



Evolutionary origin of *Ceratonova shasta* and phylogeny of the marine myxosporean lineage



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ABSTRACT

In order to clarify the phylogenetic relationships among the main marine myxosporean clades including newly established *Ceratonova* clade and scrutinizing their evolutionary origins, we performed large-scale phylogenetic analysis of all myxosporean species from the marine myxosporean lineage based on three gene analyses and statistical topology tests. Furthermore, we obtained new molecular data for *Ceratonova shasta*, *C. gasterostea*, eight *Ceratomyxa* species and one *Myxodavisia* species. We described five new species: *Ceratomyxa ayami* n. sp., *C. leatherjacketi* n. sp., *C. synaphobranchi* n. sp., *C. verudaensis* n. sp. and *Myxodavisia bulani* n. sp.; two of these formed a new, basal *Ceratomyxa* subclade.

We identified that the *Ceratomyxa* clade is basal to all other marine myxosporean lineages, and *Kudoa* with *Enteromyxum* are the most recently branching clades. Topologies were least stable at the nodes connecting the marine urinary clade, the marine gall bladder clade and the *Ceratonova* clade. Bayesian inference analysis of SSU rDNA and the statistical tree topology tests suggested that *Ceratonova* is closely related to the *Enteromyxum* and *Kudoa* clades, which represent a large group of histozoic species. A close relationship between *Ceratomyxa* and *Ceratonova* was not supported, despite their similar myxospore morphologies. Overall, the site of sporulation in the vertebrate host is a more accurate predictor of phylogenetic relationships than the morphology of the myxospore.

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1. Introduction

Myxosporeans (Cnidaria: Myxozoa) are microscopic parasites of vertebrates (fish, amphibians, rarely reptiles, birds and mammals) and invertebrates (polychaete and oligochaete worms). As myxosporean morphology is extremely simplified and unique, it took until the end of 20th century to demonstrate their taxonomic affinity to metazoan cnidarians (Siddall et al., 1995). The cnidarian origin was under discussion for more than 20 years until multigene analyses (Jiménez-Guri et al., 2007; Nesnidal et al., 2013) and the identification of synapomorphic genes between the Cnidaria and Myxozoa (Holland et al., 2011) confirmed the myxozoan origin within Cnidaria. Myxosporeans evolved from a cnidarian ancestor closely related to the Medusozoa (Jiménez-Guri et al., 2007). They developed two novel forms, myxospores

and actinospores, which are essential for their parasitic way of life. The only apparent synapomorphic morphological feature shared by both Cnidaria and Myxozoa are cells with extrudible filaments, referred to as nematocysts and polar capsules, respectively.

Taxonomy of the class Myxosporea has been based traditionally on morphology of myxospores, which develop in the intermediate vertebrate host. Myxospore morphology (structure, shape and size of spore, position of polar capsules etc.) has been the basis for assigning species to the ~60 myxosporean genera (Fiala and Bartošová, 2010), which contain ~2200 species (Lom and Dyková, 2006). Molecular studies have revealed discrepancies between this myxospore morphology-based taxonomy and phylogenetic relationships based on ribosomal DNA sequences. In many cases, morphologically distinct myxosporean species that had been assigned to different genera were shown by DNA sequencing to be related closely and some species with very similar spore morphologies are distantly related (Bartošová et al., 2009; Fiala, 2006; Holzer et al., 2004; Kent et al., 2001).

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