., 2012; Nava et al., 2018).

[☆] Sequence data reported in this study are available from GenBank under the following accession numbers (MW429381, MW429382, MW429383, MW430655, MW430656, MW430657) and from SRA (PRJNA688827).

* Corresponding author.

E-mail address: jan.slapeta@sydney.edu.au (J. Šlapeta).

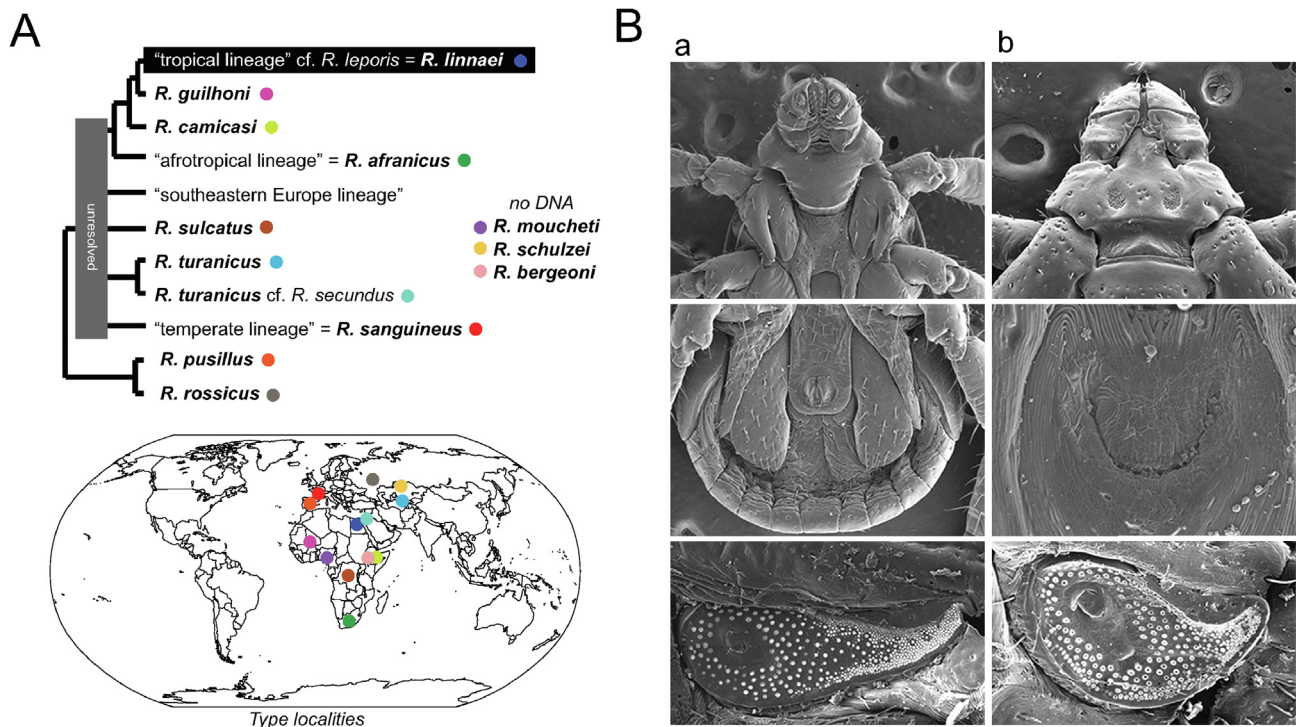


Fig. 1. *Rhipicephalus linnaei* (Audouin, 1826) within the *Rhipicephalus sanguineus* species complex. (A) Simplified schematic relationship based on available DNA sequences of 14 potential species as genetic lineages. Further, three species do not have publicly available DNA. World map with colour coded type localities of the named species (bold). (B) Scanning electron microscopy of *Rhipicephalus linnaei* specimen from Australia (Coominya strain, Chandra et al., 2020). Head from ventral view, adanal plates and spiraculum of a male specimen (a). Head from dorsal view, genital pore area and spiraculum of a female specimen (b).

We recognise 14 species within the *R. sanguineus* complex (Fig. 1A). The morphological differentiation of these species has perplexed authors for centuries, and recent detailed canonical variate analysis of data from the male adanal plate and female spiracle/spiraculum confirmed difficulties in distinguishing among them (Bakkes et al., 2020). The recognition of multiple species within the *R. sanguineus* species complex in recent literature, especially by the use of molecular markers (in particular mtDNA) has raised a significant nomenclatural issue, because at least four suspected species have been referred to by the informal term “lineage” (Fig. 1A). Two of these “lineages” have now been formally named – the “temperate lineage” is *R. sanguineus* s.s. (Nava et al., 2018) and the “afrotropical lineage” is *R. afranicus* Bakkes et al., 2020. The remaining two “lineages” are yet to be resolved (Fig. 1A).

