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Ciliates as Symbionts

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Abstract

Although many ciliates are free-living, more than 140 families of ciliates (Alveolata, Ciliophora) include symbiotic species of animals. Symbiosis, defined as an interaction between two species, is analyzed in this chapter to show a wide diversity of symbiotic systems in ciliates (epibiosis, commensalism, mutualism, and parasitism), providing some data about ciliate strategies showing their success as symbionts. Some species are free-living as well symbionts, facultative symbionts, and obligate symbionts. Analysis of reconstructions of ancestral state evidence that the parasitism arose numerous times and independently among the lineages of ciliates. At least three evolutionary routes can be traced: (1) transition from free-living to mutualism and parasitism, (2) transition from free-living to parasitism, and (3) regression from parasitism to free-living. The evolution of the symbiosis in ciliates demonstrates a higher diversification rate concerning free-living ciliates. The analysis of the evolution of the life cycles complexity, exploring molecular data of the phases of the ciliate cycle in their hosts is also essential. We propose new approaches for an integrative study of symbiotic ciliates.

Keywords: Ciliophora, diversity, ecology, macroevolution, morphology, physiology, symbiosis, taxonomy

1. Introduction

Ciliates (Alveolata: Ciliophora) comprise free-living and symbiotic species. According to Corliss, [1] 2,600 species of ciliates have been described as symbionts, mainly of individuals of metazoan phyla. This is equivalent to 33% of all the known species of the phylum. They belong to eight classes (Armophorea, Heterotrichea, Litostomatea, Nassophorea, Oligohymenophorea, Plagiopylea, Phyllopharyngea and Spirotrichea), 31 orders, 151 families, and almost 700 genera [2]. These symbiotic ciliates have been reported in aerobic and anaerobic environments and from aquatic and terrestrial habitats [2, 3].

The term symbiosis can be defined as a sustained relationship between at least two individuals from different species, either living in direct contact or close enough to each other during a part or the whole life cycles of the partners. This interaction is transmitted vertically (from one generation to the next) or horizontally (acquired *de novo* in each generation). The intricate associations are believed to have an essential driving force in evolutionary biology, as a host and their symbiotic microbiota acclimatize on scales of short time [4].

Due to the diversity of symbioses, a classification system for symbiotic associations has been developed. This classification is based on several features: i) the dependence, where symbionts can be obligate or facultative; ii) specificity of the symbionts; iii) nutrients obtention, then biotrophic and necrotrophic symbionts are distinguished on the basis of whether nutrients are obtained from a living or dead partner, and iv) location of the symbionts, ectosymbionts or endosymbionts [5]. The symbiotic relationships can be categorized into mutualistic, commensalistic, or parasitic [2, 6]. The boundary between these categories sometimes is not clear, and there are frequent transitions between them.

Several papers have been focused on providing taxonomic reports for symbiotic ciliates, some of them as general works, and a few directed to certain groups [7–16], and some were focused on certain geographic areas [17–24]. Critical reviews of some species as *Balantidium coli* were done by Schuster and Ramirez-Avila [25]; for chonotrichs [26]; peritrichs [27] and suctorians [28].

Also, very different topics about ciliates and their hosts have been developed as shown: symbiotic interactions [epibiotic, hyperepibiotic, commensals, parasites (obligates and facultatives)], codiversification: [29–37]. Morphology (variation, molecular characterization): [38], clellandellid, *Nyctotheroides*; [39], *Dicontophrya*; [40, 41] peritrichs. Taxonomy (new family, genus or species), redescription, revision: Apostomatia: [42]; Apostomatida: [43]; *Trichodina*: [44]; *Epistylis* and *Opercularia*: [45]; *Spirochona*: [46]; *Buetschlia* and *Charonina*: [31, 47–51]. Life cycles, encystment/excystment process: [52–54]. Pathogenicity, damages, infestation degree, virulence: [55–59]. Molecular and phylogeny: [30, 60–68]. Ecological aspects: [69, 70]. Immunity: [71, 72]. Stomatogenesis: [73]. Ultrastructure: [74].

