Balantidium
(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 litostomes ('simple mouthed') with a noncurved tubular cytopharyngeal apparatus (rhabdos). Vestibuliferid ciliates have a pronounced vestibulum and the balantidids are monoxenous (one-host) endocommensals in vertebrates, sometimes becoming histophagous parasites. Infections by *Balantidium* may cause diarrhoeal disease in mammals, notably in pigs and humans.

Classification:

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:	Litostomatea (simple mouths, special somatic kineties)
Subclass:	Trichostomatia (endosymbionts, holotrichous ciliation)
Order:	Vestibuliferida (distinct oral depression (= vestibulum))
Family:	Balantidiidae (monoxenous symbiotes, in vertebrates, sometimes histophagous)
Genus:	*Balantidium* (parasitic in pigs/primates, large intestine, direct (faecal-oral))
Species:	*B. coli* (causes balantidiasis in vertebrates, esp. pigs and humans)

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 transversodesmata (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 Litostomatea contains ciliates with a unique infraciliature consisting of 2 transverse microtubular ribbons (tangential and radial), a convergent postciliary ribbon, and a laterally directed kinetodesmal fibril not overlapping adjacent kineties. Litostome ciliates are 'lower' holotrichs as there is little distinction between the oral and somatic ciliature. Most possess an apical cytostome (sometimes subapical or midventral) and a conspicuous cytopharyngeal apparatus. They are found in many diverse habitats ranging from free-living to endoparasitic, and are often carnivorous in feeding habit. Three litostome subclasses are recognized, each containing 2-3 orders: namely, Haptoria (containing free-living Haptorida, Pleurostomatida and Spathidiida); Rhynchostomatia (containing free-living Dileptida and Tracheliida); and Trichostomatia (containing endosymbiotic Vestibulifera and Entodiniomorphida). Trichostomes have mouths lined with cilia derived from the anterior somatic kineties and leading through a noncurved rhabdos to the cytostome. Most species occur in the gastro-intestinal tracts of vertebrates, either as endocommensals, some as mutualists (e.g. 'rumen protozoa' in ruminants), and a few as parasites. The order Entodiniomorphida contains some 33 genera classified in 6 families in 3 suborders, most characterized by the possession of rigid bodies with posterior rudder-like projections and somatic ciliature present as specialized tufts or bands. The order Vestibuliferida contains 13 genera grouped into 5 families (Amylovoracidae, Balantidiidae, Isotrichidae, Paraisotrichidae, and Pycnotrichidae), all characterized by the possession of ovoid bodies with distinct oral depressions (= vestibula) and holotrichous somatic ciliation. Balantidiids are monoxenous endocommensals in vertebrates, but some can become histophagous parasites. More than 80 species of the genus *Balantidium* (syn. *Balantidiopsis, Balantioides, Parabursaria, Paranyctotherus*) have been recorded throughout the world in various species of crustaceans, insects, fish, amphibians, reptiles, birds and mammals (including humans). Infections by *B. coli* are particularly prevalent in pigs, monkeys and humans, especially in the tropics, with zoonotic transmission from pigs to humans frequently implicated by epidemiological studies. While few morphotypic differences have been observed between trophozoites and/or cysts of most *Balantidium* spp., recent molecular characterization studies have revealed distinct genotypic differences between isolates from mammals and amphibians (with a new genus *Neobalantidium* being proposed for the latter) as well as genotypic similarities between some isolates from primates and another ciliate (*Buxtonella sulcata*) from cattle. Several genotypes have been detected in *B. coli* isolates from mammals: including genotypes A and B in pigs and genotype C in gorillas. *B. struthionis* isolates from ostriches were also found to be similar to *B. coli* genotypes A and B prompting their amalgamation. Further studies are required to determine the extent and significance of such genetic variation, particularly with respect to host occurrence and specificity.

