

REVIEW

**Planktic morphospecies of the cyanobacterial genus *Anabaena*
= subg. *Dolichospermum* – 1. part: coiled types.**Jiří KOMÁREK^{1,3} & Eliška ZAPOMĚLOVÁ^{2,3}¹ Institute of Botany, Academy of Science of the Czech Republic, Dukelská 135, CZ-37982 Třeboň, Czech Republic² Institute of Hydrobiology, Academy of Science of the Czech Republic, Na sádkách 7, CZ-37005 České Budějovice, Czech Republic³ Faculty of Biological Science, University of South Bohemia, Branišovská 31, CZ-37005 České Budějovice, Czech Republic

Abstract: The traditional cyanobacterial genus *Anabaena* contains several groups of morphospecies, which should be classified in different genera according to modern phenotypic and molecular criteria. The separation into several clusters was confirmed by 16S rRNA sequencing. The generic name *Anabaena* must be maintained for the benthic species without gas vesicles, the type species of which is *Anabaena oscillarioides*. The planktic types are divided also in several subclusters; one of them can be provisionally designated as subg. *Dolichospermum* THW. ex WITTR. et NORDST. 1889 with the type species *Anabaena flos-aquae* [LYNGB.] BRÉB. ex BORN. et FLAHL. 1888. The taxonomy of this cluster, which contains types with coiled as well as straight filaments, is not yet satisfactorily solved. The interspecific features are particularly problematic. However, the review of stable coiled morphotypes from the subg. *Dolichospermum* which are known and repeatedly occur in natural populations, is presented in this article. This review should help to the orientation of phenotype diversity of coiled *Dolichospermum*-types, especially in populations occurring in natural habitats.

Key words: Cyanobacteria, *Anabaena*, *Dolichospermum*, taxonomy, identification, morphology, variability, morphospecies, phytoplankton, coiled trichomes

Introduction

The traditional cyanobacterial genus *Anabaena* BORY ex BORN. et FLAHL. 1888 contains several morphologically different clusters, which should be classified as separate genera according to modern taxonomic criteria. Separation of planktic from benthic *Anabaena*-species was proved by molecular sequencing (ITEMAN et al. 2002, GUGGER et al. 2002a, RAJANIEMI et al. 2005a, 2005b, HOFFMANN et al. 2005, WILLAME et al. 2006). However, the group of planktic types (with gas vesicles in cells) is also heterogeneous and contains several subclusters, the diversity of which needs further studies on both, molecular and morphological levels. The heterogeneous genus *Aphanizomenon* is related closely to planktic *Anabaena* clusters (i.e., cf. also KOMÁREK & KOMÁRKOVÁ 2006).

A part of typical planktic *Anabaena*-species (subg. *Dolichospermum* THW. ex WITTR. et NORDST. 1889, type species *Anabaena flos-aquae* [LYNGB.] BRÉB. ex BORN. et FLAHL. 1888) contains lot of traditional species characterized by solitary trichomes and by obligatory occurrence of gas vesicles in vegetative cells. These types form populations in nature with straight or differently coiled trichomes. The characteristic morphotypes occur repeatedly in various distant and delimited geographic regions, and therefore they represent a special stable entities, which sometimes differ also by ecological demands. They should be therefore distinguished and classified in the system of cyanobacterial diversity. They are considered traditionally as species, but these different planktic *Anabaena* morphotypes from natural populations were not yet supported by the method of molecular sequencing.

Morphological changes of the *Anabaena* strains were observed many times in cultures. Coiling of trichomes seems to be the particularly unstable morphological feature under culture conditions. Straightening of trichomes or loosening of the trichome coiling occur in the majority of coiled *Anabaena* strains after several years of cultivation. In some strains, it can be even observed during the first months after the isolation from natural population. Long-term cultivation can also cause other serious morphological changes that do not correspond to the situation in natural conditions. Deformation of vegetative cells and akinetes can be noticed and the cell dimensions can be modified. Some strains can lose their ability to form heterocytes, akinetes or gas vesicles. Nevertheless, short-term cultivation is a useful tool how to study the influence of various growth conditions on particular morphological features. The cultivation can also indicate the possible trends of morphological changes in natural populations.

The evaluation of water bloom forming coiled *Anabaena*-species by sequencing of 16S rRNA did not support the taxonomic value of different morphospecies known from nature and described in this article. It is interesting, that only *Anabaena compacta* was classified as an isolated cluster. Another separation appeared more or less between the complex of (both straight and

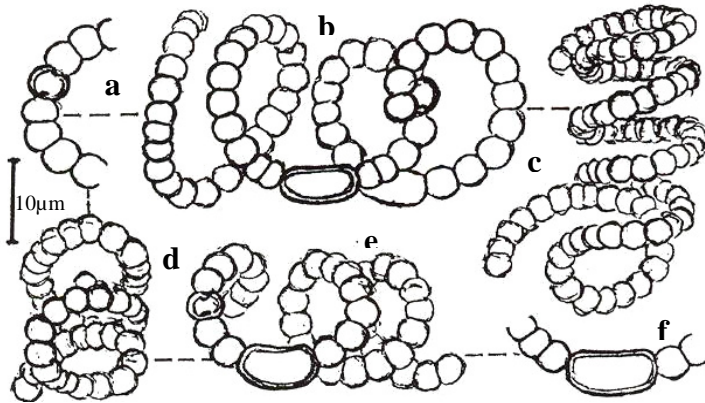
coiled) “large” species (e.g. *A. planctonica* + *A. crassa* + *A. circinalis* + *A. mucosa*, etc.) and “smaller” types (*A. flos-aquae*, *A. lemmermannii*). Strains of *A. sigmoidea* were found also heterogeneous (cf. ITEMANN et al. 2002, GUGGER et al. 2002a, 2002b, RAJANIEMI et al. 2005a, 2005b, WILLAME et al. 2006). What a taxonomic status should be ascribed to different known morphospecies of planktic *Anabaena*, must be solved by future combined molecular and phenotype studies of both strains and natural populations. The satisfactory taxonomic solution depends, therefore, on further studies and on the concept of category ‘species’ in cyanobacterial taxonomy.

We demonstrate the part of the traditional genus *Anabaena* subg. *Dolichospermum* in this article, which summarize the morphological types (species) described from nature. Only the morphospecies occurring in natural populations mostly in coiled trichomes are included. It is known, that the differences between populations with coiled and straight trichomes are not sharp (particularly in cultures), but we hope that our review will be useful for further studies. All morphospecies are divided in two parts, types with spherical and lemon-shaped cells (1–16) and with barrel-shaped and cylindrical cells (17–26).

Results (review of morphospecies)

1. *Anabaena bituri* CRONBERG et KOMÁREK, Nova Hedwigia 78: 75, 2004.

