Trypanosoma (fish 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 4 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 freshwater and marine fish. Piscine trypanosomes are transmitted by leech vectors and infections are generally nonpathogenic although several species may cause anaemia and anorexia in cultured fish.

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 fish

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. 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 fish clustered together with those from tortoises (both groups being transmitted by aquatic leeches). Fish trypanosomes have previously been allocated to two large groupings, comprising pleomorphic (polymorphic) and monomorphic species. The trypomastigotes of monomorphic species are more or less consistent in morphology for each species with little variation in size and/or shape/index (length:width ratio). Those of pleomorphic species demonstrate considerable variation in size, shape index, position of internal organelles (kinetoplast and nucleus), presence/absence of nuclear karyosome, surface striations and/or cytoplasmic granules, architecture of undulating membrane and length of free flagellum. Many pleomorphic species apparently undergo sequential development involving 'young', 'intermediate' and 'adult' forms generally becoming larger and more complex in structure, but often with mensural (morphometric) overlap. It was earlier suggested that pleomorphic trypanosomes of fish be allocated to a distinct *Trypanosoma* subgenus called *Haematomonas*, but molecular phylogenetic studies do not support their separate classification from other piscine trypanosomes. Different species have been identified in bony and cartilaginous fishes as well as from freshwater and marine fish (with a few recorded in estuarine or brackish water species), but little information is available on their actual host specificity. To date, the only known vectors of piscine trypanosomes have been leeches as determined by field observations, dissections and some experimental studies.

Trypanosoma species	Mastigote length (µm)	Hosts [disease]	Vectors	Distribution
Species in freshwater fish				
T. abeli		Siluriformes: loricariid (armoured catfish)		South America
T. abramidis		Cypriniformes: cyprinid (common bream, blue bream, white bream, common roach)		Eurasia
T. acanthobramae		Cypriniformes: cyprinid (Tigris bream)		Iraq
T. acerinae	33-49	Perciformes: percid (Eurasian ruffe); Cypriniformes: leuciscid (minnows)	Clitellata: glossiphoniid (*Hemiclepsis marginata*)	Eurasia, North America
T. affonsoi	58	Siluriformes: loricariid (armoured catfish)		Brazil
T. albopunctatus	23-41	Siluriformes: loricariid (pleco catfish)		Brazil
T. alhussaini		Siluriformes: clariid (African sharptooth catfish)		Africa
T. aligaricus		Anabantiformes: channid (spotted snakehead) [anaemia]		India
T. amurense	23-32	Scorpaeniformes: cottid (Kessler's sculpin, Amur sculpin)		Asia
T. anabasi		Anabantiformes: anabantid (climbing perch)		India
T. andradesilvae		Siluriformes: clariid (African sharptooth catfish)		Mozambique
T. anguillicola	35-40	Anguilliformes: anguillid (giant mottled eel, long-finned eel, speckled longfin eel)		Australasia
T. anurum	25-33	Acipenseriformes: acipenserid (Japanese sturgeon)		China
T. anusi		Siluriformes: loricariid (cascudo viola)		Brazil
T. aori		Siluriformes: bagrid (Gangetic mystus)		India
T. arabica		Siluriformes: silurid (Tigris catfish)		Iraq
T. aristichthysi	32	Cypriniformes: cyprinid (bighead carp)		China
T. armeti		Synbranchiformes: mastacembelid (zig-zag eel)		India
T. ataevi		Gobiiformes: gobiid (ratan goby, Kessler's goby, monkey goby, Caspian tadpole goby)		Eurasia
T. atti		Siluriformes: silurid (helicopter catfish)		India
T. aurangabadense		Synbranchiformes: mastacembelid (zig-zag eel)		India
T. azoubeli		Siluriformes: loricariid (armoured catfish)		South America
T. baigulensis		Cypriniformes: cyprinid (reba carp, chela carp)		India
T. bancrofti	27-50	Siluriformes: plotosid (eeltail catfish)		Australia
T. barbae/barbi		Cypriniformes: cyprinid (common barbel)		Europe
T. barretoi	36	Siluriformes: loricariid (armoured catfish)		Brazil
T. barrosi	54	Siluriformes: loricariid (suckermouth catfish)		Brazil
T. basrensis		Cypriniformes: cyprinid (Tigris asp)		Iraq
T. batai		Cypriniformes: cyprinid (bata)		India
T. batrachi		Siluriformes: clariid (walking catfish, broadhead catfish) [anaemia]		India, Asia
T. batrachocephali		Gobiiformes: gobiid (toad goby)		Russia
T. bengalensis	17	Siluriformes: bagrid (Day's mystus)		India
T. birmanii	57	Siluriformes: loricariid (Commerson's pleco)		Brazil
T. blenclini		Blenniformes: blenniid (horned blenny), clinid (snaky clipfish)		Atlantic
T. bliccae		Cypriniformes: cyprinid (common bream, blue bream, bronze bream, common roach)		Eurasia
T. bourouli		Synbranchiformes: synbranchid (marbled swamp eel)		Brazil
T. breindli (syn. *T. laverani nom. preocc.*)		Cypriniformes: cyprinid (bleak)		Europe
T. cancili		Beloniformes: belonid (freshwater garfish)		India
T. carasobarbi		Cypriniformes: cyprinid (Mesopotamian himri)		Iraq

