***Trichodina***
(protist: ciliate)

**Overview**

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of three membranelles. Peritrichous ciliates are filter-feeders with a left-hand spiral of oral cilia leading to cytostome. They live attached permanently (sessilines) or temporarily (mobilines) to substrates, which may include other aquatic animals. Trichodinids form mobile discoid trophonts with an aboral holdfast organelle comprising an elaborate concave disc with proteinaceous denticles (thorns and blades) subtended by radial pins. Several genera are recognized on the basis of differences in their oral ciliary wreaths and adhesive discs. Most species are ectoparasitic on fish and many cause skin lesions, although a few species have been found as endozoic organisms in the digestive tracts of elasmobranchs and some fishes where they apparently do no harm.

**Classification**:

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| Domain: | Eukaryota (membrane-bound nucleus) |
| Supergroup: | SAR (Stramenopiles + Alveolata + Rhizaria) |
| Group: | Alveolata (with cortical alveoli) |
| Phylum: | Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation) |
| Subphylum: | Intramacronucleata (microtubules occur inside macronuclear envelope during division)) |
| Class: | Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles) |
| Subclass: | Peritrichia (lacking somatic kineties, oral cilia extend from infundibulum, predominantly bactivores, often stalked) |
| Order: | Mobilida (mature trophont mobile, aboral holdfast organelle) |
| Family: | Trichodinidae (stout cylindrical body, posterior adhesive disc with denticular ring) |
| Genus: | *Trichodina* (ectoparasitic on skin/gills of fish) |
| Species: | many species cause skin lesions on freshwater and marine 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. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

| Class | Etymology | Defining characters | Lifestyles* | Genera covered |
|---|---|---|---|---|
| Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)] | | | | |
| Karyorelictea | 'primitive-nucleus' | macronuclei not dividing but replaced by division of micronuclei | free-living (aquatic benthic/planktonic) | |
| Heterotrichea | 'different-hair' | compound ciliary organelles around mouth, macronuclei divided by external microtubules | free-living (aquatic planktonic/benthic) | |
| Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules] | | | | |
| Spirotrichea | 'coiled-hair' | conspicuous right and left oral ciliature, left polykinetids leading into oral cavity | free-living (aquatic, terrestrial) | |
| Litostomatea | 'simple-mouths' | cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos) | free-living (often predatory), symbiotic | *Balantidium* |
| Phyllopharyngea | 'leaf-throated' | mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles | free-living (aquatic), epizoic, symbiotic | *Chilodonella* |
| Colpodea | 'breast-shaped' | reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons) | terrestrial, some aquatic (bactivores) | |
| Nassophorea | 'pot-bearer' | oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx) | free-living (aquatic, terrestrial) | |
| Prostomatea | 'before-mouth' | simple apical mouths, some with oral microtubular band, some with oral brush | free-living (often predatory) | |
| Plagiopylea | 'misshapen-marker' | with twisted oral tubes, most with hydrogenosomes | free-living (anoxic habitats) | |
| Oligo-hymenophorea | 'few membrane-bearer' | typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles) | free-living, epizoic, symbiotic (micro-phagous) | *Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella* |

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed in aquatic habitats (fresh, brackish and marine waters) where they occur as free-living stages (free-swimming or attached to substrates), some being epizoic (rarely endozoic) on aquatic animals (mainly crustacea and fish). Free-living aquatic species are highly sensitive to environmental changes and a range of species are used as bioindicators for the assessment of water quality (saprobic classifications) and even sludge activity in wastewater treatment. The class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. Peritrichous ciliates are filter-feeders with inverted bell-shaped bodies having prominent buccal ciliature encircling the apical pole (forming a peristomial field) and winding counterclockwise (left hand spiral) to plunge into the oral cavity (infundibulum) to the cytostome (mouth). The peristomal border consists of a dikinetid file (considered homologous to the paroral membrane) surrounding a triple row of cilia (considered homologous to the polykinetid membranelles). The narrow antapical pole of the cells possess barren kinetosomes as part of a holdfast apparatus (scopula or adhesive disc). Mature trophonts (often called zooids) lack somatic kineties but the transient dispersal telotroch (swarmer) stages may develop temporary ciliary rings for locomotion. Two peritrich orders are recognized depending on whether mature trophonts live attached permanently (Sessilida) or temporarily (Mobilida) to substrates, which in many cases may include other aquatic animals and plants.

| Higher taxonomy | Family | Exemplar genera | Hosts | Site | Trans-mission |
|---|---|---|---|---|---|
| Subclass: Peritrichia (lacking somatic kineties, oral cilia extend from infundibulum) | | | | | |
| Order: Mobilida (mature trophont mobile, aboral holdfast organelle) | Trichodinidae (stout cylindrical body, posterior adhesive disc with denticular ring) | *Trichodina* | fish | skin, gills | direct |
| Order: Sessilida (mature trophont sessile, attached to substrate by scopula (special flat thigmotactic area) with or without stalk) | Epistylididae (scopula produces noncontractile stalk, retractile lip encircles elevated peristomial disc) | *Apiosoma* | fish | skin, gills | direct |
| | | *Epistylis* | fish, crustacea | exoskeleton | direct |
| | Scyphidiidae (solitary ciliates, attached by scopula) | *Scyphidia* | fish, crustacea | exoskeleton | direct |
| | | *Ambiphrya* | fish, crustacea | exoskeleton | direct |
| | Vorticellidae (solitary, gregarious or colonial, retractile stalks with central myoneme) | *Vorticella* | fish, crustacea | exoskeleton | direct |
| | | *Carchesium* | fish, crustacea | exoskeleton | direct |
| | Zoothamniidae (solitary or colonial, retractile stalks with shared myonemes) | *Zoothamnium* | fish, crustacea | exoskeleton | direct |
| | Vaginicolidae (upright lorica) | *Cothurnia* | crustacea | exoskeleton | direct |
| | | *Vaginicola* | crustacea | exoskeleton | direct |
| | Lagenophryidae (discoid lorica) | *Lagenophrys* | crustacea | gills | direct |

The order Mobilida contains species whose mobile trophonts have conical-cylindrical discoid bodies with an aboral holdfast organelle. The holdfast functions as a slightly contractile adhesive disc with complex ring-like skeletal armature of denticles and fibres surrounding a vestigal scopula. The oral region is not contractile and contains a permanently-ciliated trochal band typically comprising 3 ciliary wreaths (2 locomotory oral polykinetids and a third short perpendicular polykinetid with immobile tactile cilia). The ciliates are usually ectosymbiotic, often on the skin or gills of aquatic invertebrates and some vertebrates. They are essentially bactivorous, obtaining prey from the water column and sometimes being microphagous on cellular debris from their hosts. A total of 5 families have been recognized on the basis of various biologic and morphologic differences: with members of the Leiotrochidae (genus *Leiotrocha*), Polycyclidae (genus *Polycycla*), Trichodinopsidae (genus *Trichodinopsis*) and Urceolariidae (genus *Urceolaria*,) comprising ciliates with smooth denticles in their adhesive discs; and only members of the Trichodinidae having complex denticles in their adhesive discs. Trichodinids have stout cylindrical-discoidal bodies, adoral (peristomial) ciliary wreaths spiraling from half a turn to 3 turns, and an aboral concave adhesive disc consisting of a ring of hollow conical elements with flat lateral projections (denticles) with centrifugal processes (blades) and centripedal rays (thorns). The denticles are inserted into each other and subtended by a ring of fine skeletal rods (radial pins). Over 20 trichodinid genera have been proposed, with recent revisions combining them into 9 genera primarily on the basis of differences in oral ciliary wreaths and adhesive disc morphology: namely, *Hemitrichodina*, *Heterobladetrichodina*, *Pallitrichodina*, *Paratrichodina*, *Semitrichodina* (syn. *Trichodoxa*)*, Trichodina* (syn. *Acyclochaeta, Anhymenia, Cyclochaeta, Cyclocyrrha, Nummulella, Paravauchomia, Poljanskina, Torquatina*)*, Trichodinella* (syn. *Brachyspira, Dipartiella, Dogielina, Foliella*), *Tripartiella* and *Vauchomia.*

| Genus | Turns to adoral spiral | Denticle composition | No. spp. | Hosts* | Site |
|---|---|---|---|---|---|
| *Vauchomia* | 2-3 | well-developed blades and thorns | 2 | fw fish | urinary tract |
| *Hemitrichodina* | 1-2 | blades stunted, well developed thorns | 1 | fw fish | skin, fins |
| *Trichodina* | 1-1½ | well-developed blades and thorns | 170 | fw & mar fish | gills, skin |
| *Pallitrichodina* | ¾ | well-developed blades, short thorns | 2 | terrestrial snails | mantle cavity |
| *Semitrichodina* | ½-¾ | well-developed blades and thorns | 3 | terrestrial snails | mantle cavity, genitals |
| *Paratrichodina* | ½-¾ | perpendicular blades, prominent thorns | 15 | fw & mar fish | gills, bladder |
| *Tripartiella* | ½-¾ | oblique blades, prominent thorns | 19 | fw & mar fish | gills |
| *Trichodinella* | ½-¾ | prominent blades, vestigial thorns | 11 | fw & mar fish | gills |
| *Heteroblade-trichodina* | <½ | rays with thin perpendicular projections | 2 | fw fish | gills |

*fw = freshwater; mar = marine

Most species are epizoic on aquatic organisms, including the skin, fins and gills of a range of ornamental, farmed and wild fishes, both freshwater and marine. Some species are thought to be host specific while others occur over a wide range of hosts, but information on their actual host specificity is often lacking. Some infections persist in euryhaline habitats (over a wide range of salinities such as encountered by estuarine fish), while others apparently survive catadromous or anadromous migrations (fish

moving from freshwater to seawater to spawn, or vice versa). A growing number of species have been associated with eruptive or ulcerative skin lesions, particularly in cultured fishes in crowded conditions. A few species have also been found as endozoic organisms in the urogenital tracts of elasmobranchs and some fish but they apparently live as endocommensals and do no harm.