Fig. 1. After CRONBERG & KOMÁREK 2004.



Shape of vegetative cells: **spherical**

Width of trichomes: **3.5–3.8 μm** (diameter of cells)

Shape of akinetes: **kidney-shaped**

Size of akinetes: **9–10 x 4.5–5 μm**

Position of akinetes: **solitary, distant from heterocytes**

Diacritical features:

- type of coiling
- dimensions
- position and form of akinetes

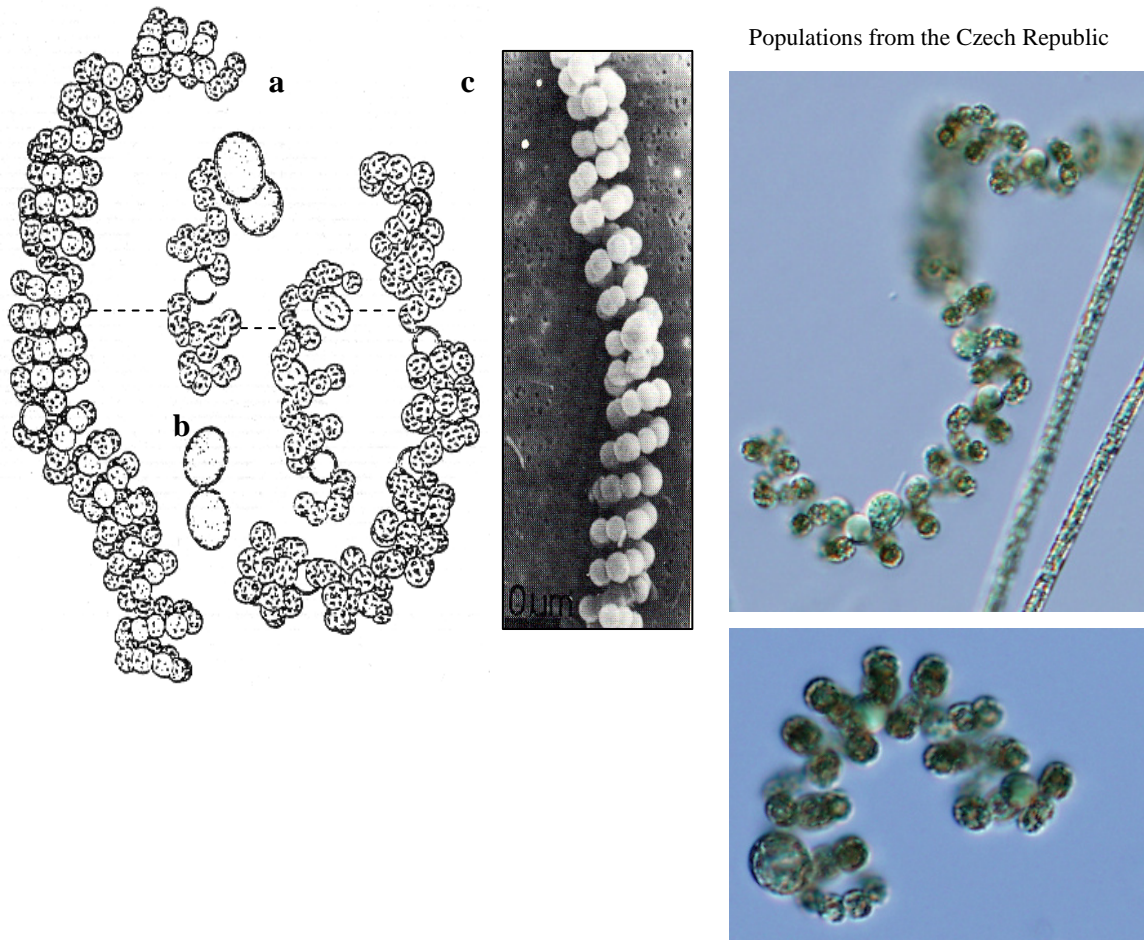
Variability: Not yet studied, little known species.

Distribution: Planktic in water reservoirs; known only from Southern and Central Africa.

2. *Anabaena compacta* (NYGAARD) HICKEL, *Algological Studies* 38/39: 269, 1985.

Synonym: *Anabaena spiroides* var. *minima* f. *compacta* NYGAARD 1949.

Fig. 2. After NYGAARD 1949 and HICKEL 1985.



Shape of vegetative cells: **spherical**
 Width of trichomes: **(3.8)4–5(5.9) µm**
 Shape of akinetes: **widely oval to almost spherical**
 Size of akinetes: **(8.2)8.9–12.5 x (7.0)7.6–11 µm**
 Position of akinetes: **solitary or in pairs,**
distant from heterocytes

Diacritical features:

- typical dense coiling
- dimensions
- shape of akinetes

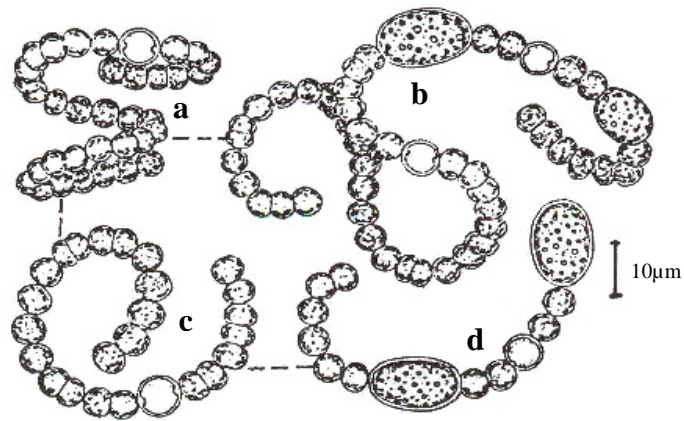
Variability: *A. compacta* was confirmed as a special taxon by 16S rRNA sequencing (RAJANIEMI et al. 2005a). Variability of all morphological features is low when compared various natural populations. Trichomes can loose their coiling up to entirely straight filaments under culture conditions, but other morphological features are not markedly modified.

Distribution: Mesotrophic and eutrophic water-bodies, locally common, mainly northern parts of temperate zone (mostly in Central and Northern Europe).

3. *Anabaena nygaardii* CRONBERG et KOMÁREK, Nova Hedwigia 78: 77-78, 2004.

Synonyms: *Anabaena flos-aquae* var. *intermedia* f. *spiroides* VORONICHIN 1923 sensu NYGAARD 1932; *Anabaena flos-aquae* f. sensu G.S.WEST 1907.

Fig. 3. After NYGAARD 1932 from CRONBERG & KOMÁREK 2004.