T. carassii (syn. *T. nikitini, scardinii, tincae, T. wincheniense, winitschenkae*)	15-40	Cypriniformes: cyprinid (common carp, crucian carp, goldfish, asp, tench, ide, rudd, common bream, blue bream, common roach), cobitid (spined loach, Siberian spined loach, weatherfish); Esociformes: esocid (northern pike); Perciformes: percid (European perch, ruffe); Salmoniformes: salmonid (Baikal black grayling, Arctic charr); Scorpaeniformes: cottid (Kessler's sculpin) [anaemia]	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Eurasia
T. catostomi	50	Cypriniformes: catostomid (white sucker)		North America
T. chagasi		Siluriformes: loricariid (suckermouthed catfish)		Brazil
T. channai	23-44	Anabantiformes: channid (spotted snakehead)		India
T. chaudhuryi		Cichliformes: cichlid (Mozambique tilapia)		Africa
T. cheni		Anabantiformes: channid (northern snakehead)		China
T. chetostomi	27-35	Siluriformes: loricariid (catfish)		Brazil
T. choudhuryi		Cichliformes: cichlid (Mozambique tilapia)		India
T. clariae		Siluriformes: clariid (walking catfish, broadhead catfish)		India, Asia
T. cobitis (syn. *T. barbatulae, elegans, langeroni, occidentalis, phoxini*)	25-47	Cypriniformes: cyprinid (crucian carp, gudgeon), cobitid (spined loach), leuciscid (common minnow, Eurasian minnow), nemacheilid (stone loach); Scorpaeniformes: cottid (inland riffle sculpin, torrent sculpin, European bullhead, weatherfish), gasterosteid (three-spined stickleback, nine-spine stickleback) [emaciation]	Clitellata: glossiphoniid (*Hemiclepsis marginata*)	Eurasia, North America
T. colisi		Anabantiformes: osphronemid (banded gourami)		India
T. commersoni		Siluriformes: loricariid (Commerson's pleco)		Brazil
T. ctenopharyngodoni		Cypriniformes: cyprinid (grass carp)		China
T. cyanophilum		Cichliformes: cichlid (redbelly tilapia)		Africa
T. cyprinioni		Cypriniformes: cyprinid (kangal fish)		Iraq
T. danilewskyi (possible synonym of *T. carassii*)	15-40	Cypriniformes: cyprinid (common carp, crucian carp, goldfish, tench, barbel, Malabar danio, common shiner), catostomid (white sucker); Perciformes: percid (rainbow darter); Siluriformes: heteropneustid (Asian stinging catfish), ictalurid (brown bullhead); Anguilliformes: anguillid (European eel) [anaemia]	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Eurasia
T. dogieli		Cypriniformes: cyprinid (ide, white-finned gudgeon, Cherskii's thicklip gudgeon); Gobiiformes: gobiid (gobies)		Asia
T. dominguesi	31	Siluriformes: loricariid (armoured catfish)		Brazil
T. dorbygnii	35-48	Siluriformes: doradid (marbled thorny catfish)		Brazil
T. elongatus		Anabantiformes: channid (spotted snakehead)		India
T. ezenami		Salmoniformes: salmonid (brown trout)		Atlantic
T. ferreirae	50-62	Characiformes: characid (tetras)		Brazil
T. francirochai	45	Siluriformes: loricariid (franciroch catfish)		Brazil
T. fulvidraco		Siluriformes: bagrid (yellowhead catfish)		China
T. gachuii		Anabantiformes: channid (dwarf snakehead)		India
T. gadrii		Siluriformes: clariid (walking catfish)		India
T. ganderi		Cypriniformes: cyprinid (largelip labeo)		Africa
T. gandhei		Cypriniformes: cyprinid (carp)		West Africa
T. garrae		Cypriniformes: cyprinid (red garra)		Iraq
T. gasimagomedovi		Anabantiformes: channid (dwarf snakehead); Scorpaeniformes: gasterosteid (Ukrainian stickleback)		Asia
T. gerraroi		Cichliformes: cichlid (Mozambique tilapia)		Africa
T. godavariense		Anabantiformes: channid spotted snakehead)		Asia
T. gracile		Cypriniformes: cyprinid (koi carp)		Eurasia

