Trypanosoma (reptile and amphibian species)
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by invertebrate vectors to a wide range of vertebrate hosts, including reptiles and amphibians. Trypanosomes in aquatic poikilotherm (cold-blooded) hosts are often transmitted by leeches or mosquitoes, while those of terrestrial poikilotherms are transmitted by sandflies and bugs. Few infections have been associated with clinical disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Excavata (with conspicuous ventral feeding groove)
Group:	Discoba (diverse group supported robustly by molecular studies)
Phylum:	Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class:	Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass:	Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order:	Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family:	Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus:	*Trypanosoma* (vector-borne haemoparasites)
Species:	various species cause infections in reptiles and amphibia

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans are a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera (*Trypanomorpha* for those in birds, *Trypanosoma* for those in amphibians, and *Haematomonas* for those in fish). Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Comparative phylogenetic studies have shown trypanosomes from major reptilian groups (chelonians, crocodilians and lizards) were polyphyletic and separated into distant clades. Trypanosomes from tortoises clustered together with those from fish (both groups being transmitted by aquatic leeches), whereas trypanosomes from crocodiles (transmitted by tsetse flies) were closest to avian trypanosomes. Trypanosomes from varanid, phrynosomatid and gekkonid lizards clustered together whereas those from chameleons grouped with anuran trypanosomes.

Trypanosoma species	Mastigote length (µm)	Hosts [disease]	Vectors	Distribution
Species in lizards				
T. anolisi	19-42	Sauria: dactyloid (slender anole, bridled anole, giant green anole, tropical anole, ghost anole)		Panama, Belize
T. betschii	20-32	Sauria: gerrhosaurid (Madagascar girdled lizard)		Madagascar
T. boueti	18-33	Sauria: scincid (African striped skink, Guinea mabuya, speckle-lipped mabuya)	Diptera: psychodid sand-fly (*Sergentomyia bedfordi*)	West and East Africa
T. chamaeleonis		Sauria: chamaeleonid (Mediterranean chameleon, graceful chameleon)		Sudan
T. cnemaspi	19-32	Sauria: gekkonid (Barbour's gecko, flathead leaf-toed gecko)		Tanzania
T. cordyli	32-62	Sauria: cordylid (East African spiny-tailed lizard)		Tanzania
T. domerguei	19-29	Sauria: oplurid (collared iguana)		Madagascar
T. egerniae	22-28	Sauria: scincid (Cunningham's skink, tree-crevice skink)		Australia
T. fairchildi	36-59	Sauria: dactyloid (bighead anole)		Panama
T. gallyi		Sauria: eublepharid (African fat-tailed gecko)		Africa