The name *Rhipicephalus leporis* Pomerantzev, 1946 was recently associated with GenBank data for specimens collected from Iraq (KM235720, HQ323697, HQ323725, FJ536557), Kenya (KX757911), and Cote d'Ivoire (KX757912, KX757913, KX757917), and their phylogenetic relationship showed that they match the *R. sanguineus* s.l. “tropical lineage” (Hornok et al., 2017). However, we believe that there may be other, older names that take priority as the valid name for what has been referred to as the “tropical lineage” of *R. sanguineus* s.l. To determine the correct name for the *R. sanguineus* s.l. “tropical lineage”, we therefore reviewed all the available junior synonyms of *R. sanguineus*.

The oldest available names listed as potential synonyms of *Ixodes sanguineus* Latreille, 1806 are *Acarus plumbeus* Panzer, 1795 and *Ixodes Linnæi* Audouin, 1826 (Zumpt, 1950; Camicas et al., 1998; Nava et al., 2018). Both of these names require careful examination.

Acarus plumbeus Panzer, 1795 was described and illustrated from specimens collected on a bird in Germany. Koch (1844) transferred it into *Ixodes* as *Ixodes plumbeus* (Panzer). That name has been considered as a synonym of *Hyalomma marginatum* Koch,

1844 (Pomerantzev, 1950; Camicas et al., 1998), or listed as *incertae sedis* (Guglielmone et al., 2015). *Ixodes plumbeus* Leach, 1815 is a junior homonym of *Ixodes plumbeus* (Panzer), and was replaced by *Ixodes lividus* Koch, 1844. *Ixodes plumbeus* Dugès, 1834 (originally *Ixode plombé*) is also a junior homonym of *Ixodes plumbeus* (Panzer), and was replaced by *Ixodes dugesi* Gervais, 1844. The specific name *dugesi* has sometimes been misspelled as *dugesii*. *Ixodes dugesi* Gervais, 1844 is regarded either as a synonym of *R. sanguineus* (e.g. by Camicas et al., 1998), or as *incertae sedis* (Guglielmone et al., 2015). This analysis shows that *Acarus plumbeus* Panzer, 1795 cannot be the valid name for the *R. sanguineus* s.l. “tropical lineage”.

Ixodes Linnæi Audouin, 1826 was described from an unidentified host in Egypt. The name was introduced by Jean Victor Audouin in “Explication Sommaire des Planches d'Arachnides de l'Égypte et de la Syrie” (<https://doi.org/10.11588/diglit.4820#0727>) for the illustration “Planche 9” (<https://doi.org/10.11588/diglit.4742#0051>), where the tick illustration is Figure 12 (Audouin, 1826). The date of the publication is considered 1826 based on the ICZN ruling (1987), however the alternative 1825 has been suggested and used by El-Hennawy (2000). The type locality is not fixed by Audouin (1826); for the current purpose, the type locality is considered Egypt. The specific name must be corrected to *linnaei* (ICZN, 1999, Article 32.5.2), but it has often been misspelled as *linnei*. The authorship and date of this name have been confirmed (Sherborn, 1897; Tollitt, 1986; ICZN, 1987). Koch (1844, 1847) transferred this species to *Rhipicephalus*. Later authors have referred to *Ixodes linnaei* as *incertae sedis* in *Rhipicephalus* (Neumann, 1897, 1901, 1911; André, 1935), as a synonym of *R. sanguineus* (Zumpt, 1950; Camicas et al., 1998), or as a *nomen dubium* (Guglielmone et al., 2015). It appears that no type specimens exist for this species, and the interpretation of the name remains uncertain because the original description was very brief and vague.

A recent survey of brown dog ticks from Egypt found both the *R. sanguineus* s.l. “tropical lineage” and “southeastern Europe lineage” (Chitimia-Dobler et al., 2017). On the other hand, only the “tropical lineage” occurs in Australia (Fig. 1B). This has been confirmed by molecular identification of both freshly collected specimens (Chandra et al., 2020) and museum material (Chandra et al., 2021). The museum material characterised as “tropical lineage” by Chandra et al. (2021) was the same material used in the morphological description of the Australian brown dog tick by Roberts (1965). We identify this material as conspecific with that of Audouin (1826), because the only population of *R. sanguineus* s.l. that exists in Australia is the “tropical lineage”, which genetically matches extant material from Egypt.