Symbiotic systems between ciliates/animals are present in a broad spectrum of kingdom Animalia, and some examples are the following (animal group alphabetically arranged, different taxonomic levels): acari: [75]; amphipods: [76]; antelope: [77]; anuran: [78]; Asian elephant: [79]; baboon: [80]; bryozoans: [81]; buffaloes: [82]; capybara: [83–85]; cattle: [86]; chimpanzees: [87]; cirripedians: [88]; crustaceans: [89]; ctenophores: [90]; cuttlefish: [91]; dromedary camels: [92]; elephants: [93]; fishes: [94, 95]; frogs: [96]; great apes: [97]; horses: [98, 99]; humans: [100, 101]; polyps of hydras: [102]; insects: [103]; isopods: [104, 105]; kinorhynch: [106]; llamas: [107]; maccacus: [108]; mammals: [109]; mollusks: [71, 76]; nematodes: [29, 110]; nemertean: [13]; oligochaetes: [111, 112]; ostracods: [113]; polychaetes: [114, 115]; rhinoceroses: [116]; sea urchins: [117]; thoroughbreds: [118]; turbellarians: [119]; wood-feeding roaches: [120].

Some examples of ciliate taxa that include symbiotic species are the following:

Heterotrichea: Folliculinids attach to the integument of various invertebrates as bivalve shells, crustaceans exoskeleton, polychaete tubes, hydroid perisarc, bryozoan tests, with a widespread occurrence [121], and may cause the skeletal eroding band or brown band diseases of scleractinian corals [2]; their life cycle includes a migratory swimming stage.

Spirotrichea: Hypotrichs are known mainly as free-living organisms, but some species such as *Euplotes balteatus* have been recorded in some sea urchins' intestinal tract [122]. Some species of stichotrichids as *Plagiotoma lumbrici* are endosymbionts of oligochaetes [123].

Armophorea: Class Armophorea includes clellandellids as Nyctotheridae, with obligate endosymbionts usually as commensals of invertebrates and vertebrates; life cycles include a phase of the cyst [2].

Litostomatea: Trichostomes are symbionts of vertebrates as ruminants and foregut fermenters [2], including the human pathogen, *Balantidium coli*, species that have a life cycle including two phases: trophozoites and cysts [25]. This species

has been considered to be included in a new genus, *Neobalantidium coli* [124]. The genus *Balantidium* has a more significant number of species that have been reported as endocommensals in the digestive tracts of a widely diverse range of metazoan, as mollusks, arthropods, fishes, reptiles, birds, and mammals [124]. In the rumen ecosystem, ciliates can account for up to 50% of the total microbial nitrogen, reaching densities of 10^5 to 10^6 cells/ml rumen fluid, being *Charonina ventriculi* one of the smallest rumen ciliates [125].

Ophryoscolecidae and Cycloposthiidae include species as endosymbionts of ruminants and equids, respectively [126]. Entodiniomorphid ciliates of the genus *Triplumaria* are found in the intestine of elephants and rhinoceroses [60]. Entodiniomorphida do not form cysts, and in non-ruminant mammals, the infections of hosts occur by coprophagy [47].

Phyllopharyngea: Chonotrichs live on marine and freshwater hosts and divide by forming external or internal buds [127], with a dimorphism where the adults live attached to several appendages of crustaceans, and the larva is free and swims to reach a new host [128].

Suctorians, as a rule, reproduce by different modes of budding, produce one to several larvae, with a short swimming existence, and then lose their cilia and metamorphose into adults or trophonts [127]. The non-ciliated mature stages of suctorians are usually sessile, attached to the substrate by a non-contractile stalk, and reproduce by ciliary larvae called swarmers or migrators [129].

Oligohymenophorea: Yi et al. [130] documented that the life cycle of *Ichthyophthirius multifiliis*, a parasite of fish, consists of three key developmental stages: the infective theront, the parasitic trophont, and the reproductive tomont.