T. garnhami	18-39	Sauria: gekkonid (Brooke's house gecko)	Hemiptera: reduviid (*Rhodnius prolixus*); Ixodida: argasid (*Ornithodoros parkeri*)	Kenya
T. gekkonis	42-59	Sauria: gekkonid (Tokay gecko)		Thailand
T. gerrhonoti	50-70	Sauria: anguid (southern alligator lizard)	Diptera: psychodid (*Lutzomyia vexator*)	North America
T. gonatodi	34-47	Sauria: sphaerodactylid (yellow-headed gecko)		Panama
T. kimbozae	25-49	Sauria: gekkonid (flathead leaf-toed gecko)		Tanzania
T. leschnaulti	56-60	Sauria: gekkonid (Leschenault's leaf-toed gecko)		Sri Lanka
T. lygodactyli	25-39	Sauria: gekkonid (flathead leaf-toed gecko, dwarf yellow-headed gecko, Cape dwarf gecko)		Tanzania
T. martini (syn. *T. mabuiae*)	dimorphic: 19-40, 17-25	Sauria: scincid (speckle-lipped skink, red-sided skink, striped skink, five-lined skink, Guinea mabuya)		Africa
T. mochli		Sauria: scincid (fire skink)		Congo
T. ndumoensis	24-45	Sauria: cordylid (Limpopo girdled lizard)		South Africa
T. ocumarensis		Sauria: phyllodactylid (turnip-tailed gecko)		Africa
T. pertenue	15-42	Sauria: gekkonid (termite hill gecko)		India
T. perroteti		Sauria: scincid (red-sided skink)		Africa
T. petteri	43-50	Sauria: gekkonid (Madagascar day gecko)		Madagascar
T. phlebotomi (possible syn. *T. hemidactyli*)		Sauria: gekkonid (common house gecko)	Diptera: psychodid (*Sergentomyia babu,* earlier misidentified as *Phlebotomus minutus*)	India
T. phylluri	36-48	Sauria: carphodactylid (broad-tailed gecko)		Australia
T. platydactyli	26-39	Sauria: phyllodactylid (common wall gecko(, gekkonid (Kotschy's gecko, grey thin-toed gecko, Turkestan thin-toed gecko, Caspian bent-toed gecko)	Diptera: psychodid (*Sergentomyia minuta, Phlebotomus parroti*)	Tunisia, Malta, Italy, France
T. plicae	49-64	Sauria: tropidurid (blue-lipped tree lizard)		Brazil
T. plicaplicae	26-45	Sauria: tropidurid (collared tree lizard)		Guyana
T. poinsetti	31-42	Sauria: phrynosomatid (crevice spiny lizard)		North America
T. rudolphi		Sauria: scincid (agile skink)		Americas
T. ryukyuense	26-45	Sauria: eublepharid (Kuroiwa's leopard gecko)		Japan
T. scelopori	35-47	Sauria: phrynosomatid (western fence lizard), crotaphytid (eastern collared lizard)	Diptera: psychodid (*Lutzomyia vexator*)	North America
T. scincorum	17-34	Sauria: scincid (many-striped skink, bronze grass skink, spotted forest skink, Sabah slender skink)		Asia
T. serveti	20-45	Sauria: phrynosomatid (Teapen rosebelly lizard, rose-bellied lizard), dactyloid (greater scaly anole, bridled anole, dappled anole, slender anole), corytophanid (Hernandez's helmeted basilisk)		Mexico
T. striatae	25-34	Sauria: scincid (striped skink, speckle-lipped skink)		Tanzania
T. superciliosae	87-124	Sauria: tropidurid (diving lizard)		Brazil
T. takydromi	25-48	Sauria: lacertid (Asian grass lizard, green grass lizard)		Japan
T. thecadactyli	19-24	Sauria: phyllodactylid (turnip-tailed gecko)	Diptera: psychodid (*Lutzomyia*	Panama

			trinidadensis)	
T. therezieni	28-33	Sauria: chamaeleonid (short-horned chameleon, Malagasy giant chameleon, carpet chameleon, warty chameleon, Parson's chameleon) [experimental fatalities]	Diptera: culicid (*Culex pipiens*)	Madagascar
T. tokoloshi	29-54	Sauria: cordylid (Zoutpansberg girdled lizard)		South Africa
T. torrealbai	27-38	Sauria: sphaerodactylid (Estado Aragua gecko, Margarita leaf-toed gecko)		Venezuela
T. turcici	28-35	Sauria: gekkonid (Mediterranean house gecko)		Iraq
T. uluguruensis	25-49	Sauria: gekkonid (flathead leaf-toed gecko, dwarf-yellow-headed gecko, Cape dwarf gecko, turquoise dwarf gecko)		Tanzania
T. urosauri	29-38	Sauria: phrynosomatid (long-tailed brush lizard)		North America
T. varani		Sauria: varanid (Nile monitor, savannah monitor)	Diptera: psychodid (*Phlebotomus duboscqi*)	Senegal
T. zonuri	22-36	Sauria: cordylid (Cape girdled lizard)		Tanzania
Species in snakes				
T. brazili	40-79	Serpentes: colubrid (olive keelback, Wagler's snake)	Clitellata: glossiphoniid (*Placobdella brasiliensis, catenigera*)	Brazil
T. butantanense		Serpentes: colubrid (Wagler's snake), viperid (crossed pit viper, tropical rattlesnake)		Brazil
T. cascavelli		Serpentes: viperid (tropical rattlesnake)		America
T. closeli	82-122	Serpentes: colubrid (African brown water snake, Smith's African water snake)		West Africa
T. constrictor	54-82	Serpentes: boid (Bolivian short-tailed boa)		Brazil
T. enhydris		Serpentes: colubrid (buff-striped keelback, rainbow water snake)		Asia
T. erythrolampri	28-34	Serpentes: colubrid (Aesculapian false coral snake)		South America
T. floridana	38-49	Serpentes: colubrid (eastern green water snake, Florida banded water snake)		North America
T. haranti	20-21	Serpentes: pseudoxyrhophiid (lateral water snake)		Madagascar
T. hogei	36-47	Serpentes: colubrid (Brazilian bird snake)	Clitellata: glossiphoniid (*Haementeria lutzi*)	Brazil
T. hydrae	31-41	Serpentes: colubrid (banded water snake, western ribbon snake, Texas rat snake)	Clitellata: glossiphoniid (*Placobdella parasitica*)	North America
T. manguinhensis	64-77	Serpentes: colubrid (Wagler's snake)		Brazil
T. mattogrossense	49-53	Serpentes: colubrid (false water cobra)		South America
T. merremii	64-77	Serpentes: colubrid (Wagler's snake)		Brazil
T. najae	50	Serpentes: elapid (black-necked spitting cobra)		Sudan
T. phylodriasi		Serpentes: colubrid (Paraguay green racer), viperid (crossed pit viper)		South America
T. primeti	dimorphic: 82-105, 44-57	Serpentes: colubrid (checkered keelback), homalopsid (Chinese water snake)		Vietnam
T. psammophis		Serpentes: psammophiid (olive grass snake)		Africa