We now provide three whole genome sequences for *Rhipicephalus linnaei* from Australia, Fiji and Laos. The three assembled mtDNA (~15 kb) sequences of *R. linnaei* are > 99% identical (29–37 differences, Fig. 2A). The whole genome sequencing (PRJNA688827) was performed as previously described using 2 × 150 bp Illumina paired-end sequencing (Kanduma et al., 2020). The newly obtained mtDNA of *R. linnaei* (MW429381,

MW429382, MW429383) are closely related to mtDNA from a brown dog tick from China (JX416325; Liu et al., 2013) that we consider conspecific, representing *R. linnaei*. The mtDNA of *R. linnaei* are 88.5–88.8% identical to *R. sanguineus* s.s. from the US (AF081829; Black and Roehrdanz, 1998) with 1684–1691 differences from each other (Fig. 2A). Phylogenetic analysis and the pairwise distance (p-distance) between the mtDNA genomes of *R. linnaei* from the closely related mtDNA from within the *R. sanguineus* species complex (12% from *R. sanguineus* (NC_002074) and 10% from *R. turanicus* (NC_035946)) exceeds pairwise mtDNA distance between the cattle tick species *Rhipicephalus australis* and *Rhipicephalus microplus* (4% between NC_023335 and NC_023348) (Fig. 2B). We have further obtained complete rDNA units (~7 kb, including 18S rDNA, ITS1 rDNA, 5.8S rDNA, ITS2 rDNA and 28S rDNA) from *R. linnaei* from Australia, Laos and Fiji (MW430655, MW430656, MW430657). The ITS2 rDNA was only 99.5–99.7% identical to *R. sanguineus* (MH616087, MH616087) and not informative for robust resolution of the *R. sanguineus* species complex taxa (see also Nava et al., 2018). The complete mtDNA provides robust resolution between the *R. sanguineus* s.l. lineages.

