PATHOLOGIE PARASITAIRE

Trypanosoma vivax in the Americas: morphometry and host range

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Key words

Trypanosoma vivax - Body conformation - Dimension - Host - America.

Summary

The African *Trypanosoma vivax* is classically described as being club-shaped. However, slender forms are present in several stocks. In the Americas this basic club-shaped characteristic has also been observed, but is dependent on the host species. The South American *T. vivax* has a range length of 16 to 26.5 µm, and therefore appears shorter than the originally described species. Recent biometrical studies showed that the South American *T. vivax* varies from mean lengths of 15.86 to 23 µm and the minimum length reported is 11.34 µm. A description of morphometrical characteristics and host range of *T. vivax* in the Americas is presented since little information is currently available on the natural pathogenicity, epizootiology and morphology of the *T. vivax*-like trypanosomes infecting domestic animals in the Americas.

■ INTRODUCTION

Trypanosoma vivax, originating in Africa, was reported in Central America, South America, the West Indies and Mauritius (21) and more recently in Indonesia (2). It was reported in the Americas for the first time in French Guiana (20). In Brazil, Shaw and Lainson (26) reported the first occurrence of T. vivax in a water buffalo (Bubalis bubalis) in the vicinity of the city of Belém, Pará. Silva et al. (27) reported the first occurrence of T. vivax in the Pantanal region of Brazil on the border with Bolivia and in the same year this parasite was found in Bolivia (28) (figure 1).

Although the economic importance of *T. vivax* infection in livestock is well documented in Africa, little information is currently available on the natural pathogenicity, epizootiology and morphology of the *T. vivax*-like trypanosomes infecting domestic

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animals in South America (12). In West Africa *T. vivax* often causes a fatal disease, while in East Africa it causes a milder infection in cattle. These characteristics have been related to morphology by Fairbairn (10). The differences in pathogenicity, host range amongst African and South American stocks of *T. vivax*, as well as the suspected transmission by *Tabanidae* and *Stomoxys* of South American isolates, lead to intriguing questions on the evolutionary relationships between members of this trypanosome species.

■ MATERIALS AND METHODS

Most of *T. vivax* measurements were obtained from the literature. The number of specimens measured and the source are listed in table I. *T. vivax* measurements from the Pantanal (Brazil) and Santa Cruz Department (Bolivia) listed as unpublished data were obtained as described by Hoare (16). Unpublished biometrical data on *T. vivax* from Venezuela (TVVG1 isolate from the State of Guarica) and French Guiana (TVGF1 isolate deposited at ILRI as IL4007) were kindly supplied by M. Desquesnes and E. Espinoza (figure 2).

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CENTRAL AND SOUTH AMERICA PANAMA COLOMBIA COLOMBIA COLOMBIA BRAZIL BOLIVIA BOLIVIA BRAZIL BRAZIL BRAZIL OCEAN OCEAN

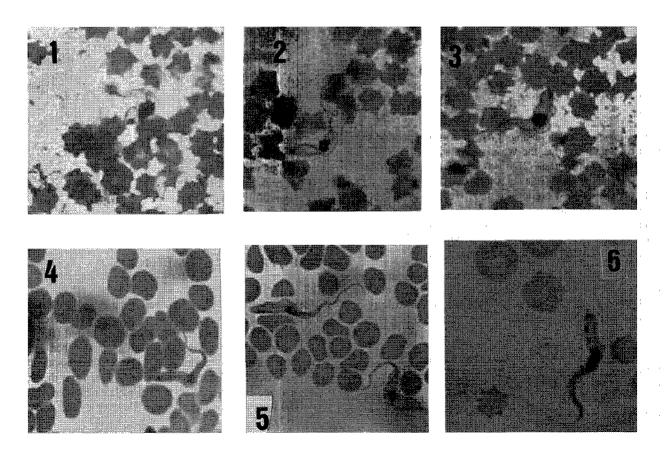
Figure 1 (above): Central and South American countries where Trypanosoma vivax was reported.