Balantidium spp.	Vertebrate* hosts	Location	Clinical signs	Distribution
Species in mammals				
B. coli (syn. *B. aragaoi, cunhamunizi, philippinensis, rhesum, simile, struthionis, suis*, *wenrichi*)	Primates: hominid (human, chimpanzee, gorilla, Sumatran orangutan), cercopithecid (chacma baboon, macaques); Artiodactyla: suid (pig), bovid (cattle, buffalo), camelid (camel); Carnivora: canid (dog); Rodentia: murid (rats, mice); Aves: Struthioniformes (ostrich)	colon	inflammation, diarrhoea, ulceration	cosmopolitan (esp. tropics)
B. caviae	Rodentia: caviid (guinea pig)	colon		cosmopolitan (pet and lab animals)
Species in amphibians				
B. amblystomatis	Urodela: ambystomatid (tiger salamander)			North America
B. amygdalli	Anura: bufonid (big-eared toad)	intestines		India
B. andianusis	Urodela: cryptobranchid (Chinese giant salamander)	intestines		China
B. aurangabadensis	Anura: dicroglossid (Asian bullfrog)	rectum		India
B. bicavata	Anura: bufonid (Asian toad)	intestines		India
B. claperedei	Anura: ranid (marsh frog)	intestines		Turkey
B. corlissi	Anura: dicroglossid (skittering frog)	rectum		India
B. cyanophlycti	Anura: dicroglossid (skittering frog)	rectum		India
B. duodeni (syn. *B. hyalinum, rotundum*)	Anura: ranid (common frog, edible frog, marsh frog), ptychadenid (grass frog), micrixalid (black torrent frog)	intestines		Europe, Asia
B. elongatum	Anura: ranid (common frog, edible frog, marsh frog), pelobatid (common spadefoot), ptychadenid (grass frog), bombinatorid (yellow-bellied toad); Urodela: salamandrid (common newt, northern crested newt, smooth newt, alpine newt)	intestines		Europe, Asia
B. entozoon [type species]	Anura: ranid (edible frog), ptychadenid (grass frog), bombinatorid (yellow-bellied toad, European fire-bellied toad), bufonid (European green toad, nutterjack toad); Urodela: salamandrid (common newt, crested newt)	intestines, rectum		Europe
B. falciformis	Anura: ranis (pickerel frog)	intestines		North America
B. ganapatii	Anura: dicroglossid (skittering frog)	rectum		India
B. giganteum	Anura: ranid (edible frog, marsh frog)			Asia, Europe
B. gracile	Anura: dicroglossid (Asian bullfrog, Indian green frog, marbled sand frog, verrucose frog), micrixalid (torrent frog)	intestines		India
B. grimi	Anura: dicroglossid (Chinese spiny frog)	rectum		China
B. helenae (syn. *B. ovale*)	Anura: ranid (edible frog, European common frog, bicolored frog, marsh frog), dicroglossid (marble sand frog, verrucose frog, Asian bullfrog), micrixalid (torrent frog)	intestines		Asia, Europe
B. honghuensis	Anura: ranid (black-spotted pond frog), dicroglossid (Asian grass frog)	rectum		China
B. kirbyi	Anura: pipid (African clawed frog)	large intestines		South Africa
B. megastomae	Anura: dicroglossid (skittering frog)	rectum		India
B. mininucleatum	Anura: dicroglossid (skittering frog)	rectum		India
B. nucleus	Anura: ranid (edible frog, European common frog)			Europe
B. ranae/ranarum	Anura: dicroglossid (Asian bullfrog)	rectum		India
B. rayi	Urodela: salamandrid (Himalayan newt)	intestines		Indochina
B. sinensis	Anura: ranid (black-spotted pond frog, eastern golden frog); Urodela: cryptobranchid (Chinese giant salamander)	intestines		China
B. singaporensis	Anura: bufonid (Asian toad)	rectum		Singapore

