

Extensive uncharted biodiversity: the parasite dimension

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Running title: Uncharted parasite diversity

Synopsis

Parasites are often hidden in their hosts and exhibit patchy spatial distributions. This makes them relatively difficult to detect and sample. Consequently we have poor knowledge of parasite diversities, distributions and extinction. We evaluate our general understanding of parasite diversity and highlight the enormous bias in research on parasites such as helminths and arthropods that infect vertebrate hosts. We then focus on Myxozoa as an exemplary case for demonstrating uncharted parasite diversity. Myxozoans are a poorly recognised but speciose clade of endoparasitic cnidarians with complex life cycles that have radiated to exploit freshwater, marine and terrestrial hosts by adopting strategies convergent to those of parasitic protists. Myxozoans are estimated to represent some 20% of described cnidarian species – greatly outnumbering the combined species richness of scyphozoans, cubozoans, and staurozoans. We summarise limited understanding of myxozoan diversification and geographical distributions, and highlight gaps in knowledge and approaches for measuring myxozoan diversity. We close by reviewing methods and problems in estimating parasite extinction and concerns about extinction risks in view of the fundamental roles parasites play in ecosystem dynamics and in driving host evolutionary trajectories.

Introduction

Diversity in terms of species richness in any one place and at any one time will be a manifestation of both ecological and evolutionary processes. The latter will be a function of patterns of speciation and extinction resulting from responses to abiotic and biotic environments while immigration and emigration will determine the distributions of locally adapted species. Because species are typically comprised of genetically distinct populations and species ranges vary, the outcomes of species interactions with their environments will continuously change in space and time according to geographical selection mosaics (Thompson 1999). Such ongoing evolutionary and ecological dynamics organise biodiversity on Earth. Coevolution in reciprocally interacting species continually reshapes interactions across different spatial and temporal scales and is a major biodiversity driver. However, accelerated environmental change effected by anthropogenic activities now challenges such biodiversity dynamics (Hoberg & Brooks 2015).

Parasites form intimate associations by living on or in another organism, the host, from which they derive nutrition. Because they are often hidden within their hosts, and exhibit patchy distributions parasites are inherently difficult to sample. Such difficulties no doubt have contributed to the typical absence of data on parasites in ecological surveys, in indices of biological assessment, in many food web studies, and in evaluations of extinction risk. Other factors contributing to neglect of parasites include lack of taxonomic expertise, time required for pathological investigation and charismatic appeal – parasites often elicit disgust and avoidance responses. Parasites are also overlooked over long time scales with their paltry fossil record promoting a narrow view of the history of life on Earth. Our consequent poor knowledge of parasite diversities, distributions, origins and extinctions creates a 'parasite void'.

We examine this parasite void by evaluating our general understanding of parasite diversity and then more particularly explore uncharted diversity patterns revealed by the Myxozoa, a speciose radiation of endoparasites that exploit vertebrate and invertebrate

hosts. Long regarded as enigmatic, it is now clear that myxozoans are a clade of parasitic cnidarians – an affinity that is increasingly but not yet broadly recognised by biologists. By focusing on patterns of myxozoan diversity we illustrate generic problems of estimating parasite diversities while highlighting patterns of diversification that have enabled endoparasitic cnidarians to exploit marine, freshwater and terrestrial hosts. We then go on to review parasite extinction and its implications in our changing world.

Parasite diversity

The present-day diversity of parasites results from evolutionary transitions to parasitism by a broad array of organisms and their subsequent diversification and extinction. Thirteen of the approximately 50 eukaryotic phyla recognised by de Meeûs & Renaud (2002) are comprised entirely of parasites and a further 23 phyla contain parasites. Within Metazoa, parasitism appears to have evolved independently at least 223 times in 15 of the 35 generally recognised animal phyla (Weinstein & Kuris 2015) with subsequent diversification to large numbers of species in some cases (e.g. nematodes; Poulin & Morand 2000; Poulin 2011a; Blaxter & Koutsovoulos 2015). These estimates are likely to increase as metazoan relationships are better resolved, unknown life-history strategies are described and new species are discovered (Weinstein & Kuris 2015). Although free-living lifestyles have been regained on occasion (Poulin 2011a) and some transitions to parasitism may ultimately have failed, parasitism as a lifestyle has clearly been highly successful.

Parasitologists have long recognised that parasites are ubiquitous, that co-infections are common and that host species are often infected by numerous parasite species (Schmid-Hempel 2011). For example, Kennedy (1978) found that brown trout from nine British lakes harboured 17 species of metazoan parasites (mostly helminths), and Valtonen et al. (1997) recorded 42 and 38 species of metazoan and protozoan parasites from perch and roach, respectively, from four Finnish lakes. Even though some parasites may be generalists (equivalent stages infecting \geq one host species) such data have led to the

conclusion that there are more parasitic than host species on the planet (Windsor 1988, Schmid-Hempel 2011). Many estimates of parasite species diversity are based on extrapolations of patterns of host specificity using simple equations. For example, Poulin and Morand (2000) inferred that every metazoan host has at least one parasite species. Poulin and Morand (2004) proposed that there are at least twice as many endohelminth species (77,000 species) as species of vertebrate hosts, and Dobson et al. (2008) suggested a greater estimate (300,000 endohelminth species) after correcting for cryptic species. Such extrapolations may be overestimates if local patterns of host-specificity cannot be scaled up to global patterns and across all host types (Costello 2016). In addition, the decelerating nature of species accumulation curves is not accounted for (the discovery of new parasite species becomes less likely as more host species are investigated; Strona & Fattorini 2014). Another approach to estimate parasite species diversity is to rely on expert opinion, although recent evidence suggests this may be unreliable (Poulin 2014).

Estimating parasite diversities is compromised by various issues. Many parts of the world (e.g. deep sea, meiofaunal zones) and many host groups (e.g. invertebrates) are poorly sampled (e.g. Leung et al. 2015; Rohde 2015; Costello 2016; Okamura 2016). Unrecognised cryptic species and geographic bias also confound diversity estimates. Furthermore, invalid taxa may not be accounted for (e.g. species synonymous with species already described). Perhaps most remarkable, however, is our extremely poor knowledge of microparasite diversity (Okamura 2016). Indeed, Dobson et al. (2005) conceded that 'we have no credible way of estimating how many parasitic protozoa, fungi, bacteria, and viruses exist'— hence nearly all estimates of parasite diversity are based on extrapolation of data on metazoan parasites (especially helminths). Poulin (2014) stated that there are 'no solid estimates of parasite diversity and no adequate method for obtaining one'. Accordingly, cumulative curves of known parasite species are still rising or only beginning to slow down.

We note, however, that our very poor understanding of microparasite diversity is beginning to improve. Molecular approaches are now revealing extensive diversities of eukaryotic protistan groups through the analysis of environmental samples from marine,

freshwater and terrestrial habitats (see Bass et al. 2015 for review). For example, de Vargas et al. (2015) found an unsuspected diversity of parasites in metabarcoding studies of eukaryotic plankton from the photic oceanic realm. General primers used in amplicon sequencing identified some 21% of the hyperdominant cosmopolitan OTUs as parasitic alveolates and excavates. Most notable was novel excavate diversity (>12,300 OTUs) that was associated with reference sequences of diplomonads (for which there are only two described genera). This unanticipated and surprising excavate OTU diversity was some 50-fold, 6-fold and 3.8-fold higher than that of associated foraminifers, ciliates and diatoms, respectively. In addition, 30% of the OTUs obtained by de Vargas et al. (2015) could not be assigned to known eukaryotic groups. Given the ubiquity of parasites, it is likely that a considerable proportion of these OTUs will be representative of parasites.

