Haplosporidium*, *Minchinia
(protist: haplosporidian)

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). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea. Haplosporidia are characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several dense organelles (known as haplosporosomes). The complete developmental cycles of most species are not known. Most have two developmental stages: multinucleate plasmodia and spores (although *Mikrocytos* (and some *Bonamia* spp.) form microcells). The multinucleate plasmodia undergo modified schizogony giving rise to sporonts which eventually differentiate into spores. The spore orifice is covered by an external hinged operculum and spores often have elaborate spore wall ornamentations appearing as filamentous tails or wrappings. Most species are histozoic or coelozoic parasites of aquatic molluscs, annelids, crustaceans and helminths. Several species cause significant diseases and mortality in oysters around the world.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Rhizaria (various amoebae and flagellates)
Division:	Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus ascetospora)
Phylum:	Ascetospora (haplosporidian and paramyxean parasites forming unique spores)
Class:	Haplosporea (haplosporosomes present)
Order:	Haplosporida (spore with one sporoplasm, spore orifice covered externally by operculum or internally by diaphragm)
Family:	Haplosporididae (spores with operculum)
Genus:	*Haplosporidium* (parasitic in tissues of bivalves and crustaceans)
Genus:	*Minchinia* (parasitic in tissues of bivalves)
Species:	various species cause mortalities in oysters and blemishes in other shellfish

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). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea that lack flagella and pseudopodia. Haplosporidia are usually characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several membrane-bound electron-dense organelles (known as haplosporosomes), while paramyxeans form unique multicellular (nested) spores. Most species occur as histozoic or coelozoic parasites of aquatic invertebrates (including molluscs, annelids, crustaceans, ascidians and helminths), and several species cause significant diseases and mortality in oysters around the world.

The identification and classification of haplosporidians has a complex and turbulent history. The complete developmental cycles of most species are not known, but various members of the genera *Haplosporidium*, *Minchinia* and *Urosporidium* were shown to form 2 developmental stages: multinucleate plasmodia which undergo modified schizogony to form sporonts that eventually differentiate into uninucleate spores. The spores were surrounded by a spore wall with an orifice (micropyle) and the enclosed endosporoplasm contained a complex membranous system known as a spherulosome (or spherule). Members of several other genera (*Bonamia* and *Mikrocytos*) which produced microcells (but not spores) were nonetheless recognized as haplosporidians on the basis of perceived structural and biological similarities. However, subsequent ultrastructural and molecular characterization studies have now removed *Mikrocytos* to a separate order Mikrocytida as they do not produce plasmodia, spores or haplosporosomes, while *Bonamia* was retained with the Haplosporida as they produced haplosporosomes. Recent studies have since shown that one *Bonamia* species (*B. perspora*) does produce spores, and conversely, that a few *Haplosporidium* spp. (e.g. *H. littoralis*) do not actually produce spores as supposed. Ultrastructural studies conducted on spores demonstrated that the orifice was covered either by an external hinged operculum (adopted as a key characteristic for the family Haplosporidiidae containing the genera *Haplosporidium*, *Minchinia* and *Bonamia*) or occluded by an internal flap-like lingula (taken to characterize the monotypic family Urosporidiidae). Many spores also possessed elaborate external ornamentations, described variously as tails, filaments, folds, projections, extensions or wrappings. It was initially thought that their presence and structure could be used to differentiate taxa, but

studies demonstrated considerable variation both between and within taxa. Most *Minchinia* spores lacked ornaments, but some isolates were found with epispore cytoplasmic extensions, albeit transiently as they disappeared during the spore maturation process. It was speculated that genera could be discerned by the origins (rather than the structure) of the ornamentations, being derived from either spore wall material (as found for many *Haplosporidium* spp. and one *Bonamia* sp.) or from epispore cytoplasmic extensions (observed for *Urosporidium* spp. and a few *Minchinia* isolates). However, molecular characterization studies did not reveal any strong correlations with morphotypic (phenetic) characters. Instead, phylogenetic analyses revealed a series of polyphyletic clades, including: a basal clade of diverse *Haplosporidium* isolates; a more derived clade containing most *Urosporidium* isolates from helminths; 2 sister clades containing *Minchinia* and *Bonamia* isolates respectively; and a clade containing many *Haplosporidium* isolates from gastropods. [Note that various spore-forming organisms detected in cockroaches, copepods, rotifers, polychaetes and toads that were originally thought to be other haplosporidian genera (e.g. *Bertramia, Coelospora, Coelosporidium, Nephridiophaga*) are now considered to be fungi on the basis of molecular phylogenetic studies.]

