Nomenclatural validation of the genetically revised cyanobacterial genus *Dolichospermum* (Ralfs ex Bornet et Flahault) comb. nova

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Abstract: The traditional cyanobacterial genus *Anabaena* is heterogeneous, as follows from the modern molecular evaluation. The cluster of planktic *Anabaena*-morphotypes with gas vesicles in cells must be separated as a unique generic entity from the typical benthic mat-forming species. In the present articles all planktic morphospecies are transferred into the new genus *Dolichospermum* in agreement with Botanical nomenclatoric rules. The name *"Dolichospermum*" is based on a taxonomic category of section in starting point publication (Bornet & Flahault 1888), which is valid for heterocytous cynobacteria.

Key words: Cyanobacteria, *Anabaena, Dolichospermum*, taxonomy, nomenclatoric validation

Introduction

The diversity of organisms (both in nature and in culture) can be reviewed and characterised only by help of the taxonomic classification. However, the modern classification of cyanobacteria must be based and revised on the molecular approach, and for the generic delimitation the clustering by 16S rRNA gene sequencing is particularly required. The cyanobacterial heterocytous genus *Anabaena* in traditional sense of Bornet & Flahault (1888) and Geitler (1932) is heterogeneous. The benthic and soil inhabiting *Anabaena*-types (forming mats and never producing gas vesicles in cells) were found clearly genetically separated from the planktic cluster containing free-floating solitary trichomes or their small groups, and producing obligatorily reversible gas vesicles in cells (Iteman et al. 2002, Gugger et al. 2002 a,b, Rajaniemi et al. 2005a,b, Willame et al. 2006) (Fig. 1). Gas vesicles production is genetically fixed adaptation to the planktic way of life. Gas vesicles have a special structure and are grouped in cells into aerotopes (= previously "gas vacuoles") recognizable by optical microscopy (Walsby 1972, 1978, 1981, etc). The genetic difference between planktic and typical mat-forming *Anabaena*-morphotypes is so distinct that both these clusters must be classified in modern cyanoprocaryotic system as separate genera (Gugger et al. 2002b, Hoffmann et al. 2005, Rajaniemi et al. 2005a,b, Willame et al. 2006). Because the type species of the genus *Anabaena, A. oscillarioides* Bory ex Bornet et Flahault 1888 belongs to benthic types, the planktic *Anabaena*-cluster must be renamed and classified as a special genus. The name "*Dolichospermum*", which was used in the starting point (Bornet & Flahault 1888, p. 228) as the valid name for section ("Sectio II – *Dolichospermum* Ralfs 1850"), can be used as valid generic name for the planktic cluster. This section contains the common planktic species "*Anabaena flos-aquae* Brébisson ex Bornet et Flahault 1888", which is designated as a type species of the revised genus *Dolichospermum* (Ralfs ex Bornet et Flahault) comb. nova.

Methods

The results are based on the molecular analyses, mainly on the 16S rRNA gene sequencing, used for the study of planktic *Anabaena*-species. The methods used are described in detail in Iteman et al. (2002), Gugger et al. (2002a, 2002b), Rajaniemi et al. (2005a, 2005b) and Willame et al. (2006). The rules of botanical nomenclature (Botanical Code) are accepted for the nomenclatoric evaluation and the requests of the validation of modern, revised cyanobacterial taxa (Oren & Tindal 2005) are respected.

Results

Dolichospermum (Ralfs ex Bornet et Flahault) comb. nova

Syn. (basionym): Sectio II – *Dolichospermum* Ralfs 1850 ex Bornet et Flahault, Ann. Sci. Nat. Bot. VII, 7: 228, 1888.

Type species: *Dolichospermum flos-aquae* ([Lyngbye] Brébisson ex Bornet et Flahault) comb. nova (syn. and basionym: = *Anabaena flos-aquae* [Lyngbye] Brébisson ex Bornet et Flahault, Ann. Sci. Nat. Bot. VII, 7: 228, 1888).

Main generic diacritical characters (obligatory for all species):

- The genus *Dolichospermum* (evaluated by 16S rRNA gene sequencing) belongs genetically into the unique cluster of nostocalean heterocytous cyanobacteria.
- This genetically separated group (*Dolichospermum*) represents a complex cluster, the different members of which do not differ less than in 92% of 16S rRNA gene similarity one from another (see Fig. 1).
- Trichomes are isopolar, metameric with respect to heterocytes position, with constrictions at cross-walls, without firm sheaths, sometimes with fine mucilaginous, diffluent envelopes. The growth of trichomes is theoretically endless.
- Apical cells are morphologically similar to vegetative cells, they are not differentiated and are able to divide.