For highly divergent taxa, targeted primers may be required to reveal diversity. For example, Chambouvet et al. (2015) developed primers for *Perkinsea* (a parasitic group of alveolates associated with mass mortality of frog tadpoles) and found novel diversity in freshwater samples and tadpole livers from temperate and tropical habitats. Similarly, targeted primers identified novel lineages of haplosporidians (parasites of marine and freshwater invertebrates belonging to the Ascetosporia), increasing the total number of haplosporidians by >100% (Hartikainen et al. 2014a).

The Myxozoa: An unusual, species-rich clade of endoparasites

Introduction to Myxozoa

Myxozoans are a species-rich clade of endoparasitic cnidarians with complex life cycles, exploiting invertebrate and vertebrate hosts (Canning & Okamura 2004; Okamura et al. 2015a). Many myxozoan infections are innocuous (not readily apparent), but some cause important diseases of fish (Feist & Longshaw 2006). Myxozoans demonstrate extreme morphological simplification and miniaturisation as a result of their parasitic lifestyle (Okamura et al. 2015b). In particular, they exhibit a trend of tissue loss, they lack a gut and

nervous system, and cilia and centrioles are absent. The stinging cells or cnidocytes used by free-living cnidarians for prey capture and defense have been co-opted for transmission. Water-borne multicellular stages (spores) possess intracellular organelles (polar capsules homologous to nematocysts in cnidocytes). Filaments everted from polar capsules effect attachment to hosts. Infectious cells within spores then invade the host. Observations of meiosis identify invertebrates as definitive hosts.

According to the most recent estimate, there are some 2400 described myxozoan species (Zhang 2011), but complete life cycles have only been resolved for some 50 species (Eszterbauer et al. 2015). Current knowledge of myxozoan species diversity is largely based on infections in fish ($n \sim 2300$). The two major monophyletic myxozoan clades are distinguished by molecular data, invertebrate host use, species richness and degree of morphological simplification. Members of the species-poor Malacosporea use freshwater bryozoans (Class Phylactolaemata) and fish as hosts (Canning et al. 2000). The speciose Myxosporea use oligochaetes and polychaetes as definitive hosts and various vertebrates (primarily fish) as secondary hosts (Fiala et al. 2015a; Hallett et al. 2015).

The malacosporeans possess recognisable tissues and some develop as active vermiform stages (myxoworms) (Gruhl & Okamura 2015). There are five described species (Patra et al. 2017). Malacosporeans develop as myxoworms or sacs in the coelomic cavity of bryozoan hosts (Canning & Okamura 2004) (Fig. 1A,B). Both forms possess epithelia and tetradially arranged longitudinal muscles with obliquely-oriented muscle fibres enable helical swimming in myxoworms (Gruhl & Okamura 2012, 2015). Multicellular spores (Fig. 1C) produced within myxoworms and sacs are infectious to fish. Uninucleate pseudoplasmodia develop in kidney tubules in intermediate fish hosts (Feist et al. 2015) (Fig. 1D). Multicellular spores produced within pseudoplasmodia are secreted in urine to infect bryozoans. Extensive replication of at least one malacosporean (*Tetracapsuloides bryosalmonae*) in kidney tissue can cause the devastating Proliferative Kidney Disease (PKD) in salmonid fish hosts. The simple spores produced by malacosporeans are relatively spherical, lack a hardened outer wall and are indistinguishable amongst species, possessing

either four or two polar capsules (when developing in bryozoans and fish, respectively) (Canning & Okamura 2004).

The myxosporeans have lost proper tissues and are highly morphologically simplified. There are some 2400 described species (Zhang 2013). Myxosporeans develop as pansporocysts in their definitive annelid hosts (Fig. 2A). Cells forming the pansporocyst wall have retained features suggestive of a highly modified epithelial layer (apical adherens junctions, general cell polarity and functions such as uptake and secretion; Gruhl & Okamura 2015) although a basal lamina is lacking. Multicellular spores ('actinospores') produced within pansporocysts are infectious to vertebrates. Osmotically-driven inflation of outer valve cells upon release into the environment produces caudal processes that reduce actinospore sinking rates (Fiala et al. 2015a) (Fig. 2B-D). Multinucleate plasmodia or uninucleate pseudoplasmodia develop in intermediate vertebrate hosts (Feist et al. 2015) (Fig. 2E,F) and multicellular spores ('myxospores') infectious to annelids are produced within these stages (Fig. 2G). The hardening of myxospore walls confers viability in the environment for relatively long time periods (e.g. up to months depending on temperature; Ray et al. 2015). Morphological variation of myxospores (Fig. 2H-K) is useful for taxonomic purposes (Fiala et al. 2015a). Myxosporeans are the causative agents of some problematic fish diseases (e.g. whirling disease and enteronecrosis in salmonids; Jones et al. 2015).

The first reported myxozoan was from whitefish (Jurine 1825) and for a long time myxozoans were classified as protists despite recognition of the multicellularity of spores by early researchers (Canning & Okamura 2004). The advent of molecular tools confirmed a metazoan affinity (Smothers et al. 1994) but led to considerable controversy over placement within the Metazoa due to high levels of molecular divergence and resultant long branch attraction. It is now clear that myxozoans are cnidarians (e.g. see Foox et al. 2015; Okamura & Gruhl 2015 for review), vindicating Weill's early observation of the similarity of polar capsules and nematocysts (Weill 1938). Phylogenetic analyses enabled by transcriptomic and genomic data demonstrate that myxozoans group with *Polypodium hydriforme* (a monotypic lineage with larval forms parasitizing eggs of sturgeon and paddlefish) forming a

clade of endoparasitic cnidarians (Chang et al. 2015; Kayal et al. 2017) referred to as the Endocnidozoa (Collins 2009).

Myxozoan taxonomy and species discrimination

Traditional myxozoan taxonomy is based largely on morphologies of myxospores (Lom & Dyková 2002, Fiala et al. 2015b). This reflects the long history of research on myxosporeans in fish, myxosporean species-richness, the very recent recognition of the Malacosporea, and separate assignment of actinospores (as Actinosporea) prior to recognition of complex myxozoan life cycles (Okamura et al. 2015a). Important taxonomic characters include the number and configuration of shell valves and polar capsules, spore and polar capsule dimensions, the number of turns of the polar filament, and spore surface features (Lom & Dyková 2006, Fiala et al. 2015b). However, myxospore morphologies can be plastic, spore morphotypes may be convergent, and boundaries between many genera are vague, especially when spores are morphologically simple (Atkinson et al. 2015, Fiala et al. 2015b). Accordingly, molecular markers reveal unexpected relationships and discrepancies with myxospore-based classifications (e.g. Fiala & Bartošová 2010). Actinospores can demonstrate different morphologies even within the same species which limits their taxonomic usefulness (Eszterbauer et al. 2006). Consequently, the provision of SSU rDNA sequence data in species descriptions was encouraged (Kent et al. 2001) and such data are now routinely reported in species discrimination as the marker reliably clarifies the relationships among myxozoan species (Fiala et al. 2015b). Other features that can be useful in species discrimination include patterns of host and tissue specificity (Molnár & Eszterbauer 2015), geographical distribution (Hervio et al. 1997) and developmental stages (Lom & Arthur 1989).

Estimates of myxozoan species richness

As of October 2005 some 2180 myxozoan species had been recorded (Lom & Dykova 2006) – a three-fold increase in the number of species reported 39 years earlier ($n = 731$; Sh'ulman

1966). Zhang (2013) reported a total of 2425 myxozoan species in 2013 based on the number of named species reported by Lom and Dykova (2006) and species subsequently described by Zoological Record entries. We have determined that by the end of 2017 there were 2596 described myxozoan species (using Zoological Record and Google Scholar to identify species descriptions since 2013). This number does not incorporate many unique sequences deposited in GenBank with no associated species descriptions and includes species described before sequencing was routine. As will become clear later, we expect this is a considerable underestimate of true species richness. We note that all estimates are comparable, being based on species descriptions, and therefore collectively suggest that the number of myxozoan species being described is not levelling off over time.