T. rostellata		Serpentes: homalopsid (rice paddy snake)		Asia
T. salamantae	60-73	Serpentes: boid (Paraguayan rainbow boa)	Diptera: culicid (*Culex dolosus*)	Brazil
T. sebae		Serpentes: boid (Central African rock python)		Africa
T. thamnophis	53-66	Serpentes: colubrid (common garter snake)		Canada
T. tortilis		Serpentes: (homalopsid (Chinese water snake)		Asia
T. voltariae	42	Serpentes: elapid (black-necked spitting cobra)		Ghana
T. yaegeri	46-80	Serpentes: viperid (western cottonmouth)		North America
Species in crocodiles				
T. cecili	62-84	Crocodilia: alligatorid (spectacled caiman)		Brazil
T. grayi [syn. *kochi*]	58-87	Crocodilia: crocodylid (Nile crocodile); Sauria: varanid (savannah monitor)	Diptera: glossinid (*Glossina palpalis, pallidipes, fuscipes, tachinoides*)	Central Africa
T. ralphi		Crocodilia: alligatorid (spectacled caiman, Yacare caiman, black caiman)		Brazil
T. terena		Crocodilia: alligatorid (Yacare caiman)		Brazil, Venezuela
Species in turtles				
T. balithaensis	30-35	Testudines: trionychid (Indian flapshell turtle)	Clitellata: glossiphoniid (*Helobdella nociva*)	India
T. chelodinae	34-43	Testudines: chelid (eastern long-necked turtle, eastern short-necked turtle, Brisbane short-necked turtle, saw-shelled turtle, Krefft's turtle, northern snapping turtle)		Australia
T. chrysemydis	47-50	Testudines: emydid (painted turtle, northern map turtle(, chelydrid (common snapping turtle), trionychid (smooth softshell turtle, spiny softshell turtle, Florida softshell turtle)	Clitellata: glossiphoniid (*Placobdella multilineata, ornata, rugosa, parasitica*)	North America
T. damoniae	32	Testudines: geoemydid (Chinese pond turtle)		Asia
T. gangetica	34-37	Testudines: trionychid (Indian softshell turtle)		India
T. leroyi	59	Testudines: testudinid (Home's hingeback tortoise)		Senegal
T. lissemysi		Testudines: trionychid (Indian softshell turtle)		Asia
T. mocambicum		Testudines: pelomedusid (Upemba mud turtle, Okavango mud turtle, variable mud turtle, East African black mud turtle)		Africa
T. neitzi		Testudines: pelomedusid (serrated hinged terrapin)		Africa
T. platemysi		Testudines: chelid (twist-necked turtle)		South America
T. pontyi	47	Testudines: pelomedusid (East African black mud turtle)		Africa
T. sheppardi		Testudines: pelomedusid (serrated hinged terrapin)		Africa
T. testudinis		Testudines: cheloniid (green sea turtle)		South America
T. vittatae	25-70	Testudines: trionychid (Indian flapshell turtle)	Clitellata: glossiphoniid (*Glossosiphonia* sp.), hirudinid (*Poecilobdella granulosa*)	Sri Lanka

Over 70 trypanosome species have been recorded in amphibian hosts, not only from adult frogs and toads, but often from their tadpole stages. Although it was proposed that anuran species be allocated to a separate *Trypanosoma* subgenus, provisionally called *Trypanosoma*, their classification apart from other trypanosomes has not been supported by molecular phylogenetic studies. Instead, anuran trypanosomes appear to be polyphyletic and interwoven with other species from birds, reptiles and fish. Early workers also recognized six different types (A-F) of trypanosomes in anuran hosts on the basis of trypomastigote morphology.

