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Trypanosoma rangeli is phylogenetically closer to Old World trypanosomes than to *Trypanosoma cruzi*☆

Oneida Espinosa-Álvarez^{a,1}, Paola A. Ortiz^{a,1}, Luciana Lima^{a,1}, André G. Costa-Martins^a, Myrna G. Serrano^b, Stephane Herder^{c,d}, Gregory A. Buck^b, Erney P. Camargo^a, Patrick B. Hamilton^e, Jamie R. Stevens^e, Marta M.G. Teixeira^{a,*}

^a Department of Parasitology, Institute of Biomedical Sciences, University of Sao Paulo, Brazil

^b Virginia Commonwealth University, Richmond, VA, USA

^c Department of Parasitology, Faculty of Veterinary Medicine, Kasetsart University, Bangkok, Thailand

^d Unité Mixte de Recherche Intertryp, Institut de Recherches pour le Développement, Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, France

^e Department of Biosciences, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

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ABSTRACT

Trypanosoma rangeli and *Trypanosoma cruzi* are generalist trypanosomes sharing a wide range of mammalian hosts; they are transmitted by triatomine bugs, and are the only trypanosomes infecting humans in the Neotropics. Their origins, phylogenetic relationships, and emergence as human parasites have long been subjects of interest. In the present study, taxon-rich analyses (20 trypanosome species from bats and terrestrial mammals) using *ssrRNA*, glycosomal glyceraldehyde-3-phosphate dehydrogenase (*gGAPDH*), heat shock protein-70 (*HSP70*) and Spliced Leader RNA sequences, and multilocus phylogenetic analyses using 11 single copy genes from 15 selected trypanosomes, provide increased resolution of relationships between species and clades, strongly supporting two main sister lineages: lineage *Schizotrypanum*, comprising *T. cruzi* and bat-restricted trypanosomes, and Tra[Tve-Tco] formed by *T. rangeli*, *Trypanosoma vespertilionis* and *Trypanosoma conorhini* clades. Tve comprises European *T. vespertilionis* and African *T. vespertilionis*-like of bats and bat cimicids characterised in the present study and *Trypanosoma* sp. Hoch reported in monkeys and herein detected in bats. Tco included the triatomine-transmitted tropicopolitan *T. conorhini* from rats and the African NanDoom1 trypanosome of civet (carnivore). Consistent with their very close relationships, Tra[Tve-Tco] species shared highly similar Spliced Leader RNA structures that were highly divergent from those of *Schizotrypanum*. In a plausible evolutionary scenario, a bat trypanosome transmitted by cimicids gave origin to the deeply rooted Tra[Tve-Tco] and *Schizotrypanum* lineages, and bat trypanosomes of diverse genetic backgrounds jumped to new hosts. A long and independent evolutionary history of *T. rangeli* more related to Old World trypanosomes from bats, rats, monkeys and civets than to *Schizotrypanum* spp., and the adaptation of these distantly related trypanosomes to different niches of shared mammals and vectors, is consistent with the marked differences in transmission routes, life-cycles and host-parasite interactions, resulting in *T. cruzi* (but not *T. rangeli*) being pathogenic to humans.

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1. Introduction

Trypanosoma rangeli and *Trypanosoma cruzi* are two generalist trypanosomes of bats and all orders of terrestrial mammals, and are the only trypanosome species infective to humans in the New World. *Trypanosoma cruzi*, the agent of Chagas disease, occurs from the southern United States to southern South America, while the geographical range of *T. rangeli* extends from Central to South America, and both species share diverse ecological niches in a variety of ecosystems where triatomines of the genus *Rhodnius* – the

☆ Note: Nucleotides sequence data reported in this paper are available in GenBank under accession numbers listed in [Supplementary Table S1](#).

* Corresponding author at: Departamento de Parasitologia, Instituto de Ciências Biomédicas, Universidade de São Paulo, Av. Prof. Lineu Prestes, 1374, 05508-000, São Paulo, SP, Brazil.

E-mail address: mmgteix@icb.usp.br (M.M.G. Teixeira).

