

Trypanosoma (avian 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 (amoebflagellates), 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 birds. Avian trypanosomes have been shown to be transmitted by dipteran insects (mosquitoes, hippoboscids, black flies, sand flies) to a range of birds, particularly songbirds and raptors, but 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 birds

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 (amoebflagellates), 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)	Transmission*
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)	<i>Giardia</i>	vertebrates (gut)	direct (f-o)
			<i>Hexamita</i> <i>Spironucleus</i>	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)	<i>Histomonas</i>	birds (gut, liver)	direct (f-o)
			<i>Dientamoeba</i>	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	<i>Trichomonas</i>	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	<i>Cochlosoma</i>	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)	<i>Ichthyobodo</i> (= <i>Costia</i>)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	<i>Cryptobia</i>	fish (gills, skin)	direct (w)
			<i>Trypanoplasma</i>	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	<i>Trypanosoma</i>	vertebrates (blood, tissues)	indirect (v-b)
			<i>Leishmania</i>	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)	<i>Amyloodinium</i> <i>Crepidodinium</i> <i>Piscinoodinium</i>	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	<i>Haematodinium</i> <i>Ichthyodinium</i>	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	<i>Perkinsus</i>	gastropods, bivalves (tissues)	direct (w)

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

Euglenozoans comprise 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 bacterivores 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 trypano-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: Metakinoplastina F: Trypanosomatidae	<i>Trypanosoma</i>	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		<i>Leishmania</i>	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinoplastina F: Parabodonidae	<i>Cryptobia</i> , <i>Trypanoplasma</i>	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	<i>Ichthyobodo</i> (<i>Costia</i>)	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 *Perkinsella* (= *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. 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. Several trypanosome species in birds resembled those in mammals belonging to the subgenus *T. Megatrypanum*, but rather than amalgamate both host groups, it was tentatively proposed to group the species from birds into a separate subgenus called *T. Trypanomorpha* (comprising large species including *T. avium*, *paddae*, *hannae*, *confusum*, *corvi*, *numidae*, *gallinarum*, *macfiei* and *delhiense*). Another three morpho-groups were identified: small trypanosomes (e.g. *T. franchinii*, *langeroni*, *guyanense*); broad stumpy trypanosomes (*T. calmettei*, *caprimulgi*, *cristatae*, *ixobrychi*, *laverani*, *turdoides*, *lagonostictae*); and a few species with terminal kinetoplasts (*T. fiadeiroi*, *lobivanelli*, *oenae*, *everetti*). However, molecular phylogenetic studies have not validated any of these groupings for bird trypanosomes, but have suggested much more conservatism that their host range suggests. While over 100 bird trypanosome species have been described (predominantly on the basis of host occurrence), genotypic characterization studies have found many belong to just three clades, each with around four lineages. Clade A comprised species of small-medium trypanosomes with narrow kinetoplasts (< 500 nm) from songbirds and raptors and contained lineages VI, VII, VIII and IX (the latter lineage referable to *T. bennetti*) apparently transmitted by the ingestion of biting midges. Clade B comprised species of larger striated trypanosomes with narrow kinetoplasts from songbirds, raptors, hippoboscids flies and mosquitos and contained lineages I, XII, V (referable to *T. culicavium* which is transmitted to insectivorous passerines by the ingestion of culicine mosquitos) and IV (referable to *T. corvi* which is transmitted to songbirds and raptors by the ingestion of hippoboscids flies). Clade C comprised species of large striated trypanosomes with wide kinetoplasts (> 500 nm) from songbirds, raptors, mosquitos, black flies, hippoboscids flies and sand flies and contained lineages II, III, X and XI (the latter two lineages referable to *T. avium* which is transmitted to songbirds, owls and raptors by black fly ingestion or contamination). Clearly, many more avian trypanosome species remain to be characterized by molecular studies on isolates not only from birds but also from their putative vectors.