Shape of vegetative cells: **spherical**
Width of trichomes: **5.5–6 µm** (diameter of cells)
Shape of akinetes: **oval**
Size of akinetes: **16–16.5 x 10–11 µm**
Position of akinetes: **solitary, distant from heterocytes**

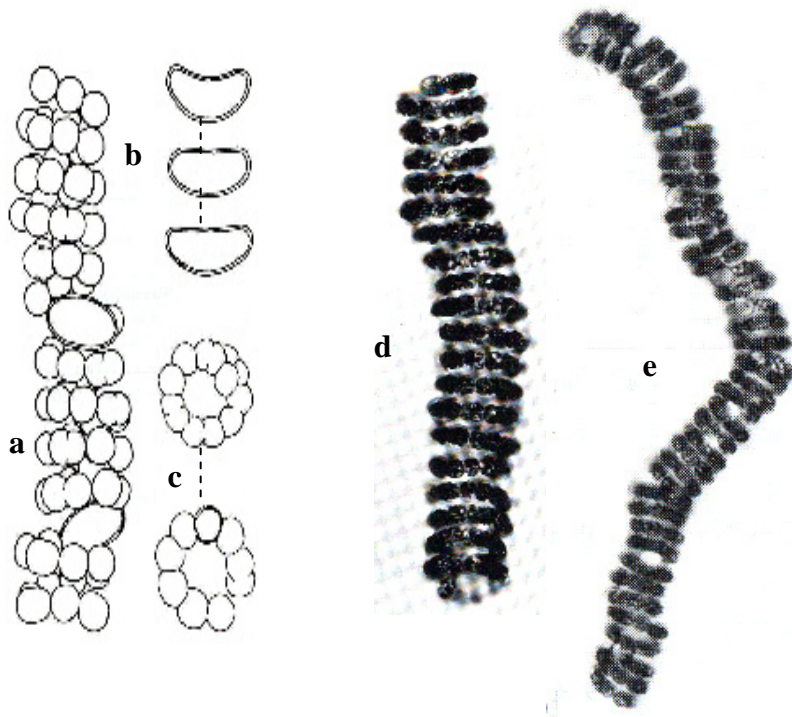
Diacritical features:
- type of coiling
- dimensions
- position and size of akinetes

Variability: Not studied.

Distribution: Known only from plankton of eutrophic water-bodies in tropical Africa.

4. *Anabaena pseudocompacta* M. WATANABE, Bull. Nat. Sci. Museum, Ser. B, 22(3): 94, 1996.

Fig. 4. After M. WATANABE 1996.



Shape of vegetative cells: **spherical**
 Width of trichomes: **5.2–7.0 μm**
 Shape of akinetes: **kidney-shaped**
 Size of akinetes: **16.8–21.3 x 7.5–11.3 μm (1.8–2.6 x l:w)**
 Position of akinetes: **solitary, remote from heterocytes**

Diacritical features:

- coiling
- size of cells
- size and shape of akinetes

Variability: Not studied.

Distribution: Known only from Japanese lakes.

Populations from the Czech Republic

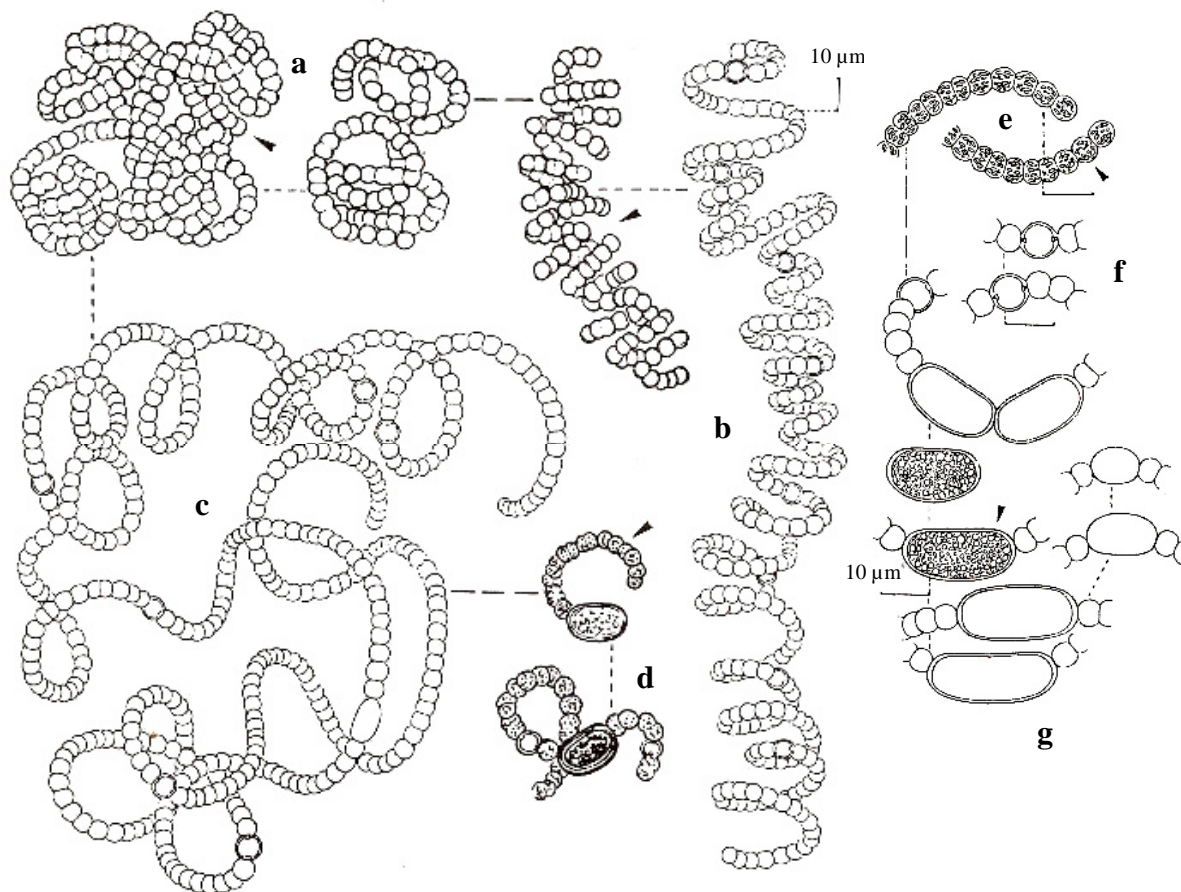
ad *A. flos-aquae* →



5. *Anabaena flos-aquae* (LYNGBYE) BRÉBISON ex BORNET et FLAHAULT, Ann. Sci. Nat. Bot., Ser. 7, 7: 228, 1888.

Synonyms: *Anabaena flos-aquae* f. *typica* ELENKIN 1938; *Anabaena contorta* BACHMANN 1921.

Fig. 5. After KOMÁREK 1958 and KONDRATEVA 1968.