Zhang (2013) also reported 10,203 extant species of free-living cnidarians. Thus, as of 2013 some 19% of described cnidarian species were endoparasitic – close to the estimate of 18% suggested by Okamura et al. (2015a) (who used Lom & Dykova's estimate of 2180 myxozoan species and did not include data for staurozoans). To determine whether the ratio of free-living:parasitic cnidarian species has remained roughly the same we updated Zhang's estimate, obtaining a total of 11,758 described species of extant free-living cnidarians by the end of 2017. This indicates that at present some 20% of described cnidarian species are endoparasitic. As depicted in Fig. 3A, the number of described myxozoan species greatly exceeds the number of described species of scyphozoans, cubozoans, and staurozoans. As we argue below these summaries are likely to greatly underestimate both myxozoan species richness and proportional representation within the Cnidaria.

To explore the issue of unknown myxozoan diversity further we determined the number of myxozoan species reported from fish in freshwater environments in Brazil over time since the first species were detected (Dunkerly 1915) (Fig. 3B) using various information sources (see Supplementary Data). The lack of any evidence of an asymptote in the cumulative number of species reported over time is a typical pattern for parasites and suggests there are many further myxozoans in this region alone.

Patterns of myxozoan diversification

A clear cut pattern of myxozoan diversification is the disparity in species richness between Myxosporea and Malacosporea. This pattern may relate to the diversity of definitive hosts, annelid hosts being relatively species rich (some 11,500 extant oligochaete and polychaete species; Ruppert et al. 2003) and phylactolaemate bryozoan hosts being notably species-poor (69 extant phylactolaemate species; Massard & Geimer 2008). Similar patterns of diversification are exhibited by the extensive independent radiations of myxosporeans that exploit oligochaete and polychaete invertebrate hosts (Fiala et al. 2015a). Such patterns are consistent with conclusions from a meta-analysis that parasite species richness is strongly correlated with that of their hosts, with richer host clades harbouring richer parasite assemblages (Kamiya et al. 2014a).

The vast majority of myxozoans are known to exploit fish as vertebrate hosts. Because fish serve as hosts of malacosporeans and myxosporeans (and also of sister taxon, *Polypodium hydriforme*) exploitation of fish may be primitive. Other vertebrate hosts have, however, been acquired by myxosporeans. These include amphibians (frogs, toads, newts, salamanders), reptiles (turtles and tortoises), waterfowl (ducks), and small mammals (shrews and probably moles) (Hallett et al. 2015). The recent discovery of infections in caecilians (Hartigan et al. 2016) confirms that myxosporeans exploit hosts in all amphibian orders and that amphibian hosts have been adopted independently on at least three occasions. All of the bird and mammal infecting species group variously within one clade (part of the large, oligochaete-infecting Freshwater Clade; Fiala et al. 2015a) and are distinct from each other. This clade will likely expand as sampling for and recognition of myxosporeans infecting terrestrial hosts continues. The small number of myxosporeans described from non-fish hosts (some 33 species), their short branches in molecular phylogenies, and molecular clock analysis suggest a scenario of relatively recent host switching in all cases (Kodádková et al. 2015; Fiala et al. 2015a). However, lack of sampling may compromise this inference.

Drivers of species richness in other parasite groups have been linked with host traits viewed to promote the colonisation and persistence of parasites. For example, in another meta-analysis Kamiya et al. (2014b) found that parasite species richness was positively associated with body size, geographical range and density of animal, plant and fungal hosts. Sympatry and gregarious host behaviour have also been linked with switching of fish hosts and subsequent speciation in monogeneans (Vanhove & Huyse 2015). These patterns have not been explored for myxozoans largely for reasons outlined in the next section.

Measuring and detecting myxozoan diversity: problems, gaps and approaches

Myxozoan species discrimination is now highly dependent on DNA sequence data (Atkinson et al. 2015). However, variable rates of molecular evolution can confound species identification. Therefore, a combination of sequence data and other traits is widely used for species discrimination. Nevertheless, measuring and detecting myxozoan diversity remains problematic. Here we outline these problems and approaches that can be employed to improve our understanding of myxozoan diversity.

The inappreciability of most myxozoan infections (Lom & Dyková 2002) suggests that many are undetected, contributing to our poor understanding of myxozoan diversity (Okamura 2016). In addition, parasites of invertebrates are generally poorly studied because there are few incentives to investigate parasites of organisms considered to be of little commercial value (Leung et al. 2015). Unsurprisingly, myxozoan-invertebrate host systems that have received the most attention are those associated with economically important fish diseases (e.g. salmonid whirling disease and PKD; Alexander et al. 2015; Hartikainen & Okamura 2015). Fieldwork focusing on the ecology of these diseases can coincidentally enable the discovery of new myxozoan diversity (e.g. Hartikainen et al. 2014b), but this will inevitably be biased in various ways (e.g. geographically and taxonomically). Further impediments to identifying myxozoan diversity by surveying invertebrates include inapparent covert infections (Okamura 2016) and low infection prevalences in annelid hosts (e.g. often < 5%; Alexander et al. 2015). Additional hindrances to detecting diversity include oversight

of infection during routine pathological examinations, lack of expertise, difficulty in identifying species, and patchy distributions of infected hosts.

As observed in other parasite groups (e.g. digenean trematodes; Poulin 2011b), there is growing indication of cryptic speciation in myxozoans. Molecular data provide evidence for complexes of morphologically indistinguishable myxozoan species that segregate with geographical or host distributions. For example, the '*Kudoa thyrsites*' complex contains isolates infecting marine fish in distant environments (Japan, Australia, eastern Pacific, eastern Atlantic) and isolates of the '*Parvicapsula minibicornis*' complex are associated with different salmonid hosts and distinct river locations (Atkinson et al. 2015). As for other taxa (Kuris 2015) the extent of cryptic speciation in myxozoans remains unknown. An open question, however, is whether knowledge of morphology and host use for all life cycle stages may resolve apparently cryptic species.

There are considerable geographical gaps in our knowledge of myxozoan diversity. Myxozoans were first recognised in Europe and since then have primarily been studied in Europe, North America, Russia, Japan, Australia, Turkey, India, China and Israel. Investigations of myxozoans from various African countries resulted in a key for some 100 myxosporean species in freshwater fish (Fomena & Bouix 1997) and there is notable ongoing work describing myxozoans in various undersampled geographical regions (e.g. in South Africa [Reed et al. 2002; 2003, 2010], Cameroon [Benoît et al. 2017] and India [Gupta & Kaur 2017a,b]). Myxozoan diversity is especially poorly known in Central and South America (with the exception of Brazil) and in many countries of Asia. Unsurprisingly, geographical knowledge of myxozoans can be biased reflecting the predilections of investigators. For example, what we know of myxozoan diversity in Brazil and Africa is largely based on investigations of myxozoans in freshwater environments. Insights on myxozoan diversity in all geographical regions are generally a direct or indirect result of concern for diseases in aquaculture.

Understanding of biogeographical patterns is also compromised. We suggest this is partly because parasites such as helminths are generally more easily and rapidly collected

and identified (e.g. potentially without a microscope), especially in difficult to sample or remote regions. Nevertheless, it is clear that myxozoans exploit fish hosts in the deep sea. For example, Moser et al. (1976) identified five myxozoan species in macrourid fishes and Kodádková et al. (2015) described a myxosporean infecting primitive chimeroid fish that is sister to the marine myxosporean lineage, forming a clade inferred to have evolved at the time of origin of cartilaginous fish. Greater sampling from such regions may reveal further novel diversity, enabling new insights into myxozoan evolution and adaptive radiations.

