Parasites & Vectors

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# The origins of the trypanosome genome strains *Trypanosoma brucei brucei* TREU 927, *T. b. gambiense* DAL 972, *T. vivax* Y486 and *T. congolense* IL3000

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**Abstract**

The genomes of several tsetse-transmitted African trypanosomes (*Trypanosoma brucei brucei, T. b. gambiense, T. vivax, T. congolense*) have been sequenced and are available to search online. The trypanosome strains chosen for the genome sequencing projects were selected because they had been well characterised in the laboratory, but all were isolated several decades ago. The purpose of this short review is to provide some background information on the origins and biological characterisation of these strains as a source of reference for future users of the genome data. With high throughput sequencing of many more trypanosome genomes in prospect, it is important to understand the phylogenetic relationships of the genome strains.

**Keywords:** Trypanosomes, Pathogen, Genome

## Review

The genome sequence of *Trypanosoma brucei brucei* TREU 927/4 was published in 2005 [1] and that of *T. b. gambiense* Dal 972 clone 1 in 2010 [2]. Genome sequencing projects for *T. vivax* Y486 and *T. congolense* IL3000 are also complete [3]. The trypanosome strains chosen for sequencing were selected because they had been well characterised in the laboratory, but all were isolated several decades ago (Table 1). The purpose of this short review is to provide some background information on the origins and biological characterisation of these strains as a source of reference for future users of the genome data. The history of the discovery of these trypanosome species has been recently reviewed [4].

### Trypanosoma brucei brucei TREU 927/4

#### *Isolation and phenotype*

*Trypanosoma brucei brucei* clone TREU 927/4 was chosen as the representative *T. brucei* for the genome project, because it displays the full range of known phenotypes for *T. brucei*, barring human infectivity. TREU 927/4 is capable of complete cyclical development within the tsetse fly, including mating [5] and produces short stumpy forms during bloodstream infection in the mammalian host [6]. TREU 927/4 is a clone derived from the isolate GPAL/KE/70/EATRO 1534 [5] that originates from Kiboko, Kenya, an area where human trypanosomiasis is unknown [7]. Nevertheless, there is some doubt about the status of TREU 927/4 with regard to human infectivity, since it has a degree of resistance to human serum [8], though it lacks the *SRA* gene that is characteristic of the human infective subspecies *T. b. rhodesiense* from East Africa [9].

The isolate GPAL/KE/70/EATRO 1534 was one of a collection of 15 *T. brucei* subgroup isolates obtained from wild caught tsetse flies of the species *Glossina pallidipes* from Kiboko, Kenya [7,10,11]. Each isolate was derived from the metacyclic population of a single infected fly by inoculation of macerated salivary glands into rodents; the bloodstream forms were subsequently used to study the antigenic types circulating in wild-caught flies [11]. Like other pleomorphic *T. b. brucei* isolates, TREU 927/4 is easily grown as bloodstream forms in rodents or procyclics *in vitro*; it has also been adapted to the bloodstream form in *in vitro* culture [6]

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**Table 1 Trypanosome genome strains**

| Species | Strain | Origin |
|---|---|---|
| *T. b. brucei* | TREU 927/4 | Isolated from tsetse *Glossina pallidipes* in 1970 in Kiboko, Kenya |
| *T. b. gambiense* | DAL 972 | Isolated from a patient in 1986 in Daloa, Ivory Coast |
| *T. vivax* | Y486 | Isolated from a bovine in 1976 in Zaria, Nigeria |
| *T. congolense* | IL3000 | Isolated from a bovine in 1966 in Transmara, Kenya |

and has been transmitted via *G. morsitans morsitans* and *G. pallidipes* in the laboratory.

#### *Relationship to other T. brucei strains*

TREU 927/4, together with other *T. b. brucei* isolates from Kiboko, has been characterised by various molecular methods in a number of different studies. The consensus from these analyses is that TREU 927/4 represents a subgroup of *T. b. brucei* that is widespread in East Africa.