Family	Genus	Biodiversity	Characters	Hosts
Order: Haplosporida (form unicellular spores/microcells with haplosporosomes)				
Haplosporidiidae (spores with operculum)	*Haplosporidium*	33	spores with external hinged lids, spores with filaments of spore wall material	oligochaetes, molluscs, crustacea, urochordates, echinoderms, polychaetes
	Minchinia	6	spores with external hinged lids, some spores with transient extensions of epispore cytoplasm	oysters, chitons, clams, tusk shells, shipworms
	Bonamia	4	microcells formed, one species forming spores with external hinged lids and filamentous projections of spore wall material	oysters
Urosporidiidae (spores without operculum)	*Urosporidium*	7	spores occluded with internal lingula (plug, flap, diaphragm)), spores with tapering extensions of epispore cytoplasm	hyperparasitic in helminths of molluscs and crabs
Order: **Mikrocytida** (form microcells without haplosporosomes)				
Mikrocytidae	*Mikrocytos*	5	form microcells, no spores, no plasmodia, no haplosporosomes	oysters, clams
	Paramikrocytos	1	form microcells, no spores, no plasmodia, no haplosporosomes	crabs

Haplosporean infections have been detected throughout the world in aquatic invertebrates in coastal waters (freshwater, marine and brackish waters). The genus *Haplosporidium* is a diverse group of species, most of which form operculate spores with elaborate spore wall ornamentations. Over 30 species have been described from freshwater oligochaetes and marine molluscs, crustacea, urochordates, echinoderms and polychaetes. Several species infect commercially important bivalves, sometimes causing epizootic mortalities in oysters, notably *H. nelsoni* and *H. costale* causing MSX (= multinucleate sphere unknown) and SSO (= seaside organism) diseases respectively, particularly in eastern oysters. A range of nominal species have also been assigned *sensu latu* (in the broadest sense) to the genus *Haplosporidium,* including some that apparently do not form spores and others that form spores without orifices (pores) or lids (opercula, clapet). Some of these enigmatic species have since been transferred to other assemblages on the basis of comparative morphological or molecular studies (notably to novel ascetosporan groups, and even to several fungal genera), while the remainder are considered *species inquirenda*, *incertae sedis* or *nomen dubium.* Members of the genus *Minchinia* form operculate spores without ornamentations and some 6 species have been described from chitons, clams, pearl oysters and shipworms. [The third haplosporidiid genus *Bonamia* is considered separately in the next section as these unique parasites form 'microcells' in oysters and generally do not produce spores, although one species has recently been reported to do so].

Parasite species	Spore size	Hosts	Location [Clinical signs]	Distribution
Haplosporidium (operculate spores with ornaments derived from spore wall)				
H. armoricanum (syn. *Minchinia*)	5.0-5.5 x 3.1-4.5 µm	Bivalvia: ostreid (European flat oyster, southern mud oyster)	viscera [brown meat disease]	Europe
H. ascidiarum (syn. *Minchinia*)		Ascidiacea: cionid (vase tunicate), polyclinid (sea-strawberry)	stomach	Mediterranean
H. caulleryi		Polychaeta: nereidid (*Neanthes* (*Nereilepas*) *fucata*)		Europe
H. cernosvitovi	10-11 x 6-7 µm	Clitellata: naidid (aquatic worm		South America