Myxozoans are also known to infect marine fish in Arctic environments (e.g. Kjøie et al. 2008; Kjøie 2009; Kodádková et al. 2014, Kristmundsson & Freeman 2013). By combining data from their own study and others Kodádková et al. (2014) compare ratios for the number of myxosporean species found:number of dissected fish species. Although based on relatively low sample sizes ratios > 1.0 suggest a large and untapped diversity of myxozoans in Arctic fishes. Myxozoans have also been described from Antarctic regions. For example, two myxosporeans were found in two species of deep sea fish in the Southern Ocean near the San Juan Archipelago, Chile (Pardo-Gandarillas et al. 2008) and Noble (1984) reports at least three myxosporeans in six species of fish (including five notothenioids) from the continental shelf of Antarctica.

Studies of Australian fish suggest substantial myxozoan diversity in coral reef environments. Gunter and Adlard (2008) found 13 myxosporeans (12 being new) by surveying for infections in 31 damselfish species from Queensland. The high host specificity of many ceratomyxids (Gunter et al. 2010, Heiniger & Adlard 2013) suggests that Australia's coral reef fish will be exploited by over 1,500 species of *Ceratomyxa* yet < 1% of these ceratomyxids have been described (Queensland Museum Network, 2010). Research in other tropical environments suggests similar problems of undersampling and undetected diversity. Freeman and Kristmundsson (2015) describe two species in two new myxosporean families from Malaysian fish hosts, one infecting marine fish and one infecting monogeneans (a case of hyperparasitism). Shaharom (2012) noted that numerous cultured

and ornamental fish in Malaysia are infected with undescribed or undocumented myxosporeans.

Molecular approaches are also revealing novel myxozoan diversity in environmental and tissue samples. For instance, myxosporean-specific primers used in amplicon sequencing enabled Hartikainen et al. (2016) to characterise novel myxozoan OTUs in water samples from freshwater and marine environments and in faeces of piscivores (otters and cormorants). Only 7% of the 107 myxosporean OTUs associated with aquatic environments clustered with previously known sequences in the molecular phylogeny. Furthermore, only one of 28 OTUs associated with otter spraints clustered with a previously known sequence. We estimate that at present some 23% of described myxozoan species have associated SSU rDNA sequence data. This estimate is based on 816 unique SSU rDNA isolates in GenBank (as of December 2017) of which 591 (= 22.8% of the 2596 myxozoan species reported here) were linked with described species. Results of sampling for myxozoans in environmental samples (eDNA analyses) therefore suggest substantial undiscovered myxosporean diversity even in regions where the myxozoan fauna is relatively well known (i.e. some 23% of 107 OTUs would be expected to represent described species). Such eDNA surveys provide a non-destructive and integrative means of characterising myxozoans present in local environments and are likely to contribute greatly and potentially in a non-biased way to revealing novel myxozoan diversity in the future. We anticipate that species richness estimates deriving from unique OTUs will sooner or later outstrip the number of described myxozoan species while further study may help to resolve redundant species. However, determining the nature of the myxozoans associated with OTUs present in environmental samples will be a considerable challenge.

Parasite extinction

Approaches and problems in estimating parasite extinctions

Current rates of species extinction greatly exceed background rates (e.g. Ceballos et al. 2015) and many species will therefore be lost before their detection. Such never-to-be-known diversity is likely to be particularly high for parasites in part due to their hidden nature and systematic oversight in surveys and checklists of threatened fauna (Rocha et al. 2016, Cizauskas et al. 2017). However, it is also predicted that coextinction, the loss of one species as a result of extinction of a species it depends on, may be the most common form of species loss (Dunn et al. 2009). Colwell et al. (2012) review how statistical host-extinction modelling approaches based on empirical matrices of hosts and affiliate species enable insights into past and future extinctions of at least some parasites by producing coextinction curves to estimate the number of extinctions of affiliate species as a function of host extinctions. For example, Dunn et al. (2009) predicted that the number of coextinctions of parasite species is more than an order of magnitude greater than that of their North American carnivore hosts. Retrospective extensions to such modelling enabled Colwell et al. (2012) to infer that between four and eight unknown affiliate species (louse, flea and cestodes) went extinct as a result of 13 known extinctions of terrestrial North American carnivores during the Holocene.

Another potential method of inferring parasite extinctions is to characterise parasite presence in extinct hosts. For example, Boast et al. (2018) examined ancient DNA in extinct New Zealand moa coprolites and identified apparently host-specific heterokoid nematodes. The first myxozoan reported (Jurine 1825) may have gone extinct along with its fish host, the whitefish *Coregonus fera*, if it failed to utilise other fish hosts.

Other research has focused on inferring risks of parasite extinction. For example, Dobson et al. (2008) considered the percentage of vertebrate species listed as threatened in the IUCN Red list and, accounting for host specificity, estimated that around 3% of helminths may therefore be endangered. Another method is to examine how projections of environmental change may cause parasite declines and loss using ecological niche modelling. Thus, a recent study (Carlson et al. 2017) estimated that 5-10% of species from eight parasite clades are committed to extinction by 2070 by considering projected range

shifts and climate-driven habitat loss. Further modelling predicted that some 30% of parasitic helminths could go extinct (without dispersal) by 2070 due to host extinction (Carlson et al. 2017). Such inferences of course rest on the availability of data on parasite distributions and these are scarce and biased. Factors other than inferred range loss of hosts or parasites of course may also influence parasite extinction rates, including dispersal capacity, availability of hosts in complex life cycles, host population density, ability to adopt novel hosts or to truncate life cycles, phenological mismatch with hosts, incompatibilities of local habitats that are not incorporated in ecological niche models, and secondary extinctions and extinction cascades (Colwell et al. 2012; Carlson et al. 2017; Cizauskas et al. 2017).

Poor understanding of host specificity and parasite distributions has compromised inferences of parasite extinction. For example, the widely cited co-extinction of two louse species with passenger pigeons was falsified with their discovery on other bird hosts (Strona 2015). Furthermore, the most comprehensive spatially explicit data set on parasites available to date (53,133 occurrences of 457 species of acanthocephalans, nematodes, cestodes, trematodes, mites, ticks, lice, and fleas) is described as a meagre subset of parasites (e.g. there are some 300,000+ species of parasitic helminths alone) (Carlson et al. 2017). Finally, poor knowledge of parasites of invertebrates and of microparasites make current estimates of parasite extinction rates highly biased. However, it may be the case that parasites such as helminths are particularly susceptible to extinction due to their high diversity relative to host diversity and associations with higher trophic level and more extinction-prone vertebrate hosts (Colwell et al. 2012). Strona (2015) synthesises the growing literature on host-parasite coextinctions and reviews approaches and difficulties in inferring vulnerabilities and risks of parasite extinctions in a changing world.

Should we care about parasite diversity and extinction?

Our understanding of both the diversity of and threats to parasites is highly compromised. If parasites were minor players exerting minimal impacts on hosts and few secondary effects,

concerns about this limited knowledge might largely relate to failure to comprehend biodiversity in general and how a significant proportion of life has radiated on Earth. However, it is clear that parasites are ubiquitous, abundant and functionally significant components of ecosystems – features that give rise to the assertion that healthy ecosystems are rich in parasites (Hudson et al. 2006). Parasites can dominate ecosystems in terms of biomass (Kuris et al. 2008; Lambden & Johnson 2013) and contribute substantially to energy transfer and food web structure and stability (e.g. Dunne et al. 2013; Cirtwell & Stouffer 2015; Michalska-Smith et al. 2017). Parasites with complex life cycles often exploit hosts at different trophic levels and free-living stages can be significant components of diets (Johnson et al. 2012). Parasites can alter host behaviour, determine host distributions and abundances, and can mediate the outcome of species interactions (e.g. competition, predation) thereby influencing population and community dynamics (Gómez et al. 2012; Hatcher et al. 2012). In addition, interactions of hosts and parasites via evolutionary arms races have driven host life history traits and have been invoked to explain such fundamental traits as the maintenance of sexual reproduction via negative frequency dependent selection (Hamilton 1980) and host body size (Guralnick et al. 2004). Finally, parasites may be potential sources of novel drugs, some helminths bioaccumulate heavy metals that would otherwise concentrate in host tissues, and contact with parasites can reduce the risk of immune-mediated disorders (Gómez et al. 2012). In short, parasites make substantial contributions to ecosystem health and function and may provide a plethora of other goods and services that contribute to the health and welfare of individual hosts and that may also benefit humankind.