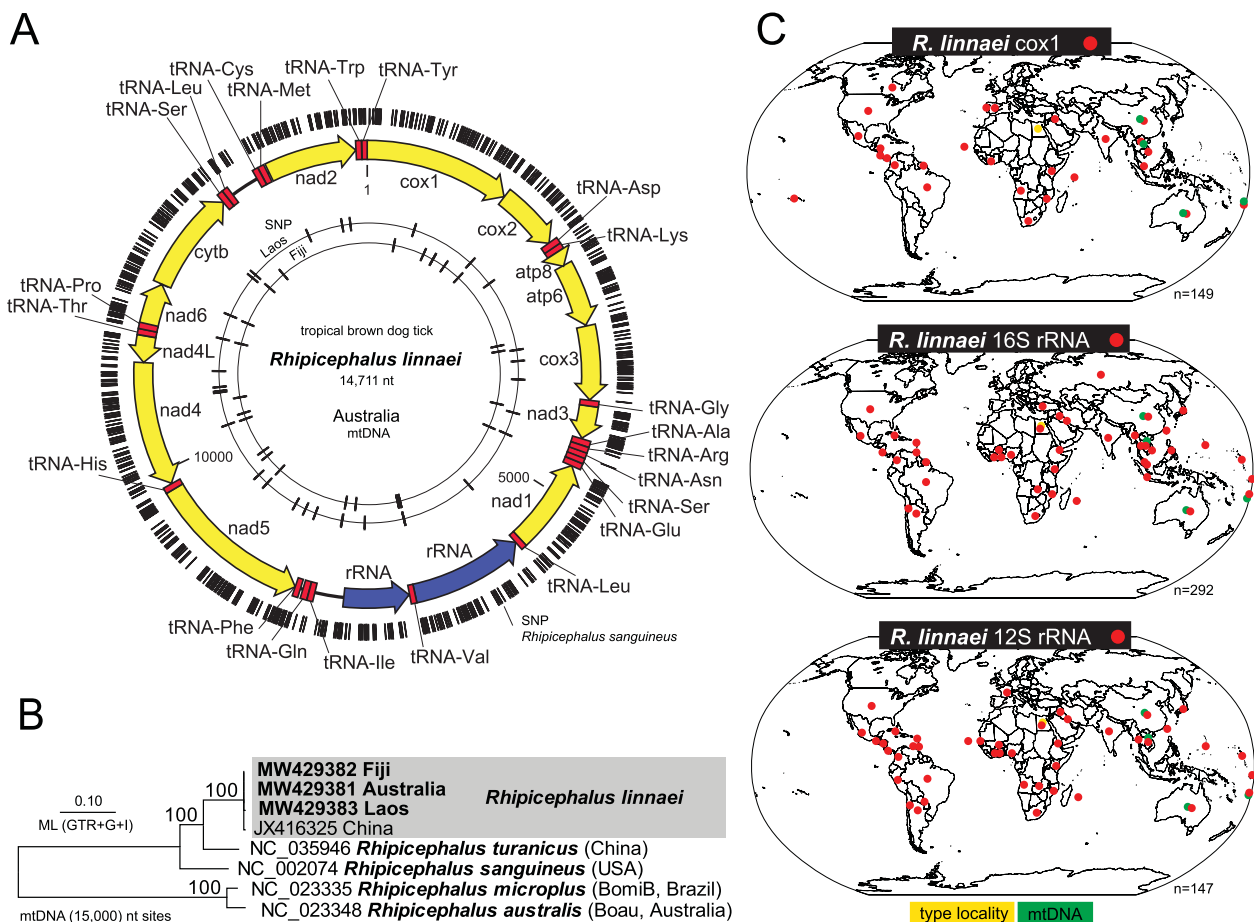


Fig. 2. *Rhipicephalus linnaei* mitochondrial genome organisation and global distribution. (A) The mitochondrial genome (mtDNA) from an Australian specimen (Coominya strain, Chandra et al., 2020) is shown including 13 protein coding genes (yellow), two rRNA genes (blue) and 22 tRNAs (red). The inner circles represent mtDNA obtained from ticks from Laos and Fiji with black lines representing single nucleotide polymorphisms (SNPs), differentiating it from the Australian mtDNA. The Fiji specimen of *R. linnaei* was collected from a dog in Viseisei, Fiji in 2011 (SC931) and the Laos specimen was collected from a dog in Luang Prabang, Laos in 2019 (#32). The Australian *R. linnaei* mtDNA is 34 and 29 SNPs different from Laos and Fiji *R. linnaei* mtDNA, respectively. The outside bars represent 1,690 SNPs between *R. linnaei* mtDNA and *R. sanguineus* mtDNA (NC_002074). (B) The mtDNA phylogenetic tree was inferred by using the Maximum Likelihood method and General Time Reversible model with a discrete Gamma distribution among sites (+G) and the rate variation model allowed for some sites to be evolutionarily invariable (+I). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The percentage of trees in which the associated taxa clustered together is shown below the branches (as the percentage from 1,000 replicates). There were a total of 15,000 positions in the final dataset. Evolutionary analyses were conducted in MEGA X. (C) Countries where molecular evidence exists for the presence of *R. linnaei* (*cox1*, 16S rDNA, 12S rDNA are shown). Available sequence data were retrieved in January 2021 from GenBank and their respective locality identified based on the annotation of original literature. Type locality of *R. linnaei* is shown as a yellow dot. Data and alignments used are available at LabArchives: <https://doi.org/10.25833/vkws-6b69>.

Searching available whole genome sequence data revealed an additional six complete mtDNA, including from *Rhipicephalus camiciasi*, *Rhipicephalus turanicus* cf. *Rhipicephalus secundus*, *R. sanguineus* s.l. “southeastern Europe lineage” from Palestine (Ravi et al., 2019) and *R. linnaei* from China (Jia et al., 2020). Phylogeny of the *R. sanguineus* s.l. lineage mtDNA using either nucleotide alignment or the amino acid sequence alignment of the 13 coding genes provided high (84–100%) bootstrap support for the lineages (Fig. 3A). Commonly used sequences (12S rDNA, 16 rDNA and *cox1*) provided weaker support, including < 60% bootstrap support and variable topology (Fig. 3B). We therefore propose that the name *R. linnaei*

is used to name the *R. sanguineus* s.l. “tropical lineage” species. Morphologically, the species is now defined by the description of Roberts (1965) from the Australian voucher material (Fig. 1B), because the morphologically well characterised *R. sanguineus* sensu Roberts, 1965 is genetically identical with *R. sanguineus* s.l. “tropical lineage” known from Egypt (Chitimia-Dobler et al., 2017). The use of Australian material is appropriate, because *R. sanguineus* sensu Roberts, 1965 and *R. australis* are the only *Rhipicephalus* spp. in Australia, both introduced species (Roberts, 1965; Estrada-Peña et al., 2012; Burger et al., 2014). Recent evaluation of genetic identity of extant and museum material at the mtDNA loci