Shape of vegetative cells: **spherical**
 Width of trichomes: **(2.5)4–7(8.3) µm**
 Shape of akinetes: **slightly kidney-shaped to cylindrical**
 Size of akinetes: **(12)15–24(35) x (5)7–12.74(14) µm**
 Position of akinetes: **solitary, rarely in pairs,**
distant (rarely aside) from heterocytes

Diacritical features:

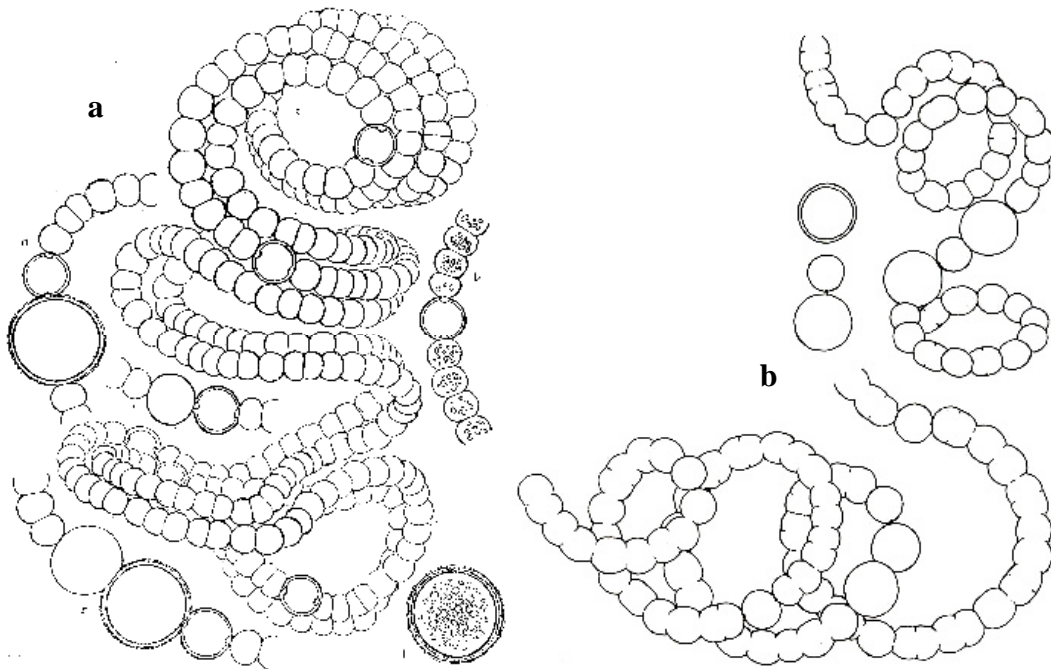
- coiling
- shape of cells
- shape and position of akinetes

Variability: Variability of morphological features is high when compared various natural populations, especially width of vegetative cells and akinete dimensions. The character of trichome coiling is obviously various in different populations. Loosening of trichome coiling and filament straightening can occur under culture conditions. Regularly and irregularly coiled filaments can occur during the cultivation in some strains. Akinete shape and cell dimensions are sometimes modified. Gas vesicles can disappear after a long-term cultivation.

Distribution: Common in eutrophic water reservoirs; considered as cosmopolitan species with exception of subpolar regions; tropical populations are less frequent and their identity with populations in temperate zones should be confirmed; in typical form less frequent in last decades of 20th century up to date.

6. *Anabaena torques-reginae* KOMÁREK, Acta Bot. Cubana 19: 14–16, 1984.Synonym: *Anabaena oumiana* M. WATANABE 1996.

Fig. 6. After KOMÁREK 1984 and M. WATANABE 1996.



Shape of vegetative cells: **spherical or slightly shorter than wide**

Width of trichomes: **5.5–7.6 μm**

Shape of akinetes: **spherical**

Size of akinetes: **10–14.5 μm**

Position of akinetes: **solitary or in pairs, at one or both sides of heterocytes**

Diacritical features:

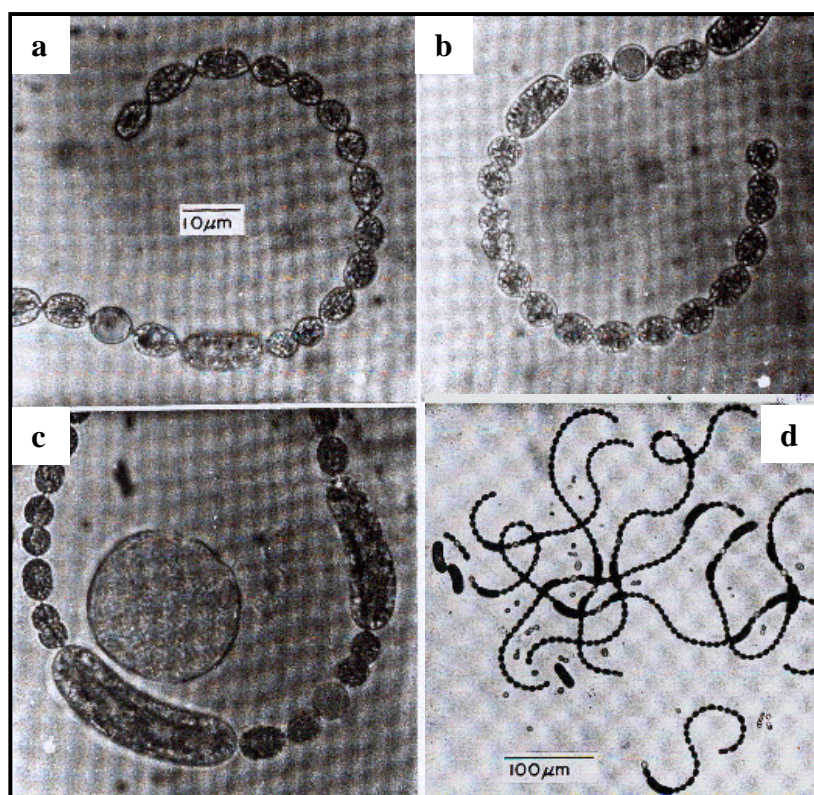
- type of spirality
- shape, position and size of akinetes

Variability: Not studied.

Distribution: Mostly tropical distribution; planktic in eutrophic lakes, known from Central and South America (Cuba, San Salvador, Brazil, Argentine), solitary in Africa (CRONBERG in lit.) and from Japan.

7. *Anabaena fusca* HILL, Phycologia 15(1): 70, 1976.

Fig. 7. After HILL 1976.