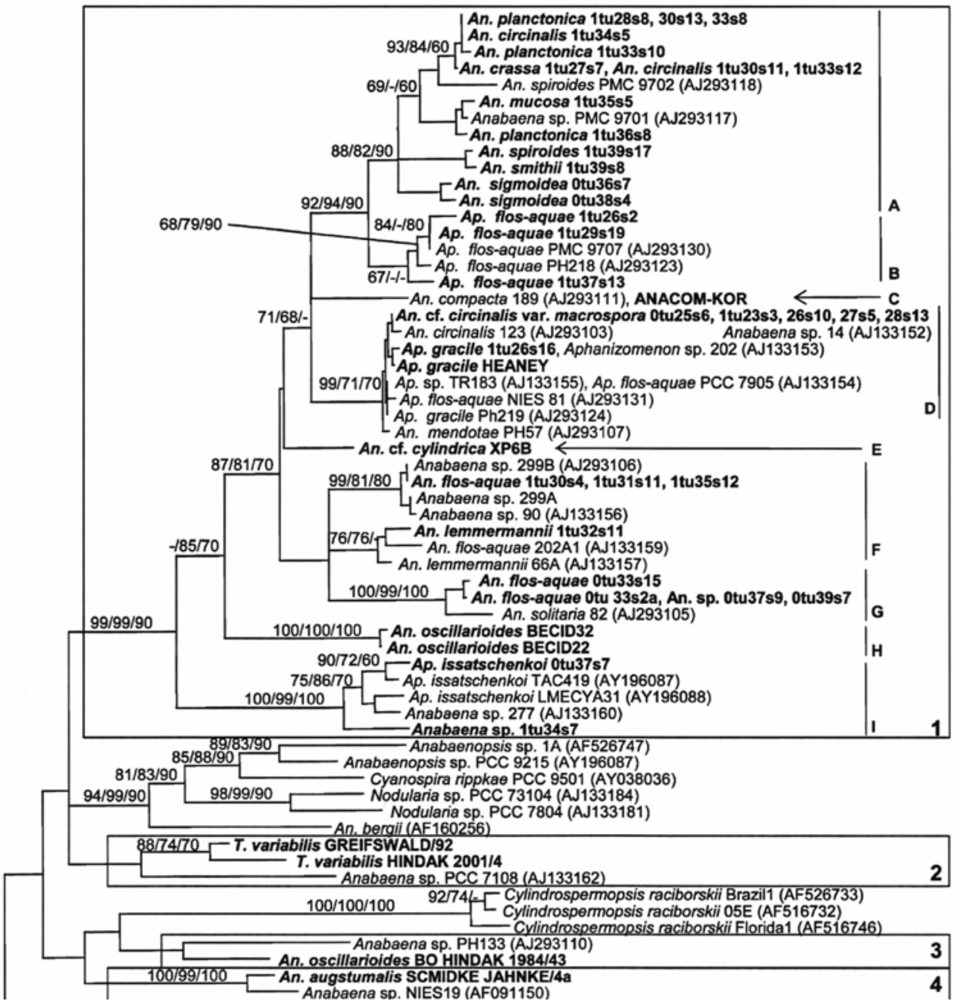

Fig. 1. The molecular evaluation of planktic *Anabaena/Aphanizomenon* clusters based on the 16S rRNA gene sequencing according to Rajaniemi et al. (2005a): (B) cluster of typical *Aphanizomenon flos-aquae*; (H) "*Anabaena oscillarioides*" (non planktic types); (I) cluster of *Aphanizomenon issatschenkoi = Cuspidothrix.* The rest of all planktic Anabaenas is also heterogeneous in certain degree, but the morphological features are mostly transient. Their taxonomic classification will be corrected and modified by further studies on basis of *Dolichospermum*.

- Gas vesicles occur obligatorily in cells in vegetative phase. They are joined into irregular aerotopes (sooner "gas vesicles") over the whole cell volume; aerotopes are recognizable in cells under optical microscope.
- Heterocytes arise intercalarly, solitary (exceptionally in pairs); they develop from vegetative cells in ± metameric position.
- Akinetes develop paraheterocytically, it means connected with heterocytes, rarely aside heterocytes from both sides or (more commonly) separated from them by several cells, solitary up to 5(6) in a row. They develop successively in the direction from heterocytes and often arise after fusion of two or few neighbouring vegetative cells. The ripe akinetes are usually three or more-times larger than vegetative cells.
- All species (morphotypes) are planktic in vegetative state, never form sessile mats on the substrate. The filaments live solitary or in small clusters.