Mesanoophrys pugettensis, is a scuticociliate that was observed with a diphasic life history, the larger phase or trophont, and the smaller phase resembling tomites [34], is a facultative parasite of the Dungeness crab. *Conchophthirus* species are generally considered an endocommensal inhabiting the mantle cavity of freshwater clams or mussels [30].

Thigmotrichids from several families were analyzed by Raabe [131–134], where species of Hemispeiridae are symbionts of the mantle cavity and nephridia of molluscan, those of Ancistrocomidae, Sphenopryidae and Thigmophryidae are ectosymbionts of mantle cavity and gills of molluscan, and Hysteroconinetidae species were categorized as endoparasites of the gut of prosobranch mollusks; life cycles include tomites.

The apostomes is a small group of oligohymenophorean ciliates, with four major life histories: 1-exuviotrophic, that remain encysted on the exoskeleton of a crustacean host, and excyst to feed on exuvial fluid, reproducing during the host ecdysis, 2-sanguicolous, penetrate the cuticle of the host, feed on the cells and fluid of the hemocoel and reproduces, 3-chromidinid, found in the renal organs and opalinopsids found in the liver and intestines of cephalopods ingesting fluids and cells, 4-histotrophs, such as *Vampyrophrya* [135]. Apostome ciliates have life cycles typically involving crustaceans, with a non feeding microstome tomite and a macrostomous trophont [127]. Species of apostome of genus *Collinia* are endoparasites able to reproduce rapidly within the host that invariably kill the euphausiid within 40 hours of infection; *Gymnodinioides* genus includes exuviotrophic species that feed on the fluid within the exuviae of crustacean hosts and Landers *et al.*, [136] documented for *Gymnodinioides pacifica* the presence of trophonts, phoronts, tomonts and tomites. For *Synophrya* the phoront, hypertrophont, hypertomont, and hypertomites were observed [137].

Pilisuctorian ciliates spend most of their lives perched on cuticular setae of crustaceans, and complete their life cycle on a single host, having the stages tomite, tomont and trophont [138].

In peritrichs, a significant character is the scopula which is the region that originates the stalk to attach the organism to the substrate and modifies to a highly complicated adhesive apparatus in mobiline [127]; two phases are known, the trophont and the dispersive telotroch.

Species of sessile peritrichs genera such *Ambiphrya*, *Epistylis*, *Heteropolaria*, *Rhabdostyla*, and *Zoothamnium* are epibionts of zooplanktonic invertebrates, larval stages of aquatic insects, aquatic mollusks, crustaceans, fish, amphibians, and reptiles as the main groups of organisms [139]. Members of genus *Epistylis* have been reported as epibionts in several metazoans, but also as an important fish ectoparasite being considered an emerging pathogen [140]. Genus *Lagenophrys* comprises only symbiotic species of freshwater and marine crustaceans [89]. Trichodinids are the most devastating ectoparasites of cultured fish, causing severe damage [141], and for genus *Trichodina* about 300 species have been described, mostly from freshwater environments [142]. Also, there are reports of trichodinids from the gills of limpets [143] and have been documented as symbionts of a broad spectrum of aquatic and terrestrial invertebrates and vertebrates hosts [65]. *Trichodinella epizootica* is one of the most widely distributed freshwater trichodinids in Europe and Asia, but has also been reported from Africa, the Pacific region and North America [55]. *Urceolaria* includes species ectosymbionts of freshwater turbellarians, marine polychaetes, and mollusks; *Leiotrocha* species are ectocommensals and endocommensals of marine mollusks, and species of *Polycycla* are endocommensals of Holothuroidea [144].

2. Ecological relationships: Classical definitions and approaches

2.1 Epibiosis

Epibiosis is a facultative association of two organisms: the epibiont, which colonizes the surface of live substrates, and the basibiont, which hosts the epibionts [145]. Some species of epibiotic communities show preferences for specific location sites on the host [76]. According to Wahl and Mark [146], when the effects associated with epibiosis are neutral or positive for a basibiont species and beneficial for an epibiont species, selection should favor the evolution of the epibiotic relationship, which tends to increase specificity through evolutionary history. Although many epibiont ciliates are not harmful to their basibionts, some studies have shown that the epibionts can cause deleterious effects on their hosts [147–149].