Shape of vegetative cells: **lemon-shaped**
Width of trichomes: **5.5–6.5 μm**
Shape of akinetes: ± **cylindrical, slightly arcuated**
Size of akinetes: **(16)26–42(52) x (7.5)8–10(12) μm**
Position of akinetes: **solitary, rarely two in series, near to heterocytes (separated by one or two cells)**

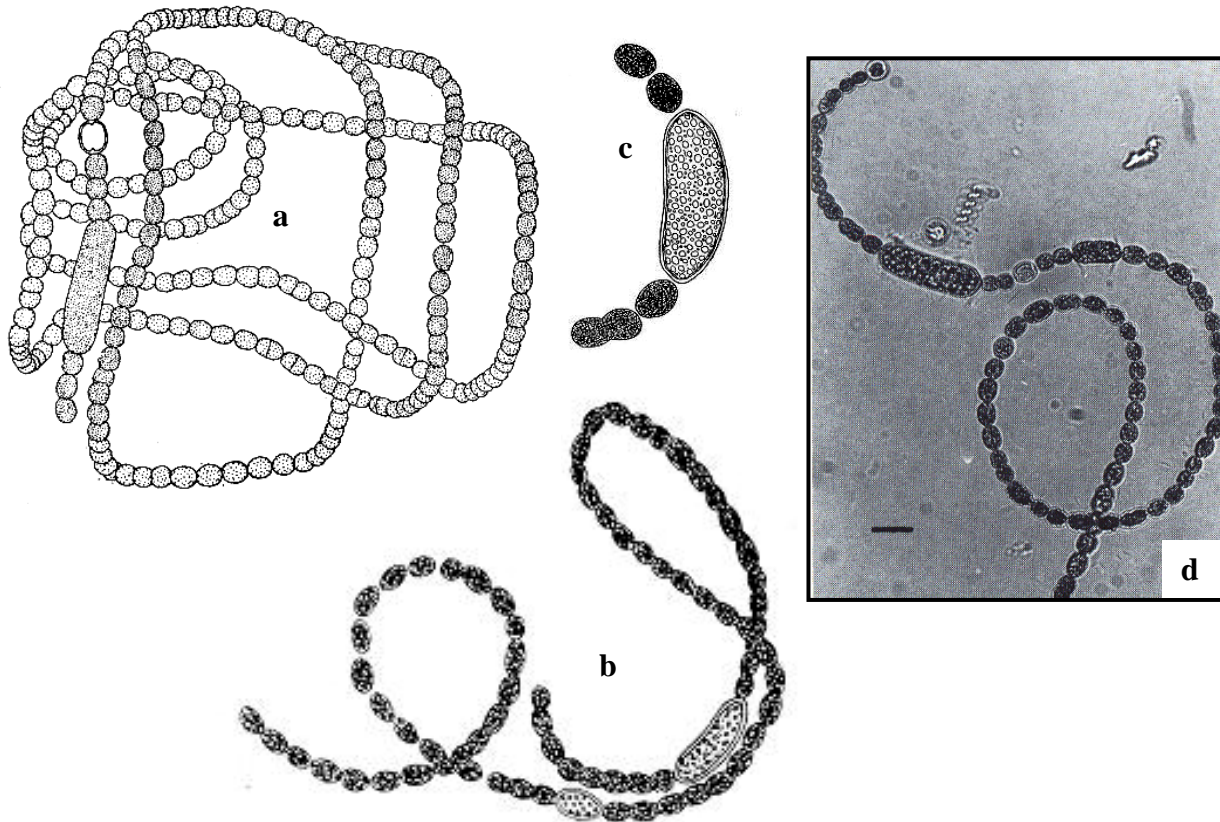
Diacritical features:
- type of coiling
- form of cells
- position, shape and size of akinetes

Variability: Not studied.

Distribution: Known from lakes of North America.

8. *Anabaena ellipsoides* BOLOCHONCEV ex VORONICHIN, Tr. Bot. Sada AN SSSR 44: 221, 1931.Synonym: *Anabaena circinalis* var. *macrospora* (WITTROCK) LEMMERMANN 1904.

Fig. 8. After G.M.SMITH 1920, VORONICHIN from STARMACH 1966 and KOMÁRKOVÁ-LEGNEROVÁ & ELORANTA 1992.

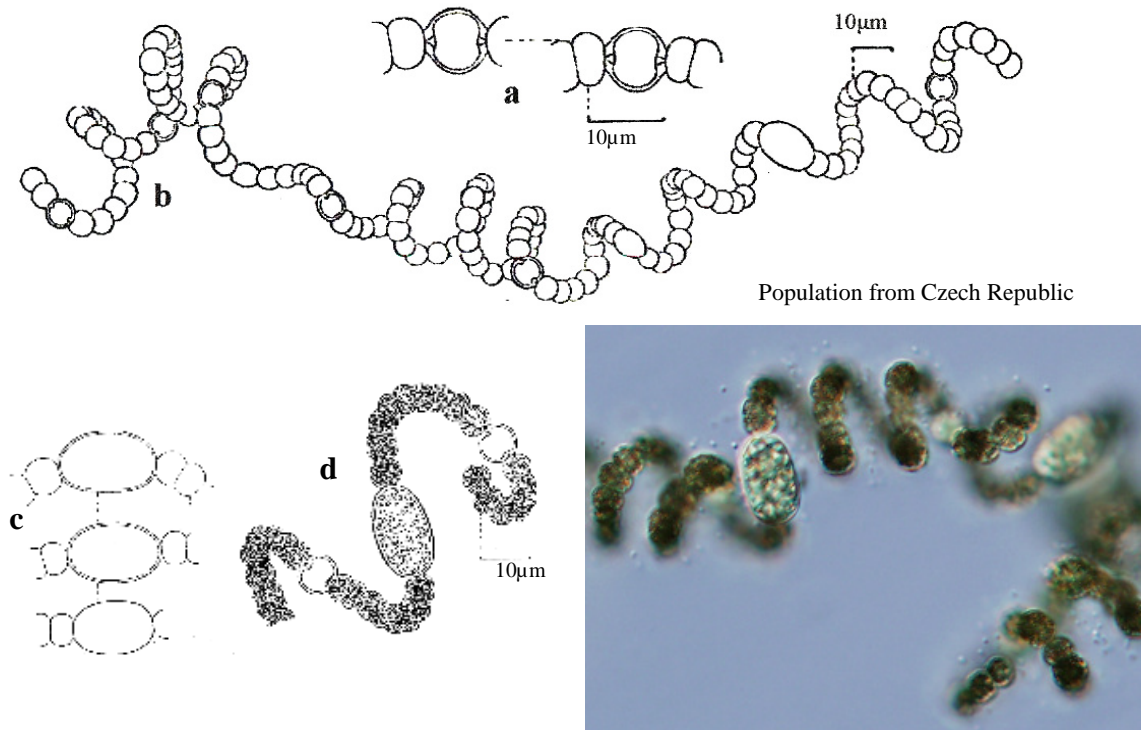
Shape of vegetative cells: **spherical to slightly oval**Width of trichomes: **(5)6.4–8 µm**Shape of akinetes: **cylindrical with rounded ends,
sometimes slightly arcuated**Size of akinetes: **20–42 x (8)9–10.5 µm**Position of akinetes: **solitary, distant from heterocytes****Diacritical features:**

- free irregular coiling
- shape and size of cells
- shape and size of akinetes

Variability: The shape of cells varies probably from spherical to slightly elongated and barrel-shaped.**Distribution:** Stagnant waters, rarely part of water-blooms, known sporadically only from temperate zone.