T. granulosum	20-80	Anguilliformes: anguillid (European eel)	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Europe
T. gorbygnii		Siluriformes: doradid (thorny catfish)		South America
T. guaibensis		Siluriformes: loricariid Commerson's pleco, whiptail catfish)		Brazil
T. hypostomi	25-40	Siluriformes: loricariid (gold speckled pleco)		Brazil
T. iheringi	42	Siluriformes: doradid (marbled spiny catfish)		Brazil
T. immanis	105-132	Siluriformes: loricariid (whiptail catfish)		Brazil
T. inexpectata (syn. *T. leucisci*)		Cypriniformes: cyprinid (orfe, dace, roach)		Eurasia
T. itoi	26	Siluriformes: loricariid (unspecified catfish)		Brazil
T. lamanoi	57	Siluriformes: loricariid (suckermouth catfish)		Brazil
T. langeroni		Scorpaeniformes: cottid (European bullhead)		Europe
T. larai	32-47	Characiformes: prochilodontid (prochilos)		South America
T. latinucleata		Siluriformes: silurid (Amur catfish)		Asia
T. limae	67	Characiformes: erythrinid (trairao)		Brazil
T. liocassis		Siluriformes: bagrid (Ussuri catfish)		Asia
T. lopesi	32	Siluriformes: loricariid (northeast Brazilian pleco)		Brazil
T. loricariae	20	Siluriformes: loricariid (unspecified catfish)		Brazil
T. lotai		Gadiformes: lotid (burbot)		Europe
T. luciopercae		Perciformes: percid (zander, Volga zander)		Eurasia
T. macrodonis	48	Characiformes: erythrinid (wolf fish)		Brazil
T. magdalenae		Cichliformes: cichlid (Krauss' cichlid)		South America
T. magna		Scorpaeniformes: cottid (stone sculpin, deepwater sculpin, pallid sculpin)		Russia
T. maguri		Siluriformes: clariid (walking catfish), bagrid (striped dwarf catfish) [anaemia]		India
T. malopteruri	39	Siluriformes: malapterurid (electric catfish)		Africa
T. mansouri		Cichliformes: cichlid (redbelly tilapia)		Africa
T, marathwadense		Cypriniformes: cyprinid (brown mahseer)		Asia
T. margaritiferi	22-46	Siluriformes: loricariid (yellow-spotted hypostomus)		Brazil
T. markewitschi		Siluriformes: silurid (wels catfish)		Asia
T. mastacembeli		Synbranchiformes: mastacembelid (zigzag eel)		India
T. micropteri		Perciformes: centrarchid (largemouth bass)		China
T. minutum	25	Cypriniformes: cyprinid (lake skygazer)		China
T. mrigali		Cypriniformes: cyprinid (mrigal carp)		India
T. mukasai	25-50	Cichliformes: cichlid (thinface cichlid, Alluaud's haplo, purpleface largemouth, yellowbelly bream, cinereus haplo, Lake Victoria cichlid, blue Victoria mouthbrooder, banded tilapia, three-spotted tilapia, Nile tilapia, Singida tilapia, Mozambique tilapia, Victoria tilapia); Siluriformes: bagrid (semutundu), clariid (African sharptooth catfish, snake catfish), clareotid (Zambezi grunter), mochokid (spotted squeaker, upside-down catfish), nemacheilid (Kashmir triplophysa-loach), schilbeid (silver catfish); Cypriniformes: cyprinid (crucian carp, sattar snowtrout); Osteoglossiformes: mormyrid (elephant-snout fish)		Africa
T. mukundi		Siluriformes: heteropneustid (Asian stinging catfish)		India

T. murtii		Synbranchiformes: mastacembelid (zigzag eel)		Asia
T. mylopharyngodoni	44	Cypriniformes: cyprinid (black carp)		China
T. mysti		Siluriformes: bagrid (Gangetic mystus)		India
T. mystuii		Siluriformes: bagrid (Tigris mystus)		Iraq
T. nandi		Perciformes: nandid (Gangetic leaffish)		India
T. napolesi		Cichliformes: cichlid (Mozambique tilapia)		East Africa
T. neinavana	33-38	Cypriniformes: cyprinid (shabout)		Iraq
T. notopteri		Osteoglossiformes: notopterid (bronze featherback)		Asia
T. nupelianus	18	Siluriformes: loricariid (black armoured catfish)		Brazil
T. orientalis		Cypriniformes: cyprinid (spotted steed, stone moroko); Siluriformes: silurid (Amur catfish)		Asia
T. pancali		Synbranchiformes: mastacembelid (barred spiny eel)		India
T. parasiluri		Siluriformes: silurid (Amur catfish)		Asia
T. pelligrini		Anabantiformes: osphronemid (fork-tailed paradisefish)		Asia
T. percae	18-57	Perciformes: percid (European perch, yellow perch); Salmoniformes: salmonid (brook trout)	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	North America, Eurasia
T. petenuscii	50	Siluriformes: loricariid (unspecified armoured catfish)		Brazil
T. phaleri	12- 89	Amiiformes: amiid (bowfin)	Clitellata: glossiphoniid (*Desserobdella phalera*)	North America
T. piavae	44	Characiformes: characid (tetras)		Brazil
T. pingi		Cypriniformes: cyprinid (goldfish)		China
T. pintoi	45	Siluriformes: loricariid (armoured catfish)		Brazil
T. piracicaboe	36-42	Siluriformes: loricariid (cascudo espada)		Brazil
T. piscidium		Anabantiformes: osphronemid (banded gourami)		India
T. plecostomi	20-38	Siluriformes: loricariid (armoured catfish)		Brazil
T. pradoi	20-48	Siluriformes: loricariid (cascudo)		Brazil
T. pseudobagri		Siluriformes: bagrid (unspecified catfish)		Asia
T. punctati	34	Anabantiformes: channid (spotted snakehead)		India
T. puntii		Cypriniformes: cyprinid (kolus barb)		India
T. qadrii		Siluriformes: clariid (walking catfish)		Asia
T. rayi		Cypriniformes: cyprinid (minnow)		Europe
T. rebeloi		Cichliformes: cichlid (Mozambique tilapia)		East Africa
T. regani	21-53	Siluriformes: loricariid (giant white-spot pleco)		Brazil
T. remaki (possible synonym of *T. schulmani*)	bimorphic: 10-25, 45-70	Esociformes: esocid (northern pike); Cypriniformes: cyprinid (ide, tench, common roach)	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Eurasia, North America
T. rohilkhandae		Anabantiformes: channid (spotted snakehead)		India
T. roulei		Synbranchiformes: synbranchid (Asian swamp eel)		Asia
T. rupicola		Cypriniformes: nemacheilid (stone loach)		Asia
T. saccobranchi		Siluriformes: heteropneustid (Asian stinging catfish)		India
T. salihi		Siluriformes: sisorid (Tigris cat)		Iraq
T. sauli		Anabantiformes: channid (spotted snakehead)		India
T. schulmani		Esociformes: esocid (northern pike)		Asia
T. serranoi		Cichliformes: cichlid (Mozambique tilapia)		East Africa