On the other hand, novel parasites acting in conjunction with ecological change may contribute to host declines or extinctions (Plowright et al. 2008). Parasites also of course contribute to the global burden of human disease and may hinder socioeconomic development (e.g. malaria; Sachs & Malany 2002), prompting programmes of control and eradication for parasites of medical or veterinary importance. Clearly, the costs and benefits of such programmes require careful evaluation in view of the consequences for ecosystem

dynamics and the removal of lineages with unique co-evolutionary histories and future co-evolutionary potentials (Gómez et al. 2012). By extension, the roles of parasites (e.g. in providing protective immunity to hosts) should also be evaluated and appropriately incorporated in conservation programmes (Dougherty et al. 2015).

Conclusion

Parasites are the result of unique evolutionary radiations driven by intimate species interactions. As a result of these interactions parasites demonstrate striking evolutionary trajectories involving e.g. the loss, gain and co-option of traits. Myxozoans illustrate this perhaps most dramatically (Okamura et al. 2015a). As they have miniaturised over time, myxosporeans have lost proper tissues and occur as unicellular plasmodia, evolving endoparasitic strategies comparable to parasitic protists. Nevertheless within these plasmodia multicellular spores develop. Myxozoans have co-opted the intracellular organelles (nematocysts) of their free-living ancestors deploying them to achieve transmission to new hosts rather than for prey capture or defense. Adoption of this endoparasitic strategy has been highly successful – myxozoans represent a substantial proportion of cnidarian species richness and it is entirely possible that myxozoan species may outnumber those of their free-living relatives. Whether this question is ever adequately resolved will depend on future expertise in and funding for taxonomic research.

It is clear that parasites substantially contribute to biodiversity on Earth and play fundamental ecological and evolutionary roles. We can expect that molecular approaches will continue to refine our insights on parasite diversification and macroecological patterns. Key questions here include revealing parasite diversity gradients (Rohde 2016) and the relative responses of hosts and parasites to rapid environmental change. Because parasites cannot persist below a critical threshold of host density the latter issues are of fundamental and practical interest. Fortunately, the unique and complex roles of parasites are increasingly being appreciated, spawning recent academic (Wood & Johnson 2015) and

media attention with the British Broadcasting Corporation posing the question ‘What would happen if all the parasites disappeared?’ (Jones 2015). Answering such ‘what if’ scenarios may help to identify strategic areas for research on the past, present and future biodiversity of these uncharismatic and hidden players.

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Figures

Fig. 1 Malacosporean stages. **(A)** Sacs (s) of *Buddenbrockia bryzoides* developing within the body cavity surrounding the digestive tract of its bryozoan host *Cristatella mucedo* which is extending tentacular crowns (lophophores). Scale bar = 0.8 mm. **(B)** Sacs in various stages of development of *B. bryzoides* extruded from *C. mucedo* by applying pressure to the bryozoan body wall. Multicellular spores can be seen filling the lumen of more mature sacs on right. Scale bar = 200 μm . **(C)** Spores of *Tetracapsuloides bryosalmonae* with 4 polar capsules (pc) and 2 enclosed amoeboid sporoplasms (sp) that invade fish host. Scale bar = 20 μm . **(D)** Pseudoplasmodium (p) of *Buddenbrockia* sp. attached to kidney tubule (t) of fish host *Barbatula barbatula* (stone loach). Note the projections (arrows) attaching the pseudoplasmodium to the tubule wall. Scale bar = 1 μm .

Fig. 2 Myxosporean stages. **(A)** Unicapsula pansporocyst isolated from the coelomic cavity of polychaete host *Diopatra neapolitana*. Seven developing spores (ds) can be seen enclosed by the plasmodium wall (W). Scale bar = 10 μm (photo courtesy of L. Rangel). **(B-D)** Morphological types of spores that develop in annelid hosts (known as actinospores) showing three caudal processes (cp) and polar capsules (pc) (B, C photos courtesy of S. Feist; D courtesy of S. Atkinson); B - Aurantiactinomyxon-type; scale bar = 20 μm , C - Neoactinomyxon-type; scale bar = 20 μm , D - Triactinomyxon-type; scale bar = 50 μm . **(E)** *Myxobolus* sp. cysts (white masses) in *Leuciscus leuciscus* (dace) gill filaments. Scale bar = 1 mm (photo courtesy of C. Williams). **(F)** Transmission electron micrograph of multinucleate plasmodium of *Myxobolus* sp. in gill of fish host *Salminus franciscanus* (dorado) showing outer wall (arrow) enclosing developing spores. Scale bar = 10 μm . **(G)** Closer view of F, showing developing myxospores and sections of filaments within polar capsules (arrows). Scale bar = 5 μm . **(H-K)** Variation in spores that develop in fish hosts (known as myxospores); H) - *Sphaerospora* sp. spore within monosporic plasmodium in *Oncorhynchus mykiss* (rainbow trout) kidney, scale bar = 5 μm (photo courtesy of S. Atkinson), (I) -

Myxobilatus gasterostei from *Gasterosteus aculeatus* (three-spined stickleback) kidney showing polar capsules (pc) and elongated caudal processes (cp); scale bar = 10µm (photo courtesy of S. Feist), (J) - *Hofferellus* sp. showing short, fine caudal filaments (arrow) infecting *Carassius auratus* (goldfish) kidney; scale 5 µm (photo courtesy of S. Atkinson), K) - *Myxobolus* sp. spores from *Anguilla anguilla* (eel) showing detail of enclosed polar filament (arrow) and thickened valve walls (W), scale bar = 5 µm (photo courtesy of C. Williams).

Fig. 3 Species diversity of myxozoans. **(A)** Pie-chart showing the proportions (and numbers) of described species within the major cnidarian clades, Anthozoa, Hydrozoa and Myxozoa. 'Others' includes described species in Scyphozoa, Cubozoa, Staurozoa and the monotypic *Polypodium hydriforme*. **(B)** The cumulative number of myxosporean species reported in Brazilian freshwater fish over 10 year increments from 1915 except for the last point which incorporates species reported during the period 2005-2017.

Supplementary Data

To determine the number of myxozoan species reported infecting freshwater fish from Brazil over time we consulted Zoological Record, PubMed, Brazilian check lists (Gioia & Cordeiro 1996, Walliker 1969), and check lists for *Henneguya* (Eiras 2002, Eiras & Adriano 2012), *Myxobolus* (Eiras et al. 2005b, Eiras et al. 2014) and *Myxidium* (Eiras et al. 2011) to confirm species identity. The below table provides records and sources for the following genera (and number of species reported in Brazil from 1915: *Myxobolus* (45 species), *Henneguya* (58 species), *Myxidium* (6 species), *Ceratomyxa* (4 species), *Thelohanellus* (1 species), *Tetrauronema* (1 species), *Agarella* (1 species), *Meglitschia* (1 species), *Ellipsomyxa* (1 species), *Triangulomyxa* (2 species), *Kudoa* (2 species).

Table 1. Records for myxozoans found in Brazil, including species, site of infection in fish, fish host, locality and reference. Studies that included molecular data identified with asterisk (*).