9. *Anabaena spiroides* KLEBAHN, Flora – allg. bot. Ztg. 1895: 268, 1895.

Fig. 9. After KOMÁREK 1958.



Shape of vegetative cells: **spherical**
 Width of trichomes: **(5.8)6–9(9.3) µm**
 Shape of akinetes: **oval, rarely slightly kidney-shaped**
 Size of akinetes: **15–20.8(22.8) x 9–14 µm**
 Position of akinetes: **solitary, distant from heterocytes**

Diacritical features:

- coiling with slight irregularities
- size of cells
- size and form of akinetes

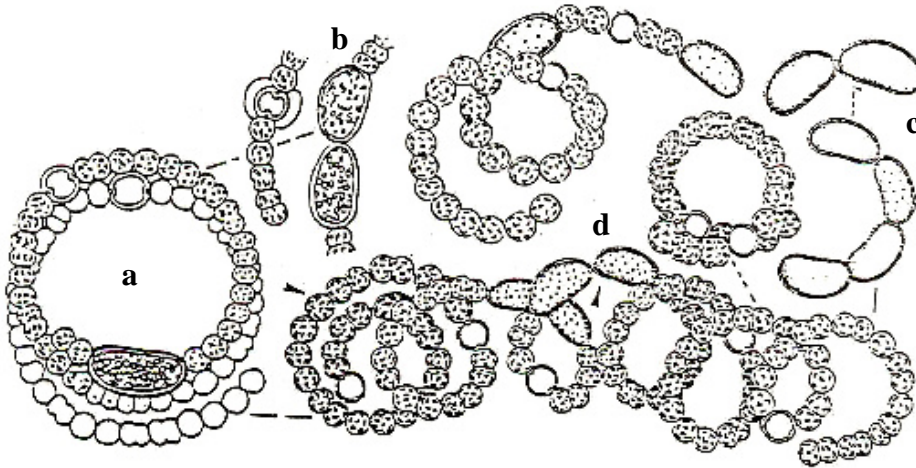
Variability: Regularity of trichome coiling is stable under culture conditions. Between *A. spiroides* and *A. flos-aquae* is not a clear morphological limit.

Distribution: Not common, eutrophic stagnant reservoirs, rarely in large rivers, temperate zones.

10. *Anabaena perturbata* HILL, Phycologia 15(1): 67, 1976.

Synonyms: *Anabaena flos-aquae* f. *aptekariana* ELENKIN 1938; *Anabaena spiroides* f. *tumida* NYGAARD 1949.

Fig. 10. After APTEKAR' ex KONDRATEVA 1968 and NYGAARD 1949.



Shape of vegetative cells: **spherical**
 Width of trichomes: **(6)7–9(10) µm**
 Shape of akinetes: **kidney-shaped**
 Size of akinetes: **(11)13–18(23) x (9.5)11–12(14) µm**
 Position of akinetes: **solitary up to 4 in rows,**
distant from heterocytes

Diacritical features:

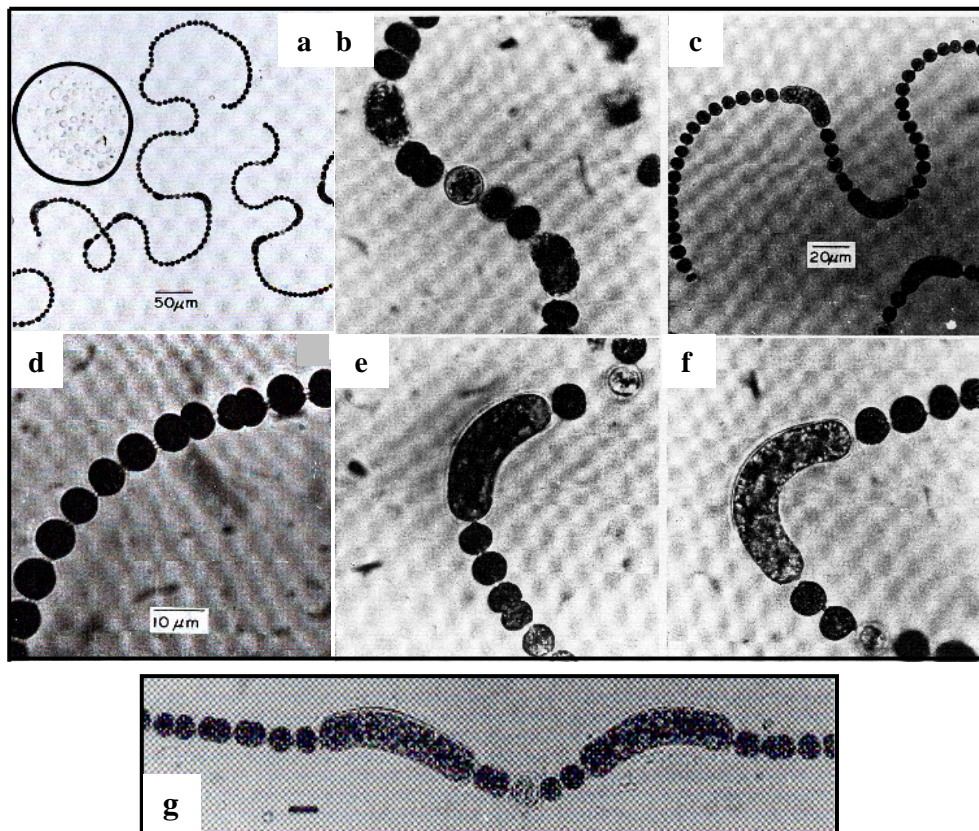
- coiling
- dimensions
- shape and position of akinetes

Variability: The differences from *A. flos-aquae* are not clear, transient forms occur also in nature. In the original HILL's concept are presented wider (ellipsoid) akinetes.

Distribution: Mesotrophic and slightly eutrophic, clear water reservoirs; temperate zones, more frequently in northern areas.

11. *Anabaena curva* HILL, Phycologia 15(1): 62, 1976.

Fig. 11. After HILL 1976 and KOMÁRKOVÁ-LEGNEROVÁ & ELORANTA 1992.