Initial studies of isoenzyme variation showed that the Kiboko isolates had a high frequency of rare polymorphisms for several enzymes, notably threonine dehydrogenase (TDH) and malate dehydrogenase (MDH), and that these unusual isoenzyme patterns were shared by *T. brucei* subgroup isolates from other areas with abundant wild animals in Kenya (Kibwezi, Meru and Maasai Mara), Zambia (Luangwa valley) and Tanzania (Serengeti) [12-14]. As a consequence, these isolates appeared as a separate clade distinct from other *T. brucei* subgroup isolates in cluster analysis [12-14]. The clade was initially dubbed the *kiboko* group [12] and later split into 2 groups: *kiboko* and *kakumbi* [13]. Only a minority (estimated < 7%) of the many isolates of the *T. brucei* subgroup that have been characterised belong to the *kiboko/kakumbi* isoenzyme group [12,13]. The association with areas of abundant wildlife in East Africa suggests transmission cycles primarily involving wild mammals and tsetse. However, some *kiboko/kakumbi* strains have been isolated from domestic animals and three came from humans in the Luangwa Valley, Zambia [13].

The molecular karyotype of TREU 927/4 was deduced from chromosome-separation gels and hybridisation with a comprehensive set of gene probes [15]. The nuclear genotype has been analysed by restriction fragment length polymorphisms (RFLPs), mini- and microsatellites. Reinforcing the isoenzyme results, analysis of *T. brucei* subgroup isolates using RFLP data from repetitive DNA probes placed TREU 927/4 in a discrete cluster with 2 other Kiboko tsetse isolates [16,17]. Minisatellite analysis of the original trypanosome population from which TREU 927/4 was cloned showed it to contain several genotypes [18]. Minisatellites are hypervariable and the Kiboko strains, like other collections of trypanosome isolates from particular locations, show population specific alleles [19]. A recent study using STRUCTURE to analyse microsatellite genotype data from a total of 142 *T. brucei* subgroup strains placed TREU 927/4 in a cluster designated Kiboko B, including 18 other *T. b. brucei* isolates derived from wild animals (mostly lions and hyenas) in Serengeti, Tanzania, and other tsetse and livestock isolates from Kiboko and Meru in Kenya [20]. In summary, there is agreement from all genotyping analyses to date that TREU 927/4 belongs to a particular group of *T. b. brucei* isolates that is found predominantly in wildlife areas of East Africa.

Complementary to these data from analyses of the nuclear genome, are data on variation in the sequence of kinetoplast DNA maxicircles, which constitute the mitochondrial genome of trypanosomes. Initial analysis of RFLPs showed that the maxicircles of *kiboko/kakumbi* strains could be distinguished from those of other *T. brucei* subgroup isolates by several polymorphisms [21]. Sequencing of the maxicircle COI (cytochrome c oxidase subunit I) gene allowed detailed analysis of mitochondrial haplotypes and revealed that isolates of the *kiboko/kakumbi* group, including TREU 927/4, share a limited range of haplotypes not found among other *T. brucei* subgroup isolates [20]. There was a particularly striking correlation between maxicircle haplotypes and the corresponding microsatellite data for the cluster of 19 *T. b. brucei* isolates designated Kiboko B, which included TREU 927/4 [20]. This reinforces the distinctive nature of this group of strains and also demonstrates that genetic exchange between this group and other *T. brucei* genotypes is not sufficiently frequent to break up this association.

### Trypanosoma brucei gambiense DAL 972 clone 1

#### *Isolation and phenotype*

*T. b. gambiense* is the causative organism of human trypanosomiasis in West and Central Africa and has been divided into two groups or types based on phenotypic and genotypic characteristics [22]. Most isolates belong to Tbg1, which conforms to the classical description of *T. b. gambiense* as a pathogen that causes a chronic disease in human patients and manifests very low parasitaemia; it is typically slow growing in experimental rodents and is better adapted to transmission by *palpalis* than *morsitans* group tsetse flies [23]. Tbg1 is responsible for most cases of human trypanosomiasis in Africa. By contrast Tbg2 grows well in experimental

rodents and is easily transmitted by *morsitans* group tsetse [23]; it has rarely been isolated from patients and has thus far been found only in Côte d'Ivoire (Ivory Coast) and Burkina Faso (Upper Volta) [16,24]. Tbg2 isolates are genetically heterogeneous [16,24,25].