***Trypanosoma* species**	**Mastigote length (µm) (Type)***	**Hosts**	**Vectors**	**Distribution**
Species in frogs/toads				
T. andersoni	47-72	Anura: hylid (grey tree frog, spring peeper)		North America
T. arcei (syn. *T. ocellati*?)	40 (A)	Anura: leptodactylid (butter frog)		South America
T. aurorae		Anura: ranid (red-legged frog)		
T. belli	25-41 (D)	Anura: ranid (European common brown frog, edible frog)		China
T. bocagei	71 (B)	Anura: bufonid (African common toad, Asian common toad, Asiatic toad, European toad, Berber toad), ranid (common green frog, Hose's frog), dicroglossid (rice field frog)	Diptera: psychodid (*Phlebotomus squamirostris*), and mosquito?	Africa, East Asia
T. bufophlebotomi		Anura: bufonid (California toad), ranid (American bullfrog)	Diptera: psychodid (*Lutzomyia vexator*)	North America
T. borelli (syn. *T. hylae*)	20-80 (A)	Anura: hylid (red-snouted tree frog, European tree frog), dicroglossid (Indian bullfrog)		Brazil, Europe
T. boyli		Anura: hylid (foothill yellow-legged frog)		North America
T. canadensis		Anura: ranid (northern leopard frog)	Clitellata: glossiphoniid (*Placobdella* sp.)	Canada
T. chattoni (syn. *T. celestinoi*?)	18-25 (F)	Anura: ranid (northern leopard frog, southern leopard frog, Hose's frog, American bullfrog, common green frog, Ryukya tip-nosed frog, crab-eating frog, rice field frog), ptychadenid (Mascarene grass frog), ceratophryid (Argentine horned frog), hylid (European tree frog, white-banded tree frog, waxy monkey tree frog), phrynobatrachid (Natal dwarf puddle frog), leptodactylid (butter frog), bufonid (Asian common toad, Argentine common toad)		Americas, Eurasia, Africa
T. clamatae	33-42 D)	Anura: ranid (northern green frog)		North America
T. clelandi (syn. *T. tasmaniensis*)	41-58 (D)	Anura: limnodynastid (ornate burrowing frog, spotted marsh frog)		Australia
T. diamondi		Anura: ranid (northern leopard frog)		Mexico
T. fallisi		Anura: bufonid (American toad)		Canada
T. galbae		Anura: ranid (Mexican cascades frog, Montezuma leopard frog)		North America
T. gaumontis	15-21 (D)	Anura: bufonid (America toad), ranid (northern leopard frog)		North America
T. grande		Anura: ranid (northern leopard frog)		North America
T. grandicolor	84-151	Anura: pipid (African clawed frog)		Africa
T. grylli	~30-40 (E)	Anura: hylid (southern cricket frog, grey tree frog, spring peeper)		North America
T. hosei		Anura: ranid (Hose's frog)		Asia
T. inopinatum (syn. *T. undulans, elegans,*	12-54 (D)	Anura: ranid (edible frog, common grass frog, northern leopard frog, American bullfrog, Gunther's Amoy frog), dicroglossid (Indian	Clitellata: glossiphoniid (*Helobdella algira*)	Africa, Europe, Russia,