T. siluri		Siluriformes: silurid (Amur catfish)		Asia
T. simondi		Siluriformes: claroteid (giraffe catfish)		Africa
T. singhii		Siluriformes: heteropneustid (Asian stinging catfish)		Asia
T. sinipercae		Perciformes: sinipercid (mandarin fish)		China
T. splendorei (syn. *T. rhamdiae*)	40-48	Siluriformes: heptapterid (silver catfish, South American catfish)		South America
T. squalli		Cypriniformes: cyprinid (ide)		Europe
T. stigmai		Cypriniformes: cyprinid (pool barb)		India
T. striati (syn. *T. ophiocephali*)	32-54	Anabantiformes: channid (northern snakehead, striped snakehead)		Asia
T. striatum	27-30	Siluriformes: bagrid (Braschikow's catfish)		China
T. strigaticeps	21-23	Siluriformes: loricariid (cascudo pintado)		Brazil
T. synodontis		Siluriformes: mochokid (mandi, onespot squeaker)		Africa
T. tandoni		Siluriformes: silurid (helicopter catfish)		Asia
T. tchangi		Centrarchiformes: sinipercid (bigeye mandarin fish)		China
T. tobeyi		Siluriformes: clariid (Angolan walking catfish)		West Africa
T. toddi		Siluriformes: clariid (Angolan walking catfish, mudfish)		Africa
T. trichogasteri		Anabantiformes: osphronemid (banded gourami, three-spot gourami)		Asia
T. venustissimum	72	Siluriformes: loricariid (suckermouth catfish)		Brazil
T. vittati		Siluriformes: clariid (walking catfish, striped dwarf catfish) [anaemia]		India
T. wangi		Cypriniformes: cyprinid (rainbow gudgeon)		China
T. zilli		Cichliformes: cichlid (Guinean tilapia)		Africa
T. zungaroi	62	Siluriformes: pimelodid (gilded catfish)		Brazil
Species in marine fish				
T. aulopi		Aulopiformes: aulopid (Sergeant baker)		Australia
T. balistes		Tetraodontiformes: balistid (grey triggerfish)		Caribbean
T. burresoni		Anguilliformes: anguillid (American eel)		North America
T. callionymi	65-70 striated	Callionymiformes: callionymid (common dragonet)		European Atlantic
T. cataphracti (*nomen nudem*)		Scorpaeniformes: agonid (pogge)		England
T. caulopsettae	26-95	Pleuronectiformes: pleuronectid (large scald flounder, New Zealand sand flounder)		New Zealand
T. cephalacanthi	24-32	Syngnathiformes: dactylopterid (flying gurnard)		West Africa
T. coelorhynchii		Perciformes: haemulid (javelin fish); Gadiformes: morid (red codling)		New Zealand
T. congiopodi		Scorpaeniformes: congiopodid (southern pigfish)		New Zealand
T. cotti	45-55 striated	Scorpaeniformes: cottid (long-spined bullhead)	Clitellata: piscicolid (*Calliobdella punctata*)	European Atlantic
T. delagei	21-33 nonstriated	Blenniiformes: blenniid (shanny)		Northeast Atlantic
T. dohrni	37-41 nonstriated	Pleuronectiformes: soleid (whiskered sole)		Mediterranean
T. epinepheli	9-28	Perciformes: latid (barramundi), serranid (tiger grouper, humpback grouper)		China
T. froesi		Mugiliformes: mugilid (Lebranche mullet)		West Atlantic
T. gobii	38-56 nonstriated	Gobiiformes: gobiid (black goby)		European Atlantic
T. heptatreti	56-98	Myxiniformes: myxinid (broadgilled hagfish)		New Zealand
T. laternae	44-57 nonstriated	Pleuronectiformes: pleuronectid (lefteye flounder)		Northeast Atlantic