Figure 2 (below): Trypanosoma vivax isolates. 1, 2, 3: from bovines of the Santa Cruz Department, Bolivia. 4, 5: from bovines of Pantanal of Poconé, State of Mato Grosso, Brazil. 6: from bovines of Venezuela.

Falkland Islands

800

Miles



Trypanosoma vivax mean length, number of measurements and host of isolation

Arca (Beforeace)	1	Total January	Moss longth
		11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31	(mrl)
Bolivia, Santa Cruz (28) Bolivia, Puerto Suarez (Silva et al., 1997, unpubl.)	Bovine 80 Bovine 45		15.86
Brazil, PA (26) Brazil, MT (27) Brazil MS	Buffalo 43 Sheep 50 Bovine 100		22.9 22.6 18.73
(Silva et al., 1997, unpubl.)			21.0
French Guiana (20) (8)	Bovine - 50		22.5 20.3
Panama (17)	Bovine 100		21.38
Martinique (4)	1		24.0
Mauritius (15) (10)	Bovine 200 Goat 100 Goat 100		25.0 26.4 23.9 24.4
Venezuela (8) (30) (11) (18)	Sheep 50 Bovine - Bovine -		21.52
Suriname (24) (23)	Bovine 100 Sheep 100 Sheep 100 Goat 150		21.0 22.4 21.5 21.7 22.7
Uganda, Kenya, Tanzania (10)	Bovine 500		26.0
Nigeria (10)	Sheep 7830		21.36 to 24.58
,			

• Places where means are located

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RESULTS AND DISCUSSION

Distribution

South American countries where *T. vivax* has been confirmed are: French Guiana (20), Suriname (24), Venezuela (18, 30), Colombia (25), Brazil (26, 27), Bolivia (28).

Using an indirect fluorescent antibody test (IFAT) with a South American *T. vivax* as antigen, Wells *et al.* (31) tested cattle sera from different South American countries. The results were positive (probably for *T. vivax*) in the participating countries as follows: El Salvador 15%, Costa Rica 23%, Colombia 48%, Ecuador 23%, Peru 14%, Brazil, Mato Grosso, 54% and Paraguay 40%. In addition, the authors reported that blood films containing trypanosomes resembling *T. vivax* had been received from Pucallpa in Peru. Recently, observations of this parasite in sheep have been recorded in the vicinity of the Department of Lima in Peru (Prof. Rosa Martinez Rojas-UNMSM, pers. commun.).

Host range

According to Gardiner and Mahmoud (13) T. vivax is predominantly a pathogenic livestock parasite in South America. Horses, water buffalo, sheep, goats, deer, alpacas and llamas can be infected. The three latter species usually develop only mild symptoms, but presumably can act as reservoir hosts. In Venezuela, the deer species where T. vivax has been found is Odocoileus gymnotis. Dipaka (Lama pasos) and llama (Lama glama) may also be infected. There is no potential wild reservoir in French Guiana, except for deer whose population has been reduced by hunting. Although T. vivax was found in deer, the existence of a wild reservoir has never been demonstrated. Whether it can infect dogs, cats and horses still needs investigating (6, 7). Rodents can be infected reliably with only some stocks and after periods of adaptation (13) through the inoculation of forms isolated from early natural infections into irradiated or non-irradiated laboratory rodents using serial and rapid passages (14, 19, 22). Mixed infections with other trypanosome species are possible. In the Santa Cruz Department of Bolivia the authors recorded T. vivax/ T. evansi and T. vivax/Megatrypanum spp. mixed infections in one bovine and in several bovines, respectively (unpublished data).

Morphometry

Trypanosoma v. viennei is morphologically identical to African T. vivax and its pattern of motility is similar (13). T. viennei is a synonym for T. vivax. Some authors, such as Stephen (29), suggested the nomenclature Trypanosoma (Dutonella) vivax viennei (Lavier, 1921) to designate T. vivax from the Americas.

According to Hoare (16), *T. vivax* length range is between 18 and 31 μm (including the free flagellum which is 3-6 μm long), with means from 21 to 25.4 μm . More than 90% of the measurements are between 20 and 26 μm .

