

Richness of morphological hypotheses in ciliate systematics allows for detailed assessment of homology and comparisons with gene trees*

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Abstract: Morphological investigations are central to ciliate systematics. Morphology has provided most species delimitations as well as almost all hypotheses on the ciliate tree of life. Moreover, emerging analyses of molecular markers are generally concordant with morphology-based ciliate taxonomies. Despite the richness of morphology-based hypotheses, there are challenges to ciliate morphological systematics that include the decreasing numbers of trained morphologists and the difficulty in establishing homology for some morphological traits. There are also open questions about ciliate morphology, such as the cause of morphological stasis in cryptic species, and the contrasting pattern of considerable morphological variation with little underlying genetic variation.

Key words: Ciliates, Colpodea, Halteriids, morphology, systematics.

Introduction

Ciliates are unique among microbial groups in that their diverse morphology, abundance and relatively large sizes have enabled the creation of a comprehensive morphology-based taxonomy. Analyses of morphological and ontogenetic characters, first gathered using light microscopy and more recently in analyses of electron micrographs, have led to detailed hypotheses on the relationships among ciliates that extend across taxonomic levels. Hence, those of us working on the systematics of ciliates find ourselves in the enviable position of having numerous hypotheses that can be assessed through both reexamination of morphology and characterization of molecular characters. Here, we describe the strengths of morphological approaches to ciliate taxonomy, the challenges to these types of analyses, the concordance between morphological and molecular characters, and the nature of some of the open questions in ciliate systematics.

Strengths of morphology

Species delimitations

The diverse morphology among ciliates has allowed for many in-depth studies that have defined the limits of ciliate species. In general, the morphological species concept is the standard for ciliates (e.g., FOISSNER et al. 2002), although species have been named using other

methods (e.g., SONNEBORN 1975; NANNEY & MCCOY 1976; FOISSNER & BERGER 1999). These morphological investigations provide us with an estimate of the minimal number of extant ciliate species. Although it is argued that the number is around 3000 by ecologists (FINLAY et al. 1996; FINLAY 2002), the actual number may be “near-imponderable” (FOISSNER 1999). Estimates of ciliate species numbers require highly trained taxonomists exploring new environments and different parts of the Earth: the more they look, the more they find (e.g., BERGER 1999, 2006, BERGER et al. 2006; FOISSNER 1994, 1995, 1997a, 1998, 2003, 2005a; FOISSNER et al. 2002, 2003, 2005a, c, FOISSNER & STOECK 2006, FOISSNER & XU 2007; KIM et al. 2007; LIN et al. 2007; MA et al. 2006; PETZ et al. 1995). Molecular investigations using environmental sampling of SSU-rDNA (small subunit ribosomal DNA) haplotypes also point to such a high number (DOHERTY et al. 2007; STOECK et al. 2006). Hence, there are likely many more ciliates that have yet to be discovered, maybe even up to 30,000 to 40,000 (CHAO et al. 2006; FOISSNER 1997b, 1999, FOISSNER et al. 2008).

Ciliate tree of life

Analyses of morphological characters, including somatic and oral ciliature, and ontogenesis have generat-

* We want to express our deepest appreciation and esteem to Wilhelm FOISSNER for his fundamental and wide-ranging contributions to ciliate systematics.

ed almost all hypotheses on the topology of the ciliate tree of life for many diverse clades (CORLISS 1979; LYNN & SMALL 1997, 2002; PUYTORAC 1994; SMALL & LYNN 1981, 1985). Recently, morphological depictions, along with supporting molecular evidence, have divided ciliates into two subphyla – the Postciliodesmatophora and Intramacronucleata – and eleven classes (LYNN 2003; ADL et al. 2005). Detailed morphological hypotheses have also generated almost all hypotheses of relationships within these eleven classes (e.g., MATTHES et al. 1988; BERGER 1999, 2006; FOISSNER 1993, FOISSNER & XU 2007; LYNN & SMALL 2002).

Challenges to morphological analyses

Decline in number of trained taxonomists

Like in many eukaryotic clades (LEE 2000; WHEELER 2008), one principal impediment to our understanding of ciliate diversity is the lack of trained morphological taxonomists. As much of science in the past century shifted to a focus on model organisms, fewer and fewer students received training in collection, identification and analysis of diverse lineages, particularly microorganisms. This problem is particularly acute today as there is increasing interest in microbial diversity on Earth but few professors positioned to train students in microbial morphological analysis of microbes and traditional taxonomy.