| **Ciliate species** | **Adhesive disc (AD) diameter (µm), number of denticles (ND)** | **Habitat (Hosts)** | **Location** | **Distribution** |
|---|---|---|---|---|
| Genus ***Hemitrichodina*** (adoral ciliary spiral makes between 1-2 turns, denticles with reduced blades but well-developed central parts and thorns) | | | | |
| *H. robusta* [type species] | AD 43-70 ND 18-24 | freshwater, epizoic on fish (Characiformes: alestid (sharptooth tetra), hepsetid (African pike, African pike characin); Osteoglossiformes: mormyrid (bulldog)) | skin, fins | Africa |
| Genus ***Heterobladetrichodina*** (adoral ciliary spiral less than one turn, denticles with thorns ending in thin projections folded underneath at right angles) | | | | |
| *H. punctatus* [type species] | | freshwater, epizoic on fish (Siluriformes: ictalurid (channel catfish)) | | China |
| *H. kazubski* (syn. *Dipartiella*) | AD 14-19 ND 23-33 | freshwater, epizoic on fish (Siluriformes: bagrid (tengra), silurid (helicopter catfish)) | gills | India |
| Genus ***Pallitrichodina*** (adoral ciliary spiral makes ¾ turn, denticles with well-developed blades, short thorns, body with distinct indentations due to microfibrillar attachments) | | | | |
| *P. rogenae* [type species] | AD 27-44 ND 18-22 | terrestrial, endozoic in snails (Gastropoda: achatinid (*Achatina fulica, panthera*)) | mantle cavity | Mauritius, Taiwan |
| *P. stephani* | AD 30-53 ND 18-30 | terrestrial, endozoic in snails (Gastropoda: achatinid (*Achatina fulica, panthera*)) | mantle cavity | Mauritius |
| Genus ***Paratrichodina*** (adoral ciliary spiral makes ½-¾ turns, denticles wedged together only by central parts, well-developed thorns, blades attached perpendicularly) | | | | |
| *P. africana* | AD 12-25 ND 17-27 | freshwater, epizoic on fish (Cichliformes: cichlid (Nile tilapia, mango tilapia); Perciformes: latid (Nile perch)) | gills, skin | Africa, South America |
| *P. alburni* (syn. *Trichodina*) | AD 25-44 ND 23-29 | freshwater, endozoic in fish ( Cypriniformes: cyprinid (common bleak), leuciscid (common minnow)) | urinary tract | Europe |
| *P. bassonae* | AD 11-15 ND 18-21 | freshwater, epizoic on fish (Siluriformes: bagrid (Gangetic mystus)) | gills | India |
| *P. corlissi* | AD 19-25 ND 18-24 | freshwater, epizoic on fish (Cypriniformes: cyprinid (gudgeon, Kessler's gudgeon); Gobiiformes: gobiid (marbled goby)) | gills | Eurasia |
| *P. degiustii* | AD 31-36 ND 27-32 | freshwater, endozoic in fish (Cypriniformes: cyprinid (blackchin shiner)) | urinary tract | North America |
| *P. erectispina* | AD 20-31 ND 23-27 | freshwater, epizoic on fish (Cypriniformes: cyprinid (bullhead minnow)) | gills | North America |
| *P. globonucleata* [type species as subgenus of *Tripartiella*] | AD 12-30 ND 15-28 | marine, epizoic on fish (Gadiformes: lotid (shore rockling); Ophidiiformes: ophidiid (snake blenny); Scorpaeniformes: agonid (spinycheek starsnout), cottid (slim sculpin), psychrolutid (spinyhead sculpin scorpaenid (Korean rockfish); Syngnathiformes: syngnathid (long-snouted seahorse)) | gills | Atlantic, Pacific, Mediterranean |
| *P. incissa* (*incisa*) (syn. *Tripartiella*, *Paratrichodina*) | AD 11-36 ND 15-31 | freshwater, epizoic on fish (Cypriniformes: cyprinid (common carp, roach, rudd, dace, ide, zope), leuciscid (Eurasian minnow, lake minnow, Pacific redfin), nemacheilid (stone loach); Salmoniformes: salmonid (Arctic grayling); and amphibians (Anura: ranid (edible frog, tadpoles)) | gills | Eurasia |
| *P. lizae* | AD 13-20 ND 18-21 | estuarine, epizoic on fish (Mugiliformes: mugilid (goldspot mullet)) | gills | Brazil |

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| *P. obliqua* | AD 17-19<br>ND 19-21 | marine, epizoic on fish (Perciformes: mullid (red mullet); Pleuronectiformes: paralichthyid (olive flounder)) | gills | Europe |
| *P. phoxini*<br>(syn. *Trichodina*) | AD 25-44<br>ND 23-39 | freshwater, endozoic in fish (Cypriniformes: leuciscid (common minnow)) | urinary tract | Eurasia |
| *P. uralensis* | AD 20-26<br>ND 18-25 | freshwater, epizoic on fish (Acipenseriformes: acipenserid (sterlet)) | gills | Russia |
| *P. tasmaniensis* | AD 24-32<br>ND 26-29 | marine, epizoic on fish (Atheriniformes: atherinid (small-mouth hardyhead, small-scale hardyhead, short-snout hardyhead, pikehead hardyhead, silver fish)) | gills | Australia |
| *P. voikarensis* | AD 18-26<br>ND 22-25 | freshwater, epizoic on fish (Salmoniformes: salmonid (broad whitefish, peled)) | gills | Russia |
| *P. yangtzeus* | AD 20-26<br>ND 20-22 | freshwater, epizoic on fish (Siluriformes: silurid (Amur catfish)) | gills | China |
| Genus ***Semitrichodina*** (syn. *Trichodoxa*) (adoral ciliary spiral makes ½ to ¾ turn, denticles with well-developed blades and thorns, interlocked by central parts, body with oblique grooves or circumferential spines) | | | | |
| *S. sphaeronuclea*<br>[type species as subgenus of *Trichodinella*] | AD 28-54<br>ND 26-38 | terrestrial, endozoic in slugs (Gastropoda: limacid (*Limax maximus, cineroniger, Lehmannia marginata, Bielzia coerulans*), vitrinid (*Semilimax semilimax*), zonitid (*Aegopinella epipedostoma, Oxychilus* (*Schistophallus*) *orientalis*) | pallial cavity | Eurasia |
| *S. convexa* | AD 32-47<br>ND 22-25 | terrestrial, endozoic in snails (Gastropoda: clausiliid (*Cochlodina laminata*)) | pallial cavity | Europe |
| *S. genitalis*<br>(syn. *Trichodoxa, Trichodina*) | AD 33-72<br>ND 12-39 | terrestrial, endozoic in snails (Gastropoda: charopid (*Trachycystis leucocarina, contrasta*)) | genital system | Africa |
| *S. phalli*<br>(syn. *Trichodoxa*) | AD 39-67<br>ND 23-31 | terrestrial, endozoic in snails (Gastropoda: charopid (*Trachycystis menkeana*)) | genital system | Africa |
| Genus ***Trichodina*** (adoral ciliary spiral makes 1-1½ turns, denticles with well-developed blades and thorns, some species with aboral cirri, most species epizoic on skin, fins, gills, nasal pits of aquatic animals; some endozoic in gut, urinary or reproductive tracts) | | | | |
| *T. achatinae*<br>*nomen nudum* | | terrestrial, endozoic in snails (Gastropoda: achatinid (*Achatina zebra*)) | receptaculum seminis | Europe (ex Africa) |
| *T. acuta* | AD 30-66<br>ND 17-33 | freshwater, epizoic on fish (Cichliformes: cichlid (redbelly tilapia, redbreast tilapia, banded tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: acheilognathid (Amur bitterling), cyprinid (goldfish, grass carp, European carp, silver carp, sunbleak, bitterling, threespot barb, tench), leuciscid (Eurasian minnow); Cyprinodontiformes: fundulid (seminole killifish), poeciliid (barred killifish); Gadiformes: lotid (burbot); Perciformes: centrarchid (pumpkinseed, largemouth bass), percid (European perch, redfin perch, yellow perch, zander); Salmoniformes: salmonid (rainbow trout, brown trout); Siluriformes: bagrid (Day's mystus), ictalurid (brown bullhead, speckled madtom)) | skin, fins, gills | North America, Eurasia |
| *T. algonquinensis* | AD 43-57<br>ND 35-42 | freshwater, endozoic in fish (Cypriniformes: cyprinid (common shiner); Perciformes: percid (yellow perch)) | urinary tract | Canada |
| *T. amblypharyngodoni* | AD 60-65<br>ND 31-33 | freshwater, epizoic on fish (Cypriniformes: cyprinid (mola carplet)) | gills | Bangladesh |
| *T. anabantidarum* | AD 39-54<br>ND 21-28 | freshwater, epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch, manyspined climbing perch) | gills, skin, fins | Africa |
| *T. anguilli* | AD 23-28<br>ND 20-22 | estuarine, epizoic on fish (Anguilliformes: anguillid (European eel)) | gills | Europe |
| *T. arctica* | | marine, epizoic on fish (Scorpaeniformes: agonid (butterfly sculpin)) | surface | Atlantic |
| *T. asterisci* | | marine, epizoic on starfish (Echinodermata: | dorsal papules | Europe |

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| (syn. *Cyclochaeta*) | | asterinid (*Asterina gibbosa*)) | | |
| *T. astericola* (syn. *Cyclochaeta*) | cell 40-50 | marine, epizoic on starfish (Echinodermata: asterinid (*Asterias rubens*)) | tube feet | Europe |
| *T. astropectinis* | | marine, epizoic on starfish (Echinodermata: astropectinid (*Astropecten bispinosus*)) | surface | Eurasia |
| *T. australis* | AD 32-44<br>ND 20-24 | marine, epizoic in fish (Atheriniformes: atherinid (small-mouth hardyhead, small-scale hardyhead, short-snout hardyhead, pikehead hardyhead, silver fish)) | gills | Australia |
| *T. bassonae* | AD 30-38<br>ND 23-26 | freshwater, epizoic on fish (Perciformes: scatophagid (spotbanded scat)) | skin | Australia |
| *T. bellottii* | AD 50-64<br>ND 21-26 | freshwater: epizoic on fish (Cyprinodontiformes: rivulid (Argentine pearl fish)) | skin, fins | South America |
| *T. bidentata* | cell 60 | marine, epizoic on fish (Scorpaeniformes: scorpaenid (unspecified scorpionfish)) | skin | Europe |
| *T. blennii* | AD 24-27<br>ND 24-32 | marine, epizoic on fish (Blenniiformes: blenniid (tentacled blenny)) | gills | Europe |
| *T. borealis* | AD 33-40<br>ND 24-30 | marine, epizoic on fish (Pleuronectiformes: pleuronectid (European plaice); Blenniiformes: blenniid (zebra blenny)) | gills | Scotland, Hawaii |
| *T. borokensis* | AD 43-67<br>ND 24-31 | freshwater, epizoic in fish (Cypriniformes: cyprinid (goldfish, sabrefish)) | gills | Eurasia |
| *T. branchicola* | AD 19-33<br>ND 20-26 | marine, epizoic on fish (Blenniiformes: blenniid (shanny, tompot blenny); Gadiformes: lotid (fivebeard rockling, shore rockling); Perciformes: cottid (longspined bullhead); Pleuronectiformes: pleuronectid (European plaice); Scorpaeniformes: gasterosteid (sea stickleback), triglid (tub gurnard)) | gills | North America |
| *T. caecellae* | AD 25-32<br>ND 20-24 | marine, epizoic on invertebrates (Bivalvia: mesodesmatid (*Coecella chinensis*)) | gills | China |
| *T. californica* (syn *Tripartiella*) | AD 35-50<br>ND 25-32 | freshwater, epizoic on fish (Salmoniformes: salmonid (chinook salmon, Siberian salmon, cherry salmon, pink salmon, chum salmon, king salmon, dolly varden, Far East char)) | skin, gills | Pacific |
| *T. cancilae* | AD 42-60<br>ND 28-32 | freshwater, epizoic on fish (Beloniformes: belonid (freshwater gar)) | gills | Asia |
| *T. canton* | AD 43-57<br>ND 25-31 | freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia)) | skin, gills | China |
| *T. cardii* (syn. *Cyclochaeta*) | | marine, epizoic on cockle (Bivalvia: cardiid (*Cardium edule*)) | pallial cavity | Europe |
| *T. caspilosae* | | marine, epizoic on fish (Clupeiformes: alosid (Caspian shad), clupeid ('dolgina' herring)) | gills | Caspian Sea |
| *T. centrostrigeata* | AD 30-48<br>ND 23-30 | freshwater, epizoic on fish (Cichliformes: cichlid (southern mouthbrooder, Nile tilapia, Mozambique tilapia, redbreast tilapia, redbelly tilapia, banded tilapia, threespot tilapia, banded jewel cichlid, thinface cichlid, redeye labeo); Characiformes: alestid (striped robber); Cypriniformes: cyprinid (common carp, common barb); Perciformes: latid (Nile perch); Siluriformes: mochokid (leopard squeaker)) | gills, skin, fins | Africa, Asia |
| *T. chelidonichthys* | AD 19-32<br>ND 30 | marine, epizoic on fish (Scorpaeniformes: triglid (Cape gurnard)) | gills | Africa |
| *T. chlamydis* | AD 29-33<br>ND 22-25 | marine, epizoic on shellfish (Bivalvia: pectinid (*Azumapecten farreri*)) | gills | China |
| *T. claviformis* | AD 47-67<br>ND 25-29 | marine, epizoic on fish (Gadiformes: gadid (Atlantic cod, merling); Pleuronectiformes: pleuronectid (European flounder)) | gills, skin | Baltic Sea |
| *T. clini* | AD 20<br>ND 24 | marine, epizoic on fish (Blenniiformes: clinid (snaky klipfish) | gills | Africa |
| *T. cobitis* | AD 32-52 | freshwater, epizoic on fish (Cypriniformes: cobitid | gills | Eurasia |