Autapomorphic characteristics: Filaments living isolated or in free clusters; metameric structure of trichomes with heterocytes developing solitary; obligatory gas vesicles in vegetative cells; akinetes develop paraheterocytically.

List of species:

- *Dolichospermum affinis* (Lemmermann) comb. nova – basionym: *Anabaena affinis* Lemmermann, Abh. Naturw. Ver. Bremen 14: 261, 1897.
- *Dolichospermum akankoensis* (M. Watanabe) comb. nova – basionym: *Anabaena akankoensis* M. Watanabe, Bull. Natn. Sci. Mus.,Tokyo, Ser. B, 29: 9–13, 2003.
- *Dolichospermum arcticum* (Kiselev) comb. nova - basionym: *Anabaena arctica* Kiselev, Gosud. Hidrol. Inst., Issled. Morej SSSR 15: 98, 1932.
- *Dolichospermum bituri* (Cronberg et Komárek) comb. nova – basionym: *Anabaena bituri* Cronberg et Komárek, Nova Hedwigia 78: 75, 2004.
- *Dolichospermum berezowskii* (Usačev) comb. nova – basionym: *Anabaena berezowskii* Usačev, Tr. Sibir. Naučn. Ribochoz. Stan. Krasnojarsk 3(2): 32, 1928.
- *Dolichospermum bothai* (Welsh) comb. nova – basionym: *Anabaena bothai* Welsh, Rev. de Biol. 2(3/4): 259–260, 1961
- *Dolichospermum caspicum* (Ostenfeld) comb. nova – basionym: *Anabaena caspica* Ostenfeld, Vidensk. Medd. Naturh. Fören. Kjøbenhavn 1901: 138, 1902.
- *Dolichospermum circinalis* (Rabenhorst ex Bornet et Flahault) comb. nova – basionym: *Anabaena circinalis* Rabenhorst ex Bornet et Flahault, Ann. Sci. Nat. 7, Bot 7: 230, 1888.
- *Dolichospermum citrisporum* (M. Watanabe) comb. nova – basionym: *Anabaena citrispora* M. Watanabe, Bull. Nat. Sci. Mus., ser. B, 18(4): 124–126, 1992.
- *Dolichospermum compactum* (Nygaard) comb. nova – basionym: *Anabaena spiroides* var. *minima* f. *compacta* Nygaard Kong. Danske Vidensk. Selsk., Biol. Skr. 7(1): 205, 1949 [syn.: *Anabaena compacta* (Nygaard) Hickel, Algological Studies 38/39: 269, 1985].
- *Dolichospermum crassum* (Lemmermann) comb. nova – basionym: *Anabaena spiroides* var. *crassa* Lemmermann Bot. Centralbl. 76(5-6): 155, 1898 [syn.: *Anabaena crassa* (Lemmermann) Komárková-Legnerová et Cronberg, Algolog. Stud. 67: 24–25, 1992].
- *Dolichospermum curvum* (Hill) comb. nova – basionym: *Anabaena curva* Hill, Phycologia 15(1): 62, 1976.
- *Dolichospermum danicum* (Nygaard) comb. nova – basionym: *Anabaena viguieri* var. *danica* Nygaard, Kong. Danske Vidensk. Selsk., Biol. Skr. 7(1): 212, 1949 [syn.: *Anabaena danica* (Nygaard) Komárková–Legnerová et Eloranta, Algolog. Stud. 67: 112, 1992].
- *Dolichospermum delicatulum* (Lemmermann) comb. nova – basionym: *Anabaena delicatula* Lemmermann, Bot. Centralbl. 70: 155, 1898
- *Dolichospermum ellipsoides* (Bolochoncev ex Voronichin) comb. nova – basionym: *Anabaena ellipsoides* Bolochoncev ex Voronichin, Tr. Bot. Sada AN SSSR 44: 221, 1931.
- *Dolichospermum fallax* (Komárek et Komárková-Legnerová) comb. nova – basionym: *Anabaena fallax* Komárek et Komárková-Legnerová, Preslia 74: 223. 2002.
- *Dolichospermum farciminiformis* (Cronberg et Komárková-Legnerová) comb. nova – basionym: *Anabaena farciminiformis* Cronberg et Komárková-Legnerová, Algolog. Stud. 50–53: 278, 1988.
- *Dolichospermum fusca* (Hill) comb. nova – basionym: *Anabaena fusca* Hill, Phycologia 15(1): 70, 1976.
- *Dolichospermum halbfassii* (Bachmann) comb. nova – basionym: *Anabaena halbfassii* Bachmann, Ber. Dtsch. Bot. Ges. 31: 187, 1913.
- *Dolichospermum helicoideum* (Bernard) comb. nova – basionym: *Anabaena helicoidea* Bernard, Protococc. & Desmid. d'Eau Douce, p. 52, 1908.
- *Dolichospermum heterosporum* (Nygaard) comb.

nova – basionym: *Anabaena heterospora* Nygaard, Kong. Danske Vidensk. Selsk., Biol. Skr., 7(1): 195, 1949.