Genera	Species	Site of infection	Host	Locality	Reference
<i>Myxobolus</i>	<i>batalhensis</i>	liver and ovary	<i>Salminus hilarii</i>	Batalha river, Brazil	Vieira et al. 2017*
	<i>marajoensis</i>	muscular layer of the intestine	<i>Rhamdia quelen</i>	Paracauri river, Brazil	Abrunhosa et al. 2017*
	<i>axelrodi</i>	Brain and retinas	<i>Paracheirodon axelrodi</i>	Brazil	Camus et al. 2017*
	<i>prochilodus</i>	gill	<i>Prochilodus lineatus</i>	Mogi Guaçu river, Brazil	Zatti et al. 2016*
	<i>hilarii</i>	Kidney	<i>Brycon hilarii</i>	Mogi Mirim, Brazil	Capodifoglio et al. 2016*
	<i>niger</i>	the membrane of the gill arch	<i>Corydoras melini</i>	Negro River, Brazil	Mathews et al. 2016a
	<i>filamentum</i>	gill filaments	<i>Brycon orthotaenia</i>	São Francisco river, Brazil	Naldoni et al. 2015*
	<i>curimatae</i>	gill	<i>Prochilodus costatus</i>	São Francisco river, Brazil	Zatti et al. 2015*
	<i>lomi</i>	gill filaments	<i>Prochilodus lineatus</i>	Peixes river, Brazil	Azevedo et al. 2014*
	<i>umidus</i>	spleen	<i>Brycon hilarii</i>	Pantanal wetland, Brazil	Carriero et al. 2013*
	<i>piraputangae</i>	kidney	<i>Brycon hilarii</i>	Pantanal wetland, Brazil	Carriero et al. 2013*
	<i>aureus</i>	liver	<i>Salminus brasiliensis</i>	Pantanal wetland, Brazil	Carriero et al. 2013*
<i>pantanalis</i>	gill filaments	<i>Salminus brasiliensis</i>	Pantanal	Carriero et al.	

			wetland, Brazil	2013*
<i>flavus</i>	gill arch	<i>Pseudoplatystoma corruscans</i> and <i>Pseudoplatystoma reticulatum</i>	Pantanal wetland, Brazil	Carriero et al. 2013*
<i>myleus</i>	gall-bladder	<i>Myleus rubripinnis</i>	Pará, Brazil	Azevedo et al. 2012
<i>brycon</i>	gill	<i>Brycon hilarii</i>	Pantanal, Brazil	Azevedo et al. 2011a
<i>oliveirai</i>	gill	<i>Brycon hilarii</i>	Pantanal wetland, Brazil	Milanin et al. 2010*
<i>franciscoi</i>	fins	<i>Prochilodus argenteus</i>	São Francisco river, Brazil	Eiras et al. 2010
<i>sciades</i>	gill	<i>Sciades herzbergii</i>	Poti river Brazil	Azevedo et al. 2010
<i>salminus</i>	gill	<i>Salminus brasiliensis</i>	Pantanal, Brazil	Adriano et al. 2009a
<i>cordeiroi</i>	skin, gill arch, eyes, urin. bladder	<i>Zungaro jahu</i>	Pantanal, Brazil	Adriano et al. 2009b*
<i>heckelii</i>	gill	<i>Centromochlus heckelii</i>	Tocantins river, Brazil	Azevedo et al. 2009a
<i>platanus</i>	spleen	<i>Mugil platanus</i>	Lagoa dos Patos, Brazil	Eiras et al. 2007
<i>cuneus</i>	connective tissue	<i>Piaractus mesopotamicus</i>	São Paulo, Brazil	Adriano et al. 2006 Milanin et al. 2015*
<i>peculiaris</i>	gills (smears)	<i>Cyphocharax nagelli</i>	Brazil	Martins & Onaka 2006
<i>metynnis</i>	connective subcutaneous tissue of the orbicular region	<i>Metynnis argenteus</i>	Brazil	Casal et al. 2006
<i>testicularis</i>	testis	<i>Hemiodopsis microlepis</i> = <i>Hemiodus microlepis</i>	Brazil	Tajdari et al. 2005
<i>insignis</i>	gills (intralamellar)	<i>Semaprochilodus insignis</i>	Amazon river, Brazil	Eiras et al. 2005a
<i>porofilus</i>	visceral cavity	<i>Prochilodus lineatus</i>	Mogi Guaçu river, Brazil	Adriano et al. 2002 Zatti et al. 2016*
<i>desaequalis</i>	gill lamellae	<i>Apteronotus albifrons</i>	Amazon, Brazil	Azevedo et al. 2002

	<i>maculatus</i>	kidney	<i>Metynnis maculatus</i>	Amazon river, Brazil	Casal et al. 2002
	<i>absonus</i>	opercular cavity	<i>Pimelodus maculatus</i>	Piracicaba river, Brazil	Cellere et al. 2002
	<i>macroplasmodialis</i>	abdominal cavity	<i>Salminus maxillosus</i> = <i>S. brasiliensis</i>	Mogi Guaçu river, Brazil	Molnar et al. 1998 Carriero et al. 2013*
	<i>brasiliensis</i>	gills (interlamellar)	<i>Bunocephalus coracoideus</i>	Brazil	Casal et al. 1996
	<i>colossomatis</i>	connective tissue	<i>Colossoma macropomum</i>	Brazil	Molnar & Bekesi 1993 Müller et al. 2013*
	<i>inaequus</i>	brain	<i>Eigenmannia virescens</i>	Brazil	Kent & Hoffman 1984
	<i>serrasalmi</i>	spleen, kidney, liver	<i>Serrasalmus rhombeus</i>	Brazil	Walliker 1969
	<i>kudoii</i>	integument	<i>Nemathognata</i> sp.	Brazil	Guimarães & Bergamin 1938
	<i>stokesi</i>	nose integument	<i>Pimelodella</i> (?) sp.	Brazil	Pinto 1928a
	<i>noguchii</i>	gills (blood smear)	<i>Serrasalmus spilopleura</i>	Brazil	Pinto 1928a
	<i>pygocentrus</i>	intestinal content	<i>Pygocentrus piraya</i>	Brazil	Penido 1927
	<i>cunhai</i>	intestinal content	<i>Pygocentrus piraya</i> = <i>Pimelodus clarias</i>	Brazil	Penido 1927
	<i>associatus</i>	kidney	<i>Leporinus mormyrops</i>	Brazil	Nemeczek 1926
	<i>lutzi</i>	testis	<i>Girardirnus januarius</i> = <i>Phalloptychus januarius</i>	Brazil	Aragão 1919
	<i>inaequalis</i>	skin of head	<i>Piramutana blochii</i>	South American rivers (Brazil, Guiana, Surinam)	Pinto 1928b
<i>Henneguya</i>	<i>gilbert</i>	gills	<i>Cyphocharax gilbert</i>	Rio de Janeiro, Brazil	Casal et al. 2017*
	<i>melini</i>	gill filaments	<i>Corydoras melini</i>	Negro river, Brazil	Mathews et al. 2016b
	<i>paraensis</i>	gill	<i>Cichla temensis</i>	Tocantins river, Brazil	Velasco et al. 2016*
	<i>aequidens</i>	gills	<i>Aequidens plagiozonatus</i>	Peixe-boi river, Pará,	Videira et al. 2015