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| | ND 22-30 | (spined loach)) | | |
| *T. colisae* | AD 24-40<br>ND 17-25 | freshwater, epizoic on fish (Characiformes: characid (Mexican tetra), serrasalmid (small-scaled pacu, pirapatinga)) | mucus from skin, gills | Americas |
| *T. compacta* | AD 29-49<br>ND 15-21 | freshwater, epizoic on fish (Characiformes: distichodontid (multibar citharine); Cichliformes: cichlid (redbreast tilapia, three-spotted tilapia, mango tilapia, Mozambique tilapia, banded tilapia, Zambezi happy, canary kurper, southern mouthbrooder, thinface cichlid); Cypriniformes: cyprinid (Eurasian carp, redeye barb, orangefin barb, threespot barb, redeye labeo, largemouth yellowfish, largescale yellowfish, river sardine); Cyprinodontiformes: poeciliid (barred killifish, lowland livebearer, Sinaloa livebearer), procatopodid (Johnston's topminnow); Osteoglossiformes: mormyrid (bulldog, churchill); Perciformes: latid (Nile perch); Siluriformes: mochokid (shortspine suckermouth)) | skin, fins | Africa, Middle-East, Asia |
| *T. cooperi* | AD 81-107<br>ND 24-29 | marine, epizoic on fish (Gadiformes: gadid (Atlantic cod); Siluriformes: callichthyid (mottled corydoras)) | skin | Americas |
| *T. corydori* | AD 28-37<br>ND 23-27 | freshwater, epizoic on fish (Siluriformes: callichthyid (pepper cory)) | gills | South America |
| *T. cottidarum* | AD 25-44<br>ND 19-30 | marine, epizoic on fish (Gadiformes: lotid (fourbeard rockling); Gobiiformes: gobiid (ashishirohaze); Pleuronectiformes: pleuronectid (marbled flounder); Scorpaeniformes: agonid (saburo); cottid (antlered sculpin, belligerent sculpin, long-spined bullhead, longhorn sculpin, fourhorn sculpin, shorthorn sculpin, tidepool sculpin), pholid (rock gunnel)) | gills | Holarctic |
| *T. cribbi* | AD 40-60<br>ND 25-37 | freshwater, epizoic on fish (Cyprinodontiformes: anablepid (one-sided livebearer); Gobiiformes: eleotrid (firetail gudgeon)) | skin, gills | Australia, South America |
| *T. cubanensis* | AD 29-43<br>ND 22-26 | freshwater, epizoic on fish (Cichliformes: cichlid (Cuban cichlid)) | skin | Cuba |
| *T. cyprinocola* | AD 45-55<br>ND 22-24 | freshwater, epizoic on fish (Cypriniformes: cyprinid (common carp)) | gills | China |
| *T. dampanula* | AD 38-48<br>ND 28-35 | freshwater, endozoic in amphibians (Anura: bufonid (guttural toad)) | urinary bladder | Africa |
| *T. davisi* | AD 41-67<br>ND 21-25 | freshwater, epizoic on fish (Moroniformes: moronid (striped bass)) | skin, gills | North America |
| *T. decipiens* | AD 18-27<br>ND 23-34 | marine, epizoic on fish (Scorpaeniformes: agonid (tubenose poacher, saburo, tilesiin, silver-spotted sculpin), cottid (padded sculpin, snowy sculpin), hexagrammid (masked greenling), liparid (suna-bikunin), stichaeid (nagazuka, scaly prickleback)) | gills | Pacific |
| *T. diaptomi* | AD 31<br>ND 18-20 | marine, epizoic on invertebrates (Branchiopoda: bosminid (*Bosmina huaroensis*), daphniid (*Daphnia laevis*); Copepoda: diaptomid (*Arctodiaptomus dorsalis*, *Diaptomus*, *Leptodiaptomus siciloides*, *Mastigodiaptomus albuquerquensis*, *montezumae*, *Notodiaptomus deitersi*)) | carapace | Eurasia, Africa, Australia, Americas |
| *T. digitodiscus* | ND 12-14 | freshwater, epizoic on invertebrates (Hydrozoa: hydrid (*Hydra vulgaris*)) | surface | Europe |
| *T. discoidea* | AD 35-51<br>ND 18-30 | freshwater, epizoic on fish (Perciformes: centrarchid (bluegill, black crappie, rock bass); Siluriformes: ictalurid (channel catfish)) | gills | North America |
| *T. domerguei* (syn. *Cyclochaeta*) | AD 33-68<br>ND 18-31 | freshwater and marine, epizoic on invertebrates (Copepoda: diaptomid (*Diaptomus, Eudiaptomus*); | skin, fins, gills | Holarctic |

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| | | fish (Cypriniformes: cyprinid (goldfish, Eurasian carp, crucian carp, grass carp, sunbleak, Amur bitterling), Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp), poeciliid (eastern mosquitofish, twospot livebearer); Esociformes: esocid (northern pike); Gadiformes: gadid (merling); Gobiiformes: gobiid (round goby, monkey goby, marbled goby); Labriformes: labrid (five-spotted wrasse, pointed-snout wrasse); Moroniformes: moronid (European seabass); Perciformes: lateopercid (Japanese sea bass), mullid (red mullet), percid (European perch, Eurasian ruffe, zander); Pleuronectiformes: pleuronectid (European flounder), soleid (common sole); Salmoniformes: salmonid (Arctic grayling); Scorpaeniformes: cottid (shorthorn sculpin, moustache sculpin, buffalo sculpin, European bullhead), cyclopterid (lumpfish), gasterosteid (three-spined stickleback, ninespine stickleback, Sakhalin stickleback), pholid (rock gunnel); Spariformes: sparid (gilt-head bream) and amphibians (Anura: bufonid (common toad), bombinatorid (European fire-bellied toad), hylid (European tree frog), ranid (common frog, edible frog, marsh frog)) | | |
| *T. elegans* | AD 15-21<br>ND 21-25 | freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (Sakhalin stickleback)) | surface | Asia |
| *T. elegini* | AD 25-40<br>ND 22-27 | marine, epizoic on fish (Gadiformes: gadid (saffron cod, Alaska pollock); Scorpaeniformes: cottid (antlered sculpin, belligerent sculpin), zoarcid (viviparous eelpout)) | | Pacific |
| *T. elizabethae* | AD 25-37<br>ND 19-24 | marine, epizoic on fish (Scorpaeniformes: stichaeid (radiated shanny)) | gills | North Atlantic |
| *T. entzii* | | freshwater, endozoic in amphibians (Anura: ranid (marsh frog, edible frog, pool frog)) | urinary bladder | Europe |
| *T. equitoralis* | | freshwater, epizoic on fish (Cichliformes: cichlid (tilapia)) | gills | Africa |
| *T. erbilensis* | AD 22-27<br>ND 23-27 | freshwater, epizoic on fish (Siluriformes: silurid (Tigris catfish)) | surface | Iraq |
| *T. esocis* | AD 38-69<br>ND 20-28 | freshwater, epizoic on fish (Esociformes: esocid (northern pike), Perciformes: percid (European perch, zander)) | skin, gills | North America |
| *T. fahaka* | AD 26-28<br>ND 24-27 | freshwater, epizoic on fish (Tetraodontiformes: tetraodontid (Fahaka pufferfish)) | gills | Africa |
| *T. fariai* | AD 20-42<br>ND 24-28 | marine, endozoic in fish (Tetraodontiformes: tetraodontid (checkered puffer)) | intestines | Caribbean |
| *T. faurefremieti* | AD 49-54<br>ND 30-34 | freshwater, endozoic in amphibians (Urodela: salamandrid (northern crested newt)) | urinary bladder | Europe |
| *T. frenata* | AD 25-32<br>ND 19-23 | freshwater, epizoic on fish (Cichliformes: cichlid (mango tilapia); Perciformes: latid (Nile perch); Synbranchiformes: mastacembelid (long-tailed spiny eel)) | gills | Africa |
| *T. frequentis* | AD 25-35<br>ND 27-36 | marine, epizoic on fish (Gadiformes: gadid (saffron cod); Pleuronectiformes: pleuronectid (yellow striped flounder); Scorpaeniformes: cottid (plain sculpin), hexagrammid (masked greenling, fat greenling, whitespotted greenling, Arabesque greenling), stichaeid (scaly prickleback), zoarctid (viviparous eelpout); Tetraodontiformes: tetraodontid (Japanese puffer, panther puffer)) | surface | Pacific |
| *T. fultoni* | AD 62-90<br>ND 25-31 | freshwater, epizoic on fish (Anguilliformes: anguillid (European eel); Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (tench, | skin, gills (pathogenic to eels) | North Atlantic, Eurasia |

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| | | white sucker, cutlips minnow, gudgeon, common shiner, rosyface shiner, mirror shiner, blacknose dace, pearl dace, creek chub), nemacheilid (stone loach); Perciformes: centrarchid (rock bass, smallmouth bass, largemouth bass, speckled bass, green sunfish, pumpkinseed, bluegill); Salmoniformes: salmonid (rainbow trout, brook trout); Siluriformes: clariid (African sharptooth catfish), ictalurid (channel catfish)) | | |
| *T. funduli* | AD 54-65<br>ND 23-27 | freshwater, epizoic on fish (Cyprinodontiformes: fundulid (starhead topminnow)) | skin | North America |
| *T. galyae* | AD 48-65<br>ND 25-28 | marine, epizoic on fish (Scorpaeniformes: cyclopterid (lumpfish)) | gills | North Atlantic |
| *T. gasterostei* | AD<br>ND | freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (three-spined stickleback)) | skin | North America |
| *T. globosa* | AD 25-34<br>ND 20-23 | freshwater, epizoic on fish (Perciformes: percid (orangebelly darter)) | skin | North America |
| *T. glossogobae* | AD 31-47<br>ND 22-24 | freshwater, epizoic on fish (Gobiiformes: gobiid (tank goby)) | gills | India |
| *T. gobii* | AD 20-41<br>ND 18-27 | marine, epizoic on fish (Anguilliformes: anguillid (European eel); Callionymiformes: callionymid (common dragonet); Gadiformes: gadid (merling); Gobiiformes: gobiid (round goby, sand goby); Labriformes: labrid (grey wrasse, ocellated wrasse); Ophidiiformes: ophidiid (snake blenny); Pleuronectiformes: soleid (Egyptian sole)) | gills | Eurasia, Americas, Australia |
| *T. guberleti* | AD 50-100<br>ND 28-32 | freshwater, epizoic on fish (Cypriniformes: cyprinid (redside shiner, speckled dace)) | gills, skin | North America |
| *T. gulshae* | AD 44-71<br>ND 21-28 | estuarine, epizoic on fish (Siluriformes: bagrid (Gangetic mystus)) | gills | India |
| *T. haldari* | AD 34-45<br>ND 20-22 | freshwater, epizoic on fish (Gobiiformes: gobiid (tank goby)) | gills | India |
| *T. halli* | AD 30-54<br>ND 26-34 | marine, epizoic on fish (Tetraodontiformes: tetraodontid (northern puffer)) | gills, skin | North America |
| *T. heterodentata* | AD 38-82<br>ND 20-30 | freshwater, epizoic on fish (Anabantiformes: anabantid (three-spot gourami), osphronemid (three spot gourami); Atheriniformes: melanotaeniid (Pacific blue-eye); Characiformes: alestid (elongate tigerfish, sharptooth tetra), serrasalmid (small-scaled pacu); Cichliformes: cichlid (redbreast tilapia, redbelly tilapia, Mozambique tilapia, Nile tilapia, redbelly tilapia, banded tilapia, Canary kurper, southern mouthbrooder, electric blue hap); Cypriniformes: cobitid (pond loach), cyprinid (goldfish, common carp, European carp, bighead carp, grass carp, silver carp, straightfin barb, orangefin barb, threespot barb, Mexican stoneroller, Taiwan horsemouth, Conchos chub, redeye labeo, largescale yellowfish, river sardine, rainbow gudgeon), gastromyzontid (tassel-mouthed loach); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp), poeciliid (eastern mosquitofish, western mosquitofish, guppy, green swordtail, southern platyfish, molly), procatopodid (Johnston's topminnow); Galaxiiformes: galaxiid (mountain galaxias, inanga); Gobiiformes: eleotrid (empire gudgeon, firetail gudgeon, western carp gudgeon, flathead gudgeon), gobiid (tank goby, monkey goby, marbled goby, tubenose goby), oxudercid (Amur goby); Kurtiformes: apogonid (mouth almighty); Osteoglossiformes: mormyrid (bulldog, churchill); Perciformes: ambassid | skin, fins, gills | Australasia, Middle-East, South America, Africa |