T. lotae		Gadiformes: lotid (burbot)		Europe
T. mugilicola (= *mugicola*)	30	Mugiliformes: mugilid (flathead grey mullet); Pleuronectiformes: achirid (hogchoker)		Mexico, Africa
T. mugili		Mugiliformes: mugilid (Lebranche mullet)		Brazil
T. murmanense	32-94 striated	Scorpaeniformes: anarhichadid (Atlantic wolffish, spotted wolffish, northern wolffish), cottid (longhorn sculpin, shorthorn sculpin), cyclopterid (Atlantic spiny lumpfish), liparid (Atlantic snailfish, polka-dot snailfish); Anguilliformes: anguillid (American eel); Gadiformes: gadid (Atlantic cod, polar cod, Atlantic tomcod, saithe), macrourid (roughhead grenadier), phycid (longfin hake, white hake); Labriformes: labrid (cunner); Perciformes: cottid (Arctic hookear sculpin), zoarcid (Newfoundland eelpout, Arctic eelpout, checker eelpout, ocean pout); Pleuronectiformes: pleuronectid (winter flounder, witch flounder, yellowtail flounder, American plaice, Atlantic halibut, Greenland halibut) [anaemia, emaciation]	Clitellata: piscicolid (*Johanssonia arctica*)	North Atlantic, Arctic
T. myoxocephali	41-49 striated	Scorpaeniformes: cottid (longhorn sculpin)		North Atlantic, Arctic
T. nudigobii (syn. *T. capigobii, blenniclini,* on molecular grounds)	bimorphic: 25-46, 55-98	Gobiiformes: gobiid (barehead goby); Blenniiformes: blenniid (horned blenny), clinid (snaky klipfish, agile klipfish, bluntnose klipfish, bull klipfish)	Clitellata: piscicolid (*Zeylani-cobdella arugamensis*)	South Africa
T. pacifica		Pleuronectiformes: pleuronectid (English sole)		East Pacific
T. parapercis		Trachiniformes: pinguipedid (blue cod)		New Zealand
T. platessae (syn. *T. bothi, flesi, limandae*)	23-38 nonstriated	Pleuronectiformes: pleuronectid (European plaice, European flounder, common dab, long rough dab), scophthalmid (brill)		Northeast Atlantic
T. pleuronectidium (syn. *T. aeglefini*)	40-74 striated	Gadiformes: gadid (Atlantic cod, poor cod, haddock, pollock, saithe, Norway pout), lotid (cusk, common ling, fourbeard rockling, American plaice), merlucciid (European hake), phycid (greater forkbeard); Scorpaeniformes: triglid (grey gurnard); Pleuronectiformes: pleuronectid (European flounder, European plaice, witch, common dab, lemon sole), scophthalmid (megrim)	Clitellata: piscicolid (*Calliobdella nodulifera*)	Northeast Atlantic
T. pulchra	40-52	Perciformes: serranid (seaperch)		Australia
T. radiale		Anguilliformes: muraenid (spotted moray)		Atlantic
T. scorpaenae	65-70 nonstriated	Scorpaeniformes: scorpaenid (small red scorpionfish)		Mediterranean
T. senegalense	45 striated	Scorpaeniformes: triglid (streaked gurnard)		West Africa
T. soleae	32-47 striated	Pleuronectiformes: soleid (common sole)	Clitellata: piscicolid (*Calliobdella punctata, Hemibdella soleae*)	Northeast Atlantic
T. sphaeroidis		Tetraodontiformes: tetraodontid (bandtail puffer)		West Africa
T. triglae	54-62 nonstriated	Scorpaeniformes: triglid (streaked gurnard, tub gurnard, grey gurnard)		Mediterranean
T. tripterygium	36-85	Blenniiformes: tripteryglid (variable triplefin, black-faced blenny), clinid (orange clinid)		New Zealand
T. yakimovi	31-36 nonstriated	Syngnathiformes: syngnathid (greater pipefish)		Mediterranean
T. zeugopteri (*nomen nudem*)		Pleuronectiformes: scophthalmid (common topknot)		England