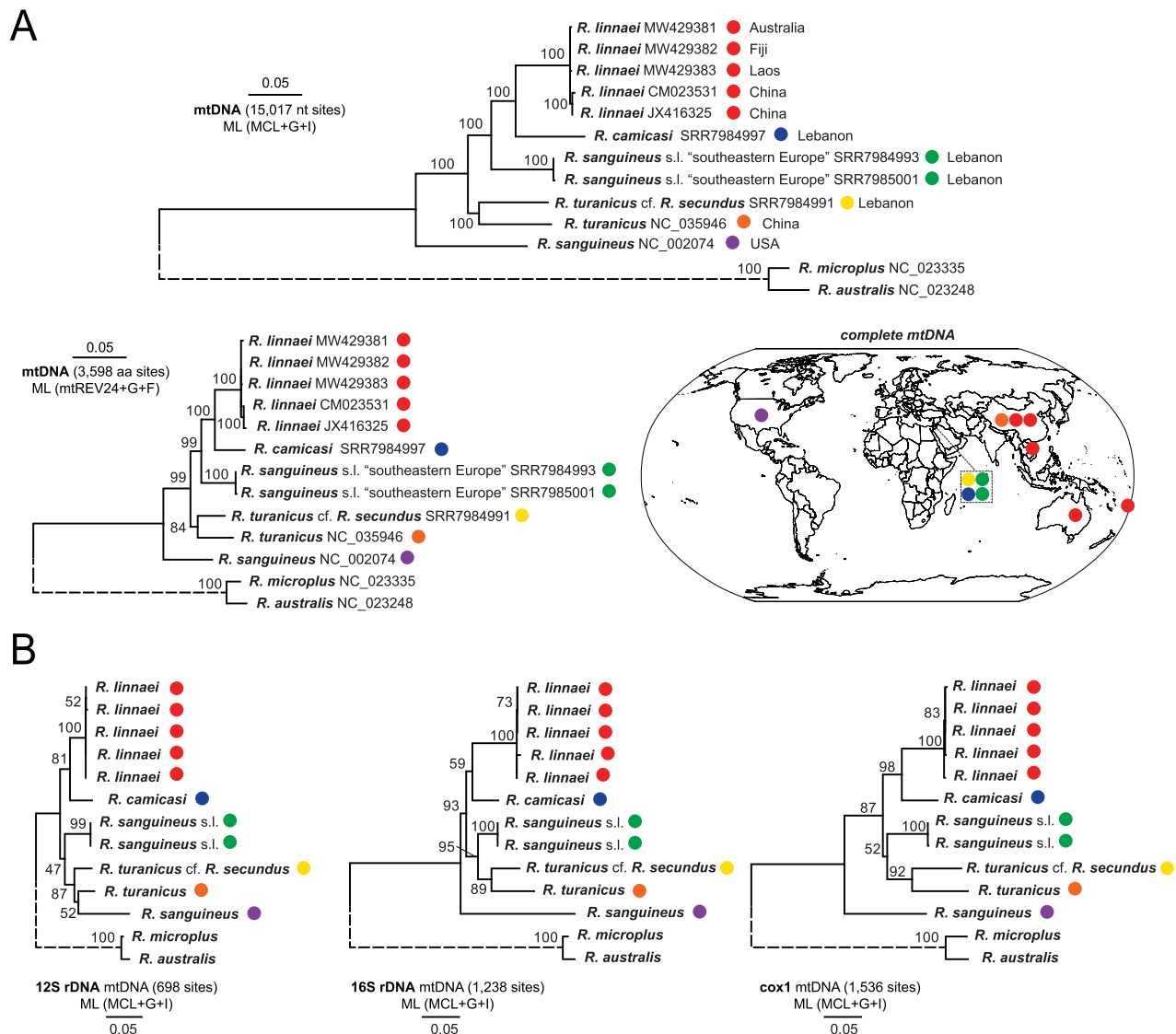


Fig. 3. *Rhipicephalus sanguineus* sensu lato (s.l.) mitochondrial genome phylogeny. (A) The mitochondrial genomes (mtDNA) for *Rhipicephalus linnaei* from this study (Australia, Fiji, Laos), as well as the previously available reference genomes for *R. sanguineus*, *R. linnaei* and *Rhipicephalus turanicus*, were aligned with additional mtDNA from genome projects data. The complete mtDNA were assembled de novo from fastq reads belonging to *R. turanicus* cf. *Rhipicephalus secundus* (SRR7984991) from Palestine: Nablus (tick_13, NST3.1, sheep), *R. camiciasi* (SRR7984997) from Palestine: Tubas (tick_8, TDT3.1, dog) and two *R. sanguineus* s.l. “southeastern Europe” (SRR7984993, SRR7985001) from Palestine: Hebron (tick_10, NST2.1, sheep) and Nablus (tick_12, HDT1.1, dog), respectively (Ravi et al., 2019). In addition, we included a complete mtDNA from a whole genome sequencing project of *R. linnaei* (China: Guangxi, dog, Rsan-2018, CM023531, PRJNA674886, Jia et al., 2020). The mtDNA phylogenetic tree based on nucleotide data (nt) was inferred by using the Maximum Likelihood method and Maximum Composite Likelihood approach with a discrete Gamma distribution among sites (+G) and the rate variation model allowed for some sites to be evolutionarily invariable (+I). The mtDNA phylogenetic tree based on amino acid data from all 13 coding genes was inferred by using the ML method and General Reversible Mitochondrial + Freq. (mtREV24 + F) model with a discrete Gamma distribution among sites (+G). Both nt and aa trees are drawn to same scale, with branch lengths measured in the number of substitutions per site. Map and colour coded markers indicate the location of the tick on the world map. (B) Phylogenetic relationship of 12S rDNA, 16S rDNA and *cox1* genes from complete mtDNA. The phylogenetic trees were inferred using the ML method and MCL + G + I. Trees are drawn to scale, with branch lengths measured in the number of substitutions per site. The percentage of trees in which the associated taxa clustered together is shown below the branches (as the percentage from 200 replicates). Evolutionary analyses including selection of models were conducted in MEGA X. Data of assembled mtDNA and alignments used are available at LabArchives: <https://doi.org/10.25833/vkws-6b69>.