African *T. vivax* is classically described as being club-shaped. However, slender forms have been observed in several stocks. In some of these trypanosomes, the posterior end of the body is rounded but not swollen. In other cases, it ends in a short blunt or even sharp point. In some individuals the undulating membrane is fairly well developed. This might be mistaken for the slender or intermediate forms of *Trypanozoon*, except for the presence of a voluminous kinetoplast (16).

In Africa two types of strains have been observed differing in morphological and biological features. One is represented by relatively short forms with mean lengths from 21.4 to 24.6 µm, and the other by long forms whose mean lengths vary from 23.6 to 27.0 µm (10). According to Chardome and Peel (3) there are two types of T. vivax in Rwanda-Burundi, which differ in the appearance of blood forms and metatrypanosomes. The blood forms of type 1 are typical of this species, the body being broad and club-shaped, with a rounded posterior end, inconspicuous undulating membrane and voluminous kinetoplast. These trypanosomes measure 20-30 µm (mean 26 µm) in length, but their sizes vary in different hosts (cattle, sheep, goats). The trypanosomes of type 2, which were found only in cattle, are slender and shorter than in the classical T. vivax. The posterior end of the body is narrower, while the undulating membrane is conspicuous and the kinetoplast smaller. These trypanosomes are 18-26 µm long (mean 22 µm). Based on these observations, slender forms should be predominant in bovine strains from Zaire (Congo) and Rwanda-Burundi. According to Hoare (16), when this parasite is transmitted mechanically, either in tsetse-free areas of Africa and in the Americas, or in the case of rodent-adapted laboratory strains, it tends to lose the tadpole forms and retains only the slender ones, presenting a behavior comparable to trypanosomes of the brucei-complex, whose laboratory strains become monomorphic.

Hoare (16) reported that the South American T. vivax has a length range from 16 to 26.5 μ m. In addition, he reported that although the lengths of T. vivax and T. uniforme overlap slightly, they can be differentiated in pure infections by measuring only 10 trypanosomes, while, in mixed infections, 100 should be measured. Moreover, if the length exceeds 20 μ m the species is T. vivax, if less than 18 μ m it is T. uniforme.

Recent morphological and biometrical studies on South American T. vivax showed different results from those mentioned by Hoare (16). According to the data in table II, the South American T. vivax varies from mean lengths of 15.86 to 23 µm in bovines from Bolivia (Santa Cruz Department) and French Guiana (27, 20), respectively. The minimum length of South American T. vivax was reported to be 11.34 µm by Silva et al. (27) in bovines from the Mato Grosso State of Brazil (table I). This review does not consider Hoare's concerns (16) on the differentiation of T. vivax from *T. uniforme* based on morphometrical observations. In a recent paper Silva et al., with the collaboration of the Institute of Tropical Medicine "Prince Leopold" in Antwerp, Belgium, confirmed through PCR analysis that the trypanosome with a mean length of 15.86 µm is T. vivax (28). In his review, Gardiner (12) notified that the last report of T. uniforme from a giraffe in Tanzania was in 1967. It is not known whether this is because T. uniforme has become truly uncommon or whether modern researchers do not generally apply mensural determinations to the parasites in their work. In addition, Gardiner emphasized that the biometrical study of a number of T. vivax stocks by Allshop and Newton (1) revealed no evidence of *T. uniforme* amongst them.

Leger and Vienne (20) described the French Guianan $T.\ vivax$ as elongated and with tapered final regions, where the posterior end is less tapered than the anterior end. The nucleus is oval and central, located at the posterior end. The kinetoplast is rounded or oval, but terminal. In Panama (17), $T.\ vivax$ has a swollen rounded posterior end and a narrow tapering anterior end. The undulating membrane is very feebly developed and in most instances cannot be seen. The flagellum extends beyond the anterior end for a distance of 4 to 6 μ m. The kinetoplast is large and usually located at the posterior end, but, in some cases, it is lateral and slightly subterminal.