Number of characters

While the number of characters needed for phylogenetic analyses is debated (ROKAS et al. 2003; GATESY et al. 2007), morphological characters are limited, particularly when compared to molecular characters (GIVNISH & SYTSMAN 1997; HILLIS & WIENS 2000; SCOTLAND et al. 2003). This lack of numerous unambiguous morphological characters remains problematic, particularly when compared to most macrobes (e.g., DOYLE & ENDRESS 2000; GIRIBET & WHEELER 2002). In light of this, we agree with SCOTLAND et al. (2003) that in ciliates it may be more critical for morphological studies to investigate fewer characters in depth, such as in the studies of the cysts of *Meseres corlissi* (FOISSNER 2005b, FOISSNER & PICHLER 2006, FOISSNER et al. 2005b, 2006).

Homology assessment

Likewise, homology assessment of morphological characters can be difficult in all eukaryotic clades (SCOTLAND et al. 2003), and it is not surprising that this problem is amplified in microbial groups. The aim is to equate homology with synapomorphy (share derived character), which is essential for inferring evolutionary relationships (PATTERSON 1982; STEVENS 1984; DE PINNA 1991). Establishing homology is a two-step process.

In a primary homology assessment, similarity among characters is initially established and shared ancestry is hypothesized. In a secondary homology assessment, the primary assessment is tested via congruence with other morphological or molecular characters (DE PINNA 1991). Hence, inferring robust phylogenies requires independent data sets and reassessment of primary homology statements.

While primary homology statements in ciliates can be relatively straight forward, establishing secondary homology statements is problematic because of issues in executing congruence tests. First, cladistic analyses using morphological characters in ciliates are rare and often deal with few taxa (e.g., PUYTORAC et al. 1994; BERGER & FOISSNER 1997, FOISSNER et al. 2007; AGATHA 2004, AGATHA & STRÜDER-KYPKE 2007). As a result, most primary homology statements just have not been tested. Like in all systematic analyses, there is a difficulty in these few ciliate examples of how many taxa – both ingroup and outgroup – need to be sampled and coded; the paper by FOISSNER et al. (2007) stands out in increasing outgroups for the problem of placing the halteriids.

Second, the question of the level of generality of the homology of many ciliate morphological characters remains unresolved because most molecular estimates of ciliate relationships rely on single locus, SSU-rDNA (e.g., SHINE et al. 2000; SNOEYENBOS-WEST et al. 2002, 2004; HEWITT et al. 2003; SCHMIDT et al. 2007a, b; STRÜDER-KYPKE et al. 2006, 2007; WILLIAMS & CLAMP 2007; DUNTHORN et al. 2008). With the well-known gene tree versus species tree problem (DOYLE 1997; MADDISON 1997), we do not know yet if the SSU-rDNA locus accurately reflects species phylogeny. For example, the homology of halteriid oral membranes with other spirotrichs remains to be satisfactorily answered, although there are numerous hypotheses (explicit or implicitly implied) and molecular tests (SZABÓ 1935; PETZ & FOISSNER 1992; AGATHA 2004, AGATHA & STRÜDER-KYPKE 2007; STRÜDER-KYPKE & LYNN 2003; FOISSNER et al. 2004, 2007). Development of additional molecular markers is essential for robustly testing morphological homology statements.

Concordance with molecular hypotheses

Hypotheses of the ciliate tree of life are generally congruent with gene trees. For example, the most inclusive clades proposed – ranked at the class level – have, for the most part, either been supported or at least not refuted by molecules (LYNN 2003). Molecules also generally support less inclusive ciliate clades. For example, much of FOISSNER's (1993) morphological classification

of the class Colpodea is largely congruent with SSU-rDNA gene trees (DUNTHORN et al. 2008; LASEK-NESSELQUIST & KATZ 2001; LYNN et al. 1999).