Historically, studies involving epibiont ciliates focus on the following interests: new records and checklists [27, 28], descriptions of new taxa using morphological and molecular data [150], possible deleterious effects on hosts [149, 151], distribution and preferred sites of epibiont populations and communities [152], spatial and temporal distribution of the epibiotic relationship [153], laboratory rearing and experimentation studies [154–156], and even investigations into extrinsic and intrinsic factors involved in the kinetics of epibiont ciliate populations [157, 158].

2.2 Mutualism

Mutualism is a relationship with high metabolic dependence, where both organisms, ciliate and their hosts, obtain benefits [159, 160]. In the phylum Ciliophora, this type of relationship is seen, mainly in the subclass Trichostomatia, which includes the ciliates of the digestive tract of herbivorous mammals [161]. The symbiont ciliates represent approximately 2,600 of the described organisms, of which around 1000 species belong to the subclass Trichostomatia [2]. This subclass comprises ciliated protists, mostly mutualists of the digestive tract of

several vertebrate hosts, with only one species showing parasitism in humans, *Balantidium coli* [2, 162, 163]. The subclass Trichostomatia is divided into three orders: Vestibuliferida, Entodiniomorpha, and Macropodiniida.

Ruminant ciliates and the host have a fundamental symbiosis relationship for the digestion and absorption of large amounts of plant material by the ruminant [164, 165]. On the one hand, the host provides an ideal environment for the survival of the symbiotic microbiota. The rumen is a strictly anaerobic environment, with temperatures ranging from 38 to 41° C, redox potential around 250 to 450 mV (millivolts), osmolarity ranging from 260 to 340 mOsm (millivolts), and pH levels between 5.0 and 7.5. Maintaining these characteristics is essential for microbial enzymatic activity to occur. In return, symbionts provide energy, protein, and vitamins to the host [166]. In energy terms, about 50–70% of the energy obtained by the host comes from the absorption of volatile fatty acids (VGAs) (eg. acetate, butyrate, and propionate), which are absorbed after the breakdown and fermentation of plant fiber by ruminal microorganisms [165]. Ciliates also represent a great source of protein for the ruminant (about 2 to 5%). Still, the ruminal microbiota also synthesizes B and K vitamins in sufficient quantities for the maintenance and growth of the animal. Due to the important participation in the physiology of the ruminant, the evolutionary dynamics of ruminal ciliates has been suggested as closely associated with the radiation of their hosts [167–169].

2.3 Commensalism and parasitism

Commensalism occurs when the symbiont inhabits in the host with no evident benefit or harm [170].

Parasitism, which is less common in ciliates, involves the parasites that usually cause disease being pathogens. They may be localized or spread throughout a host, defined as the independent and dominant member of the symbiotic pair. Here, the parasite inhabits on or inside the host to obtain resources and to harm it [171].

3. Ecological relationships: evolutionary approach

From an evolutionary point of view, there are species that are entirely free-living, those which can live equally well both free or as symbionts, species that are almost entirely symbiotic with only occasional periods of “free” existence during their life cycles (facultative symbionts), and species which are entirely symbiotic (obligate symbionts). Most of the well documented associations between Ciliophora and Metazoa are the ones leading to a certain degree of metabolic dependence. We will use in this topic the idea of metabolic dependence to define the ecological relationships: “free-living” (no metabolic dependence), “epibiont” (facultative metabolic dependence), “mutualistic” (mutual metabolic dependence) or “parasitic” (unilateral metabolic dependence, including commensalism).