Table II

Measurements (µm) of *Trypanosoma vivax* isolated from Central and South American countries

Area (Reference)	L	PK	KN	PN	NA	F	PN/KN (KI)	PN/NA (NI)
(16)	18-31					3-6		
Bolivia, Santa Cruz	15.86	0.54	5.05	5.59	5.90	4.35		0.96
(28)	(2.23)*	(0.51)	(1.07)	(1.15)	(0.76)	(1.26)		(0.24)
Bolivia, Puerto Suarez	17.37	0.99	5.25	6.24	5.77	5.33		0.87
(Silva <i>et al.</i> , 1997, unpubl.)	(1.65)	(0.51)	(0.68)	(0.83)	(0.68)	(0.83)		(0.12)
Brazil , Pará	22.77	0.65	6.16	7.60	8.22	6.92		0.94
(26)	(1.38)	(0.25)	(0.57)	(0.57)	(1.08)	(1.03)		(0.24)
Brazil, Mato Grosso	18.73	1.02	6.10	7.18	5.40	6.15		1.50
(27)	(3.8)	(1.16)	(1.29)	(1.18)	(1.63)	(2.38)		(0.72)
Brazil, Mato Grosso do Sul	18.1	0.30	7.46	7.76	6.03	4.3		1.34
(Silva et al., 1997, unpubl.)	(2.04)	(0.53)	(1.56)	(1.59)	(1.18)	(0.87)		(0.37)
Colombia (25)	21.00							
French Guiana (20)	22-23	0.80	5.50	6.3	7.20	6.00	1.14	0.87
French Guiana	20.3	1.10	6.00	7.1	5.70	7.50	1.18	1.24
(8)	(0.55)	(0.17)	(0.22)	(0.16)	(0.37)	(0.40)	(0.04)	(0.08)
Panama (17)	21.38							
Venezuela	21.52	0.82	6.02	6.83	7.83	6.86	1.13	0.87
(8)	(1.17)	(0.19)	(0.47)	(0.54)	(1.03)	(1.32)	(0.06)	(0.14)
(18)	22.00							
Suriname (24) (23)	21.00 21.50							

PK = distance from posterior end to kinetoplast; KN = from kinetoplast to middle of nucleus; PN = from posterior end to middle of nucleus; NA = from nucleus to anterior end; F = free flagellum length; L = total length including free flagellum; KI = kinetoplast index; NI = nuclear index (Hoare, 1972, Oxford, UK, Blackwell Scientific Publ.)

* (mean)

According to Nieschulz *et al.* (24) *T. vivax* from Suriname generally appears more or less club-shaped, with the nucleus mostly located in the anterior part of the body center. The anterior end is strung-out and the posterior part of the nucleus is wider and commonly swollen compared with the anterior part of the nucleus. The posterior end is broad-rounded and the kinetoplast is remarkably big and located quite near the posterior end. In general, the undulating membrane is poorly developed and a relatively long flagellum is always observed. In addition, these authors mentioned that mice, rats, guinea pigs and dogs cannot be infected by *T. vivax*.

In the first report of *T. vivax* in Brazil, Shaw and Lainson (26) described this parasite as being monomorphic with a body characteristically broader at the rounded posterior end, and tapered toward the anterior. The undulating membrane is weakly developed

in the mature trypomastigotes and slightly more pronounced in the dividing forms. The kinetoplast is oval in shape, although rounded forms are sometimes seen, the nucleus is centrally located. The trypanosome size ranges from 19.0 to 25.5 µm.

According to Dávila *et al.* (5), the biometrical differences between *T. vivax* isolates from Belém-Brazil (26), Poconé-Brazil (27) and Santa Cruz de la Sierra-Bolivia (28) are highly significant. In addition, their results showed that there is a similarity in the subterminal position of kinetoplast among Belém and Santa Cruz de la Sierra trypanosomes. The body of the Bolivian parasite at the rounded posterior end is broader than that of the Poconé trypanosome. However, the Poconé parasite is more tapered than the Bolivian toward the anterior and posterior ends. The kinetoplast of the Poconé parasite is more oval than that of the Bolivian. In the former, the kinetoplast is lateral and subterminal

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and in the latter it is more terminal. The free flagellum of Bolivian trypanosomes is shorter than that of trypanosomes from Poconé and Belém. The nucleus of the Bolivian parasite is bigger and more rounded than that of the Poconé (5).