demonstrated homogeneity of *R. sanguineus* sensu Roberts, 1965 with *R. sanguineus* s.l. “tropical lineage”, and the absence of *R. sanguineus* s.s. (Chandra et al., 2020, 2021). Unambiguous characterisation of *R. sanguineus* s.l. “tropical lineage” in Australia enables association of the biological traits to be extrapolated to the species globally, because all other continents are occupied by additional *R. sanguineus* s.l. lineages that can only be differentiated using molecular data. We used reference sequences from Australia (*cox1*, 16S rDNA, 12S rDNA) to search GenBank for all available *R. linnaei* (= *R. sanguineus* s.l. “tropical lineage”) to demonstrate its presence on all continents except Antarctica (Fig. 2C). We propose to associate the name *R. linnaei* (Audouin, 1826) with the specimens characterised genetically as *R. sanguineus* s.l. “tropical lineage” sensu Chitimia-Dobler et al. (2017).

The modern morphological description of *R. linnaei* is presented by Roberts (1965) and those of Chandra et al. (2020), Chandra et al. (2021) from Australia. The Australian material of *R. linnaei* is available from the Australian National Insect Collection (ANIC, Commonwealth Scientific and Industrial Research Organisation, CSIRO, Canberra, Australia). The differential diagnosis of *R. linnaei* from *R. sanguineus* s.l. remains complex as outlined by Nava et al. (2018) and Bakkes et al. (2020), but in the absence of robust morphological differences, molecular data provides unequivocal identification of specimens. There is no exceptional need to designate a neotype for *R. linnaei* (ICZN, 1999, Article 75), because the material we are associating with the name is unambiguous and there is currently no doubt about the identity of what was formerly known as the “tropical lineage” of *R. sanguineus* s.l. (ICZN, 1999, Article 75.3. Qualifying conditions).

In conclusion, the identity of *R. sanguineus* s.l. “tropical lineage” is clarified by the restoration of *Rhipicephalus linnaei* as a valid name. The derivation of “linnaei” is a tribute to Carl Linnaeus who formalised binominal nomenclature. The use of the name *R. linnaei* reduces the list of dubious names and is preferred to the introduction of a new potential synonym. The name *R. linnaei* is now associated with the material of Roberts (1965) from Australia, where there is no other *Rhipicephalus* sp. that parasitises dogs (Barker and Walker, 2014; Barker et al., 2014). The species *R. linnaei* is defined by a detailed morphological and genetic description, as well as deposition of material in a reputable museum collection. Utilisation of whole genome sequencing to assemble mtDNA and rDNA units is an affordable approach and should be used to improve the characterisation of all taxa within the *R. sanguineus* species complex.

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