For many years the evolutionary studies for Ciliophora were based only on morphological data, mainly those related to the ultrastructural characterization of its complex infraciliature [2]. However, in recent years this scenario has been modified with the implementation of modern tools that use multidisciplinary methods to integrate morphological, phylogenetic, molecular, and ecological data [161, 172–174]. A reliably dated phylogeny is fundamental to infer a broad macroevolutionary scenario for Ciliophora [172]. The inference of diversification rates from molecular phylogenies has increasingly been used to derive macroevolutionary patterns of lineages. Understanding how the different ecological relationships evolve in Ciliophora along time is a complex task that has been developed for many years. Different hypotheses

about the origin and evolution of parasitic life have been proposed. Parasitologists suggest that the symbiotic way of life probably descended from free-living lineages that subsequently adapted to life in special habitats. Besides this, several authors suggest multiple origins of parasitism based on a comparison of morphological and ultrastructural aspects between them and their free life co-specifics [175], however, the processes that lead to its emergence are still imprecise [176–178].

Concerning the phylum Ciliophora, the vast majority of ciliates are categorized as free-living, and studies suggested that symbiosis apparently arising independently among various classes [179]. For genus *Tetrahymena* (subclass Hymenostomatia, order Hymenostomatida), all gradations of adaptations to symbiosis occur. There are species that live totally free, those that can live equally well both free and as symbionts, species that are almost entirely symbiotic with only occasional periods of “free” existence during their life cycles (optional symbionts), and species that are totally symbiotic (mandatory symbionts) [180]. Different transition routes between ecological associations have also been proposed, based on morphological and ecological characteristics. The first one proposes that free-living organisms assume habits of low metabolic dependence (mutualism, commensalism, among others), and with the strengthening of relationships, where they become parasites [176, 181]. The second hypothesis suggests that a free-living organism, when it comes into contact with a host accidentally, adapts itself to live both freely and within that host (optional parasite) [179], that is, free-living organisms adapt to live inside a host, which becomes something advantageous and increases fitness, making this a favorable way of life for the species.

Previous studies aimed to test these hypotheses based on phylogenetic analyzes of small groups within Ciliophora [174, 182, 183]. The macroevolutionary analyzes from the whole Ciliophora phylogeny presented **Figure 1** suggested that the ancestral way of life of the ciliates originated from a free-living organism and that the parasitic way of life arose numerous times and independently in Ciliophora, which was induced by two types of ancestors, free life and mutualistic (**Figure 1**). The transition to the parasitic way of life was recovered from two different origins: 1) a free-living ancestor evolved into a mutualistic organism and, later, to a parasitic organism, and 2) a free-living ancestor evolved into an organism parasite (highest number of cases). There are also cases where there has been a regression in the ciliate’s way of life, where parasite clades evolved to free-living clades (**Figure 1**).

