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Nodularia (Cyanobacteria, Nostocaceae): a phylogenetically uniform genus with variable phenotypes

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Abstract

The taxonomy of cyanobacteria currently faces the challenge of overhauling the traditional system to better reflect the results of phylogenetic analyses. In the present study, we assessed the phylogenetic position, morphological variability, ability to produce the toxin nodularin, and source habitat of 17 benthic and soil isolates of *Nodularia*. A combined analysis of two loci (partial 16S rRNA gene and *rbc*LX region) confirmed the genus as a monophyletic unit and the close relationship of its members. However, the taxonomic resolution at the subgeneric level was extremely problematic. The phylogenetic clustering did not show any reasonable congruence with either morphological or ecological features commonly used to separate taxa in heterocytous cyanobacteria. Despite the near phylogenetic similarity of planktonic, benthic and soil *Nodularia* strains, we did not find any new nodularin-producing strains among the non-planktonic isolates. The relatively low variability in conserved molecular markers within the genus *Nodularia* exemplifies the limitations of the currently accepted taxonomic workflow and polyphasic approach. Elucidation of mechanisms that drive the phenotypic variability in such groups presents a major challenge in cyanobacterial research.

Key words: Benthos, Cyanobacteria, *Nodularia*, nodularin, plankton, taxonomy

Introduction

Among heterocytous cyanobacteria, the genus *Nodularia* Mertens ex Bornet & Flahault (1886: 243) forms a monophyletic lineage within Nostocaceae—unbranched filamentous types with both heterocytes and akinetes (Komárek 2013). The genus consists of three distinct ecological groups: planktonic types with aerotopes (gas vesicles), and benthic and soil types without aerotopes (Komárek & Mareš 2012). The planktonic *Nodularia* often create massive water blooms, especially in the Baltic Sea and Australia (Sellner 1997, Koskenniemi *et al.* 2007, McGregor *et al.* 2012). The blooms are highly toxic because the planktonic types produce the cyclic pentapeptide hepatotoxin nodularin (e.g., Lopes & Vasconcelos 2011). The frequent occurrence of harmful blooms, especially of the toxic planktonic type, has attracted the attention of scientists (Sellner 1997, Moffit *et al.* 2001, Jodłowska & Latała 2010). On the other hand, benthic and soil representatives of *Nodularia* have been rather overlooked because they are not dominant in the soil or benthic biotopes and they usually do not produce nodularin. The only known exception is strain PCC 7804/SAG 50.79 from a benthic mat in a thermal spring in France, a strain of *Nodularia sphaerocarpa* Bornet & Flahault (1886: 245) that has been proven to produce nodularin in several studies (Beattie *et al.* 2000, Moffitt *et al.* 2001). It is difficult to transfer benthic and soil *Nodularia* into cultures because of their low density in phototrophic populations, and only few such strains are currently kept in algal culture collections worldwide. Thus, only a few studies have dealt with benthic species (*N. harveyana* Thuret ex Bornet & Flahault (1886: 243), *N. sphaerocarpa*, *N. moravica* Hindák, Šmarda & Komárek (2003: 243)) and included them in phylogenetic reconstructions (Lehtimäki *et al.* 2000, Laamanen *et al.* 2001, Lyra *et al.* 2005, Lopes & Vasconcelos 2011, Hašler *et al.* 2011). Soil isolates were almost completely neglected.

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