Species in marine elasmobranchs (cartilaginous fishes)				
T. boissoni	45-67	Rhinopristiformes: zanobatid (striped panray)		East Atlantic
T. carchariasi	35-70	Lamniformes: odontaspidid (sand sharks)		Australia
T. gargantua	67-131	Rajiformes: rajid (New Zealand rough skate)		New Zealand
T. giganteum	100-130	Rajiformes: rajid (long-nosed skate)	Clitellata: piscicolid (*Pontobdella muricata*)	Mediterranean
T. haploblephari	20-112	Carcharhiniformes: scyliorhinid (dark shyshark, puffadder shyshark, leopard catshark)		South Africa
T. harriottae	24-38	Chimaeriformes: rhinochimaerid (narrownose chimaera)		Cape Verde Islands
T. humboldti	78-93	Carcharhiniformes: scyliorhinid (Chilean catshark)		Chile
T. mackerrasi	118-125	Orectolobiformes: hemisculliid (epaulette shark)		Australia
T. marplatensis	60-65	Rajiformes: arhynchobatid (softnose skate)		Argentina
T. rajae (syn. *T. variabile*)	55-80	Rajiformes: rajid (common skate, winter skate, little skate, thorny skate, starry ray, mosaic ray, thornback ray, small-eyed ray) [anaemia]	Clitellata: piscicolid (*Pontobdella muricata*)	European Atlantic, Mediterranean
T. scyllii	54-75	Carcharhiniformes: scyliorhinid (large-spotted dogfish, lesser spotted dogfish)	Clitellata: piscicolid (*Pontobdella muricata*)	Northeast Atlantic
T. squalii		Squaliformes: squalid (spurdog)		Northeast Atlantic
T. taeniurae	50-55	Myliobatiformes: dasyatid (blue-spotted ribbontail ray)		Australia
T. torpedinis		Torpediniformes: torpedinid (marbled electric ray)		European Atlantic

Parasite morphology: Piscine trypanosomes form several different developmental stages in their hosts: trypomastigotes in fish and epimastigotes (sometimes sphaeromastigotes, rarely amastigotes, promastigotes and metacyclic trypomastigotes) in leeches. Species were originally identified on the basis of differences in host occurrence (zoogeography) and parasite morphology (morphometrics, presence/absence of granules/striations) but considerable variation has been observed within these characters for many species (variable host specificity, parasite pleomorphy). More recently, molecular techniques (proteins, DNA) have been used to characterize species and indicate phylogenetic relationships. All stages have an oval-round kinetoplast (containing mitochondrial DNA) located separately from the cell nucleus and the flagellar basal body (complex of microtubules) is located adjacent to the kinetoplast. The basal body gives rise to a single flagellum which emerges from the cell in all stages except amastigotes. Observation of live organisms indicates that they move in the direction of the free flagellum, so that cellular aspect has been designated anterior. This sometimes causes confusion when considering the orientation of trypomastigotes which have a long flagellum often mistakenly termed recurrent or trailing when in fact it extends forwards (in contrast to bodonids such as *Cryptobia* and *Trypanoplasma* which do have a recurrent flagellum directed posteriorly). Trypomastigotes are long and slender ranging from 20-90 µm in length and 1-10 µm in width. The kinetoplast is located posterior to the cell nucleus and the emergent flagellum is attached to the cell body forming a long undulating membrane before extending freely beyond the anterior margin. The trypomastigotes of most piscine species are monomorphic (e.g. *T. danilewskyi*), although those of some species may be pleomorphic (e.g. *T. murmanense* with small, intermediate and large forms). They have well-developed cytostomes (mouths) located subapically near the nucleus and they usually possess numerous dense granules juxtaposed to the cytopharyngeal tube. The cell body is membrane-bound with a thin fibrillar surface coat, which in some species bears longitudinal striations. Epimastigotes are elongate ranging in size from 8-26 by 1-4 µm (sometimes comprising short thick forms, long thick forms and longer slender forms). The kinetoplast is located anterior to the cell nucleus and the emergent flagellum is attached to the cell body forming a short undulating membrane before extending freely beyond the anterior margin. Sphaeromastigotes are rounded stages ranging from 3-7 µm in diameter that have an anterior kinetoplast and a short free flagellum emerging from a small depressed pocket. Amastigotes are small rounded stages ranging from 5-7 µm in diameter that do not have emergent flagella or undulating membranes. A few studies have also reported the rare occurrence of promastigotes (kinetoplast anterior to nucleus) and possibly early metacyclic (infective) trypomastigotes (with kinetoplast posterior to nucleus) in leeches.

Site of infection: Trypomastigotes occur as extracellular organisms in the blood stream of their fish hosts. Over 200 species have been described in almost 300 fish species: with 165 parasite species reported in 181 freshwater fish species belonging to 48 families in 19 orders (esp. cyprinids and catfish), and 51 parasite species found in 115 marine fish species belonging to 49 families in 24 orders (esp. flounder, but also including some cartilaginous fishes). *Trypanosoma* epimastigotes, sphaeromastigotes and amastigotes infect the crop and intestines of leech vectors, while metacyclic trypomastigotes invade the proboscis sheath. Infections have been demonstrated in 9 leech species: 2 glossiphoniid and one piscicolid species recovered from freshwater fish, and 6 piscicolid species from marine fish.