- *Dolichospermum jacuticum* (Kiselev) comb. nova – basionym: *Anabaena jacutica* Kiselev, Gosud. Hidrol. Inst., Issled. Morej SSSR 15: 100, 1932.
- *Dolichospermum lemmermannii* (Richter in Lemmermann) comb. nova – basionym: *Anabaena lemmermannii* Richter in Lemmermann, Forschungsber. Biol. Stat. Plön 10: 153, 1903.
- *Dolichospermum longicellularis* (Pankow) comb. nova – basionym: *Anabaena spiroides* var. *longicellularis* Pankow, Limnologova, Berlin, 3(2): 163–172, 1965 [Syn.: *Anabaena longicellularis* (Pankow) Komárková-Legnerová et Eloranta, Algolog. Stud. 67: 125, 1992].
- *Dolichospermum macrosporum* (Klebahn) comb. nova – basionym: *Anabaena macrospora* Klebahn, Flora 80: 269, 1895.
- *Dolichospermum maximum* (Cronberg et Komárek) comb. nova – basionym: *Anabaena maxima* Cronberg et Komárek, Nova Hedwigia 78(1/2): 77, 2004.
- *Dolichospermum mendotae* (Trelease) comb. nova – basionym: *Anabaena mendotae* Trelease, Trans. Wisconsin Acad. Sci. 7: 123, 1889.
- *Dolichospermum mucosum* (Komárková-Legnerová et Eloranta) comb. nova – basionym: *Anabaena mucosa* Komárková-Legnerová et Eloranta, Algolog. Stud. 67: 125–126, 1992.
- *Dolichospermum nathii* (Vasishta) comb. nova – basionym: *Anabaena nathii* Vasishta, Res. Bull. (N.S.) Panjab Univ., 11(I–II): 67, 1960.
- *Dolichospermum nygaardii* (Cronberg et Komárek) comb. nova – basionym: *Anabaena nygaardii* Cronberg et Komárek, Nova Hedwigia 78: 77–78, 2004.
- *Dolichospermum perturbatum* (Hill) comb. nova – basionym: *Anabaena perturbata* Hill, Phycologia 15(1): 67, 1976.
- *Dolichospermum planctonicum* (Brunnthaler) comb. nova – basionym: *Anabaena planctonica* Brunnthaler, Sitzungsb. K. Akad. Wiss. Wien, mat.–nat., 103(1): 4, 1903
- *Dolichospermum pseudocompactum* (M. Watanabe) comb. nova – basionym: *Anabaena pseudocompacta* M. Watanabe, Bull. Nat. Sci. Museum, Ser. B, 22(3): 94, 1996.
- *Dolichospermum sigmoideum* (Nygaard) comb. nova – basionym: *Anabaena sigmoidea* Nygaard, Kong. Danske Vidensk. Selsk. Biol. Skr. 7(1): 199, 1949.
- *Dolichospermum skujae-laxum* (Komárek et Zapomělová) comb. nova – basionym: *Anabaena skujae-laxa* Komárek et Zapomělová, Fottea 7(1): 27, 2007 [syn.: *Anabaena flos-aquae* var. *laxa* Skuja, N. Acta R. Soc. Sci. Upsal., Ser. 4, 16(3): 78, 1956].
- *Dolichospermum smithii* (Komárek) comb. nova – basionym: *Anabaena solitaria* f. *smithii* Komárek, Algolog. Studien p. 129, 1958 [*Anabaena smithii* (Komárek) M. Watanabe, Bull. Nat. Sci. Mus., ser. B, 18(4): 131, 1992].
- *Dolichospermum solitarium* (Klebahn) comb. nova – basionym: *Anabaena solitaria* Klebahn, Flora 80: 270, 1895.
- *Dolichospermum spiroides* (Klebahn) comb. nova – basionym: *Anabaena spiroides* Klebahn, Flora – allg. bot. Ztg. 1895: 268, 1895.
- *Dolichospermum torques-reginae* (Komárek) comb. nova – basionym: *Anabaena torques-reginae* Komárek, Acta Bot. Cubana 19: 14–16, 1984.
- *Dolichospermum viguieri* (Denis et Frémy) comb. nova – basionym: *Anabaena viguieri* Denis et Frémy, Bull. Soc. Linn. Normandie, Ser. 7, 6: 122, 1924.
- *Dolichospermum werneri* (Brunnthaler) comb. nova – basionym: *Anabaena werneri* Brunnthaler, Sitzungsb. K. Akad. Wiss. Wien, mat.–nat., 112(1): 292, 1903.
- *Dolichospermum zinserlingii* (Kosinskaja) comb. nova – basionym: *Anabaena zinserlingii* Kosinskaja, Russ. Arch. Protistol. 8(3/4): 245, 248, 1929.