		Opisthocysta flagellum)		
H. comatulae	6 x 4 µm	Crinoidea: colobometrid (sawtoothed feather star)	haemal spaces in intestinal wall	Australia
H. costale (syn. *Minchinia*) [SSO = seaside organism]	3.1 x 2.6µm	Bivalvia: ostreid (eastern oyster, Pacific oyster)	connective tissues, digestive gland	North America, Eurasia
H. diporeiae	4-7 x 3-5 µm	Amphipoda: pontoporeiid (*Diporeia* sp.)	coelom, connective tissue, digestive tissue, muscle	North America
H. edule	3.2 x 2.2 µm	Bivalvia: cardiid (common cockle)	digestive gland	Europe
H. heterocirri (syn. *Minchinia*, *Aplosporidium*)	not stated	Polychaeta: cirratulid (*Heterocirrus viridis*)		Europe
H. hinei	3.5-4.0 x 2.5-3.0 µm	Bivalvia: pteriid (South Sea pearl oyster)	connective tissue of digestive gland	Australia
H. limnodrilli	10-12 x 8-10 µm	Clitellata: naidid (worm *Limnodrilus udekemianu*)		Europe
H. louisiana (syn. *H. cadomensis*, *Minchinia*)	12 x 8 µm	Decapoda: panopeid (dwarf crab, Atlantic mud crab)	gut wall	North America, Europe
H. lusitanicum	3.0 x 2.1 µm	Gastropoda: patellid (limpet *Helicon pellucidus*)	gills, viscera	
H. marchouxi		Polychaeta: serpulid (tubeworm *Salmacina dysteri*)		Europe
H. meligethi	3.3-4.8 x 1.6-2.6 µm	Coleoptera: nitidulid (rape blossom beetle)	intestines	Europe
H. montforti	2.4 x 2.3 µm	Gastropoda: haliotid (green ormer)	connective tissue, gill, digestive gland, foot muscle	Europe
H. nelsoni (syn. *Minchinia*) [MSX = multinucleate sphere unknown]	5-11 x 5-8 µm	Bivalvia: ostreid (eastern oyster, Pacific oyster)	gills, gonads, digestive gland [blemishes, mortalities]	North America, Asia
H. nemertis	7 x 4 µm	Nemertea: lineid (ribbonworm *Lineus hilineatus*)		Europe
H. parisi	not stated	Polychaeta: serpulid (calcareous tubeworm)		Atlantic
H. patagon	4.2 x 2.5 µm	Gastropoda: siphonariid (false limpet)	digestive gland	South America
H. pickfordi	8-11 x 4-5 µm	Gastropoda: lymnaeid (great pond snail), physid (broadshoulder physa), planorbid (bell-mouthed ramshorn)	digestive gland	North America
H. pinnae	3.6-5.7 x 2.7-4.5 µm	Bivalvia: pinnid (fan mussel)	digestive gland tubules	Mediterranean
H. potamillae	?	Polychaeta: sabellid (tubeworm *Potamilla torelli*)		Europe
H. raabei	6-9 x 4-6 µm	Bivalvia: dreissenid (zebra mussel)	gills, gonads, digestive gland	Europe
H. scolopli (syn. *Aplosporidium*)	not stated	Polychaeta: orbiniid (bristleworm *Scoloplus mulleri*)		Europe
H. simulii	4.8 x 3.6 µm	Diptera: simuliid (white-stockinged black fly larva)	viscera	North America
H. tipulae	2.4 x 1.8 µm	Diptera: tipulid (crane fly larva)	viscera	Europe
H. tumefacientis	8-11 x 5-8 µm	Bivalvia: mytilid (California mussel)	digestive gland [tumefactions = swellings]	North America
H. tuxtlensis	3.6 x 2.7 µm	Gastropoda: siphonariid (striped false limpet)	visceral tissues	North America
H. vejdovskii	10-12 x 8-10 µm	Clitellata: enchytraeid (iceworm)		Europe
Minchinia (spores without ornaments)				