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| | | (Agassiz's perchlet), centrarchid (largemouth bass), percichthyid (golden perch), percid (zander); Siluriformes: mochokid (brown squeaker)) | | |
| *T. hexagrammi* | AD 19-26<br>ND 20-25 | marine, epizoic on fish (Pleuronectiformes: pleuronectid (barfin flounder); Scorpaeniformes: agonid (tubenose poacher), hexagrammid (whitespotted greenling, fat greenling, masked greenling), zoarctid (viviparous eelpout)) | surface | Pacific |
| *T. histiocotti* | AD 20-26<br>ND 21-27 | marine, epizoic on fish (Scorpaeniformes: agonid (crested sculpin)) | surface | Pacific |
| *T. hoffmani* | AD 28-41<br>ND 17-25 | freshwater, epizoic on fish (Perciformes: percid (brown darter, blackside darter); Siluriformes: bagrid (Tengara catfish)) | skin | North America, Bangladesh |
| *T. hypsilepsis* | AD 40-57<br>ND 20-24 | freshwater, epizoic on fish (Cypriniformes: cyprinid (highscale shiner) and amphibians (Anura: unidentified tadpoles)) | skin | North America |
| *T. indica* | AD 45-50<br>ND 14-32 | freshwater, epizoic on fish (Anabantiformes: channid (spotted snakehead, dwarf snakehead); Cypriniformes: cyprinid (mrigal carp, reba carp, mola carplet, catla, large razorbelly minnow, rohu, orangefin labeo); Perciformes: ambassid (elongate glassy perchlet, Indian glassy fish)) | gills, skin | India |
| *T. intermedia* | AD 25-46<br>ND 22-37 | freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian minnow)) | gills, skin | Eurasia |
| *T. izyumovae* | AD 52-69<br>ND 29-32 | freshwater, epizoic on fish (Cypriniformes: cyprinid (ide)) | gills | Eurasia |
| *T. jadranica* | AD 17-35<br>ND 15-27 | freshwater and marine, epizoic on fish (Blenniiformes: blenniid (zebra blenny), tripterygiid (network triplefin); Callionymiformes: callionymid (common dragonet); Cypriniformes: cobitid (spiny loach); Gadiformes: gadid (Atlantic cod); Gobiiformes: eleotrid (Sandwich Island sleeper), gobiid (sand goby, monkey goby); Labriformes: labrid (grey wrasse); Perciformes: mullid (red mullet); Pleuronectiformes: paralichthyid (bay whiff, olive flounder), pleuronectid (European flounder, stone flounder, marbled flounder, barfin flounder, rock sole), scophthalmid (Black Sea turbot), soleid (common sole, blackhand sole); Scorpaeniformes: agonid (saburo), cottid (threaded sculpin, aikajika), hexagrammid (masked greenling), liparid (suna-bikunin)) | gills, skin | Atlantic, Pacific, Mediterranean, Black Sea |
| *T. japonica* | AD 17-28<br>ND 18-23 | catadromous, epizoic on fish (Anguilliformes: anguillid (Japanese eel); Perciformes: lateolabracid (Japanese sea bass); Spariformes: sparid (red seabream)) | gills | Asia |
| *T. jarmilae* | AD 23-30<br>ND 19-23 | marine, epizoic on fish (Gobiiformes: gobiid (ashishirohaze); Scorpaeniformes: agonid (sea raven, silver-spotted sculpin, tubenose poacher, saburo, tilesiin), cottid (plain sculpin, snowy sculpin, Steller's sculpin, elegant bero), liparid (unspecified snailfish), pholid (nishikiginpo), stichaeid (scaly prickleback)) | gills | Pacific |
| *T. jenynsii* | AD 55-67<br>ND 23-26 | freshwater, epizoic on fish (Cyprinodontiformes: anablepid (one-sided livebearer)) | skin | South America |
| *T. jiroveci* | AD 29-35<br>ND 24-27 | freshwater, epizoic on fish (Gobiiformes: gobiid (monkey goby)) | gills | Europe |
| *T. kalimbeza* | AD 21-30<br>ND 16-19 | freshwater, epizoic on fish (Characiformes: distichodontid (multibar citharine); Cichliformes: cichlid (redbreast tilapia); Cypriniformes: cyprinid (African banded barb)) | skin, fins | Africa |
| *T. kazubski* | AD 27-45 | freshwater, epizoic on fish (Cypriniformes: | skin, fins, gills | China, |

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| | ND 19-26 | cyprinid (goldfish, bighead carp, straightfin barb, threespot barb)) | | Africa |
| *T. korschelti* (syn. *Cyclochaeta*) | cell 30-35 | marine, epizoic on chitons (Polyplacophora: chitonid (*Chiton marginatus*) | mantle | Europe |
| *T. kuleminae* (syn. *T. rectangli*, *meridionalis*) | AD 35-40<br>ND 18-21 | freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish, crucian carp, European carp, white bream, vimba bream, common shiner, golden shiner, blacknose shiner, common roach); Perciformes: percid (yellow perch)) | nasal cavity, skin | Eurasia, North America |
| *T. kupermanni* | AD 29-44<br>ND 20-28 | freshwater, epizoic on fish (Cypriniformes: cyprinid (blue bream, grass carp)) | gills | Eurasia |
| *T. kwando* | AD 32-39<br>ND 25-27 | freshwater, epizoic on fish (Characiformes: alestid (striped robber, sharptooth tetra)) | gills, skin, fins | Africa |
| *T. labrorum* | AD 30-34<br>ND 21 | marine, epizoic on fish (Labriformes: labrid (corkwing wrasse, East Atlantic peacock wrasse)) | gills | Atlantic |
| *T. labyrinthipicis* | AD 31-48<br>ND 20-26 | freshwater; epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch, manyspined climbing perch) | gills, skin | Africa |
| *T. lairdi* | AD 59-81<br>ND 30-35 | marine, epizoic on fish (Scorpaeniformes: cottid (tidepool sculpin)) | gills | Pacific |
| *T. lepsi* | AD 19-27<br>ND 18-25 | marine, epizoic on fish (Mugiliformes: mugilid (flathead grey mullet, golden grey mullet); Perciformes: percid (European perch)) | gills, skin | Atlantic |
| *T. liana* | AD 31-41<br>ND 21-25 | marine, epizoic on shellfish (Bivalvia: solenid (*Solena gracilis*)) | gills | China |
| *T. lieni* | AD 31-43<br>ND 20-24 | estuarine, epizoic on fish (Cypriniformes: cyprinid (crucian carp, grass carp, Changchun bream, variegated carp, silver carp); Anabantiformes: channid (snakehead); Perciformes: sinipercid (mandarin fish); Clupeiformes: engraulid (long-tailed anchovy)) | skin, gills | China |
| *T. linyanta* | AD 30-50<br>ND 24-28 | freshwater, epizoic on fish (Cichliformes: cichlid (banded jewel cichlid, three-spotted tilapia)) | skin, gills | Africa |
| *T. liparisi* | | marine, epizoic on fish (Scorpaeniformes: liparid (striped seasnail)) | gills | Barents Sea |
| *T. lishuiensis* | AD 29-38<br>ND 26-31 | freshwater, endozoic in amphibians (Anura: ranid (piebald odorous frog)) | urinary bladder | China |
| *T. luba* | AD 30-40<br>ND 26-37 | marine, endozoic in fish (Acanthuriformes: acanthurid (yellowfin surgeonfish)) | colon | Africa, Pacific |
| *T. luciopercae* | | freshwater, epizoic on fish (Perciformes: percid (zander)) | gills | Eurasia |
| *T. macomarum* | AD 39-47<br>ND 22-25 | marine, epizoic on clams (Bivalvia: mactrid (*Mactra veneriformis*)) | gills | China |
| *T. mactrae* | AD 33-40<br>ND 22-24 | marine, epizoic on clams (Bivalvia: mactrid (*Mactra veneriformis*)) | gills | China |
| *T. magna* | AD 46-95<br>ND 24-30 | freshwater, epizoic on fish (Characiformes: hepsetid (African pike, African pike characin); Cichliformes: cichlid (redbreast tilapia, redbelly tilapia, banded tilapia, three-spotted tilapia, mango tilapia, thinface cichlid, Mozambique tilapia, Nile tilapia, southern mouthbrooder); Cypriniformes: cyprinid (river sardine); Cyprinodontiformes: procatopodid (Johnston's topminnow); Osteoglossiformes: mormyrid (bulldog, churchill); Perciformes: centrarchid (largemouth bass), latid (Nile perch); Siluriformes: clariid (African sharptooth catfish), schilbeid (African butter catfish)) | skin, fins, gills | Africa |
| *T. major* | | freshwater, epizoic on fish (Gadiformes: lotid (burbot)) | gills | Holarctic |
| *T. mandarin* | AD 45-55<br>ND 24-30 | freshwater, epizoic on fish (Cypriniformes: cobitid (pond loach), cyprinid (rainbow gudgeon, Taiwan | skin, fins, gills | China |