DAL 972 (MHOM/CI/86/DAL972) clone 1 was chosen as the representative Tbg1 for the genome project, because it was originally isolated from a patient in West Africa (Daloa focus in Côte d'Ivoire) [26], and has the phenotypic features typical of Tbg1. DAL 972 clone 1 has been very little passaged and has an extremely chronic phenotype in normal experimental rodents, but can be grown in immunosuppressed or immunodeficient mice such as SCID (severe combined immunodeficiency) mice. It has been transmitted via *G. palpalis gambiensis, G. m. morsitans* and *G. pallidipes* in the laboratory, and grows satisfactorily as procyclics *in vitro* in Cunningham's medium.

#### *Relationship to other T. brucei strains*

By biochemical characterisation, DAL 972 is a typical Tbg1 with specific isoenzyme patterns for alanine and aspartate aminotransferases [27], and has all three characteristic Tbg1 genetic markers, namely genes for the variant surface glycoproteins LiTat 1.3 and VSG AnTat 11.17, and the flagellar pocket glycoprotein, TgsGP [28,29]. Note that *TgsGP* is not correctly annotated in the DAL 972 genome, because this gene has been subject to a rearrangement relative to TREU 927 resulting in lack of synteny for one homologue of chromosome 2 [30]. In addition, DAL 972 was shown to have the characteristic Tbg1 RFLP pattern for *VSG 117* (*AnTat 1.8*) [31,32].

Tbg1 isolates typically have low DNA contents compared to other members of the *T. brucei* subgroup [33,34]. The DNA content of DAL 972 was at the high end of the range for Tbg1, but lower than *T. b. brucei* or *T. b. rhodesiense* [34]. In addition, the molecular karyotypes of Tbg1 isolates typically have lower numbers of minichromosomes than *T. b. brucei* or *T. b. rhodesiense* [33] and this is also true for DAL 972 [34].

### Trypanosoma vivax Y486

#### *Isolation and phenotype*

*T. vivax* is a major pathogen of ruminants both in Africa, where it is transmitted cyclically by tsetse flies, and in South America, where it is transmitted mechanically by biting flies such as tabanids. Despite its importance as a livestock pathogen, *T. vivax* has received little attention because it is difficult to cultivate in the laboratory. Unlike *T. brucei, T. vivax* is typically not infective to laboratory rodents, but can be gradually adapted to these hosts by for example co-injection with ruminant serum or immunosuppression by sublethal irradiation [35]. However, three strains of *T. vivax* (Y486, Y58, V953) from naturally infected cattle in Zaria, Nigeria were isolated directly into mice [36]. These spontaneously mouse infective strains grow to high parasitaemia in outbred mice and have been widely used in laboratory studies. The ability to clone antigenic variants of *T. vivax* Y486 [37] led to the purification and characterization of *T. vivax* variant surface glycoproteins [38]; *T. vivax* Y486 is ILRAD *Duttonella* antigen repertoire 1, ILDAR 1. As the most well characterized of the three Zaria *T. vivax* strains, Y486 was chosen for the genome project.

The Zaria *T. vivax* strains are infective to calves, sheep and goats, as well as mice, rats and rabbits, and are readily transmissible by a wide range of tsetse species (*G. m. centralis, G. m. morsitans, G. pallidipes, G. austeni, G. brevipalpis, G. tachinoides, G. palpalis palpalis, G. p. gambiensis, G. fuscipes fuscipes*) [37,39-42]. Infection in these flies was typically found in the labrum and hypopharynx and sometimes also in the cibarium [41,42]. Unlike *T. brucei* and *T. congolense, T. vivax* does not multiply in the tsetse midgut and hence does not grow *in vitro* as procyclics. Although culture systems to maintain *T. vivax* bloodstream forms *in vitro* were developed by several groups [43-45], none has come into general use. Likewise, there are several published methods from the same era for *in vitro* differentiation of bloodstream forms into epimastigotes and subsequent development to infective metacyclics [46-48]. Recently, a simple *in vitro* cultivation method for epimastigotes of IL 1392, a derivative of Y486, has been described that is robust enough to allow transfection and also gives rise to infective metacyclics [49].