M. chitonis	9-11 x 6-8 µm	Polyplacophora: tonicellid (gray chiton)	digestive gland, muscles, gills [brown colourations]	Europe
M. dentali	4.6 x 2.8 µm	Scaphopoda: dentaliid (tusk shell)	radula and connected tissues	Mediterranean
M. mercenaria	5.4 x 3.7 µm	Bivalvia: venerid (hard clam)	connective tissues, muscles	North America
H. orchestiae	not observed	Amphipoda: talitrid (sandhopper *Orchestia* sp.)	connective tissues of digestive glands and other organs [tissue disruption]	Europe
M. occulta	4.5-5.0 x 3.5-4.1 µm	Bivalvia: ostreid (hooded oyster)	connective tissue of gills, mantle, reproductive follicles, digestive gland	Pacific
M. teredinis	fresh 10-11 x 8-9 µm fixed 5.5-7.5 x 4.5-6.0 µm	Bivalvia: teredinid (Bartsch shipworm, Naval shipworm, deepcleft shipworm)	gill, visceral tissues [shipworm disease]	North America
Species inquirenda				
H. aulodrili	spores without orifice or lid	Clitellata: naidid (tubificid bloodworm Aulodrilus)		Europe
H. aselli (transferred to ascetosporan genus *Claustrosporidium*)	spores without orifice or lid	Isopoda: asellid (pond slater)		North America
H. babyloniae	not stated	Gastropoda: babyloniid (sea snail *Babylonia areolata*)	internal organs [tissue disruption]	Asia
H. bayeri	spores without orifice or lid	Ephemeroptera: heptageniid (unspecified mayfly)		Europe
H. carcini	not observed	Decapoda: carcinid (European green crab)	haemolymph, gills, hepatopancreas	Europe
H. cranc	not observed	Decapoda: carcinid (European green crab)	haemolymph, gills, hepatopancreas	Europe
H. ecdyonuris (transferred to fungal genus *Polycarum* then *Endoblastidium*)	spores without operculum	Ephemeroptera: heptageniid (mayfly *Ecdyonurus lateralis*)	connective tissues	Europe
H. echinogammari	not observed	Amphipoda: gammarid (scud *Echinogammarus marinus*)	connective tissues of internal organs [tissue disruption]	Europe
H. gammari (transferred to ascetosporan genus *Claustrosporidium*)	spores up to 10 µm long, without orifice, operculum or lingula	Amphipoda: gammarid (*Rivulogammarux pulex*)	adipose tissue [destroy fat cells]	Europe
H. guarani	?	Oligochaeta: enchytraeid (worm *Guaranidrilus oiepe*)		South America
H. littoralis	not observed	Decapoda: carcinid (European green crab)	haemolymph, gill, hepatopancreas	Europe
H. malacobdellae	3.5 x 2.5-3.0 µm, spores without orifice	Nemertea: amphiporid (ribbonworm *Amphiporus lactifloreus*), lineid (ribbonworm *Lineus bilineatus*)		Europe
H. mesnili (transferred to the ichthyosporean genus *Caullerya*)	10-16 x 8-12 µm	Branchiopoda: daphniid (water fleas, *Daphnia pulex, D. longispina, D. magna, D. galeata, D. obtusa* and *D. galeata x hyalina* hybrid*)*	gut epithelia	Europe
H. mytilovum (transferred to the microsporan genus *Steinhausia* or *Chytridiopsis*)	1-2 µm, spores without orifice	Bivalvia: mytilid (blue mussel, Mediterranean mussel)	ova [mussel egg disease]	Atlantic, Pacific, Mediterranean

H. periplanetae (syn. *Nephridiophaga*) (now considered to be fungi)	spores without orifice or lid	Blattodea: blattid (cockroach)		Europe
H. prostomae	6.5 x 4.5 µm, spores without orifice	Nemertea: prostomatid (ribbonworm *Prostoma eilhardi*)		Europe
H. typographi	spores without orifice or lid	Coleoptera: curculionid (European spruce bark beetle)		Europe
*M. tapetis** (syn. *Haplosporidium*)	4-6 µm, spores without operculum	Bivalvia: cardiid (common cockle), venerid (Palourde clam, European littleneck clam)	gills, mantle, digestive gland tubules	Europe

*Not to be confused with *Urosporidium tapetis* hyperparasitic in trematode from Manila clams.