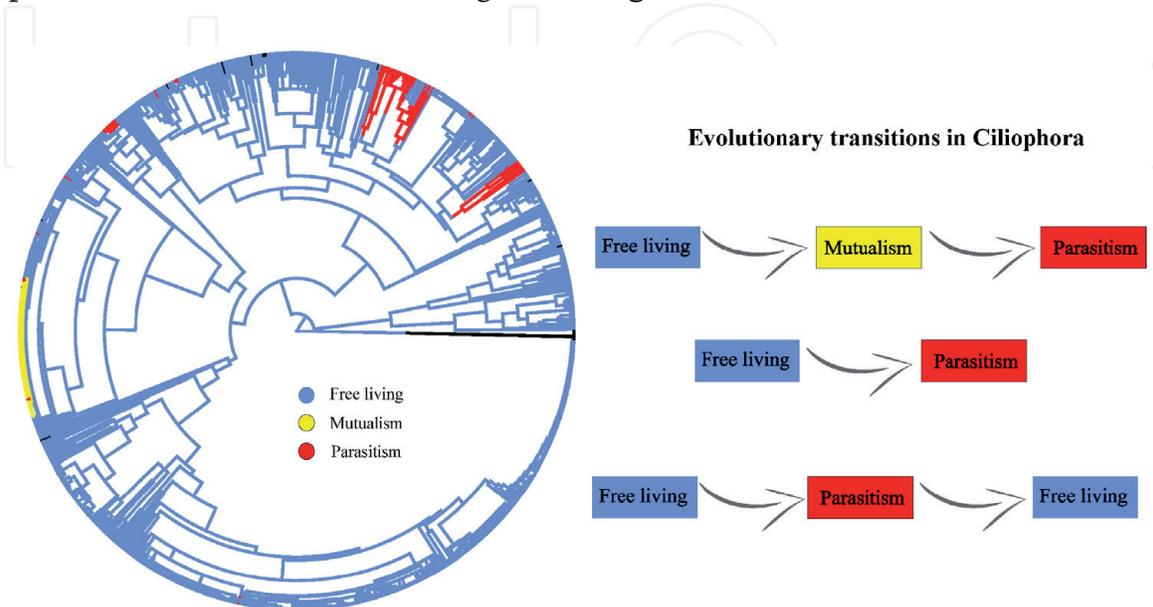


Figure 1. Ancestral habit reconstruction for Ciliophora showing the main routes of transitions. Blue: Free-living. Yellow: Mutualism. Red: Parasitism/commensalism.

4. Future perspectives

The analytical improvement for morphological, ultrastructural, molecular, and evolutionary characterizations in Ciliophora culminated in an “Age of Integration”, which several disciplines interact to infer patterns of biodiversity [184]. Although it is an age in full expansion, several gaps often prevent a study of diversity in its diverse areas in a complete way.

We are in a period of the paradigm shift, where Next Generation Sequencing (NGS) techniques have been applied exponentially, and, therefore, it is expected that new discoveries will emerge and new panoramas will be drawn on the diversity of the strains, as well as their respective ecological interactions. The transition from phylogenetic studies to phylogenomics is based on technological progress combined with exponential sequencing of molecular sequences (DNA, RNA), reduced associated costs, increased computational capacity, and improved analytical protocols. It is important to make efforts in studies to expand such technologies to lineages with little sampling in databases. For example, the classes Prostomatea, Oligohymenophorea, Litostomatea, and Phyllopharyngea, which present several examples of symbiosis, do not have available molecular sequences which prevents the evolutionary inferences of these lineages, requiring in the future more studies to refine the evolutionary hypotheses about the phylum. Efforts to expand metataxonomy using metagenomics and metatranscriptome methods have fed the databases exponentially in several lineages, revolutionized the analysis of environmental microbial diversity [175, 185, 186]. In fact, the generation of data for the target sequencing of phylogenetic, metagenomic, and metatranscriptomic markers is now reasonably well established, and several DNA sequencing platforms based on different technologies are currently available as well as different bioinformatics programs for each level of data extraction. However, due to the limited size of the molecular sequences produced by the platforms (~ 500 bp), phylogenetic estimates may be inadequate. With longer readings comes an improved phylogenetic signal, and we show that it is possible to employ a complete phylogenetic signal approach to taxonomically classify sequences and obtain a robust evolutionary structure of environmental diversity. New sequencing technologies such as nanopore sequencing, which offer long reads, improved the phylogenetic signal and more robust taxonomic patterns, can be an alternative in future studies [187].

With the significant increase in the number of available sequences from NGS sequencing, more effective and less subjective methodologies have been proposed to define the limits and number of independent evolutionary entities, to accelerate the biodiversity assessment process. In the last two decades, the field of species delimitation has intensified in relation to the number of methods available. For this, several methodologies have been proposed, based on biological [188], ecological [189], and molecular data [190], in addition to combining phylogenetic theory and population genetics [191–193]. The use of these methodologies in ciliates performed very recently to delimit organisms of free life, as species of the genus *Frontonia*, using the mitochondrial gene COX1 [194], species of the genus *Spirostomum*, using the ITS spacer region genes [195], and COI and 18S markers of the *Paramecium* genus.

Finally, several authors have emphasized the lack of studies on the distribution and occurrence of ciliates associated with Metazoa in natural conditions and the the lack of information on the ecology and interactions between epibionts and hosts. Few studies are exploring the natural history and complexity of life cycles, which makes it difficult to characterize optional and mandatory relationships. The absence of the characterization of the ciliate at the stage it is in the host, most studies, only in the environment, making it difficult to characterize the life cycle. Relevant information about habitat, life cycle, infection site is rare for Ciliophora [160, 196, 197].

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