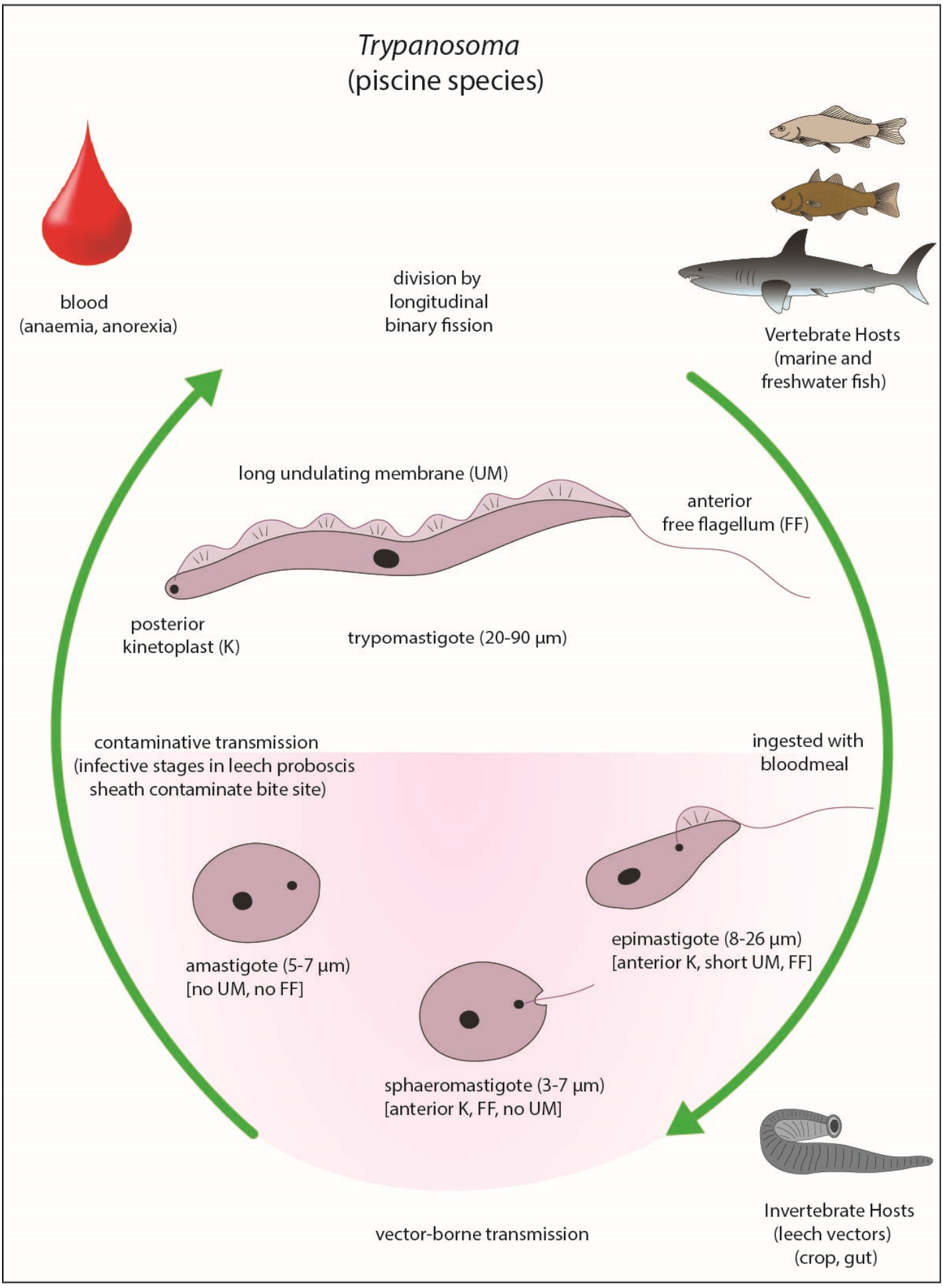
Pathogenesis: Trypanosomes feed on host fluids by absorbing nutrients through their surface membranes and digesting proteins, carbohydrates and fats by enzyme systems within their protoplasm. Most infections in the blood of fishes have not been associated with any clinical disease, although several species are thought to be responsible for mild anaemia in their hosts, due partly to haemolysis and exacerbated by haemodilution. For example, infections by *T. danilewskyi* may cause progressive anaemia in goldfish resulting in anorexia, poor condition and even death. Infections by *T. murmanense* were found to cause chronic disease with low parasitaemias and low mortalities in goldfish, barramundi, eels, grouper, and tilapia. The severity of anaemia was often correlated to the degree of parasitaemia, with numerous parasites causing greater reductions in haematocrit (packed cell volume), lower erythrocyte counts, and reduced haemoglobin levels. While the parasites were located extracellularly in the host circulation, experimental studies have shown that some trypomastigote excretory-secretory products were able to lyse host erythrocytes in the absence of antibodies. Clinical signs observed in fish have included inappetence with reduced feeding sometimes leading to emaciation, weakness and lethargy. The anorexia was found to involve low food movement through the intestines, mucosal alterations affecting digestion and absorption, increases in appetite-suppressing hormones (cholecystokinin/gastrin), and elevations in the pro-inflammatory cytokines (interleukin-1) altering gut motility. Infected fish may also develop splenomegaly, darkening of the body, exophthalmia, scale loss and respiratory disorders due to gill epithelial hyperplasia, hypertrophy and vacuolation, mucus cell hypertrophy and thrombi formation. There may be some congestion in internal organs (brain, liver, spleen, kidney) due to cellular necrosis, haemorrhages, haemosiderin deposits and melanomacrophage aggregates. There appears to be little innate or acquired immunity to infection, although some fish developed neutralizing antibodies but their trypanocidal lytic activity was lost after several weeks-months. Young fish are more susceptible to clinical disease, while adults often appear to be refractory. However, older fish often harbour small but persistent infections but do not develop disease, suggesting that some premunitive immunity (rather than sterile immunity) may be involved. Infections in freshwater fish exhibit seasonal fluctuations in prevalence and intensity, with more parasites found in warmer months, possibly due to increased fish susceptibility or greater leech activity or both. Infections are also more prevalent in fish that spend more time in shallower waters near vegetation where leeches dwell.