B. sushilii	Anura: dicroglossid (Asian bullfrog)	intestines		India
B. tigrinae	Anura: dicroglossid (Asian bullfrog)	rectum		India
B. tylototritonis	Urodela: salamandrid (Himalayan newt)	intestines		Indochina
B. vanensis	Anura: ranid (marsh frog)	intestines		Turkey
B. xenopi	Anura: pipid (Fraser's clawed frog)	intestines		Africa
Species in tortoises				
B. testudinis	Testudines: testudinid (tortoises, incl. Galapagos tortoise)	intestines		Asia, Africa, South America
B. bacteriophorus	Testudines: cheloniid (green sea turtle)	intestines		Caribbean
B. dogieli	Testudines: trionychid (Indian flapshell turtle)	intestines		India
Species in freshwater fish				
B. barbi	Cypriniformes: cyprinid (carp)	intestines		Central Asia
B. ctenopharyngodoni	Cypriniformes: cyprinid (grass carp)	intestines	enteritis	China, Europe
B. fulinensis	Cypriniformes: cyprinid (carp)	intestines	ulceration	China
B. granulosum	Salmoniformes: salmonid (brook trout)	stomach		America
B. grevolosum	Salmoniformes: salmonid (brook trout)	gut		Americas, Europe
B. mrigalae	Cypriniformes: cyprinid (mrigal carp)	intestines		Asia
B. pangasi	Siluriformes: pangasid (Pangas catfish)	intestines		Asia
B. piscicola	Characiformes: serrasalmid (pirapitinga)	intestines		South America
B. polyvacuolum	Cypriniformes: cyprinid (blackbelly, yellowtail, David's yellowfin, smallscale yellowfin, common carp)	rectum	ulceration	China, Middle-East
B. procyprini	Cypriniformes: cyprinid (carp)	intestines		China
B. semilabeai	Cypriniformes: cyprinid (carp)	intestines		China
B. senilabeai	Cypriniformes: cyprinid (carp)	intestines		China
B. spinibarbichthys	Cypriniformes: cyprinid (Chinese phoenix barb)	intestines		China
B. steinae	Cypriniformes: cyprinid (Chinese phoenix barb)	intestines		China
B. strelkovi	Cypriniformes: cyprinid (mud carp)	intestines		Asia
B. yangtzensis	Cypriniformes: cyprinid (carp)	rectum		China
B. yinjiangensis	Cypriniformes: cyprinid (carp)	rectum		China
Species in marine fish				
B. acanthuri	Acanthuriformes: acanthurid (powder blue tang)	intestines		Indian Ocean
B. jocularum	Acanthuriformes: acanthurid (bulbnose unicornfish)	intestines		Pacific
B. macrodextroral	Acanthuriformes: acanthurid (black tang, whitespotted surgeonfish, Achilles surgeonfish)	intestines		Pacific
B. prionurium	Acanthuriformes: acanthurid (yellowtail surgeonfish)	intestine		Pacific
B. sigani	Perciformes: siganid (streamlined spinefoot)	rectum		Red Sea
B. zebrascopi	Acanthuriformes: acanthurid (brown tang)	intestines		Oceania

*Other *Balantidium* species have been described from invertebrate hosts (but are not listed here)

Parasite morphology: Two developmental stages are formed: trophozoites and cysts. Trophozoites are variable in size ranging from 30-150 μm in length and 25-120 μm in width. They are oblong-spherical in shape and are covered by longitudinal kineties (rows of cilia). At the anterior end there is a depression (vestibulum) leading to the cytostome (mouth) and cytopharyngeal complex (tubular rhabdos). Internally, they contain a single large reniform macronucleus (vegetative), a small spherical micronucleus (reproductive), several contractile vacuoles (water regulation) and hydrogenosomes (instead of mitochondria). The cysts appear as membrane-bound ovoid bodies ranging from 40-60 μm in diameter.