Shape of vegetative cells: **spherical**
 Width of trichomes: **7–9(10) μm**
 Shape of akinetes: **cylindrical, arcuate**
 Size of akinetes: **(26)29–47 x 9.5–11(12) μm**
 Position of akinetes: **slightly distant from heterocytes**

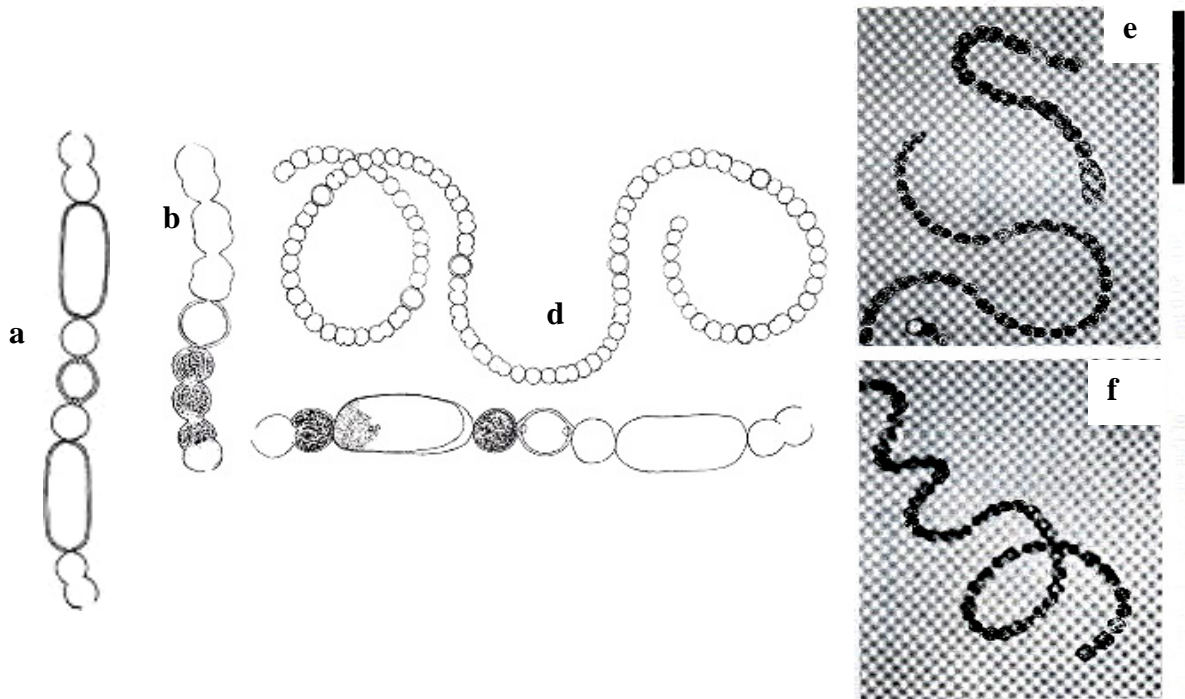
Diacritical features:
 - coiling of trichomes
 - form of cells
 - form and size of akinetes

Variability: Not studied.

Distribution: Known only from plankton of lakes in North America and Northern Europe (Finland).

12. *Anabaena akankoensis* M. WATANABE, Bull. Natn. Sci. Mus., Tokyo, Ser. B, 29: 9–13, 2003.

Fig. 12. After M. WATANABE 2003, M. WATANABE et al. 2004.



Shape of vegetative cells: \pm **spherical to lemon-shaped**
 Width of trichomes: **6.3–8.8(10.5) μm**
 Shape of akinetes: **cylindrical, sometimes slightly bent**
 Size of akinetes: **23.3–42.3 x 10.8–13 μm**
 Position of akinetes: **at both sides of heterocytes, separated by 1–3 cells from heterocytes**

Diacritical features:

- coiling
- shape of cell
- position, size and form of akinetes

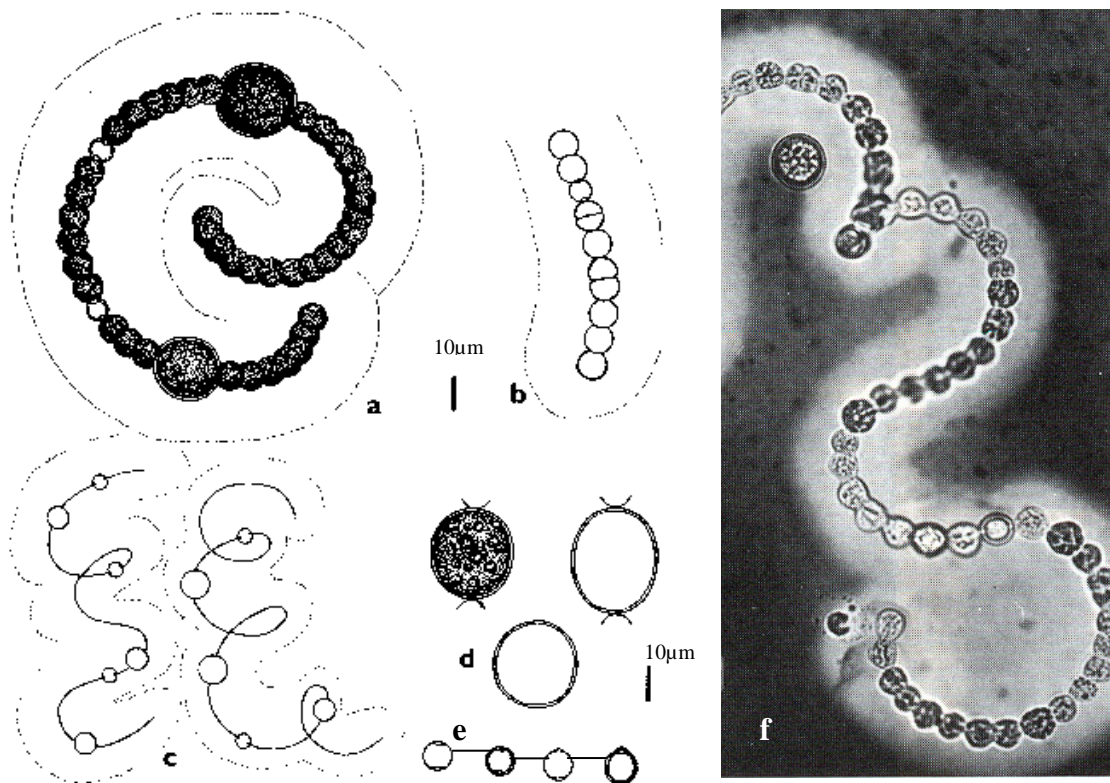
Variability: Not studied. Morphologically related to the straight species *A. solitaria* (differs by coiling).

Distribution: Known only from plankton of eutrophic reservoirs in Japan.

13. *Anabaena mucosa* KOMÁRKOVÁ-LEGNEROVÁ et ELORANTA, Algological Studies 67: 125–126, 1992.