#### *Relationship to other T. vivax strains*

The Nigerian reference isolate, *T. vivax* Y486, is a representative of the West African form of *T. vivax*. Before the advent of the Polymerase chain reaction (PCR), knowledge of genetic diversity in *T. vivax* was severely limited because of the difficulty of obtaining enough trypanosomes for analysis. However, differences in pathogenicity were recognised between East and West African *T. vivax* strains, the West African strains being generally regarded as more pathogenic to cattle than East African strains [50], although highly pathogenic haemorhaggic *T. vivax* strains are also known in East Africa [51,52]. West African *T. vivax* strains can be identified by specific repetitive DNA sequences and are phylogenetically distinct from East African strains [53-56]. South American *T. vivax* strains have been shown to have close genetic similarity to West African strains [57], in agreement with the historical evidence that *T. vivax* was imported into the New World in cattle from West Africa [58]. Thus, *T. vivax* Y486 also represents the South American form of *T. vivax*.

### Trypanosoma congolense IL3000

#### *Isolation and phenotype*

IL 3000 is a derivative of strain Transmara I, which was isolated from a bovine in the Transmara region of Kenya in 1966 [59,60]. Antigenic variation has been studied in this strain (designated ILRAD *Nannomonas* antigen repertoire 2, ILNAR 2) and variant antigen genes have been characterized from both bloodstream and metacyclic IL 3000 trypanosomes [61,62]. Presumably this was one of the deciding factors in choosing IL3000 for the genome project, although several other *T. congolense* strains such as TREU 1457 have also been widely used in experimental studies.

*T. congolense* generally grows well in laboratory rodents and bloodstream forms of IL3000 have been grown in mice as well as bloodstream form culture [60,63]. *T. congolense* is transmissible by a range of tsetse species and the life cycle is similar to that of *T. brucei* with proliferation of procyclics in the midgut and transmission of metacyclics in the saliva; for *T. congolense*, production of metacyclics occurs in the proboscis [58,64]. The tsetse developmental stages of *T. congolense* are more amenable to *in vitro* culture than those of *T. brucei* and methods for the *in vitro* production of attached epimastigotes and metacyclics pioneered by Gray and colleagues [65] have allowed the analysis of epimastigote and metacyclic as well as procyclic and bloodstream form populations. In this way epimastigote and metacyclic populations of sufficient purity for EST analysis were obtained from IL3000 [66] and recently the complete life cycle of IL3000 has been reproduced *in vitro* [63]. The ability to culture epimastigotes of IL3000 led to the characterisation of an epimastigote-specific, GPI-anchored surface glycoprotein called CESP [67], adding to the list of surface molecules specific to tsetse developmental forms of *T. congolense*, including GARP (glutamic acid/alanine rich protein) [68,69], PRS (protease-resistant surface molecule) [70] and *T. congolense* procyclin [71]. It is possible to transfect *T. congolense* procyclics fairly easily by electroporation [63,72,73], but much more difficult to transfect bloodstream forms [63].

#### *Relationship to other T. congolense strains*

Three genetically distinct subgroups are currently recognized within *T. congolense*: savannah, forest and Kenya Coast or kilifi [74]. The most abundant and widespread is *T. congolense* savannah and IL3000 represents this subgroup. The savannah and forest subgroups were originally distinguished by different isoenzyme patterns [75,76], and subsequently by unique repetitive DNA sequences which provide targets for species-specific PCR identification [77]. A further genetically distinct subgroup was isolated from livestock on the Kenya Coast [78] and appears to have a restricted distribution in East Africa. Although phylogenetic analysis places these three *T. congolense* subgroups in a single clade [79,80], they are arguably sufficiently genetically divergent to warrant recognition as separate species [81].

## Conclusions

This short review has brought together background information on the origins and biological characterisation of the four African tsetse-transmitted genome strains as a source of reference for future users of the genome data.

#### Competing interests

The author declares that she has no competing interests.

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