Parasite morphology: Haplosporidian parasites generally form 4 different types of developmental stages: namely, invasive uninucleate stages; vegetative multinucleate plasmodia; sporonts (yielding sporoblasts); and unicellular spores. The invasive stages are small rounded cells measuring 4-6 µm in diameter and they have a single central nucleus, although diplokaryotic cells are sometimes observed. The multiplicative stages are spherical to amorphous (plasmodial) in shape ranging in size from 4-100 µm in diameter. It sometimes appears that smaller plasmodia form by cleavage of larger plasmodia. These stages are multinucleate, containing up to 60 nuclei in some *Haplosporidium* spp. and up to 24 nuclei in some *Minchinia* spp. The nuclei are usually spherical measuring from 1.5-2.0 µm in diameter. The plasmodia divide by irregular multiple fission (plasmotomy) to form daughter cells (sporonts). Division begins when Golgi bodies and irregular membranes form in the cytoplasm amongst the nuclei, and culminates when each nucleus and some surrounding cytoplasm becomes encircled by limiting membranes arising from fusion of the Golgi vesicles. The resultant sporonts undergo sporoblastogenesis to form sporoblasts which are characterized by gradual thickening of their external membranes (which ultimately become spore walls), the appearance of a pre-operculum (which later differentiates into an operculum) and the formation of haplosporosomes and a spherulosome in the endosporoplasm. The sporoblasts differentiate into spores (sporogenesis) which undergo a maturation process with the development of spore wall ornamentation, degradation of the episporoplasm, rupture of the sporocyst and liberation of mature spores. Haplosporidian spores lack polar capsules (present in myxozoans) and lack polar filaments (present in microsporans). The spores are oval-ellipsoidal in shape and range in size from 3-8 x 2-5 µm (those of several species range up to 13 x 9 µm). The spores are unicellular and possess a single endosporoplasm and a small (2-3 µm) nucleus with an endosome. A rudiment of the intranuclear spindle (known as the 'kernstab') often persists in interphase nuclei. The cytoplasm bears a spherulosome (sometimes called a spherule), mitochondria with tubular cristae, and several dense organelles (known as haplosporosomes). The spores are operculate and have an orifice covered by an external lid in the genera *Minchinia* and *Haplosporidium* (whereas the orifice is occluded by an internal lingula (tongue-like plug, flange or flap) in the genus *Urosporidium*). The mature spores of *Haplosporidium* display elaborate ornamentations appearing as filamentous wrappings of spore wall material, whereas those of *Minchinia* lack ornaments, although some may have transient extensions of epispore cytoplasm during their development. In contrast, the mature spores of most *Urosporidium* spp. have long caudal extensions of epispore cytoplasm.

Site of infection: Haplosporidian parasites infect the soft tissues of aquatic invertebrates, particularly the gills, palps, suprabrachial chambers, connective tissues and epithelia of the intestines and digestive gland (hepatopancreas), with many infections eventually becoming systemic and distributed throughout host tissues. Parasites have been recorded in a wide range of animals (molluscs, crustacea, urochordates, echinoderms, polychaetes and oligochaetes) from a variety of habitats (mostly marine and estuarine, but also from some freshwater regions). Most parasite species appear to be oioxenous and only infect one or a few closely-related hosts.

Pathogenesis: Several species are notorious parasites of oysters around the world, causing significant disease and mortalities in both wild and cultured oysters. Infections may cause a range of lesions, from destruction of the gills, gonads or digestive gland to general destruction of all associated tissue, often resulting in tissue discolouration. *H. nelsoni* causes MSX (= multinucleate sphere unknown) disease characterized by pale discolouration of the digestive gland due to the presence of numerous spores in the tubule epithelia. *H. costale* causes SSO (= seaside organism) disease in oysters typified by darker discolouration of the digestive gland due to the presence of spores in the connective tissues between tubules. *H. armoricana* causes brown meat disease in flat oysters, and *M. tapetis* causes discolourations in the tissues of cockles and clams. In many cases, the first signs of infection in shellfish are mortalities. Post-mortem examination often reveals emaciation, retracted mantle with failure of shell growth, rarely brown patches of peristracum opposite lesions on the mantle surface, reduced meat yield, impaired gonadal development and lower fecundity (often a threefold increase in the proportion of females infected, possibly due to inhibition in the development of male gametes). Oysters often start to die within a month of infection, with peak mortalities occurring for 1-3 months over summer. Disease is reduced (suppressed?) by low temperatures over winter and by low salinities. There is some evidence of resistance developing in oysters that survive the first year of infection, as they were often able to suppress or rid themselves of parasites in late spring as temperatures approached 20°C in their second year. Remission was characterized by diminution of infection with localization of

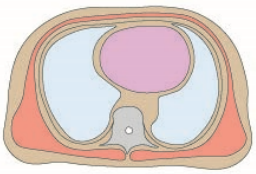
parasites to external epithelia and diapedesis resulting in the deposition of moribund parasites and necrotic tissues against the shell followed by external conchiolinous encapsulation.