Site of infection: *B. coli* is found in the large intestine, caecum and terminal ileum of their hosts. They are actively swimming organisms and they reproduce asexually (by transverse binary fission) and sexually (by conjugation involving the exchange of micronuclei between paired trophozoites).

Pathogenesis: Infections are usually not associated with any changes in the colonic mucosa. Healthy individuals often exhibit spontaneous recovery or become symptomless carriers. However, under certain conditions, the organisms produce proteolytic enzymes which digest away the epithelium producing flask-shaped ulcers. This stimulates inflammatory changes with lymphocytic

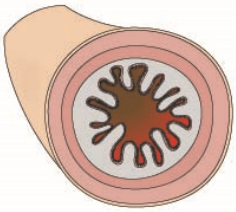
infiltration and haemorrhage and secondary bacterial invasion may follow. Infections may cause a dysentery-like syndrome, involving diarrhoea, tenesmus, nausea, vomiting, anorexia, headache, insomnia and weakness. Diarrhoea may persist for long periods resulting in acute fluid loss. Colonic ulceration involves mucosal sloughing, necrosis, fluid loss, haemorrhage, occasional abscess formation but rarely perforation of the bowel. Factors predisposing to ciliate multiplication and clinical infections have usually involved changes to the microbial gut flora associated with dietary changes, antibiotic use and stressful conditions.

Developmental cycle and mode of transmission: Infections are passed horizontally between hosts by faecal-oral transmission. Cysts passed in the faeces of infected hosts contaminate the environment. When ingested with contaminated food or water, the cysts excyst releasing trophozoites in the digestive tract. Trophozoites multiply primarily by asexual transverse binary fission across rows of cilia (homothetogenic fission), although they may occasionally pair-up in a unique sexual process of conjugation where micronuclei are exchanged via a temporary cytoplasmic bridge. Infections in humans are more prevalent in communities which farm pigs (under intensive or extensive husbandry) and in individuals working with pigs or in slaughterhouses.

Differential diagnosis: Infections are diagnosed by coprological examination and the detection of characteristic cysts in faecal material or trophozoites in colonic biopsy material. Multiple stool samples should be examined as the cysts may be excreted intermittently. Molecular techniques have been developed in several research laboratories to characterize isolates using polymerase chain reactions (PCR) to amplify specific sequences (small subunit ribosomal RNA (SSU rRNA) and internal transcribed spacer (ITS) genes].

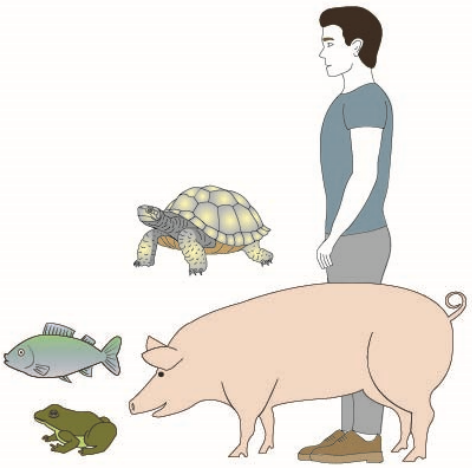
Treatment and control: Clinical infections may be treated with metronidazole, di-iodohydroxyquin, tetracycline or carbarsone. Prevention and control depend on strict hygiene to prevent the contamination of food and water supplies, particularly by faeces from humans and pigs. Sewage should be collected and treated and drinking water supplies should be purified by filtration and/or chlorination. Effluent from intensive piggeries should not be used to fertilize vegetable gardens or edible crops. In developing countries, pigs should not be left to roam free in rural villages, but are best confined to pens and sties where proper waste disposal can be practiced.