¹ These authors contributed equally to this work.

vector of *T. rangeli* – occur. *Trypanosoma rangeli* is prevalent from Central America to Amazonia, where *Rhodnius* spp. are highly abundant in palm trees, and it is also reported in other Brazilian biomes such as the Pantanal, Cerrado, and the Atlantic Forest. *Trypanosoma rangeli* is a common parasite of xenarthrans, marsupials, rodents, carnivores and primates, and recent studies have identified a relevant prevalence of *T. rangeli* in bats (Hoare, 1972; Maia da Silva et al., 2007, 2009; Vallejo et al., 2009; Dario et al., 2017).

Mixed infections with *T. cruzi* and *T. rangeli* are common in triatomines and mammalian hosts including humans (Hoare, 1972; Maia da Silva et al., 2004a,b, 2007, 2009; Ramírez et al., 2014a; Pinto et al., 2015; Dario et al., 2017). However, despite shared mammalian hosts and vectors across Central and South America, the life cycles of *T. cruzi* and *T. rangeli* differ significantly in both vertebrate and invertebrate hosts. *Trypanosoma rangeli* is not pathogenic to its mammalian hosts, in which intracellular forms have not been confirmed, and is transmitted by *Rhodnius* spp. (triatomines) through the inoculation of trypomastigotes present in the salivary glands during feeding on mammalian blood (Hoare, 1972; Vallejo et al., 2009).

Trypanosoma rangeli was originally classified in the subgenus *Herpetosoma*, based exclusively on morphological parameters. On the basis of its route of transmission, *T. rangeli* was considered to be related to African trypanosomes transmitted by tsetse flies of the *Salivaria* section (Hoare, 1972), and the subgenus *Tejeria* was proposed to accommodate this species in this section (see Hoare, 1972; Maia Da Silva et al., 2004a; Vallejo et al., 2009). However, based on molecular phylogeny, Stevens et al. (1999) confirmed *T. rangeli* to be closely related to *T. cruzi*, and thus distant from any species of the *Salivaria* section. In more comprehensive phylogenies, *T. rangeli* and *T. cruzi* clustered with trypanosomes from diverse mammalian hosts from South America, Africa and Europe, forming the *T. cruzi* clade comprising two main subgroups: one headed by *T. rangeli*, and the other by *T. cruzi* and its allied bat-trypanosome species of the subgenus *Schizotrypanum*: *Trypanosoma cruzi marinkellei* (restricted to Central and South America), *Trypanosoma dionisii* (cosmopolitan), and *Trypanosoma erneyi* of African bats (Hamilton et al., 2007, 2012; Lima et al., 2012, 2015a; Pinto et al., 2015). The *T. cruzi* clade also comprises several species of trypanosomes of Neotropical bats (clade Neobats that includes *Trypanosoma wauwau*) that clustered with *Trypanosoma noyesi* from Australian marsupials, unnamed trypanosomes from Australian rodents (Cottontail et al., 2014; Lima et al., 2015a; Pinto et al., 2015; Botero et al., 2016; Barbosa et al., 2017), and with one trypanosome reported from lemurs in Madagascar (Larsen et al., 2016); all placed basal to the assemblage including *T. rangeli* and *T. cruzi* clades. *Trypanosoma livingstonei* from African bats is currently positioned at the edge of the *T. cruzi* clade (Lima et al., 2013, 2015a; Dario et al., 2017).

Trypanosoma cruzi is widespread in virtually all terrestrial mammalian orders, and is transmitted by triatomines of both the Triatomini and Rhodniini tribes (Reduviidae: Triatominae); its development is restricted to the digestive tract of the vectors. *Trypanosoma cruzi* is a genetic complex, comprising at least six discrete taxonomic units (DTUs, TcI–TcVI), plus the Tcbat DTU tightly linked to bats, and bats are hosts of all DTUs (Marcili et al., 2009; Pinto et al., 2012; Ramírez et al., 2014b; Lima et al., 2015b; Dario et al., 2016, 2017). All species of *Schizotrypanum* exhibit intracellular (cytoplasm) multiplication of amastigote forms and differentiation to infective trypomastigote forms that are released by the cells, a trait unique to the subgenus (Molyneux, 1991; Cavazzana et al., 2010; Lima et al., 2012). To date, only *Cavernicola pilosa* of the rare Cavernicolini tribe of Triatominae has been proven to be a vector of *T. c. marinkellei*. Cimicidae bat bugs are known vectors of *T. dionisii* and *T. vespertilionis* to Old World

bats and *Trypanosoma hedricki* in North America; these ectoparasites are common in bat shelters (Bower and Woo, 1981; Gardner and Molyneux, 1988; Molyneux, 1991). The high prevalence of *T. c. marinkellei* and *T. dionisii* in regions where neither *Cavernicola* spp. nor bat bugs are reported suggests that alternative vectors (triatomines of different species) transmit (cyclically or mechanically) *Schizotrypanum* trypanosomes to bats (Cavazzana et al., 2010; Lima et al., 2015a,b).