Developmental cycle and mode of transmission: Fish trypanosomes are transmitted by haematophagous leech vectors. The parasites multiply asexually in both vertebrate and invertebrate hosts by symmetrogenic (rather than homothetogenic) binary fission

involving the production of a new flagellum, division of the kinetoplast, karyokinesis, and transverse constriction of the midbody culminating in cytokinesis. Fish become infected via leech bites when infective stages are released into the circulation where they develop into trypomastigotes which feed and multiply. Leeches become infected when they feed on host blood and ingest trypomastigotes which undergo cyclic changes forming different multiplicative stages before the formation of infective metatrypanosomes (process termed metacyclogenesis). Three basic developmental patterns have been observed: two in freshwater leeches and one in marine leeches. Some freshwater species (e.g. *T. acerinae, T. abramidis, T. barbi, T. percae, T. remaki, T. squalii*) multiply and develop exclusively in the crop with metacyclic stages migrating forwards (or being regurgitated) as the leech feeds, while other species (e.g. *T. carassii, T. cobitis, T. danilewskyi, T. granulosum, T. phaleri, T. phoxini*) multiply in the crop and intestines (forming epimastigotes, sometimes sphaeromastigotes) before eventual invasion of the proboscis sheath by infective metatrypanosomes which contaminate bite sites. In marine species (e.g. *T. cotti, T. soleae, T. murmanene*), ingested trypomastigotes lose their flagella and divide as amastigotes, then sphaeromastigotes and epimastigotes in the crop and intestines before developing into infective stages in the proboscis sheath.

Differential diagnosis: Trypomastigotes can be detected by microscopic examination of blood either in wet mounts or stained smears. Microhaematocrit tube centrifugation can also be used to concentrated trypomastigotes from blood where they band with the buffy coat layer. Piscine trypanosomes have also been cultured on a variety of blood-agar media where they usually multiply as epimastigotes by binary fission and sometimes multiple fission. Leeches may also be examined for developmental stages by microscopy of squash preparations or histological sections. Molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA, glycosomal glyceraldehyde-3-phosphate dehydrogenase).

Treatment and control: There is no specific chemotherapy available for trypanosome infections in fish, although some chemical bath treatments have reduced infection levels in cultured fish, the most effective for catfish being ethanolic extracts of *Aloe vera* leaves or *Artemisia annua* leaves, and less effective treatments involving diamidines (diminazene aceturate) and even some anthelmintics (praziquantel). Some reports have indicated that thiazole water conditioners or crystal violet disinfectants may help reduce infections in aquarium fish. A range of trypanocidal drugs effective against infections in mammals have yet to be tested against infections in fish. Preventive measures in aquaculture are based around reducing transmission rates to fish by excluding leech vectors, either by chemical treatments of infested fish (trichlorphon baths) or by clearing ponds of vegetation (which support leech populations). Preliminary immunological studies have shown some promise for the potential immuno-modulation of infections. Infected fish have been found to produce antibodies with activity against trypanosomes, but they did not persist. Nonetheless, passive immunization experiments showed antibodies purified from infected fish were able to confer some protection to recipient challenged fish. While some parasite proteins (calreticulin, glycoprotein 63) have been implicated in immuno-evasion strategies (avoiding complement lysis and macrophage phagocytosis), other proteins (beta-tubulin, hepcidin) stimulated protective immune responses in naïve fish. It should be re-iterated that most infections in fish remain asymptomatic despite the persistence of blood stages, so that any acquired immunity may be premunitive. Care should be taken in all control programs not to upset this delicate enzootic stability between hosts and parasites.


Trypanosoma
(piscine species)
blood
(anaemia, anorexia)
division by
longitudinal
binary fission
Vertebrate Hosts
(marine and
freshwater fish)
long undulating membrane (UM)
anterior
free flagellum (FF)
posterior
kinetoplast (K)
trypomastigote (20-90 µm)
contaminative transmission
(infective stages in leech proboscis
sheath contaminate bite site)
ingested with
bloodmeal
amastigote (5-7 µm)
[no UM, no FF]
epimastigote (8-26 µm)
[anterior K, short UM, FF]
sphaeromastigote (3-7 µm)
[anterior K, FF, no UM]
vector-borne transmission
Invertebrate Hosts
(leech vectors)
(crop, gut)

Trypanosoma trypomastigite in fish blood