An aspect of the incongruence between the morphological hypotheses and the SSU-rDNA gene trees in the Colpodea centers upon paraphyletic groups; e.g., the Sorogenida nesting within part of the Cyrtolophosidida, the Bursariomorphida nesting within the Bryometopida, and the Grossglockneriida nesting within the Colpodida (DUNTHORN et al. 2008). In these three cases of paraphyly there are a number of morphological characters that unite the respective groups within the gene trees (DUNTHORN et al. 2008). Another aspect of the incongruence is the challenge that plesiomorphic characters pose when trying to uncover evolutionary relationships, where the ancestral condition of the group remains in some taxa, causing them to be grouped together. An example of this is in the possibility of the Cyrtolophosidida being polyphyletic (DUNTHORN et al. 2008).

Open questions

Lack of morphological variation when there is genetic diversity

While morphology provides us with the minimal number of extant species, there are undoubtedly many more. Like in other eukaryotic clades (MAYR 1963; PFENNINGER & SCHWENK 2007), cryptic species are well-known in ciliates (SONNEBORN 1937, 1957). Underlying these ciliate cryptic species there can be both a high genetic diversity as well as ecological variation (NANNEY et al. 1998; WEISSE & LETTNER 2002, WEISSE & RAMMER 2006; KATZ et al. 2005; FOISSNER et al. 2008; SIMON et al. 2008).

There are two main reasons why cryptic species have been postulated: the species may be nascent, with little time to acquire morphological difference, or the conserved morphology of the species may be of selective value (MAYR 1976). This second reason is generally accepted for ciliates (NANNEY 1977, 1982, 1999, NANNEY et al. 1998). This selective reason is supported by the hypothesis that cryptic ciliates may be ancient clades, although the actual age is debated (NANNEY 1977, 1982, 1999; VAN BELL 1985). However, data on these ages are highly speculative.

There have been no tests, though, of the selective value of keeping the same morphology among cryptic ciliate species. Equally plausible is that selection is not driving morphological evolution and that morphology remains in stasis for other reasons such as constraints or canalization. Alternatively, the prevalence of cryptic species of ciliates may be due to disparate rates of morphological and molecular evolution enabled by the dual

nature of ciliate genomes. The separation of genome function between the unexpressed germline micronucleus and the expressed somatic macronucleus changes the dynamics of molecular evolution in ciliates as compared to other eukaryotes. Based on analyses of multiple molecular markers in diverse ciliate, the dual nature of genome evolution has been shown to be related to elevated rates of protein evolution in this lineage (MCGRATH et al. 2006; ZUFALL et al. 2006). This elevated rate of molecular evolution, coupled with the prevalence of epigenetics in development (MCGRATH et al. 2006), may contribute to the generation of cryptic species.

Lack of genetic diversity when there is morphological variation

In contrast to cryptic species, there are also cases in ciliates in which there is only limited genetic variation, at least as measured by SSU-rDNA divergence, in light of considerable morphological variation. This phenomenon is best seen in comparisons among SSU-rDNA gene trees of various clades in the class Spirotrichea. Morphological and molecular changes are relatively concordant among members of the choreotrichs, oligotrichs; in contrast, there is considerable discordance and very short SSU-rDNA branches among stichotrich taxa (SNOEYENBOS-WEST et al. 2002; STRÜDER-KYPKE & LYNN 2003; AGATHA & STRÜDER-KYPKE 2007). Intriguingly, it is only within the stichotrichs that we have evidence of gene scrambling, a process whereby coding domains are reshuffled in ciliate micronuclei (GRESLIN et al. 1989; PRESCOTT 1992; ARDELL et al. 2003). We hypothesize that this type of heritable scrambling can cause instant, or at least rapid, speciation as extensive gene scrambling will disrupt pairing of homologous chromosomes during meiosis. Under this scenario, accumulation of scrambled genes within populations can lead to a barrier to gene exchange with other populations of the same species.

Acknowledgements

We would like to thank E. AESCHT and H. BERGER for the invitation to contribute to this volume, and S. AGATHA and D. LAHR for insightful comments.

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Zeitschrift/Journal: [Denisia](#)

Jahr/Year: 2008

Band/Volume: [0023](#)

Autor(en)/Author(s): Dunthorn Micah, Katz Laura

Artikel/Article: [Richness of morphological hypotheses in ciliate systematics allows for detailed assessment of homology and comparisons with gene trees 389-394](#)