			Brazil	
<i>cuniculator</i>	gill filaments	<i>Pseudoplatystoma corruscans</i>	São Francisco river, Brazil	Naldoni et al. 2014*
<i>visibilis</i>	fins	<i>Leporinus obtusidens</i>	São Paulo, Brazil	Moreira et al. 2014a*
<i>rotunda</i>	gill arch	<i>Salminus brasiliensis</i>	São Paulo, Brazil	Moreira et al. 2014b*
<i>maculosus</i>	gill filaments	<i>Pseudoplatystoma corruscans</i> and <i>P. reticulatum</i>	Brazilian Pantanal wetland, Brazil	Carriero et al. 2013*
<i>nagelli</i>	gills	<i>Cyphocharax nagelli</i>	São Paulo, Brazil	Azevedo et al. 2013a
<i>multiplasmodialis</i>	gills arch, gill filaments	<i>Pseudoplatystoma corruscans</i>	Brazil	Adriano et al. 2012*
<i>azevedoi</i>	gill lamellae	<i>Leporinus obtusidens</i>	Brazil	Barassa et al. 2012
<i>eirasi</i>	gill filaments	<i>Pseudoplatystoma corruscans</i>	Brazil	Naldoni et al. 2011*
<i>torpedo</i>	brain, spinal chord	<i>Brachyhyopomus pinnicaudatus</i>	Brazil	Azevedo et al. 2011b
<i>hemiodopsis</i>	secondary gill lamellae	<i>Hemiodopsis microlepis</i>	Brazil	Azevedo et al. 2009b
<i>corruscans</i>	gill filaments	<i>Pseudoplatystoma corruscans</i>	Brazil	Eiras et al. 2009 Carriero et al. 2013*
<i>pseudoplatystoma</i>	gills filaments	<i>Pseudoplatystoma corruscans</i> x <i>P. fasciatum</i> (hybrid)	Brazil	Naldoni et al. 2009 Milanin et al. 2015*
<i>rondoni</i>	peripheral lateral nerves beneath lateral lines	<i>Gymnoramphichthys rondoni</i>	Brazil	Azevedo et al. 2008
<i>arapaima</i>	gill arch, gall-bladder	<i>Arapaima gigas</i>	Brazil	Feijó et al. 2008
<i>caudicula</i>	secondary gill lamellae	<i>Leporinus lacustris</i>	Brazil	Eiras et al. 2008
<i>guanduensis</i>	gills	<i>Hoplosternum littorale</i>	Brazil	Abdallah et al. 2007
<i>cyphocharax</i>	gills	<i>Cyphocharax gilbert</i>	Brazil	Abdallah et al. 2007
<i>garavelli</i>	gill filaments	<i>Cyphocarax nagelli</i>	Brazil	Martins &

				Onaka 2006
<i>caudalongula</i>	gills (intra and interlamellar spaces)	<i>Prochilodus lineatus</i>	Brazil	Adriano et al. 2005a
<i>pellucida</i>	serous membrane of visceral cavity and tunica externa of swim-bladder	<i>Piaractus mesopotamicus</i>	Brazil	Adriano et al. 2005b
<i>rhamdia</i>	connective tissue of base of gill lamellae	<i>Rhamdia quelen</i>	Brazil	Matos et al. 2005
<i>schizodon</i>	kidney	<i>Schizodon fasciatus</i>	Brazil	Eiras et al. 2004a
<i>paranaensis</i>	secondary gill lamellae	<i>Prochilodus lineatus</i>	Brazil	Eiras et al. 2004b
<i>curvata</i>	interlamellar epithelium or epithelium of secondary lamellae	<i>Serrasalmus spilopleura</i>	Brazil	Barassa et al. 2003a
<i>chydadea</i>	gill lamellae epithelium	<i>Astyanax altiparanae</i>	Brazil	Barassa et al. 2003b
<i>astyanax</i>	interlamellar spaces of gills	<i>Astyanax keithi</i>	Brazil	Vita et al. 2003
<i>pilosa</i>	gill filaments	<i>Serrasalmus altuvei</i>	Brazil	Azevedo & Matos, 2003
<i>friderici</i>	gill filaments	<i>Leporinus friderici</i>	Brazil	Casal et al. 2003 Vidal & Luque 2017 (genbank)*
<i>curimata</i>	kidney	<i>Curimata inornata</i>	Brazil	Azevedo & Matos 2002
<i>leporinicola</i>	gills	<i>Leporinus macrocephalus</i>	Brazil	Martins et al. 1999
<i>testicularis</i>	testis	<i>Moenkhausia oligolepis</i>	Brazil	Azevedo et al. 1997

<i>piaractus</i>	gills	<i>Piaractus mesopotamicus</i>	Brazil	Martins & Souza 1997 Müller et al. 2013*
<i>striolata</i>	gills	<i>Serrasalmus striolatus</i>	Brazil	Casal et al. 1997
<i>malabarica</i>	gills	<i>Hoplias malabaricus</i>	Brazil	Azevedo & Matos 1996a
<i>adherens</i>	gills	<i>Acestrorhynchus falcatus</i>	Brazil	Azevedo & Matos 1995
<i>amazonica</i>	gills	<i>Crenicichla lepidota</i>	Brazil	Rocha et al. 1992
<i>artigasi</i>	gills	<i>Astyanax scabripinnis</i>	Brazil	Gioia & Cordeiro 1987
<i>hoimba</i>	gills	<i>Astyanax fasciatus</i>	Brazil	Cordeiro & Gioia 1987
<i>intracornea</i>	cornea	<i>Astyanax scabripinis</i>	Brazil	Gioia et al. 1986
<i>theca</i>	brain	<i>Eigemannia virescens</i>	Brazil	Kent & Hoffman 1984
<i>pisciforme</i>	gills	<i>Hyphessobrycon anisitsi</i>	Brazil	Cordeiro et al. 1983/84
<i>electrica</i>	large electric organs	<i>Electrophorus electricus</i>	Brazil	Jakowska & Nigrelli 1953
<i>visceralis</i>	kidney, liver, heart, mesentery	<i>Electrophorus electricus</i>	Brazil	Jakovska & Nigrelli, 1953
<i>santae</i>	gills	<i>Tetragonopterus santae</i>	Brazil	Guimaraes & Bergamin 1934
<i>travassoi</i>	muscle	<i>Leporinus</i> sp.	Brazil	Guimaraes & Bergamin 1933
<i>bergamini</i>	body cavity	<i>Astyanax fasciatus</i>	Piracicaba river, Piracicaba City (São Paulo state), Brazil	Guimaraes 1931
<i>cesarpintoi</i>	gills cavity.	<i>Astyanax fasciatus</i>	Agua Funda (São Paulo state), Brazil	Guimaraes 1931
<i>fonsecai</i>	Fin tissue	<i>Leporinus copelandi</i>	Paraíba river, Taubate City (São Paulo state), Brazil	Guimaraes 1931
<i>iheringi</i>	gills	<i>Serrasalmus spilopleura</i>	Turvo river, Pirangy City (São Paulo state), Brazil	Pinto 1928a