Discussion

This article does not solve the taxonomy of different *Dolichospermum* species. All up to now described species which evidently belong into the "planktic *Anabaena*-cluster" according to position in phylogenetic tree (lit. cit.), and/or which correspond morphologically to this characteristical "*Anabaena*" morphotype with gas vesicles in cells are transferred into the genus *Dolichospermum*. The listed characteristic morphospecies were taxonomically described by phenotype taxonomy, they are usually well recognizable in natural samples and occur repeatedly in nature. They are all therefore transferred into a new revised genus *Dolichospermum*.

It is known that particularly the traditional *Dolichospermum* morphospecies with coiled trichomes described from nature (for review see in Komárek & Zapomělová 2007, 2008) change drastically in cultures (Zapomělová et al. 2008; in press). The questions concerning molecular and phenotype variability need therefore further studies. The relationships between different species are not yet definitely solved, but the separation of a special genus is justified and all up to date corresponding and validly described planktic *Anabaena*-species should be transferred into this genetic entity.

Different subclusters of the traditional genus *Aphanizomenon* (cf. Gugger et al. 2002b, Rajaniemi et al. 2005a; Fig. 1) also belong into the large planktic cluster with *Dolichospermum*-strains. From this point of view, also the planktic *Anabaena* (= *Dolichospermum*) cluster is not monophyletic.

Stable morphological markers of *Aphanizomenon* are unique and distinct in such a degree that its generic separation from *Dolichospermum* is justifiable. *Aphanizomenon* itself is also surely heterogeneous (Li et al. 2002, 2003, Rajaniemi et al. 2005a,b, Willame et al. 2006) and various *Aphanizomenon*-subclusters are distinguishable in the tree (Fig. 1) as isolated generic clusters. These subclusters differ from each other substantially by smaller percentage of similarity and by important and stable phenotype (autapomorphic) characters (structure of trichomes, morphology of terminal cells, facultative formation of gas vesicles, etc.). They are therefore classified in special generic units (*Aphanizomenon* sensu stricto, *Cuspidothrix*; Rajaniemi et al. 2005b, Komárek & Komárková 2006).

A few strains (morphotypes?), the position of which is very unique (Rajaniemi et al. 2005a: *Anabaena compacta*), or which differ from this cluster by percentage of 16S rRNA gene similarity distinctly lower than 95%, appeared also within the planktic cluster "*Anabaena/ Dolichospermum*". E.g. according to Zapomělová et al. (in press), the strains FM161348 and FM161349 of *Anabaena reniformis* differ from the *Dolichospermum* cluster only by about 92% 16S rRNA gene similarity, and these strains form special group containing also *Anabaena kisseleviana* and *Anabaena aphanizomenoides* (strain FM161350). The phenotype difference from other *Dolichospermum* species (form and position of akinetes in trichomes, morphology of end cells) is not doubtless, but it is separated in such a degree that the taxonomic classification in a special genus *Sphaerospermum* is proposed (Zapomělová et al. , in press). However, the final taxonomic position of several other types of "planktic Anabaenas" is still unsolved, but this our paper should be the basis for next studies.

The proposed limit for separation of different cyanobacterial genera is 95% of 16S rRNA gene similarity (Wayne et al. 1987, Stackebrand & Goebel 1994). This limit cannot be applied obligatorily. In nature sharp numerical limits (even correctly calculated) never exist, and also in this case the percentage of 16S rRNA gene similarity can serve only as one of important criteria, which can be (and should be) applied in complex in connection with other valuable genetically important and stable characters. However the autapomorphic phenotypic marker should also be applied in generic descriptions. The combined, special type of metameric structure of solitary floating trichomes, with paraheterocytic formation of akinetes and obligatory presence of gas vesicles in cells represents there special characters in *Dolichospermum*.

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