Developmental cycle and mode of transmission: The complete developmental cycles of most haplosporidian species are not known. Recent studies indicate that amoebulae released from spores undergo modified schizogony (exosporulation of the endosporoplasm) giving rise to multinucleate plasmodia. The plasmodia undergo irregular multiple fission (plasmotomy) to produce sporonts which cleave into uninucleate sporoblasts that eventually differentiate into spores. Sporoblast membranes become thickened during sporoblastogenesis, spore walls become ornamented during sporogenesis, and mature operculate spores are thought to be liberated by rupture of the sporocyst. Despite spore production, most epidemiological and experimental evidence suggests that direct transmission occurs via host-to-host contact during cohabitation. Transmission has been shown to be facilitated by oyster translocations, either deliberate by growers and/or scientists, or accidental via the fouling of ships hulls or via ballast water. Attempts to transmit infections by the experimental transplantation of infected tissues have failed, initially suggesting that another host may be involved (either as a reservoir for infective stages or as an intermediate host for development). No alternate hosts have yet been found even though environmental DNA studies were able to detect haplosporidian signals in planktonic and benthic water samples, suggesting the presence and dissemination of water-borne stages. However, several experiments attempting to transmit infections by injecting spore suspensions have been unsuccessful, suggesting that a maturation period may be required for spores to become infectious. MSX and SSO diseases in oysters usually occur when salinities are greater than 15-20 parts per thousand (ppt), and some outbreaks have been associated with drought conditions which caused estuaries to become more saline and oysters to be more susceptible.

Differential diagnosis: Infections are difficult to recognize ante-mortem as shellfish exhibit few clinical signs before death, although some may become moribund and others appear to gape due to mantle recession. At post-mortem, infected tissues often become watery-translucent and appear to be discoloured or have blemishes. Diagnosis is facilitated by the microscopic examination of host tissues for the presence of parasite developmental stages (plasmodia, sporonts, spores); either in stained haemolymph smears, tissue squash preparations or in histological sections. The sporoplasm of mature spores stains bright red with modified Ziehl-Neelsen carbol fuchsin stains. Careful examination is required to differentiate haplosporidian genera: with *Haplosporidium* spp. forming unicellular operculate ornamented spores (3-12 μm) distributed throughout host tissues, *Minchinia* spp. forming unicellular operculate unornamented spores (4-11 μm) widespread in tissues, and *Bonamia* spp. forming microcells (2-5 μm) usually within host haemocytes. Related *Mikrocytos* spp. also form microcells (2-4 μm) but usually within vesicular connective tissue cells. Transmission electron microscopy is often required to confirm haplosporidian spore identity through the detection of haplosporosomes (notably absent in *Mikrocytos*). In comparison, the paramyxean *Marteilia* spp. infecting oysters forms multicellular nested spores (4-10 μm), with haplosporosomes, usually in digestive tubules. At present, there are no techniques available to culture parasites *in vitro*. Molecular biological techniques have been used to detect, identify and characterize haplosporidian taxa following polymerase chain reaction (PCR) amplification of nuclear gene sequences, predominantly ribosomal RNA and actin genes.

Treatment and control: There is currently no effective treatment for haplosporidian infections in shellfish. Nonetheless, control programmes based on epidemiological observations have been successful in curtailing and preventing infections. Disease outbreaks exhibit a strong seasonal pattern, being most prevalent during summer when water temperatures are warmer and salinity levels are higher due to water evaporation. Spore stages also develop primarily in juvenile oysters, and studies have shown that culture in low salinity areas (< 10 ppt) reduced parasite pathogenicity and enhanced oyster survival. It is therefore recommended that growers plant and culture oysters in areas of low salinity by placing racks in intertidal zones or estuaries, and only moving them during cooler months to high salinity areas to take advantage of better growth. Stocks should be continually monitored for infections in enzootic areas so that informed decisions can be made on when to plant and harvest oysters. Some success has been made with mathematical prediction models simulating infection cycles in oyster populations under different environmental conditions and forecasting conditions that can initiate and end epizootics. Relevant factors include water temperature, salinity, turbidity, available food, host filtration, respiration, assimilation, parasite doubling times, crowding effects and mortality rates to predict disease occurrence, prevalence and intensity. Some success has also been reported selecting oysters for disease resistance based on those with increased haemocyte counts being better able to plug lesions, remove debris, repair tissue and help oysters survive infection. Triploid eastern oysters are more resistant to MSX than diploid cohorts, and some sympatric wild oyster populations appear to be more resistant than their cultured counterparts.