<i>Trypanosoma</i> species	Mastigote length (µm)	Hosts	Vectors	Distribution
<i>T. abelsalazari</i>		Passeriformes: sturnid (purple starling)		Africa
<i>T. aguedaferreirae</i>		Galliformes: phasianid (double-spurred spurfowl)		Africa
<i>T. anellobiae</i>	30-35	Passeriformes: meliphagid (little wattlebird)		Australia
<i>T. ardeae</i>		Pelecaniformes: ardeid (yellow-crowned)		Americas

		night heron, cocoi heron, little blue heron)		
<i>T. asturinulae</i>		Accipitriformes: accipitrid (lizard buzzard)		Africa
<i>T. avium</i>	26-29 striated	Accipitriformes: accipitrid (lesser spotted eagle); Anseriformes: anatid (mallard, northern pintail), Coraciiformes: alcedinid (African pygmy kingfisher), coraciid (European roller); Columbiformes: columbid (mourning dove); Cuculiformes: cuculid (black-billed cuckoo); Falconiformes: falconid (common kestrel); Galliformes: phasianid (rock partridge, Ahanta spurfowl); Passeriformes: bombycillid (cedar waxwing), cardinalid (rose-breasted grosbeak), cisticolid (grey-backed camaroptera), corvid (rook, fish crow, western jackdaw, blue jay), fringillid (canary, purple finch, chaffinch), hirundinid (barn swallow), icterid (red-winged blackbird, bobolink, Baltimore oriole, campo troupial, red-breasted meadowlark), meliphagid (regent honeyeater), mimid (grey catbird), nectariniid (olive sunbird, little green sunbird), parid (boreal chickadee), parulid (American redstart, common yellowthroat, yellow warbler, Tennessee warbler, Canada warbler, yellow-rumped warbler, chestnut-sided warbler, black-and-white warbler, Cape May warbler, Magnolia warbler, MacGillivray's warbler, Wilson's warbler), passerellid (dark-eyed junco, song sparrow, swamp sparrow, chipping sparrow, white-throated sparrow), passerid (house sparrow, northern grey-headed sparrow), ploceid (village weaver, Vieillot's black weaver), pycnonotid (common bulbul, yellow-bellied greenbul, red-whiskered bulbul, little greenbul), turdid (American robin, eastern bluebird, veery, hermit thrush, Swainson's thrush), tyrannid (western flycatcher, olive-sided flycatcher, willow flycatcher, pygmy tyrant), vireonid (red-eyed vireo); Pelecaniformes: ardeid (little blue heron, snowy egret, black-crowned night heron); Piciformes: picid (northern flicker, downy woodpecker); Strigiformes: strigid (tawny owl, long-eared owl)	Diptera: simuliid (<i>Eusimulium securiforme</i> , <i>Metacnephia lyra</i> , <i>Obuchovia albella</i> , <i>Odagmia ornata</i> , <i>erganica</i> , <i>Simulium aureum</i> , <i>latipes</i> , <i>rugglesi</i> , <i>vernnum</i> , <i>Tetisimulium coarctata</i> , <i>alajensis</i>), hippoboscid (<i>Stilbometopa podopostyla</i> , <i>impressa</i> , <i>Ornithomyia avicularia</i>)	Europe, Africa
<i>T. bakeri</i>		Psittaciformes: psittacid (blossom-headed parakeet)	Diptera: ceratopogonid (<i>Culicoides nuberculosus</i>)	Asia
<i>T. balfouri</i>		Psittaciformes: psittacid (blue-crowned parakeet); Passeriformes: thraupid (red-crested cardinal)		South America
<i>T. bennetti</i>		Falconiformes: falconid (American kestrel)		North America