hendersoni)		bullfrog, Indian green frog, rice field frog), alytid (Mediterranean painted frog), bufonid (African toad)		India, Canada
T. ishigakiense		Anura: dicroglossid (rice field frog)		Asia
T. karyozeukton	trimorphic 60-134 (D)	Anura: bufonid (African toad), hylid (southern cricket frog), dicroglossid (crowned bullfrog), ptychadenid (South African sharp-nosed frog)		Africa
T. lavalia	31-36 (D)	Anura: bufonid (American toad)		North America
T. leptodactyli	30-54 (D)	Anura: leptodactylid (butter frog, Vizcachera's white-lipped frog, Bolivian toad-frog), ceratophryid (Argentine horned frog), hylid (black-lined pond frog)	Clitellata: glossiphoniid (*Placobdella braziliensis, catenigera, Glossiphonia complanata*)	South America
T. loricatum	42-48 (C)	Anura: ranid (edible frog, common green frog, dark-spotted frog, gold-spotted pond frog, Gunther's frog, Galam white-lipped frog, Hose's frog), dicroglossid (Indian bullfrog, rice field frog), ptychadenid (South African sharp-nosed frog, Mascarene grass frog), hyperoliid (marbled rush frog), bufonid (African toad)		Eurasia, North America
T. malabaricum		Anura: ranid (fungoid frog)		India
T. mega	72 (D)	Anura: bufonid (Africa toad), ptychadenid (South African sharp-nosed frog), dicroglossid (rice field frog), pyxicephalid (warty frog), hylid (veined tree frog)		Africa
T. miyagii		Anura: ranid (Taurus frog, Okinawa tip-nosed frog)		Asia
T. montezumae		Anura: ranid (Montezuma leopard frog, Mexican cascades frog, Amazon River frog)		Americas
T. montrealis	45-68 (D)	Anura: bufonid (American toad)		North America
T. nagasakiense		Anura: hylid (Japanese tree frog)		Asia
T. nelspruitense	44-70 (D)	Anura: pyxicephalid (Angola river frog, Drakenberg river frog)		South Africa
T. neveulemairei	125-145 (D)	Anura: ranid (edible frog)		Europe
T. ocellati		Anura: leptodactylid (butter frog)		South America
T. parroti	65 (D)	Anura: alytid (Mediterranean painted frog)		Africa
T. parvum	11-14 (D)	Anura: microhylid (noisy cross frog), ranid (green frog)		North America
T. pipientis	52-82 (D)	Anura: ranid (northern leopard frog, wood frog)	Clitellata: glossiphoniid (*Placobdella phalera*)	North America
T. pseudopodium		Anura: bufonid (American toad)		North America
T. raksasa		Anura: ranid (common green frog)		Asia
T. ranarum [type II (flat spiralled form)]	71 (B)	Anura: ranid (northern leopard frog, northern green frog, edible frog, American bullfrog, mink frog, wood frog)		North America, Eurasia
T. rifae		Anura: bufonid (African toad)		Africa
T. rotatorium (syn. *T. sanguinis, T. ranarum p.p.* (simple membranous form), *costatum*)	43-62 (A)	Anura: bufonid (common toad, southern toad, European green toad, African toad, Argentine toad, Fowler's toad, Woodhouse's toad, Texas toad), alytid (midwife toad), aromobatid (yellow-throated frig), arthroleptid (forest tree frog), ceratophryid (Argentine horned frog,	Clitellata: glossiphoniid (*Batracobdella picta, Glossiphonia complanata, Haementeria lutzi,*	Eurasia, West Africa, South America