	<i>wenyoni</i>	gills	<i>Tetragonopterus</i> sp.	Brazil	Pinto 1928c
	<i>leporini</i>	urinary ducts	<i>Leporinus moormyrops</i>	Brazil	Nemeczek 1926
	<i>occulta</i>	gills	<i>Loricaria</i> sp.	Brazil	Nemeczek 1926
	<i>lutzi</i>	gall-bladder	<i>Piaractus mesopotamicus</i>	Pardo river, Brazil	Cunha & Fonseca 1918
	<i>linearis</i>	gills	<i>Pimelodus sebae</i>	Brazil and South America	Pinto 1928
<i>Myxidium</i>	<i>amazonense</i>	gall-bladder	<i>Corydoras melini</i>	Rio Negro river, Brazil	Mathews et al. 2015*
	<i>ceccarelli</i>	gall-bladder	<i>Leporinus elongatus</i>	São Francisco river, Brazil	Adriano et al. 2014*
	<i>cholecysticum</i>	gall-bladder	<i>Astyanax scabripinnis</i>	Alpes farm, Atibaia river basin, Brazil	Cordeiro & Gióia 1990
	<i>gurgeli</i>	gall-bladder	<i>Acestrorhamphus</i> sp.	Mogi Guaçu river, Brazil	Pinto 1928d
	<i>cruzi</i>	gall-bladder	<i>Chalcinus nematurus</i>	Mato Grosso state, Brazil	Penido 1927
	<i>fonsecai</i>	gall-bladder	<i>Carapus fasciatus</i>	Porto Esperança Brazil	Penido 1927
<i>Ceratomyxa</i>	<i>brasiliensis</i>	gall-bladder	<i>Cichla monoculus</i>	Tapajós river, Brazil	Zatti et al. 2017 *
	<i>vermiformis</i>	gall-bladder	<i>Colossoma macropomum</i>	Amazon river, Brazil	Adriano & Okamura et al. 2017*
	<i>amazonensis</i>	gall-bladder	<i>Symphysodon discus</i>	Amazon river, Brazil	Mathews et al. 2016c*
	<i>microlepis</i>	gall-bladder	<i>Hemiodus microlepis</i>	Amazon river, Brazil	Azevedo et al. 2013b
<i>Thelohanellus</i>	<i>marginatus</i>	gills	<i>Hypophthalmus marginatus</i>	Amazon river, Brazil	Rocha et al.

					2014*
<i>Tetrauronema</i>	<i>desaequalis</i>	ventral fins	<i>Hoplias malabaricus</i>	Amazon river, Brazil	Azevedo & Matos 1996b
<i>Agarella</i>	<i>gracilis</i>	testis	<i>Lepidosiren paradoxa</i>	Amazon river, Brazil	Dunkerly et al. 1915
<i>Meglitschia</i>	<i>mylei</i>	gall-bladder	<i>Myleus rubripinnis</i>	Amazon river, Brazil	Azevedo et al. 2011c
<i>Ellipsomyxa</i>	<i>gobioides</i>	gall-bladder	<i>Gobioides broussonnetii</i>	Amazon river, Brazil	Azevedo et al. 2013c
<i>Triangulamyxa</i>	<i>psittaca</i>	urinary bladder	<i>Colomesus psittacus</i>	Amazon river, Brazil	Rocha et al. 2011
	<i>amazonica</i>	lumen of the intestine	<i>Spherooides testudineus</i>	Amazon river, Brazil	Azevedo et al. 2005
<i>Kudoa</i>	<i>orbicularis</i>	mussele	<i>Chaetobranchopsis orbicularis</i>	Amazon, Brazil	Azevedo et al. 2016*
	<i>aequidens</i>	sub-opercular musculature	<i>Aequidens plagiozonatus</i>	Amazon, Brazil	Casal et al. 2008

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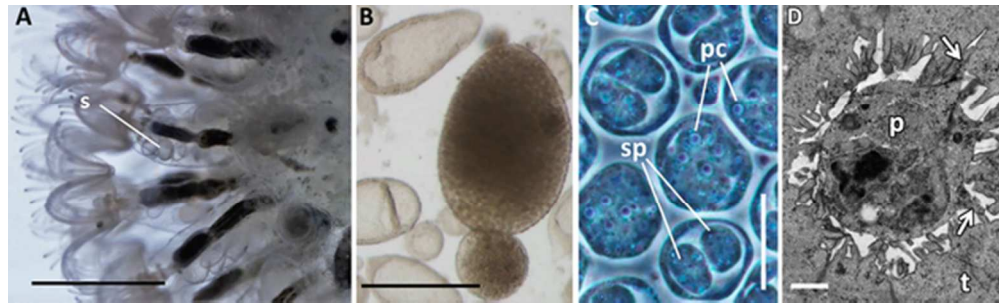
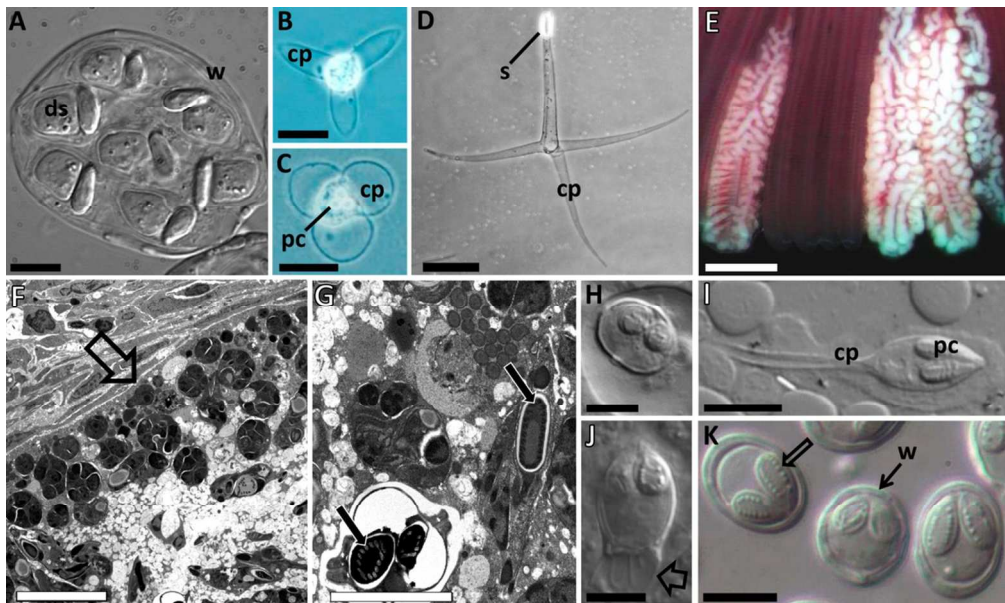
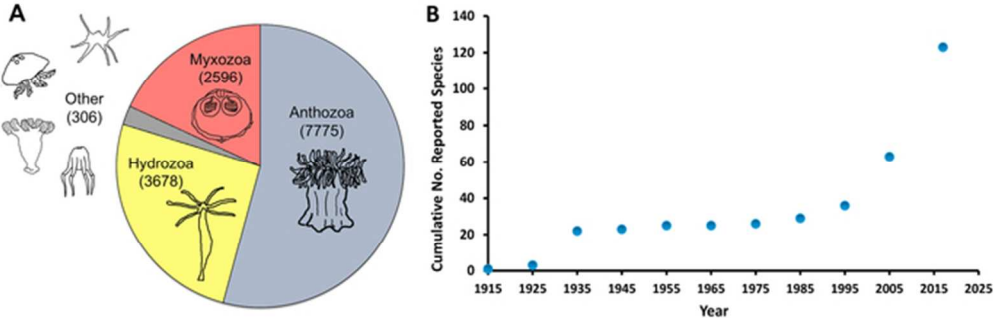


Fig. 1 Malacosporean stages. (A) Sacs (s) of *Buddenbrockia bryozoides* developing within the body cavity surrounding the digestive tract of its bryozoan host *Cristatella mucedo* which is extending tentacular crowns (lophophores). Scale bar = 0.8 mm. (B) Sacs in various stages of development of *B. bryozoides* extruded from *C. mucedo* by applying pressure to the bryozoan body wall. Multicellular spores can be seen filling the lumen of more mature sacs on right. Scale bar = 200 μ m. (C) Spores of *Tetracapsuloides bryosalmonae* with 4 polar capsules (pc) and 2 enclosed amoeboid sporoplasms (sp) that invade fish host. Scale bar = 20 μ m. (D) Pseudoplasmodium (p) of *Buddenbrockia* sp. attached to kidney tubule (t) of fish host *Barbatula barbatula* (stone loach). Note the projections (arrows) attaching the pseudoplasmodium to the tubule wall. Scale bar = 1 μ m.

53x15mm (300 x 300 DPI)



107x63mm (300 x 300 DPI)



58x18mm (300 x 300 DPI)