In their paper, Dávila et al. (5) concluded that shorter forms reported in Brazil (Poconé) and Bolivia (Santa Cruz de la Sierra) are related to acute forms of diseases which they observed in these regions, and that T. vivax probably arrived in the Americas from West Africa. Other authors, such as Fairbairn in West Africa (10) and Shaw and Lainson in Belém, Brazil (26), reached the same conclusion. Moreover, recent studies showed a similarity between the West African group parasites and those from Colombia in South America. This suggests that the generally held hypothesis that South American parasites are derived from tsetse-transmitted African trypanosomes is probably correct (9). In their work, Dirie et al. (9) also remarked that individual isolates of T. vivax from Africa are different in some characteristics such as pathogenicity, infectivity for laboratory rodents, isoenzyme and karyotypic patterns. We believe that the morphometrical characteristics observed in South American T. vivax should be included in this listing since this trypanosome species is biometrically distinct among bovine species from Brazil and Bolivia (5) and probably from other New World countries (table III).

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Table III

Mean length of *Trypanosoma vivax* isolated from bovines in the New World

Country (reference)	Num. of measurements	Mean length (μm)
Bolivia (28)	80	15.86
(Silva et al., 1997, unpubl.)	45	17.37
Brazil (27)	100	18.73
(Silva et al., 1997, unpubl.)	50	18.10
Colombia (25)	-	21.00
French Guiana (20)	-	22.50
Mauritius (15).	200	25.0
(10)	100	26.4
Panama (17)	100	21.38
Suriname (23)	600	21.50
Venezuela (18)	-	22.00

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Résumé

Dávila A.M.R, Ramirez L., Silva R.A.M.S. *Trypanosoma vivax* en Amérique : morphométrie et spectre d'hôtes

L'espèce Trypanosoma vivax, d'origine africaine, est classiquement décrite comme ayant la forme d'une massue à l'extrémité arrondie. Cependant des formes longues et flexueuses sont présentes dans plusieurs stocks. En Amérique, le maintien de cette forme classique en massue semble dépendre de l'espèce de l'hôte. Le *T. vivax* d'Amérique du Sud mesure de 16 à 26,5 µm de longueur et apparaît ainsi plus court que l'espèce décrite initialement. Des études biométriques récentes ont montré que les longueurs moyennes du T. vivax d'Amérique du Sud variaient de 15,86 à 23 µm et que la longueur minimum rapportée était 11,34 µm. Une description des caractéristiques morphologiques et du spectre d'hôtes de T. vivax en Amérique est présentée car peu d'information est disponible sur la pathogénicité, l'épizootiologie et la morphologie des trypanosomes semblables à T. vivax infectant les animaux domestiques dans cette région du monde.

 ${\it Mots-clés}$: ${\it Trypanosoma\ vivax}$ - Conformation animale - Dimension - Hôte - Amérique.

Resumen

Dávila A.M.R, Ramirez L., Silva R.A.M.S. *Trypanosoma vivax* en las Américas: morfometría y rango de huéspedes

El Trypanosoma vivax africano se describe clásicamente por presentar extremidad redondeada. Sin embargo, ciertas cepas se presentan como formas mas finas. Esta forma característica de matraca se ha observado también en las Américas, dependiendo de la especie huésped. El T. vivax sud americano tiene un rango de longitud de 16 a 26,5 µm, apareciendo mas corto que las especies descritas originalmente. Estudios biométricos recientes muestran que el T. vivax sud americano varía en longitudes promedio de 15,86 a 23 µm, con una longitud mínima reportada de 11,34 µm. Debido a que actualmente existe poca información sobre la patogenicidad natural, la epizootiología y la morfología de los tripanosomas similares a T. vivax, que infectan los animales domésticos en las Américas, se presenta una descripción de las características morfológicas y el rango de hospederos de T. vivax en las Américas.

Palabras clave: Trypanosoma vivax - Conformación animal - Dimensión - Huesped - América.