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| | | horsemouth), gastromyzontid (tassel-mouthed loach); Siluriformes: clariid (Hong Kong catfish)) | | |
| *T. maritinkae* | AD 31-50<br>ND 20-32 | freshwater, epizoic on fish (Characiformes: characid (blind cave fish); Siluriformes: clariid (blotched catfish, Hong Kong catfish, African sharptooth catfish, snake catfish, vundu)) | gills | Africa, Asia |
| *T. matsu* | AD 15-40<br>ND 20-27 | freshwater, epizoic on fish (Cypriniformes: gastromyzontid (tassel-mouthed loach); Siluriformes: bagrid (adiposalis catfish), clariid (African sharptooth catfish)) | gills, skin, fins | Africa, China |
| *T. meretricis* | AD 44-52<br>ND 23-27 | marine, epizoic on clams (Bivalvia: venerid (*Meretrix meretrix*)) | gills | China |
| *T. microbis* | | marine, epizoic on fish (Labriformes: labrid (peacock wrasse)) | gills | Pacific |
| *T. microdenticulata* | AD 12-16<br>ND 15-18 | freshwater, epizoic on fish ( Clupeiformes: dorosomatid (threadfin shad)) | skin, gills | North America |
| *T. micromaculata* | AD 28-42<br>ND 20-27 | marine, epizoic on fish (Mugiliformes: mugilid (flathead grey mullet); Scorpaeniformes: opisthocentrid (muroranginpo), pholid (nishikiginpo)) | surface | Pacific |
| *T. microspina* | AD 19-33<br>ND 18-23 | freshwater, epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch, manyspined climbing perch) | skin, fins, gills | Africa |
| *T. minima* | AD 16-17<br>ND 17-19 | marine, epizoic on fish (Scorpaeniformes: stichaeid (tauegaji)) | surface | Pacific |
| *T. mira* | | freshwater, epizoic on fish (Cypriniformes: leuciscid (lake minnow)) | gills | Russia |
| *T. miranda* | AD 38-54<br>ND 27-31 | freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (three-spined stickleback)) | surface | Pacific |
| *T. modesta*<br>(syn. *T. spathulata*) | AD 18-43<br>ND 20-26 | freshwater, epizoic on fish (Characiformes: characid (Mexican tetra); Cypriniformes: cobitid (pond loach), cyprinid (common bream, bronze bream, silver bream, vimba bream), gastromyzontid (tassel-mouthed loach); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp), poeciliid (twospot livebearer); Gobiiformes: oxudercid (Amur goby)) | gills, skin | Eurasia |
| *T. mugilis* | AD 23-28<br>ND 32 | marine, epizoic on fish (Mugiliformes: mugilid (thinlip grey mullet)) | gills | Europe |
| *T. murmanica* | AD 35-70<br>ND 21-31 | marine, epizoic on fish (Gadiformes: gadid (Atlantic cod); Spariformes: sparid (blackhead seabream)) | gills, skin | Pacific, Atlantic |
| *T. mutabilis* | AD 30-74<br>ND 21-36 | freshwater, epizoic on fish (Characiformes: characid (Mexican tetra); Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (common carp, goldfish, grass carp, European carp, silver carp, bighead carp, sunbleak, sabrefish, bitterling, roach, rudd, straightfin barb, threespot barb); Cyprinodontiformes: poeciliid (eastern mosquitofish); Salmoniformes: salmonid (rainbow trout)) | gills, skin | Eurasia, Americas, Africa, Australia |
| *T. multidentis* | AD 12-45<br>ND 30-37 | marine, epizoic on fish (Blenniformes: blenniid (blenny), clinid (orange clinid), tripterygiid (New Zealand topknot)) | gills | New Zealand |
| *T. myicola* | AD 29-46<br>ND 26-36 | marine, epizoic on clams (Bivalvia: myid (*Mya arenaria*)) | oral epithelia | North America |
| *T. nemachili* | | freshwater, epizoic on fish (Cypriniformes: nemacheilid (stone loach)) | skin, gills | Europe |
| *T. nesogobii* | AD 30-33<br>ND 19-23 | marine, epizoic on fish (Gobiiformes: gobiid (unspecified sandgoby)) | gills | Australia |
| *T. ngoma* | AD 29-50<br>ND 21-27 | marine, epizoic on fish (Characiformes: distichodontid (multibar citharine)) | skin, fins, gills | Africa |
| *T. nigra* | AD 20-70 | freshwater, epizoic on fish (Cichliformes: cichlid | skin, gills | Eurasia, |

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| | ND 16-29 | (banded tilapia, Mozambique tilapia, Nile tilapia, southern mouthbrooder); Cypriniformes: cyprinid (common bream, blue bream, common bleak, goldfish, grass carp, European carp, crucian carp, silver carp, gudgeon, Amur ide, Marmara chub, European chub, sabrefish, roach, rudd, tench, straightfin barb), leuciscid (lake minnow); Perciformes: centrarchid (bluegill), nandid (mottled nandus), nandid (Gangetic leaffish), percid (common zingel, redfin perch, zander); Salmoniformes: salmonid (Arctic char, brown trout, rainbow trout, sea trout, peled); Siluriformes: silurid (wels catfish), and amphibians (Anura: bombinatorid (European fire-bellied toad, tadpoles), bufonid (common toad, tadpoles), hylid (European tree frog, tadpoles), ranid (edible frog, common frog, tadpoles)) | | Africa |
| *T. nkasa* | AD 24-35<br>ND 19-22 | freshwater, epizoic on fish (Siluriformes: mochokid (leopard squeaker, largespot squeaker)) | gills | Africa |
| *T. nobilis*<br>(syn. *T. nobillis*) | AD 50-77<br>ND 21-28 | freshwater, epizoic on fish (Cichliformes: cichlid (unspecified tilapia); Cypriniformes: cyprinid (grass carp, European carp, bighead carp, goldfish, gold barb, silver carp); Cyprinodontiformes: poeciliid (giant sailfin molly, guppy)) | skin, gills | Eurasia |
| *T. noturi* | AD 35-45<br>ND 23-27 | freshwater, epizoic on fish (Siluriformes: ictalurid (speckled madtom)) | skin, gills | North America |
| *T. okajimae* | AD 20-40<br>ND 34-38 | freshwater, epizoic on amphibians (Urodela: hynobiid (Tokyo salamander)) | surface | Asia |
| *T. oligocotti* | AD 23-34<br>ND 19-26 | marine, epizoic on fish (Pleuronectiformes: pleuronectid (barfin flounder)) | surface | Pacific |
| *T. opeongoensis* | AD 35-51<br>ND 24-34 | freshwater, endozoic on fish (Cypriniformes: cyprinid (golden shiner, creek chub)) | urinary tract | North America |
| *T. ophiocephalus* | AD 43<br>ND 55 | freshwater, epizoic on fish (Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (blue bream)) | gills | Eurasia |
| *T. ophiotricis*<br>(syn. *Cyclochaeta*) | cell 47 | marine, epizoic on brittle star (Echinodermata: ophiothricid (*Ophiotrix fragilis*)) | surface | Europe |
| *T. orientalis* | AD 46-63<br>ND 24-27 | freshwater, epizoic on fish (Cypriniformes: cyprinid (crucian carp, black carp, grass carp, triangular bream, variegated carp, silver carp)) | skin, gills | China |
| *T. oviducti* | AD 83-271<br>ND 40-60 | marine, endozoic on fish (Rajiformes: rajid (thornback skate, winter skate, thorny skate, Magellan skate, blonde ray, raspthorn sand skate)) | oviducts [mucoid exudates] | Atlantic, Barents, Pacific |
| *T. oviformis* | AD 22-38<br>ND 24-29 | freshwater, epizoic on fish ( Cypriniformes: cyprinid (goldfish, common carp, crucian carp, black carp, grass carp, variegated carp, silver carp, common shiner, false salmon, Changchun bream, triangular bream, silvery chub, large-spined bitterling, scanty-scaled bitterling, stone moroko), cobitid (loach, spined loach); Anabantiformes: channid (snakehead); Perciformes: percid (yellow perch), sinipercid (mandarin fish)) | gills | Asia, North America |
| *T. ovonucleata* | AD 17-29<br>ND 18-26 | marine, epizoic on fish (Blenniiformes: blenniid (tentacled blenny, rusty blenny); Gadiformes: lotid (shire rockling); Labriformes: labrid (grey wrasse, five-spotted wrasse); Ophidiiformes: ophidiid (Roche's snake blenny); Perciformes: mullid (red mullet), percid (perch), Pleuronectiformes: scophthalmid (kalkan); Syngnathiformes: syngnathid (seadragons), Scombriformes: scombrid (Atlantic mackerel); Scorpaeniformes: agonid (saburo), cottid (plain sculpin), | gills | Mediterranean, Pacific, Black Sea |

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| | | hexagrammid (masked greenling)) | | |
| *T. oxystelis* | AD 32-44<br>ND 21-29 | marine, epizoic on sea snails (Gastropoda: trochid (*Oxystele sinensis, tabularis, tigrina, variegata, impervia*)) | mantle cavity, shell | Africa |
| *T. pagoda* | AD 19-43<br>ND 19-24 | freshwater, epizoic on fish (Anabantiformes: channid (small snakehead)) | skin, gills | China |
| *T. pala* | AD 24-37<br>ND 21-26 | marine, epizoic on fish (Scorpaeniformes: zoarctid (viviparous eelpout)) | surface | Pacific |
| *T. parabranchicola* | AD 10-30<br>ND 16-26 | marine, epizoic on fish (Blenniiformes: clinid (orange clinid), tripterygiid (New Zealand topknot, variable triplefin, blackhead triplefin), plesiopid (New Zealand rockfish, three-lined rockfish); Gobiesociformes: gobiesocid (striped clingfish, orange clingfish)) | gills | New Zealand |
| *T. paraheterodentata* | AD 37-55<br>ND 20-22 | freshwater, epizoic on fish (Perciformes: sinipercid (mandarin fish)) | skin | China |
| *T. parasiluri* | AD 32-58<br>ND 20-25 | freshwater, epizoic on fish (Cypriniformes: cyprinid (black carp, grass carp, variegated carp, silver carp); Anabantiformes: channid (snakehead), osphronemid (Chinese paradise fish); Perciformes: sinipercid (mandarin fish)) | gills, skin | China |
| *T. parvula* | AD 23-30<br>ND 20-23 | marine, epizoic on fish (Scorpaeniformes: psychrolutid (spinyhead sculpin)) | gills | Pacific |
| *T. patellae* | AD 40-50 | marine, epizoic on limpet (Gastropoda: patellid (*Patella vulgata*)) | gills | Europe |
| *T. pectenis* | AD 27-38<br>ND 22-31 | marine, epizoic on scallops (Bivalvia: pectinid (*Mizuhopecten yessoensis*) and sand dollars (Echinodermata: echinarachniid (*Echinarachnius parma*))) | gills | China, Russia |
| *T. pediculus*<br>[type species as *Cyclidium*] | AD 27-85<br>ND 16-36 | freshwater, epiphytic on moss (Bryozoa: cristatellid (*Cristatella mucedo*), plumatellid (*Plumatella repens*) and epizoic on invertebrates (Hydrozoa: hydrid (*Hydra attenuata, fusca, vulgaris, viridis, Pelmatohydra oligactis*); jellyfish (Cnidaria: olindiid (*Limnocnida indica*); mussels (Bivalvia: unionid (*Margaritifera margaritifera*)), fish (Cichliformes: cichlid (redbreast tilapia, banded tilapia, Mozambique tilapia, Nile tilapia, electric yellow cichlid, pindani); Cypriniformes: cyprinid (goldfish, crucian carp, Eurasian carp, grass carp, black carp, bighead carp, silver carp, common bream, common bleak, sunbleak, rudd, swamp barb, olive barb, stigma barb, common chub, common roach); Cyprinodontiformes: poeciliid (giant sailfin molly, short-finned molly); Esociformes: esocid (northern pike); Perciformes: centrarchid (largemouth bass), percid (European perch, ruffe, zander); Salmoniformes: salmonid (vendace); Scorpaeniformes: gasterosteid (three-spined stickleback); and amphibians (Anura: bufonid (common toad, tadpoles), ranid (common frog, tadpoles): Urodela: salamandrid (smooth newt, larvae) | gills, skin, fins | cosmopolitan |
| *T. percae* | AD 42-64<br>ND 22-25 | freshwater, epizoic on fish (Perciformes: percid (redfin perch)) | skin | Russia |
| *T. perforata* | AD 37-55<br>ND 22-26 | freshwater, epizoic on fish (Cypriniformes: cyprinid (crucian carp, common carp, common bleak, European carp, white-finned gudgeon, Kessler's gudgeon)) | gills | Eurasia |
| *T. platyformis* | AD 53-76<br>ND 26-35 | freshwater, epizoic on fish (Cypriniformes: leuciscid (pearl dace, blacknose dace)) | gills | North America, Europe |
| *T. ploveri* | | marine, epizoic on fish (Clupeiformes: clupeid | surface | Pacific |