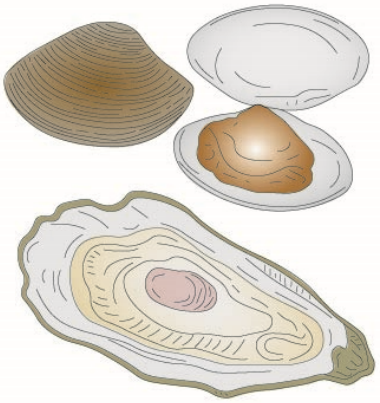
Haplosporidium, Minchina



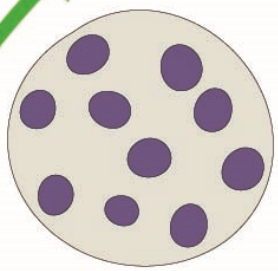
viscera, coelom
(lesions, mortalities)
(MSX disease)
(SSO disease)
(brown meat disease)

form unicellular spores
with single sporoplasm
and haplosporosomes

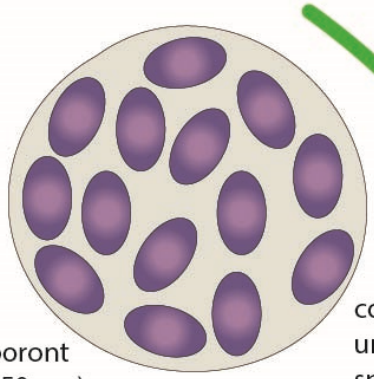
multiply by modified schizogony
within multinucleate plasmodia



Invertebrate Hosts
(aquatic molluscs)



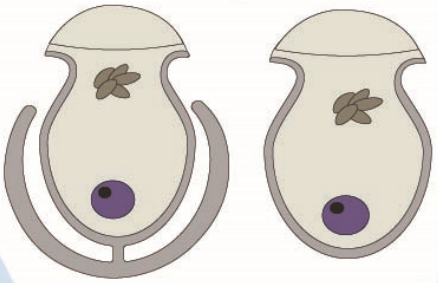
multinucleate
plasmodium
(4-100 µm)



sporont
(~ 50 µm)

containing
uninucleate
sporoblasts

spores (3-8 µm)
(with hinged lids)



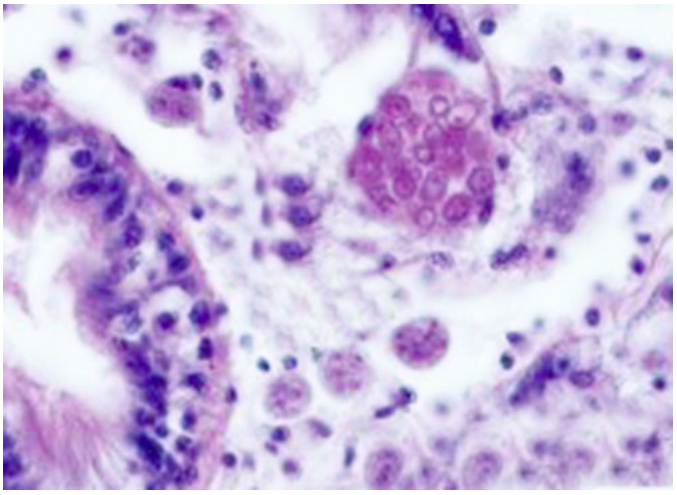
Haplosporidium

Minchinia

uninucleate
invading
stage
(4-6 µm)

?

despite spore formation, transmission between hosts
is often direct via close contact (co-habitation)



Haplosporidium plasmodia in oyster tissues