		Paraguay horned frog, Budgett's frog), dicroglossid (green pond frog, golden frog, skittering frog, rice field frog, Javan wart frog, African tigrine frog), hylid (giant leaf frog, European tree frog, bird-voiced tree frog, emerald-eyed tree frog, green tree frog, gray tree frog, ridged tree frog, veined tree frog, southern chorus frog, Brimley's chorus frog, spring peeper, waxy monkey tree frog, paradoxical frog), hyperoliid (African reed frog), leptodactylid (butter frog, rufous frog, Dumeril's striped frog, Cei's white-lipped frog, Gunther's white-lipped frog, Vizcachera's white-lipped frog, Bolivian toad-frog), limnodynastid (spotted grass frog), microhylid (red narrow-mouthed frog), pipid (African clawed frog), ptychadenid (Perret's grassland frog, Uganda grassland frog, Dakar grassland frog, Mascarene grass frog, sharp-nosed frog), pyxicephalid (Cape river frog), ranid (common green frog, common brown frog, edible frog, peeping frog, yellow frog, mink frog, white-lipped frog, wood frog, marsh frog, ringed frog, laughing frog, spring frog, green pond frog, black-spotted frog, Gunther's Amoy frog, Hose's frog, common bullfrog, American bullfrog); Urodela: plethodontid (ensatina salamander)	*Helobdella algira*, *nociva, Hemiclepis marginata, Placobdella ceylonica*, *marginata*), hirudinid (*Hirudo medicinalis),* macrobdellid (*Macrobdella ditetra*), piscicolid (*Piscicola geometra*); Diptera: culicid (*Culex territans, Aedes aegypti*)	
T. rugosae		Anura: ranid (wrinkled frog)		Asia
T. schmidti	100 (D)	Anura: ranid (southern leopard frog, Northern leopard frog), bufonid (American toad)		North America
T. sergenti	41 (E)	Anura: alytid (painted frog)		Africa
T. somalense sp. inq.		Anura: bufonid (African toad)		Africa
T. systoma		Anura: microhylid (marbled balloon frog)		India
T. taprobanicum		Anura: microhylid (painted globular frog)		India
T. tsanezomiyatai		Anura: ranid (wrinkled frog)		Asia
T. tsukanotoi		Anura: ranid (red-eared frog), dicroglossid (Namie's frog, Indian cricket frog)		Asia
T. tumida	18-35 (E)	Anura: pyxicephalid (Nutt's River frog)		East Africa
Species in salamanders/newts				
T. ambystomae	51-84	Urodela: ambystomatid (Jefferson salamander, silvery salamander, blue-spotted salamander, spotted salamander, Tremblay's salamander), salamandrid (rough-skinned newt)	Clitellata: erpobdellid (*Erpobdella* sp.)	North America
T. barbari		Urodela: salamandrid (California newt)		North America
T. cryptobranchi		Urodela: cryptobranchid (eastern hellbender salamander)		North America
T. diemyctyli	45-80	Urodela: salamandrid (vermilion-spotted newt, eastern newt)	Clitellata: glossiphoniid (*Batrachobdella picta, Placobdella parasitica*)	North America
T. granulosae	41-59	Urodela: salamandrid (rough-skinned newt)		North America
T. ogawai		Urodela: salamandrid (Jefferson salamander, blue-spotted salamander, spotted salamander)		North America
T. tritonis	57-80	Urodela: salamandrid (fire-bellied newt)		Japan

*Trypomastigote morphology: group A (body flattened, sheet-like), B (body flattened, not sheet-like), C (body thick, ellipsoidal), D (body elongate, pointed), E (body pyriform), and F (body spherical).

Parasite morphology: Reptilian trypanosomes may form up to 6 different morphological stages in their developmental cycles: with trypomastigotes invariably being found in vertebrate blood; while a variety of stages (promastigotes, amastigotes, sphaeromastigotes, epimastigotes, and metacyclic trypomastigotes) occur within their invertebrate vectors. Trypomastigotes usually appear as long slender cells (20-90 x 1-10 μm) with a single ovoid central nucleus and a smaller oval-round kinetoplast (containing mitochondrial DNA) located posterior to the cell nucleus. Flagellar basal bodies (complex of microtubules) are located adjacent to the kinetoplast and they give rise to a single long flagellum that emerges and runs forwards along the body forming an undulating membrane but projecting freely anteriorly (it is not a recurrent or trailing flagellum like that formed by *Trypanoplasma* and *Cryptobia* spp.). In reptilian blood, trypomastigotes usually exhibit 2 developmental forms: slender and stumpy forms. Most stages are slender forms which proliferate in the bloodstream and are thought to exhibit surface antigenic variation to evade host immunity. Stumpy forms, in contrast, are non-proliferative and adapted for transmission. In amphibian blood, trypomastigotes have been allocated to 6 different types whose bodies are flattened (A = sheet-like, B = not sheet-like), ellipsoidal (C), elongate (D), pyriform (E) or spherical (F). The different stages found in vectors include ellipsoidal promastigotes with a posterior kinetoplast and a short emergent flagellum that does not form an undulating membrane, rounded amastigotes without an emergent flagellum, rounded sphaeromastigotes (possibly divisional stages) with a short emergent flagellum, ovoid epimastigotes with an anterior kinetoplast and an emergent flagellum that forms a short undulating membrane, and broad stocky metacyclic trypomastigotes (infective stages) with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane.