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| | | (Atlantic herring)) | | |
| *T. polaridiae* | | marine, epizoic on mussels (Bivalvia: cardiid (*Cardium namarcki*)) | gills | Europe |
| *T. polycirra* | AD 48-58<br>ND 38-55 | freshwater, endozoic in fish (Cypriniformes: cyprinid (bream, common roach, carp bream, common carp)) | urinary tract | Eurasia |
| *T. polystriata* | | freshwater, epizoic on fish (Perciformes: centrarchid (pumpkinseed)) | gills | North America |
| *T. porocephalusi* | AD 27-42<br>ND 20-27 | freshwater, epizoic on fish (Gobiiformes: eleotrid (orange-bellied sleeper)) | gills | India |
| *T. prowazeki* | AD 39-55<br>ND 22-26 | freshwater, epizoic on fish (Cypriniformes: cobitid (loach)) | gills | Europe |
| *T. pseudoheterodentata* | AD 61-74<br>ND 23-25 | freshwater, epizoic on fish (Siluriformes: ictalurid (channel catfish)) | gills | China |
| *T. puytoraci* | AD 42-52<br>ND 25-28 | euryhaline, epizoic on fish (Gadiformes: gadid (merling); Mugiliformes: mugilid (golden grey mullet, flathead grey mullet, leaping mullet)) | gills | Europe |
| *T. raabei* | AD 22-32<br>ND 23-29 | marine, epizoic on fish (Gadiformes: gadid (saffron cod); Pleuronectiformes: pleuronectid (European flounder, common dab, marbled flounder); Scorpaeniformes: agonid (saburo), cottid (plain sculpin), hexagrammid (masked greenling, Arabesque greenling)) | gills, skin | Baltic Sea, White Sea |
| *T. rajae* | AD 69-90<br>ND 34-41 | marine, endozoic on fish (Rajiformes: arhynchobatid (raspthorn sandskate)) | oviducts | Pacific |
| *T. ranae* | AD 38-52<br>ND 28-33 | freshwater, endozoic in amphibians (Anura: ranid (marsh frog, edible frog, pool frog)) | urinary bladder | Europe |
| *T. rectuncinata* | AD 19-42<br>ND 20-35 | marine, epizoic on fish (Blenniiformes: blenniid ((butterfly blenny, tentacled blenny, peacock blenny, rusty blenny, combtooth blenny, shanny), tripterygid (network triplefin, grass goby, Molly Miller); Gadiformes: gadid (merling), lotid (shore rockling); Gobiesociformes: gobiesocid (blackstripe clingfish); Gobiiformes: gobiid (grass goby, island frillfin); Labriformes: labrid (grey wrasse, five-spotted wrasse, East Atlantic peacock wrasse, goldsinny wrasse); Perciformes: lateolabracid (Japanese seabass); Scorpaeniformes: cottid (padded sculpin), hexagrammid (spotty-bellied greenling); Syngnathiformes: syngnathid (long-snout seahorse) [possibly erroneously reported from freshwater fish (Cichliformes: cichlid (Nile tilapia); Perciformes: latid (Nile perch); Siluriformes: clariid (African sharptooth catfish)] | gills | Atlantic, Pacific, Adriatic |
| *T. reticulata* | AD 31-66<br>ND 21-34 | freshwater, epizoic on fish (Acipenseriformes: acipenserid (Siberian sturgeon); Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (goldfish, common carp, crucian carp)) | skin, gills [mortalities] | Europe, North America, Africa |
| *T. rhinobatae* | AD 29-42<br>ND 27-34 | marine, endozoic in fish (Rhinopristiformes: rhinobatid (lesser guitarfish)) | urogenital tract | Africa |
| *T. rostrata* | AD 44-55<br>ND 26-28 | freshwater, epizoic on fish (Cypriniformes: cyprinid (common roach, bronze bream, European carp, bitterling); Cyprinodontiformes: goodeid (dark-edged splitfin)) | skin | Europe, Mexico |
| *T. ruditapicis* | AD 33-52<br>ND 21-29 | marine, epizoic in shellfish (Bivalvia: venerid (*Saxidomus purpurata*, *Ruditapes philippinarum*), solenid (*Solen grandis*)) | gills | China |
| *T. salmincola* | AD 40-59<br>ND 21-26 | freshwater, epizoic on fish (Salmoniformes: salmonid (rainbow trout, brook trout) | skin | North America |
| *T. sangwala* | AD 39-59<br>ND 23-31 | freshwater, epizoic on fish (Siluriformes: clariid (African sharptooth catfish), schilbeid (African butter catfish)) | gills | Africa |

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| *T. scapharcae* | AD 23-30<br>ND 20-24 | marine, epizoic on clams (Bivalvia: arcid (*Scapharca subcrenata*)) | gills | China |
| *T. schizothoraci* | | freshwater, endozoic in fish (Cypriniformes: cyprinid (Sattar snowtrout)) | urinary tract | Asia |
| *T. scorpaenae*<br>(syn. *Cyclochaeta*) | cell 40-50 | marine, epizoic on fish (Scorpaeniformes: triglid (unspecified)) | surface | Europe |
| *T. serpularum*<br>(syn. *Cyclochaeta*) | cell 25-40 | marine, epizoic on tubeworm (Polychaeta: serpulid (*Serpula*) | surface | Europe |
| *T. shitalakshyae* | AD 30-37<br>ND 18-21 | estuarine, epizoic on fish (Gobiiformes: gobiid (tank goby)) | gills | India |
| *T. siluri* | AD 22-46<br>ND 23-27 | freshwater, epizoic on fish (Siluriformes: silurid (wels catfish)) | gills | Eurasia |
| *T. sinonovaculae* | AD 48-67<br>ND 24-27 | marine, epizoic on clam (Bivalvia: pharid (*Sinonovacula constricta*)) | gills | China |
| *T. spheroidesi* | AD 14-54<br>ND21-31 | marine, epizoic on fish (Tetraodontiformes: tetraodontid (northern puffer)) | gills, skin | North America |
| *T. spongillae* | AD 60<br>ND 37 | freshwater, planktonic and endozoic on sponge (Porifera: spongillid (*Spongilla fluviatilis*)) | inside body | Europe |
| *T. steini* | AD 40-50<br>ND 21-26 | aquatic, epizoic on flatworms (Tricladida: dugesiid (*Dugesia lugubris*), planariid (*Polycelis nigra, cornuata*)) | surface | Europe |
| *T. strelkovi* | AD 33-58<br>ND 25-28 | freshwater, epizoic on fish (Cypriniformes: cyprinid (false osman), nemacheilid (Tibetan stone loach); Mugiliformes: mugilid (Abu mullet)) [and on parasitic trematodes (Monogenea: dactylogyrid (*Dactylogyrus auriculatus, falcatus*)] | skin, gills [carapace] | Eurasia |
| *T. subtilihamata* | AD 38-48<br>ND 26-29 | freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish)) | gills | China |
| *T. sylhetensis* | AD 25-38<br>ND 23-24 | freshwater, epizoic on fish (Perciformes: nandid (mud perch)) | gills | India |
| *T. synaptae*<br>(syn. *Cyclochaeta*) | cell 56-95 | marine, epizoic on sea cucumber (Echinodermata: synatid (*Synapta*)) | surface | Europe |
| *T. tegula* | AD 30-50<br>ND 22-31 | marine, epizoic on sea snails (Gastropoda: tegulid (*Tegula funebralis, ligulata*)) | mantle cavity | North America |
| *T. tenuidens* | AD 40-79<br>ND 25-38 | anadromous/euryhaline, epizoic on fish (Cyprinodontiformes: fundulid (mummichog); Scorpaeniformes: gasterosteid (three-spined stickleback, ninespine stickleback)) | gills, skin | North America |
| *T. tisae* | AD 40-58<br>ND 23-29 | freshwater, epizoic on fish (Perciformes: percid (zander)) | gills | Eurasia |
| *T. trichiuri* | | marine, epizoic on fish (Scombriformes: trichiurid (largehead hairtail)) | surface | Pacific |
| *T. trigonofibulae* | | marine, epizoic on fish (Scorpaeniformes: agonid (butterfly sculpin)) | surface | Pacific |
| *T. truttae* | AD 76-142<br>ND 27-34 | freshwater, epizoic on fish (Cichliformes: cichlid (Nile tilapia); Salmoniformes: salmonid (humpback salmon, chum salmon, masu salmon, yellowfin cutthroat trout)) | skin, gills | North America, Russia |
| *T. tumefaciens* | AD 27-38<br>ND 19-27 | freshwater, epizoic on fish (Scorpaeniformes: cottid (mottled sculpin); Cypriniformes: cyprinid (golden shiner, creek chub); Perciformes: centrarchid (pumpkinseed), percid (yellow perch)) | gills, skin | North America |
| *T. tunnae* | AD 26-35<br>ND 19-22 | freshwater, epizoic on fish (Perciformes: percid (European perch)) | skin, gills | Australia |
| *T. uniforma* | AD 50-57<br>ND28-30 | freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish)) | skin, fins, gills | China, Africa |
| *T. unionis* | AD 41-53<br>ND 22-28 | freshwater, epizoic on snails (Gastropoda: lymnaeid (*Stagnicola*), physid (*Physella acuta*), planorbid (*Gyraulus siamensis*)) | surface | Canada, Asia |
| *T. urechi* | cell 25-50<br>ND 18-25 | marine, endozoic in worm (Polychaeta: urechid (*Urechis caupo*)) | midgut | North America |
| *T. uretra* | AD 42-65 | freshwater, endozoic in fish (Cypriniformes: | urinary bladder, | Africa |

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| | ND 47-54 | cyprinid (threespot barb)) | ureters | |
| *T. urinaria* | AD 36-60<br>ND 14-41 | freshwater, endozoic in fish (Cypriniformes: cyprinid (common shiner, golden shiner); Perciformes: percid (zander, yellow perch, redfin perch)) | urinary tract | Holarctic |
| *T. urinicola* | AD 34-35<br>ND 26-36 | freshwater, endozoic in amphibians (Anura: bufonid (common toad, tadpoles); Urodela: salamandrid (northern crested newt, smooth newt, larvae)) | urinary tract | Europe |
| *T. valkanovi* | AD 38-53<br>ND 26-29 | freshwater, epizoic on fish (Cypriniformes: cyprinid (bitterling)) | gills | Europe |
| *T. vallata* | AD 31-49<br>ND 18-23 | freshwater, epizoic on fish (Siluriformes: ictalurid (channel catfish)) | skin, gills | North America |
| *T. vancouverense* | AD 8-23<br>ND 16-25 | marine, epizoic on fish (Scorpaeniformes: cottid (padded sculpin)) | gills | Pacific |
| *T. vesicola* | | freshwater, endozoic in amphibians (Anura: ranid (Japanese wrinkled frog)) | urinary bladder | Asia |
| *T. vesicularum* | AD 19-47<br>ND 21-33 | freshwater, endozoic in amphibians (Urodela: salamandrid (smooth newt, Carpathian newt, palmate newt)) | urinary bladder | Europe |
| *T. wellborni* | AD 36-46<br>ND 21-26 | freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian carp, Amur carp); Perciformes: centrarchid (largemouth bass)) | gills | North America |
| *T. wulai* | AD 47-62<br>ND 24-26 | freshwater, epizoic on fish (Siluriformes: silurid (Amur catfish)) | gills | Asia |
| *T. xenopodos* | AD 68-94<br>ND 46-55 | freshwater, endozoic in amphibians (Anura: pipid (African clawed frog)) | urinary bladder | Africa |
| *T. zambeziensis* | AD 20-28<br>ND 16-20 | freshwater, epizoic on jellyfish (Cnidaria: olindiid (*Limnocnida tanganjicae*)) | surface of medusae | Africa |
| Genus ***Trichodinella*** (adoral ciliary spiral makes ½-¾ turns, denticles wedged together by central parts and blades, thorns absent or stunted to form short hooks) | | | | |
| *T. baltica*<br>(syn. *Trichodina*, *Brachyspira*) | cell 16-43 | estuarine, epizoic on snails (Gastropoda: neritid (*Neritina* (*Theodoxus*) *fluviatilis*), and fish (Gobiiformes: gobiid (black goby)) | mantle cavity, gills | Baltic Sea |
| *T. carpi* | AD 14-19<br>ND 15-20 | freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian carp)) | gills | Philippines |
| *T. crennulata* | AD 17-23<br>ND 21-26 | freshwater, epizoic on fish (Characiformes: characid (sharptooth tetra)) | gills | Africa |
| *T. epizootica*<br>(syn. *Tripartiella, T. carassii p.p., maior, percarum, lotae*)<br>[type species as *Brachyspira*] | AD 13-47<br>ND 16-30 | freshwater, epizoic on fish (Anguilliformes: anguillid (European eel); Cichliformes: cichlid (redbreast tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (riffle minnow, roundnose minnow, goldfish, common carp, crucian carp, European carp, bighead carp, grass carp, silver carp, common barbel, tench, straightfin barb, threespot barb, bluebream, common roach, common rudd, white bream, ziege, Amur bitterling), cobitid (weatherfish), danionid (river sardine), leuciscid (lake minnow); Esociformes: esocid (northern pike); Gadiformes: lotid (burbot); Perciformes: percid (Eurasian ruffe, redfin perch, zander, zingel); Osteoglossiformes: mormyrid (elephant-snout fish); Perciformes: percid (European perch, zander); Salmoniformes: salmonid (sockeye salmon, brown trout, rainbow trout) | gills | cosmopolitan |
| *T. lawleri* | AD 12-17<br>ND 15-19 | marine, epizoic on fish (Spariformes: sparid (pinfish)) | gills | North America |
| *T. longispira* | | freshwater, epizoic on fish (Esociformes: esocid (northern pike, Amur pike)) | gills | Asia |
| *T. lomi* | AD 15-24<br>ND 20-29 | marine, epizoic on fish (Perciformes: lateolabracid (Japanese seabass); Spariformes: sparid (red seabream)) | gills | Asia |