<i>T. bouffardi</i>	19-53 striated	Passeriformes: estrildid (lavender waxbill, black-rumped waxbill, bronze mannikin, red-cheeked cordonbleu, cut-throat finch, red-billed firefinch), ploceid (black-headed weaver, black-necked weaver, red bishop), viduid (village indigobird)		Africa, Europe
<i>T. bramae</i>		Strigiformes: strigid (spotted owlet)		Asia
<i>T. brimonti</i>		Passeriformes: pycnonotid (light-vented bulbul)		Asia
<i>T. brumpti</i> (syn. <i>T. langeroni</i> nom. preocc.)		Falconiformes: falconid (American kestrel)		North America
<i>T. bycanistis</i>		Bucerotiformes: bucerotid (trumpeter hornbill)		Africa
<i>T. calmettei</i>		Galliformes: phasianid (junglefowl)		Africa
<i>T. caprimulgi</i>		Caprimulgiformes: caprimulgid (long-tailed nightjar)		Africa
<i>T. catharistae</i>		Cathartiformes: cathartid (black vulture)		Americas
<i>T. centropi</i>		Cuculiformes: cuculid (greater coucal)		Asia
<i>T. chlamydoerae</i>		Passeriformes: ptilorhynchid (great bowerbird)		Australia
<i>T. chaubaudi</i>	42-49	Passeriformes: estrildid (orange-cheeked waxbill)		Africa
<i>T. columbae</i>		Columbiformes: columbid (rock dove)		Europe
<i>T. confusum</i> (possibly a synonym of <i>T. avium</i>)		Passeriformes: turdid (thrushes, jays), muscicapid (robins), meliphagid (honey-suckers)	Diptera: simuliid (<i>Helodon decemarticulatus</i> , <i>Simulium</i> sp.)	North America
<i>T. corvi</i>	striated	Passeriformes: corvid (rook, house crow, western jackdaw, rufous treepie), turdid (common blackbird); Accipitriformes: accipitrid (Eurasian sparrowhawk)	Diptera: simuliid (<i>Simulium latipes</i>), hippoboscid (<i>Ornithomyia avicularia</i>)	Eurasia
<i>T. cotylei</i>		Passeriformes: hirundinid (sand martin)		Eurasia, North America
<i>T. cristatae</i>		Musophagiformes; musophagid (great blue turaco)		Africa
<i>T. cuculi</i>		Cuculiformes: cuculid (Indian cuckoo)		India
<i>T. culicavium</i>	40-41	Passeriformes: fringillid (canary), (flycatchers, canaries), muscicapid (collared flycatcher)	Diptera: culicid (<i>Culex pipiens</i> , <i>modestus</i> , <i>quinquefasciatus</i>)	Europe
<i>T. cypseli</i>		Apodiformes: apodid (common swift)		Eurasia
<i>T. dabbenei</i>		Passeriformes: formicariid (short-tailed antthrush)		South America
<i>T. dafilae</i>		Anseriformes: anatid (northern pintail duck)		Europe
<i>T. davidmolyneuxi</i>	13-18	Passeriformes: estrildid (common waxbill, orange-cheeked waxbill)		Africa
<i>T. delhiense</i>		Passeriformes: estrildid (Indian silverbill)		India
<i>T. dschunkowskii</i>		Passeriformes: corvid (Eurasian jay)		Eurasia
<i>T. eudyptulae</i>	36-52	Sphenisciformes: spheniscid (little penguin)		Australia
<i>T. eurystomi</i>		Coraciiformes: coraciid (rollers)		Africa
<i>T. everetti</i>	16-20	Passeriformes: estrildid (common waxbill, orange-cheeked waxbill, black-rumped waxbill), fringillid (finch), muscicapid (flycatchers), nectariniid (sunbirds), ploceid (weavers),		Africa

		pycnonotid (bulbuls), sturnid (starlings), zosteropid (white-eyes); Bucerotiformes: bucerotid (hoopoes), Coraciiformes: coraciid (kingfishers)		
<i>T. faridi</i>		Passeriformes: fringillid (Eurasian bullfinch)		Europe
<i>T. fiadeiroi</i>		Accipitriformes: accipitrid (lizard buzzard)		Africa
<i>T. fradei</i>		Coraciiformes: coraciid (broad-billed roller)		Africa
<i>T. franchinii</i> (= <i>franchinianus</i>)		Passeriformes: fumariid (great rufous woodcreeper)		South America
<i>T. francolini</i>		Galliformes: phasianid (double-spurred spurfowl)		Africa
<i>T. fringillinarum</i>		Passeriformes: fringillid (Eurasian chaffinch, common chaffinch, common redpoll)		Eurasia
<i>T. fulicae</i>		Gruiformes: rallid (Eurasian coot)		Eurasia
<i>T. gallinarum</i>	26-29	Galliformes: phasianid (Uganda fowl)		Africa, Asia
<i>T. garruli</i>		Passeriformes: corvid (black-headed jay)		Asia
<i>T. gentilini</i>	32-40	Passeriformes: estrildid (orange-cheeked waxbill)		Africa
<i>T. grewali</i>		Passeriformes: estrildid (scaly-breasted munia)		Asia
<i>T. guyanense</i>		Accipitriformes: accipitrid (savanna hawk)		South America
<i>T. gymnochidis</i>		Passeriformes: passerid (yellow-throated sparrow)		Asia
<i>T. hanna</i>		Columbiformes: columbid (rock dove)	Diptera: hippoboscid (<i>Lynchia maura</i>)	India
<i>T. ixobrychi</i>		Pelecaniformes: ardeid (little bittern)		Africa
<i>T. johnstoni</i>		Passeriformes: estrildid (common waxbill)		Africa
<i>T. knowlesi</i>		Passeriformes: estrildid (Indian silverbill)		India
<i>T. kremeri</i>	50	Passeriformes: estrildid (orange-cheeked waxbill)		Africa
<i>T. lagopodis</i>		Galliformes: phasianid (ptarmigan)		North America
<i>T. lagonstictae</i>		Passeriformes: estrildid (red-billed firefinch)		Africa
<i>T. langeronianus</i>		Falconiformes: falconid (American kestrel)		South America
<i>T. lanii</i>		Passeriformes: laniid (long-tailed shrike)		Asia
<i>T. laverani</i>		Passeriformes: fringillid (American goldfinch), mimid (brown thrasher)		North America
<i>T. liothricis</i>		Passeriformes: leiothrichid (red-billed leiothrix)		Asia
<i>T. lobivanelli</i>		Charadriiformes: charadriid (red-wattled lapwing)		India
<i>T. loxiae</i>		Passeriformes: fringillid (red crossbill, canary, finch)	Diptera: culicid (<i>Culex pipiens</i> , <i>Aedes argenteus</i>)	Africa
<i>T. macfieii</i>		Passeriformes: fringillid (canary)		Europe
<i>T. mathisi</i>		Passeriformes: hirundinid (barn swallow)		Europe
<i>T. mayae</i>		Passeriformes: passerid (house sparrow)		Europe
<i>T. mesnili</i>		Accipitriformes: accipitrid (red-shouldered hawk, savanna hawk)		South America
<i>T. milvi</i>		Accipitriformes: accipitrid (black kite)		Eurasia