Site of infection: Infections in reptiles typically involve trypomastigote developmental stages swimming free in the circulatory system, although there are rare reports of epimastigote or amastigote stages found in host tissues. A total of 90 parasite species have been described in 130 reptilian hosts: including 47 species reported from 76 lizard species (from 18 families), 25 species from 28 snake species (6 families), 4 species from 4 crocodile species (2 families), and 14 species from 22 testudine species (8 families). Another 60 parasite species have been described from 140 amphibian hosts: including 52 parasite species from 126 anuran species (16 families), and 8 species from 14 salamander species (4 families). Infections in invertebrate vectors may involve several different developmental stages (promastigotes, amastigotes, sphaeromastigotes, epimastigotes and metacyclic (infective) trypanosomes), mainly in the stomach and crop of leeches, or the gut of dipteran vectors. A wide range of invertebrate vectors have been found: including 8 dipteran species (1 culicid, 7 psychodid), 1 hemipteran species (reduviid) and 1 ixodid species (argasid) for infections in lizards; 4 leech species (glossiphoniid) and 1 dipteran species (culicid) for infections in snakes; 4 dipteran species (glossinids) for infections in crocodiles; 7 leech species (6 glossiphoniid, 1 hirudinid) for infections in turtles; 16 leech species (12 glossiphoniid, 1 erpobdellid, 1 hirudinid, 1 macrobdellid, 1 piscicolid) and 4 dipteran species (2 culicid, 2 psychodid) for infections in amphibians.

Pathogenesis: Natural infections by *Trypanosoma* spp. have not been associated with any clinical disease in reptiles and amphibians. While some hosts exhibited mild clinical signs and even some haematological perturbations, the changes were vague and nonspecific and could not be directly attributed to trypanosome infections as the hosts often suffered from other infections or disease conditions. Under experimental conditions, infections were found to cause severe disease when blood from chameleons infected with *T. therezieni* was experimentally inoculated into sibling chameleon species resulting in massive parasitaemias, pulmonary emboli and some fatalities.

Developmental cycle and mode of transmission: In vertebrates, trypomastigotes feed by absorbing nutrients through their surface membranes and multiply by asexual symmetrogenic binary fission involving the replication of organelles, then karyokinesis followed by transverse midbody cytokinesis. While there are some rare early reports of transmission occurring between lizards via cannibalism, studies have demonstrated that infections are usually transmitted between reptilian hosts by invertebrate vectors, which act as secondary hosts in which parasites undergo asexual development forming a variety of different developmental stages. Vector-borne transmission occurs primarily via the bite of haematophagous arthropods and leeches, although some trypanosome species may be transmitted by the ingestion of infected arthropods. Molecular phylogenetic studies have shown that trypanosomes from tortoises clustered together with those from fish (both groups being transmitted by aquatic leeches), whereas trypanosomes from crocodiles (transmitted by tsetse flies) were closest to avian trypanosomes. Trypanosomes from varanid, phrynosomatid and gekkonid lizards clustered together (transmitted by flies, bugs, ticks), whereas those from chameleons (transmitted by mosquitoes) grouped with anuran trypanosomes (transmitted by leeches). In leech vectors, ingested trypomastigotes form epimastigotes in crop or stomach which multiply by binary fission and form metacyclic trypomastigotes that are injected into new hosts via leech bites (inoculative transmission). Development generally takes 14-34 days depending on the species involved and the prevailing water temperatures (faster in warmer conditions). In tsetse fly vectors for crocodilian *T. grayi*, ingested trypomastigotes form epimastigotes in the midgut, divide and enter the hindgut where they transform into metacyclic trypomastigotes that are transmitted to crocodiles when they consume fly vectors (consumptive transmission). Infections in terrestrial reptiles involve other dipteran vectors and follow a more complex developmental sequence, with ingested trypomastigotes forming promastigotes or amastigotes within hyaline cysts in the midgut, then sphaeromastigotes and finally infective epimastigotes in the hindgut which are transmitted to new vertebrate hosts when they ingest vectors during feeding or grooming (consumptive transmission). Development in the vector may take as little as 5 days.

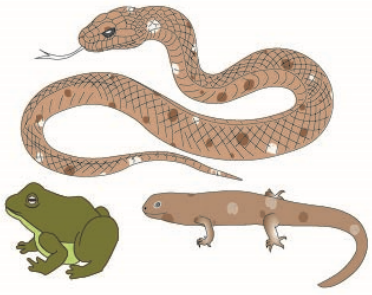
Differential diagnosis: Infections are conventionally diagnosed in reptiles and amphibians by the microscopic detection of trypomastigotes in samples of peripheral or heart blood collected into anti-coagulants. Wet mounts may be examined by high-contrast microscopy to detect motile extracellular trypomastigotes swimming around in blood, or fixed smears may be examined after staining with Giemsa or Leishman's stains. Alternatively, buffy coat layers may be examined for parasites following centrifugation in tubes or haematocrit straws. Invertebrate vectors may be examined for parasite developmental stages by microscopy of squash preparations or fixed histological sections. Parasites may be cultured *in vitro* in various media, including biphasic blood agar, Novy-MacNeal-Nicolle (NNN) media, Diamond's saline-neopeptone-blood (SNB-9) or Ponselle's hypotonic medium. Modern molecular biological techniques have been used to detect and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA).