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| *T. minuta* (syn. *Trichodina*) [possible synonym of *T. epizootica*] | AD 11-36 ND 15-24 | freshwater, epizoic on fish (Cichliformes: cichlid (banded jewel cichlid, banded tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (grass carp, bighead carp, silver carp, threespot barb)) | gills, skin, fins | Eurasia |
| *T. myakkae* (syn. *Trichodina*) | AD 11-25 ND 17-24 | freshwater, epizoic on fish (Cypriniformes: catostomid (smallmouth buffalo, river carpsucker), cyprinid (silver carp, bighead carp, grass carp, stone moroko); Perciformes: centrarchid (largemouth bass); Salmoniformes: salmonid (brook trout)) | gills | Asia, North America |
| *T. simplex* (syn. *Dipartiella, Dogielina*) | AD 10-30 ND 17-28 | marine, epizoic on fish (Gobiiformes: gobiid (black goby); Perciformes: lateolabracid (Japanese sea bass)) | gills | Baltic Sea, Yellow Sea |
| *T. subtilis* (syn. *T. carassii p.p., Trichodina*) | AD 14-32 ND 16-36 | freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian carp, goldfish, crucian carp, white bream, tench, ziege, Amur bitterling); Salmoniformes: salmonid (rainbow trout)) | gills | Eurasia |
| *T. symmetrica* (syn. *Trichodina*) [possible mixture of species, thus regarded as *nomen nudum*] | AD 24-35 ND 21-28 | freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish, Eurasian carp, common shiner, golden shiner, creek chub), leuciscid (pearl minnow, eastern blacknose dace); Perciformes: percid (yellow perch); Siluriformes: ictalurid (channel catfish)) | skin, gills | North America |
| *T. tilapae* | AD 14-20 ND 22-25 | freshwater, epizoic on fish (Cichliformes: cichlid (redbelly tilapia)) | gills | Philippines |
| Genus ***Tripartiella*** (adoral ciliary spiral makes ½-¾ turns, denticles with well-developed thorns, blades extend obliquely backwards, denticles interlocked by central parts and by anterior projections) | | | | |
| *T. bulbosa* (syn. *Trichodina, T. ovaliformis, Tripartiella leucisci)*) | AD 13-26 ND 19-28 | freshwater, epizoic on fish (Anabantiformes: osphronemid (round-tailed paradisefish, giant gourami); Cypriniformes (grass carp, silver carp, bighead carp, black carp, mrigal carp, catla, rohu, bata, dace, Allegheny pearl dace, Java barb); Gobiiformes: butid (marble goby); Perciformes: ambassid (elongate glassy perchlet); Siluriformes: bagrid (Day's mystus), clariid (broadhead catfish), pangasiid (sutchi catfish, (spot pangasius) and amphibians (Anura: bufonid (common toad, tadpoles), ranid (Japanese wrinkled frog, tadpoles)) | gills | Eurasia, North America |
| *T. bursiforms* (syn. *Trichodina*) | AD 25-36 ND 23-32 | freshwater, epizoic on fish (Perciformes: centrarchid (mud sunfish, rock bass)) | gills | North America |
| *T. cichlidarum* | AD 22-30 ND 30-32 | freshwater, epizoic on fish (Cichliformes: cichlid (blue tilapia)) | gills | Israel |
| *T. clavodonta* | AD 15-20 ND 18-24 | freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (river sardine)) | gills | Africa, Asia |
| *T. copiosa* [type species] | AD 13-45 ND 17-33 | freshwater, epizoic on fish (Cypriniformes: cobitid (spined loach), cyprinid (common carp, mrigal carp, common roach, common bleak, sunbleak, common dace, common chub, rohu, bata, catla, Amur bitterling, bronze bream, silver bream, ide); Siluriformes: bagrid (striped dwarf catfish)) | gills | Eurasia |
| *T. ctenopomae* | AD 18-32 ND 26-34 | freshwater, epizoic on fish (Anabantiformes: anabantid (manyspined climbing perch)) | gills | Africa |
| *T. dactylodentata* | AD 22-27 ND 27-32 | freshwater, epizoic on fish (Osteoglossiformes: mormyrid (elephant-snout fish), Siluriformes: schilbeid (African butter catfish)) | gills | Africa |
| *T. kashkovskyi* | AD 20-27 ND 23-29 | freshwater, epizoic on fish (Cyprinodontiformes: fundulid (starhead topminnow)) | gills | North America |
| *T. lata* | AD 17-25 ND 20-24 | freshwater, epizoic on fish (Cypriniformes: cyprinid (bullhead minnow), leuciscid (Eurasian minnow); Salmoniformes: salmonid (sockeye | gills | Eurasia |

| | | | | |
|---|---|---|---|---|
| | | salmon, rainbow trout)) | | |
| *T. lechridens* | AD 15-20<br>ND 20-26 | freshwater, epizoic on fish (Characiformes: alestid (sharptooth tetra); Cichliformes: cichlid (Mozambique tilapia); Cypriniformes: cyprinid (Eurasian carp, straightfin barb, threespot barb, redeye labeo), danionid (river sardine)) | gills | Africa |
| *T. leptospina* | AD 14-22<br>ND 16-21 | freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia)) | gills | Africa |
| *T. macrosoma* | AD 14-20<br>ND 22-25 | freshwater, epizoic on fish (Cypriniformes: cyprinid (orangefin barb); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp)) | gills | Africa, Europe |
| *T. melanogrammi* | AD 37-69<br>ND 28-32 | marine, epizoic on fish (Gadiformes: gadid (haddock) | gills, fins | Eurasia |
| *T. microctenopomae* | AD 13-23<br>ND 21-31 | freshwater, epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch) | gills | Africa |
| *T. nana* | AD 13-22<br>ND 16-19 | freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia)) | gills | Africa |
| *T. obliqua*<br>(syn. *T. inversa*) | AD 14-19<br>ND 18-26 | marine, epizoic on fish (Labriformes: labrid (grey wrasse); Mugiliformes: mugilid (flathead grey mullet); Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Atlantic mackerel), trichiurid (largehead hairtail); Scorpaeniformes: triglid (tub gurnard)) | gills | Atlantic, Black Sea |
| *T. obtusa* | AD 10-23<br>ND 17-27 | freshwater, epizoic on fish (Cypriniformes: cyprinid (gudgeon, rohu); Osteoglossiformes: notopterid (bronze featherback)) | gills | Eurasia |
| *T. orthodens* | AD 14-32<br>ND 19-28 | freshwater, epizoic on fish (Cichliformes: cichlid (redbreast tilapia, mango tilapia); Siluriformes: bagrid (rita, shining catfish)) | gills | Africa, Asia |
| *T. pseudoplatystomae* | AD 23-37<br>ND 27-31 | freshwater, epizoic on fish (Siluriformes: pimelodid (spotted sorubim)) | gills | South America |
| *T. pungitii* | | freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (ninespine stickleback); Cichliformes: cichlid (redbelly tilapia); Salmoniformes: salmonid (chum salmon)) | gills | Pacific, Iraq |
| *T. rhombi* | AD 18-30<br>ND 20-28 | estuarine, epizoic on fish (Pleuronectiformes: scophthalmid (turbot); Cypriniformes: cyprinid (common carp)) | gills | Eurasia |
| *T. tetramerii* | AD 27-38<br>ND 23-25 | freshwater, epizoic on fish (Cichliformes: cichlid (saddle cichlid)) | gills | South America |
| *T. tilapiae* | AD 16-25<br>ND 21-27 | freshwater, epizoic on fish (Cypriniformes: cyprinid (grass carp)) | gills | Asia |
| Genus ***Vauchomia*** (adoral ciliary spiral makes 2-3 turns, denticles with well-developed blades and thorns, striated border membrane with fused rings of rays and myonemes) | | | | |
| *V. nephritica*<br>(syn. *Trichodina*)<br>[type species] | AD 53-75<br>ND 33-42 | freshwater, endozoic in fish (Esociformes: esocid (muskellunge)) | urinary tract | North America |
| *V. renicola*<br>(syn. *Trichodina*) | AD 75-97<br>ND 44-65 | freshwater, endozoic in fish (Esociformes: esocid (chain pickerel, pike)) | urinary tract | North America |

**Parasite morphology**: *Trichodina* spp. form trophic stages (trophonts) that have 3 distinctive features: an oral ciliary spiral for feeding; a ring of somatic cilia for motility; and a complex adhesive disc for temporary attachment to hosts. Trophonts are discoidal to hemispherical in shape, appearing circular when viewed from above, and flattened or convex when viewed from the side. They vary considerably in size depending on species, ranging from 10-150 µm in diameter. They are covered by a thin pellicular membrane and contain a large macronucleus (usually horseshoe-shaped, rarely ellipsoidal) with a small dense adjacent micronucleus. Trophonts have specialized 'peritrichous' mouthparts located on the surface facing away from the host (termed the upper or oral surface) with a prominent paroral membrane formed by ciliary rows spiralling through 1-1½ counter-clockwise turns down to the central cytostome (mouth), accompanied by a smaller series of lateral membranelles. Other trichodinid genera may be partly distinguished by the number of spiral turns made by their paroral membranes (*Paratrichodina*, *Semitrichodina*, *Tripartiella* and *Trichodinella* making ½-¾ turns, *Pallitrichodina* ¾ turns, *Heterobladetrichodina* < 1 turn, *Hemitrichodina* 1-2 turns, and *Vauchomia* 2-3 turns). The body of the trophont bears several rings of peripheral cilia which are used for locomotion, including a compound wreath of oblique ciliary rows (6-10 cilia per row), a basal row of single cilia (separated from the compound wreath by a septum), sometimes a third ring of marginal cilia (located adoral to the basal cilia), and rarely several aboral cirri (compound ciliary organelles). The aboral surface of the trophonts contains an elaborate adhesive disc used for temporary attachment to substrates. The adhesive disc is formed by a distinctive ring of radial interlocking cytoskeletal denticles, each with a distal blade, hook-like centrum, and proximal ray (or thorn). The denticular ring is surrounded by a ring of fine skeletal rods (radial pins). The structure of the adhesive disc varies depending on the trichodinid genus and species, with *Trichodina* spp. possessing discs ranging from 10-150 µm in diameter (mostly 30-40 µm) and containing 12-55 denticles (mostly 20-30) with well-developed flat straight-semicircular blades, central parts lacking anteriorly-directed projections, and spine- or needle-shaped rays.