<i>T. moruoni</i>		Passeriformes: muscicapid (Oriental magpie-robin)		Asia
<i>T. myzanthae</i>	19-24	Passeriformes: meliphagid (noisy miner)		Australia
<i>T. noctuae</i>	26-60	Strigiformes: strigid (little owl)	Diptera: culicid (<i>Culex pipiens</i>)	Europe
<i>T. notophoxyis</i>		Pelecaniformes: ardeid (white-faced heron)		Australia
<i>T. numidae</i>		Galliformes: numidid (helmeted guineafowl), phasianid (chicken)	Diptera: simuliid (<i>Simulium adersi, impucane, nyasalandicum, vorax</i>)	Africa
<i>T. nycticoracis</i>		Pelecaniformes (black-crowned night heron)		Eurasia
<i>T. oenae</i>		Columbiformes: columbid (Namaqua dove)		Africa
<i>T. ontarioensis</i>		Passeriformes: corvid (American crow), fringillid (canary); Galliformes: phasianid (ruffed grouse, chicken); Psittaciformes: psittaculid (budgerigar)		North America
<i>T. paddae</i>		Passeriformes: estrildid (red-billed firefinch, Java sparrow, black-rumped waxbill), fringillid (canary, serin), thraupid (glistening-green tanager)		Eurasia, Americas
<i>T. pedrozi</i>		Galliformes: cracid (bare-faced curassow)		South America
<i>T. phedinae</i>		Passeriformes: hirundinid (Mascarene martin)		Mauritius
<i>T. polyplectri</i>		Galliformes: phasianid (Germain's peacock pheasant)		Asia
<i>T. pycnonoti</i>		Passeriformes: pycnonotid (common bulbul)		Africa
<i>T. queleae</i>		Passeriformes: ploceid (red-billed quelea)		Africa
<i>T. santadiasi</i>		Strigiformes: strigid (northern white-faced owl)		Africa
<i>T. schistochlamydis</i>		Passeriformes: thraupid (cinnamon tanager)		South America
<i>T. syrni</i>		Strigiformes: strigid (tawny owl)		Europe
<i>T. thiersi</i>		Caprimulgiformes: caprimulgid (European nightjar)		Europe
<i>T. thomasbancrofti</i>	28-43	Passeriformes: acrocephalid (Eurasian reed warbler), estrildid (zebra finch), fringillid (canary), hirundinid (barn swallow, sand martin), meliphagid (regent honeyeater), phylloscopid (wood warbler, common chiffchaff), sylviid (Eurasian blackcap)	Diptera: culicid (<i>Culex pipiens, molestus, quinquefasciatus</i>), hippoboscid (<i>Ornithomya fringillina</i>)	Europe, Australia
<i>T. tinami</i>		Tinamiformes: tinamid (cinereous tinamou, great tinamou)		South America
<i>T. turdoides</i>		Passeriformes: leiothrichid (jungle babbler)		India
<i>T. uruguayensis</i>		Passeriformes: fringillid (finch)		South America
<i>T. urolonchae</i>		Passeriformes: estrildid (white-rumped munia)		Asia
<i>T. viduae</i>		Passeriformes: viduid (pin-tailed whydah)		Africa
<i>T. ziemanni</i>		Coraciiformes: coraciid (broad-billed roller)		Africa
<i>T. zonotrichae</i>		Passeriformes: passerellid (rufous-collared sparrow)		Americas