Treatment and control: Infections in reptiles and amphibians do not cause clinical disease and therefore do not require treatment. If infections are a cause of concern to herpetologists in zoo or captive collections, it is recommended that some form of vector control be instituted to reduce the risks of transmission, with chemical bath treatments (e.g. trichlorphon) being effective against aquatic leeches, and topical insecticides and/or acaricides used to treat terrestrial hosts for ectoparasitic arthropods.

Trypanosoma
(reptilian/amphibian species)

blood
(nonpathogenic)

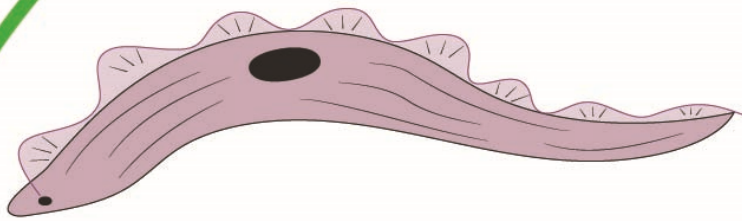
division by
longitudinal
binary fission



Vertebrate Hosts
(lizards, snakes, frogs)

long undulating membrane (UM)

anterior free
flagellum (FF)



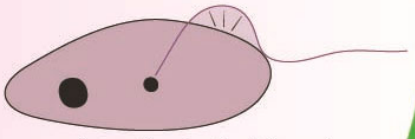
posterior
kinetoplast (K)

trypomastigote (15-120 µm)

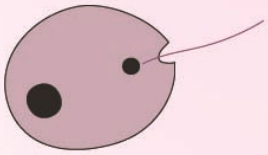
mostly inoculative transmission (infective stages injected)
sometimes consumptive (infected vectors ingested)

ingested with
bloodmeal

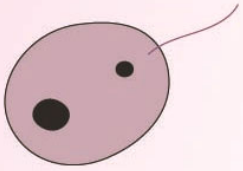
amastigote (~ 6 µm)
[no UM, no FF]



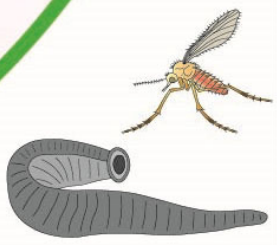
epimastigote (~ 20 µm)
[anterior K, short UM, FF]



sphaeromastigote (~ 5 µm)
[anterior K, FF, no UM]



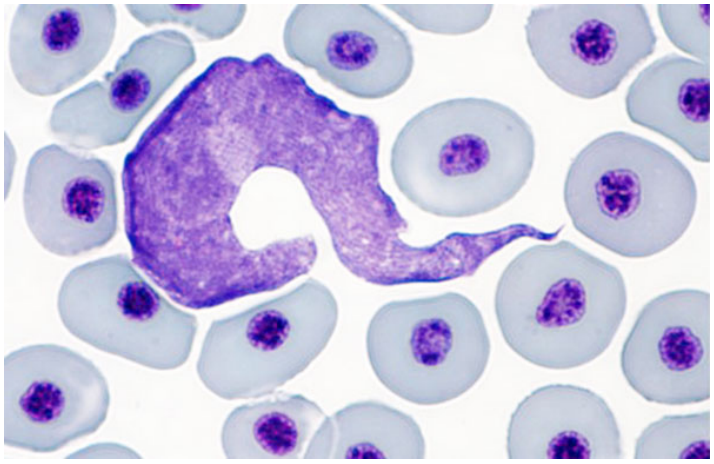
promastigote (~ 10 µm)
[anterior K, FF, no UM]



Invertebrate Hosts
(leech/sandfly vectors)
(alimentary tract)

vector-borne transmission

Trypanosoma trypomastigote in tortoise blood



Trypanosoma trypomastigote in frog blood