**Site of infection**: *Trichodina* spp. are essentially commensals, most being epizoic on superficial aspects of aquatic hosts (skin, fins, gills, nasal pits) but some being endozoic in the lumina of tubular organs (mostly the urinary tract, sometimes the intestinal or reproductive tracts). Over 125 *Trichodina* spp. have been reported as epizoic commensals/parasites on almost 290 species of freshwater fish belonging to 74 families in 29 orders (especially Cypriniformes, Cichliformes, Perciformes, Salmoniformes and Siluriformes, but also including Acipenseriformes, Anabantiformes, Anguilliformes, Atheriniformes, Beloniformes, Blenniiformes, Callionymiformes, Characiformes, Clupeiformes, Cyprinodontiformes, Esociformes, Gadiformes, Galaxiiformes, Gobiiformes, Kurtiformes, Labriformes, Moroniformes, Mugiliformes, Osteoglossiformes, Pleuronectiformes, Scorpaeniformes, Spariformes, Synbranchiformes, and Tetraodontiformes). Several freshwater species have also been reported attached to larval stages of amphibians (toads, frogs, newts and salamanders) and there have been occasional reports in association with freshwater mussels, snails, copepods, bryozoans, hydrozoans, jellyfish, sponges and flatworms. An additional 86 *Trichodina* spp. have been recorded as epizoic commensals/parasites on 165 species of marine fish belonging to 56 families in 26 orders (particularly Scorpaeniformes, but also including Anabantiformes, Anguilliformes, Atheriniformes, Blenniformes, Callionymiformes, Characiformes, Clupeiformes, Cypriniformes, Cyprinodontiformes, Esociformes, Gadiformes, Gobiesociformes, Gobiiformes, Labriformes, Moroniformes, Mugiliformes, Ophidiiformes, Perciformes, Pleuronectiformes, Salmoniformes, Scombriformes, Siluriformes, Spariformes, Syngnathiformes, and Tetraodontiformes). Another 6 marine species have been found as endozoic organisms within the urogenital tracts of marine fish (surgeonfish, guitarfish, puffers and skates) and there have been occasional reports of infestations in association with bivalves (clams, cockles, scallops, limpets, mussels), chitons, star fish, brittle stars, sea snails, sea cucumbers, branchiopods, copepods, polychaetes and tubeworms. Other trichodinid genera are found mainly on the gills of freshwater and marine fish (including 23 *Tripartiella* spp., 15 *Paratrichodina* spp., 13 *Trichodinella* spp.), some exclusively on surfaces of freshwater fish (2 *Heterobladetrichodina* spp., one *Hemitrichodina* sp.) or in the urinary tracts of freshwater fish (2 *Vauchomia* spp.) and a few in the mantle cavities of terrestrial snails (4 *Semitrichodina* spp., 2 *Pallitrichodina* spp.).

**Pathogenesis**: Trophonts use their aboral adhesive discs to attach to hosts where they filter-feed on waterborne solutes and particles, including bacteria. Most species attach to the superficial surfaces of fish, but some reside in the cavities of tubular organs. During attachment, the adhesive disc acts as a sucking cup drawing up epithelial cells and sometimes resulting in attachment-related pathologies. The discs play no part in feeding as the mouthparts and feeding ciliary spirals are located on the opposite oral surface. The presence of a few trophonts usually has little effect on healthy hosts, but in young fish or those debilitated by stress (poor water quality, inadequate nutrition, concomitant infections), skin barriers and their protective chemicals may be impaired allowing trichodinids to proliferate. The trophonts are highly mobile constantly attaching and detaching on epidermal and epithelial surfaces (sometimes colloquially referred to as 'scrubbing bubbles'). Attachment may cause irritation, cellular damage and inflammation, but does not result in distinctive lesions. Fish may develop focal patches of blotchy blue-grey skin with epithelial hyperplasia, peeling and excessive mucus production. Heavily infected fins may appear tattered and frayed. Infected gills can become congested with mucus and gill filaments can become clubbed or fused. Clinical signs may include breathing difficulties, sluggish swimming just beneath the surface or near the water's edge, sometimes flashing behaviour (abrupt movements exposing the silvery undersides of fish), lethargy, loss of appetite, cessation of feeding, rapid loss of condition, and occasionally mortalities in both wild and cultured fishes. Affected fish also become prone to secondary fungal and bacterial infections in areas of damaged tissue. Several trichodinid species are endozoic and occur in the urinary tracts of fish, sometimes the genital or intestinal tracts, where their attachment may cause extensive epithelial desquamation and occasionally yellowish mucoid exudates, but not overt disease. Trichodinids become

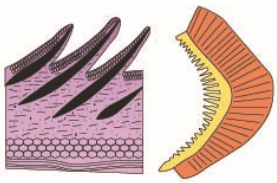
problematic in aquaculture systems when water quality is poor resulting in eutrophication with bacterial blooms providing abundant food for trichodinid growth and proliferation. Clinical infections are found more frequently in young fish fry, particularly during the spring in fish stressed by harsh winter conditions.

**Developmental cycle and mode of transmission:** Trichodinids are mobiline peritrichous ciliates in aquatic habitats, attaching to hosts using their aboral holdfast organelles but also able to swim freely. They do not form cysts so all transmission between hosts is direct via free-swimming stages, particularly when incidental contact is made between fish, but also through contact with ciliates in the water column. The discoidal trophonts swim with the aboral surface facing forwards, but upon making contact with a suitable substrate, they move laterally with the aboral surface facing the substrate. Attached trophonts reproduce asexually by binary fission, with nuclear division, replication of the adhesive disc, oral and somatic ciliature followed by transverse splitting into 2 cells. Daughter cells become free-swimming and are ready to attach to hosts within 24 hours. Under ideal growth conditions (usually when food is abundant), trophonts may divide every several days. When conditions are not ideal, ciliates may initiate sexual reproduction by conjugation which involves 2 cells coming together to form a mating pair with fusion of their cell membranes producing a cytoplasmic bridge through which genetic material is exchanged (gametic pronuclei derived from micronuclear meiotic divisions). Reproduction by conjugation enhances genetic diversity and is thought to help promote the survival of at least some offspring in adverse conditions. There has also been speculation that the transmission of some endozoic species in the urogenital tracts of fish may occur venereally, but conclusive studies are outstanding.

**Differential diagnosis**: Infections are diagnosed by the direct microscopic detection of trophonts in wet mounts of skin scrapings, mucus, fin snips, gill filaments, or the contents of tubular organs (mainly the urinary bladder). Live trophonts are best observed by high-contrast microscopy and may be seen as small motile rotating ciliated discs in fluids or as sedentary cells attached to host tissues. Differential diagnosis is afforded by enrobing specimens onto albuminized slides and subjecting them to silver staining (silver nitrate, silver proteinate (protargol) or silver carbonate) to reveal details of their adhesive discs, ciliature and nuclei. In particular, staining with silver nitrate accentuates the adhesive disc by staining the cell cytoplasm black but leaving the denticles white. Molecular biological techniques have been used to characterize trichodinid species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA).

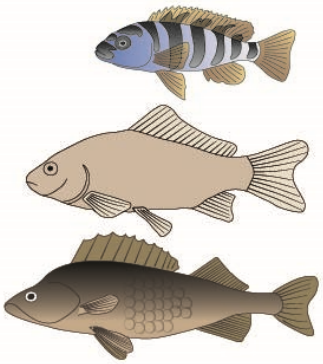
**Treatment and control**: Infected fish may be treated using a range of chemical baths, including formalin, copper sulphate, potassium permanganate, malachite green and dilute acetic acid, but some treatments may produce adverse side-effects or pose toxicity problems (many chemicals are prohibited for use in food animals). Other treatments have included freshwater baths for marine fish or saltwater baths for freshwater fish. A range of preventive measures have been suggested to control infections in aquaculture through improved hygiene, sanitation and husbandry. Regular health surveillance should be conducted to screen new stock, identify infected animals for treatment, quarantine or culling. Ponds and tanks should be decontaminated by chemical disinfection or draining and drying. Fish should be reared in clean water, with good flow or regular flushing, and any dead or dying fish should be promptly removed. Every effort should be made to avoid over-feeding and organic enrichment (eutrophication) in holding facilities as they lead to bacterial blooms that enhance ciliate growth. Fish should also be kept in good health by avoiding stressful (immunocompromising) situations (over-handling, over-crowding, inadequate nutrition, poor water quality) and any injuries or concomitant infections should be treated.

# *Trichodina*



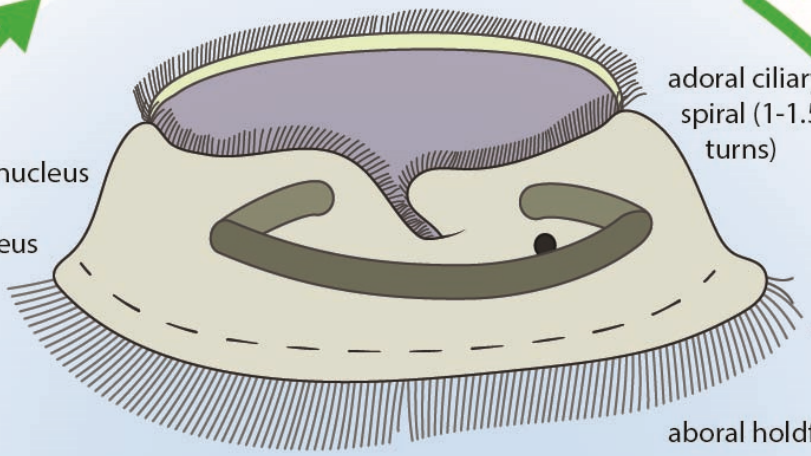
most epizoic (skin, gills)
(irritation, lesions, ulkcers)
some endozoic (tubular organs)
(nonpathogenic)

may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)

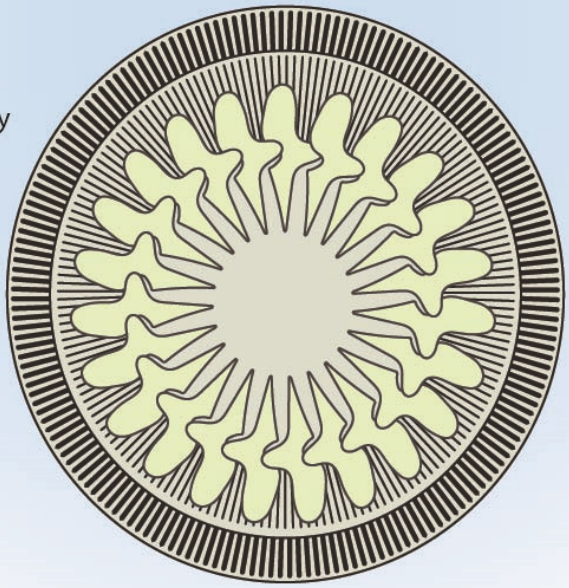


Vertebrate Hosts
(freshwater and
marine fish)

mobile trophont
(10-150 µm)



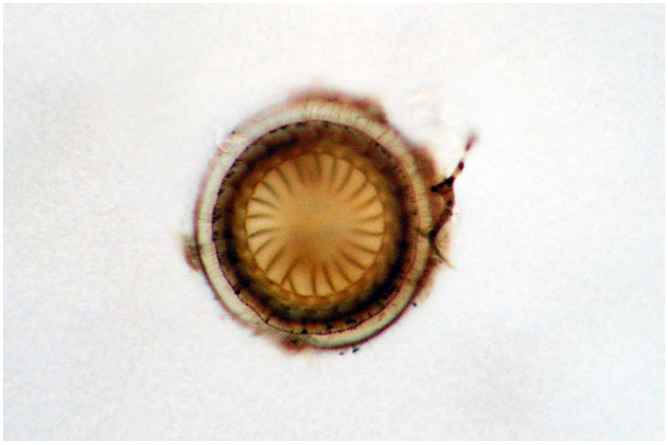

denticle comprising
distal blade, hook-like
centrum & proximal ray



concave discoid
holdfast with
interlocking denticles
subtended by
radial pins

no cyst formation

transmission via free-swimming
trophonts in water column



*Trichodina* trophont adhesive disc from fish skin

*Trichodina* trophont adhesive disc from fish skin

*Trichodina* trophont adhesive disc from fish skin