Parasite morphology: Avian *Trypanosoma* spp. form 2 different types of developmental stages: trypomastigotes in birds; and epimastigotes in invertebrate vectors. Trypomastigotes are pleomorphic depending on the species and the stage of development, but most forms are elongate and slender ranging from 20-90 µm in length and 1-10 µm in width. They contain a central ovoid basophilic nucleus as well as a smaller rounded kinetoplast (containing mitochondrial DNA) located behind the host cell nucleus. Flagellar basal bodies (microtubular arrays) are located adjacent to the kinetoplast and give rise to a single long flagellum that emerges and runs along the body surface forming a long undulating membrane before extending freely beyond the cell margin. This margin is the anterior end of the cell as live observations show the parasites moving in the direction of the flagellum (the flagellum is not recurrent or trailing like that of the bodonids *Cryptobia* and *Trypanoplasma*). The cell surface is often striated in appearance with so-called myonemes extending longitudinally or spirally along the body (e.g. *T. avium* complex). Epimastigotes are smaller cells (5-20 µm long) that have a central nucleus, an anterior kinetoplast and a short emergent flagellum that forms a short undulating membrane.

Site of infection: In birds, trypomastigotes are found extracellularly in the circulatory system of their hosts. A total of 93 *Trypanosoma* spp. have been described from 154 bird species, including 61 non-passerine species belonging to 24 families in 21 orders, and 120 passerine species belonging to 33 families. In the invertebrate vectors, epimastigotes are found extracellularly within the hindgut and midgut. Vectors for avian *Trypanosoma* spp. have included 26 dipteran species belonging to 4 families (mainly simuliids, but also some culicids, hippoboscids and one ceratopogonid).

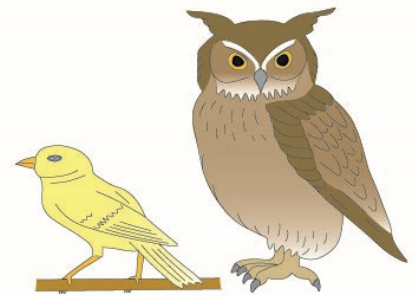
Pathogenesis: Natural infections by avian trypanosomes are considered to be nonpathogenic as they have not been associated with any specific clinical disease. Although some bird hosts may have exhibited clinical signs or haemodynamic disturbances, they were often attributable to concomitant infections or existing disease conditions. Nevertheless, some experimental infections in aviary birds have been associated with chronic disease characterized by progressive splenomegaly, myositis and myocarditis.

Developmental cycle and mode of transmission: Avian trypanosomes have cyclic heteroxenous (2-host) life-cycles with vector-borne transmission involving haematophagous dipteran insects (simuliid blackflies, culicid mosquitoes, hippoboscids louse-flies, and ceratopogonid biting midges). Trypomastigotes swim freely in bird blood where they feed by absorption of nutrients across their surface membranes and multiply asexually by binary fission involving organelle replication, karyokinesis and then transverse cytokinesis. Vectors acquire infections by ingesting trypomastigotes while feeding on bird blood. The parasites are localized in the hindgut where they form rosettes of dividing stages by binary and multiple fission, eventually releasing free epimastigotes that may stay in the hindgut, move forward to the midgut or become localized on the stomodeal valve. Transmission to birds does not occur via vector bite but rather by birds ingesting vectors when feeding or grooming (i.e. consumptive transmission rather than inoculative transmission). Several studies have also implicated transmission via bird conjunctival contamination by vector urine droplets, possibly the consequence of prediuresis (the excretion of water by the vector to concentrate the bloodmeal).