Balantidium



large intestines
(mucosal ulceration,
haemorrhages,
diarrhoea)

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

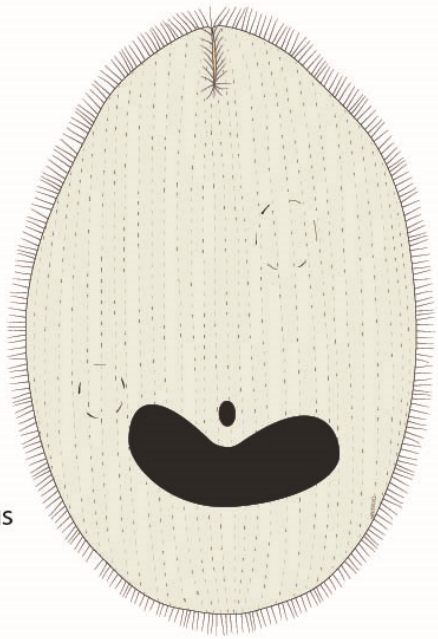


Vertebrate Hosts
(mammals, frogs,
tortoises, fish)

contractile vacuoles

micronucleus

macronucleus

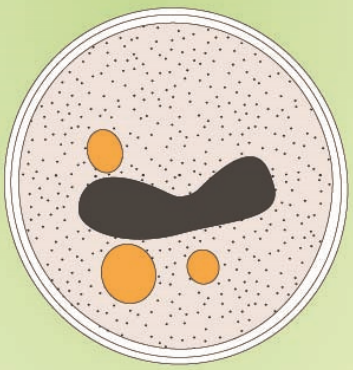


numerous
longitudinal
kineties
(cilary rows)

trophozoite
(30-150 µm)

cysts
ingested

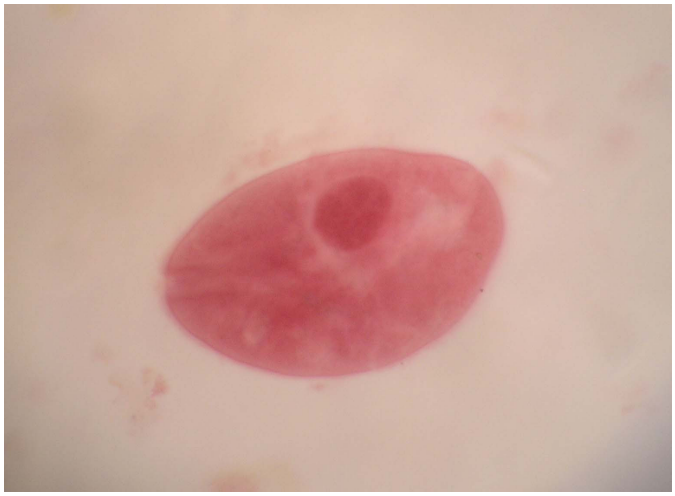
cysts excreted
in faeces



conspicuous
macronucleus

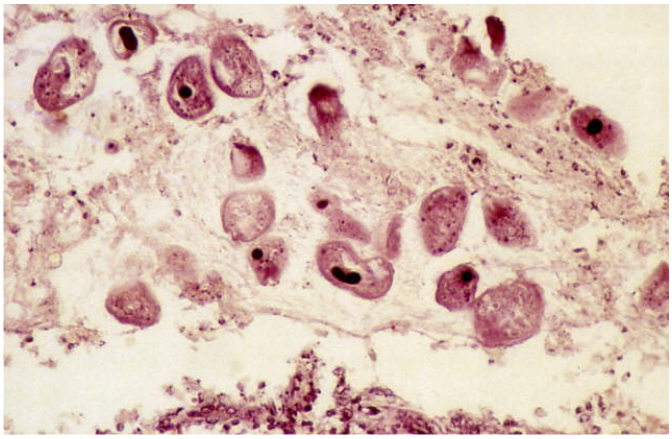
cyst
(40-60 µm)

direct faecal-oral transmission
via contaminated environment (soil, water, food)



Balantidium trophozoite in human bowel

Balantidium cyst from human faeces



Balantidium lesion in pig bowel