Trypanosoma vespertilionis appears to be restricted to bats and transmitted by cimicids (development being restricted to the digestive tract) in Europe and Africa (Hoare, 1972; Gardner and Molyneux, 1988; Molyneux, 1991). *Trypanosoma conorhini* is a parasite of *Rattus* spp. (restricted to the bloodstream), and is thought to be transmitted exclusively by *Triatoma rubrofasciata* (with development restricted to the digestive tract); *Tr. rubrofasciata* is known to transmit at least two trypanosomes: *T. cruzi* in Latin America and *T. conorhini* worldwide. *Trypanosoma conorhini* was first reported in *Tr. rubrofasciata* in India, and has since been reported throughout the tropical world, especially in Asian-Pacific, African and Latin American seaports (Hoare, 1972; Dujardin et al., 2015). *Trypanosoma conorhini* and *Tr. rubrofasciata* likely dispersed together with domestic rats (Patterson et al., 2001; Hyspa et al., 2002; Dujardin et al., 2015). The presence of *T. conorhini* in field monkeys and *Tr. rubrofasciata* has never been confirmed by molecular methods, and only a single isolate derived from *Rattus rattus* from Brazil has been included in phylogenetic trees (Stevens et al., 2001; Rodrigues et al., 2006; Hamilton et al., 2009).

Phylogenetic analyses of isolates of *T. rangeli* from different vertebrates and vectors have to date identified five phylogenetic lineages: TrA–TrE (Maia da Silva et al., 2004a,b, 2007, 2009; Ortiz et al., 2009; Caballero et al., 2015). In contrast to *T. rangeli* and *T. cruzi*, both constituted by an increasing number of genotypes supported by different molecular markers, there are no studies on the genetic diversity of *T. conorhini* and *T. vespertilionis*, whose ranges of host species, geographical distribution, and relationships with other species of trypanosomes remain unclear. Recent phylogenies based on ssrRNA and glycosomal glyceraldehyde-3-phosphate dehydrogenase (gGAPDH) have left uncertainty regarding the relationships of *T. rangeli* with *T. cruzi*, *T. conorhini*, European *T. vespertilionis* and African trypanosomes from bats, monkeys and civets (Stevens et al., 1999, 2001; Hamilton et al., 2007, 2009; Lima et al., 2013, 2015a; Barbosa et al., 2016).

The unresolved relationships of *T. rangeli* with Old World trypanosomes of bats and non-volant hosts, and *Trypanosoma teixeirae* of Australian bats have challenged the earlier hypotheses about the origin and hosts of recent ancestors of *T. rangeli*, and the usually assumed close relationships with *T. cruzi*. The addition of new taxa into the weakly supported lineage comprising *T. rangeli* and the use of multilocus analyses appear critical to resolution of these relationships. With this aim, we characterised eight new African (Guinea Bissau (GW)) trypanosomes from bats and one from a bat cimicid related to *T. vespertilionis*, plus nine trypanosomes morphologically resembling *T. conorhini* isolated from *Rattus* spp., *Tr. rubrofasciata*, and Asian (Malaysia) monkeys. To clarify the tangled phylogenetic relationships of *T. rangeli* with Old World trypanosomes related to *T. conorhini* and *T. vespertilionis*, and with *T. cruzi* and other species of the subgenus *Schizotrypanum*, we performed taxon-rich phylogenetic analyses using ssrRNA, gGAPDH and heat shock protein-70 (HSP70) sequences. Thereafter, trypanosomes from bats and non-volant mammals representative of the genetic diversity of the whole data set of trypanosomes transmitted by triatomines and cimicids, from the New and Old Worlds, were selected for Spliced Leader (SL) RNA and multilocus phylogenetic analyses.

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