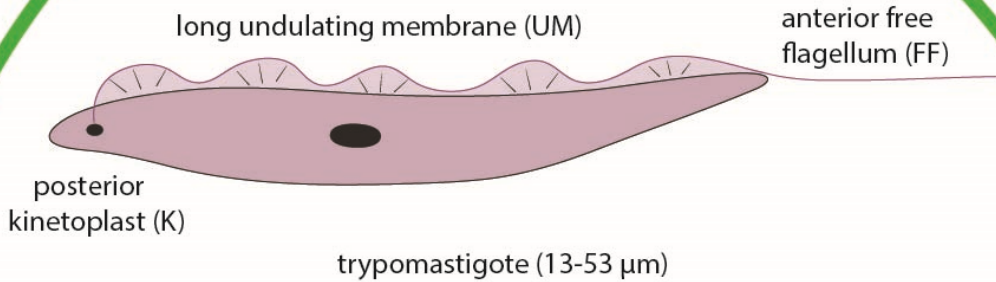
Differential diagnosis: Infections are normally detected in birds by the direct microscopic demonstration of trypomastigotes in blood samples (peripheral or heart blood collected into anticoagulant). Wet mounts may be examined by high-contrast microscopy looking for motile parasites thrashing between blood cells, or fixed smears may be examined after staining with Giemsa or Leichman's stains. Trypomastigotes may also be concentrated from blood samples into the buffy coat layer by centrifugation in capillary or haematocrit tubes. Infections in vectors are usually revealed by examining squash preparations or histological sections. Parasites may be cultured in vitro in a variety of media, including biphasic blood agar with RPMI liquid media or Schneider's *Drosophila* medium with foetal calf serum. Molecular biological techniques have recently been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA, internal transcribed spacer regions 1 and 2, and glycosomal glyceraldehyde 3-phosphate dehydrogenase).

Treatment and control: Infections are nonpathogenic in birds so chemotherapy is not required. If infections are of concern to managers of captive bird collections in zoos or aviaries, measures may be instituted to prevent the spread of infections by excluding potential vectors using physical or chemical barriers in holding facilities or applying topical or systemic insecticides to birds at risk.

Trypanosoma (avian species)

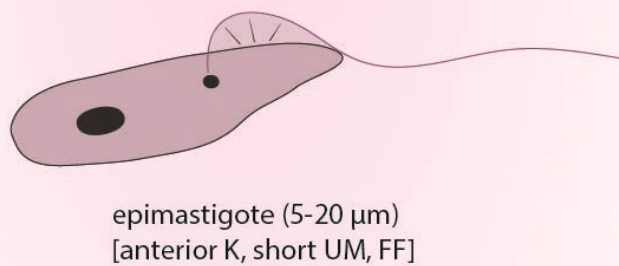


division by
longitudinal
binary fission

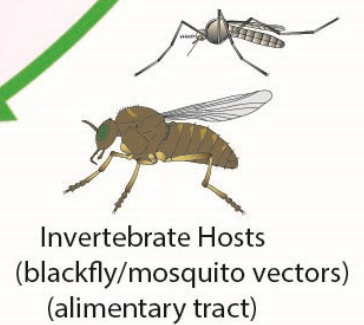


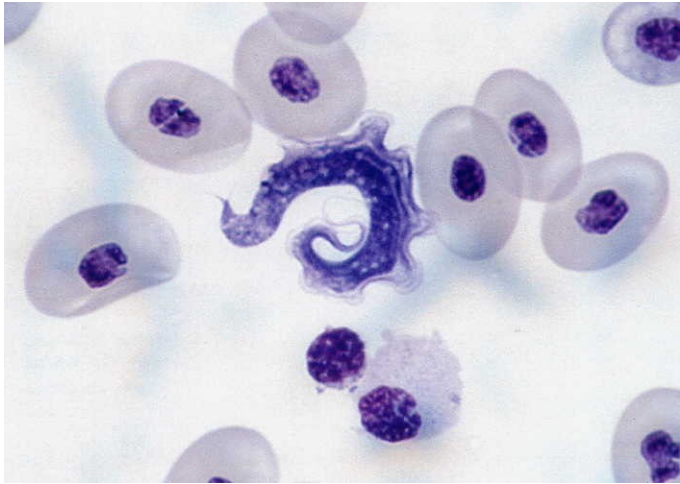
mostly consumptive transmission
(infected vectors ingested)

ingested with
bloodmeal



vector-borne transmission





Trypanosoma trypomastigote in bird blood