Synonyms: *Anabaena spiroides* f. *ucrainica* (ŠKORBATOV) ELENKIN 1938;
Anabaena ucrainica (ŠKORBATOV) M. WATANABE 1996.

Fig. 13. After KOMÁRKOVÁ-LEGNEROVÁ & ELORANTA 1992.



Shape of vegetative cells: **spherical**
Width of trichomes: **7–10 µm**
Shape of akinetes: **spherical to wide oval**
Size of akinetes: **18–25 µm in diameter**
Position of akinetes: **distant from heterocytes**

Diacritical features:

- irregular coils, 60–200 µm in diameter
- shape, position and dimensions of akinetes
- mucilaginous envelopes around trichomes

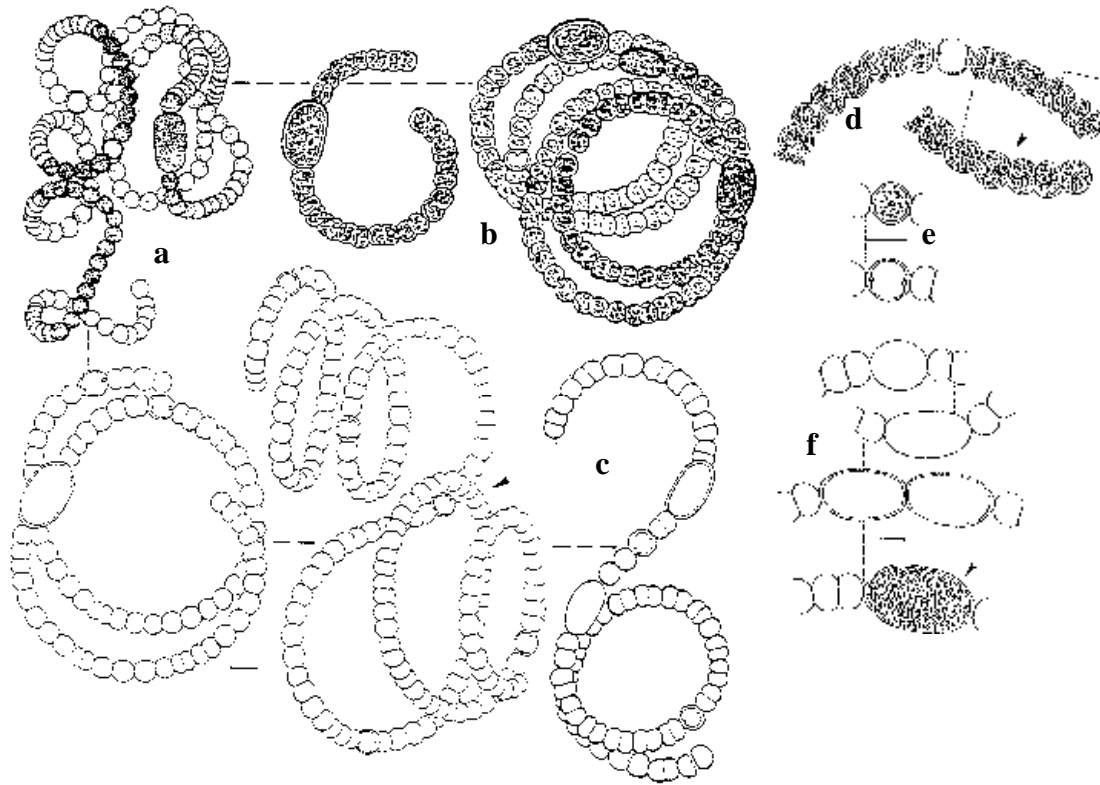
Variability: Not studied.

Distribution: Planktic in lakes, North Europe, Ukraine, Japan.

14. *Anabaena circinalis* RABENHORST ex BORNET et FLAHAULT, Ann. Sci. Nat. 7, Bot 7: 230, 1888.

Synonym: *Anabaena hassallii* WITROCK ex LEMMERMANN 1907.

Fig. 14. After G.M.SMITH 1920, KOMÁREK 1958, KONDRATEVA 1968.



Shape of vegetative cells: **spherical**

Width of trichomes: **(7)8–11 μm**

Shape of akinetes: **oval**

Size of akinetes: **(12.5)20–28(42) x (9)15–21 μm**

Position of akinetes: **solitary, rarely two together, distant from heterocytes**

Diacritical features:

- coiling (spirals 1.4–3.2 : 1; coils 68–120 μm wide)

- form and position of akinetes

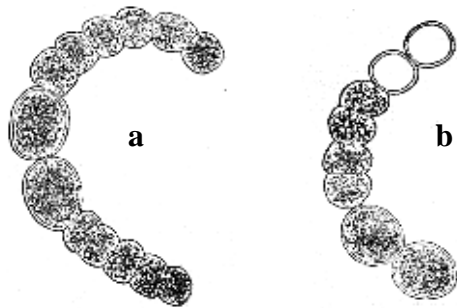
- dimensions

Variability: Loosening of trichome coiling and filament straightening can be often observed under culture conditions. Regularly coiled trichomes are more common but irregularly coiled filaments are also formed during the cultivation. Akinete shape and cell dimensions are sometimes modified. Gas vesicles can disappear in some cells of a trichome after a long-term cultivation. There occur the transient forms between *A. circinalis* and *A. crassa*.

Distribution: Plankton of eutrophic waters, often forming heavy water blooms; cosmopolitan distribution considered with exception of subpolar regions; massive populations known mainly from Central Europe, South America and Australia; genetic identity of populations from mentioned three areas not confirmed.

15. *Anabaena caspica* OSTENFELD, Vidensk. Medd. Naturh. Foren. Kjøbenhavn 1901: 138, 1902.

Fig. 15. After OSTENFELD 1902.



Shape of vegetative cells: **spherical or shortly barrel-shaped**
Width of trichomes: **8–12 μm**
Shape of akinetes: **spherical to widely ellipsoid**
Size of akinetes: **15–17 x 14–15 μm**
Position of akinetes: **solitary or in pairs, distant from heterocytes**

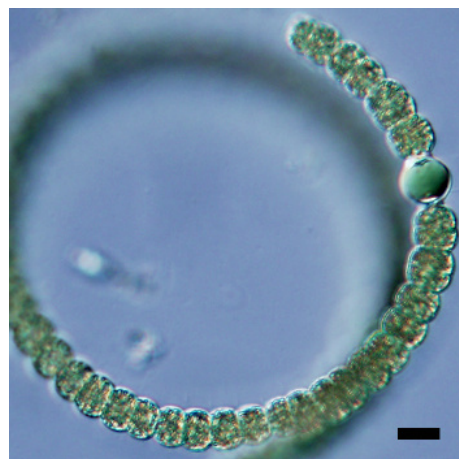
Diacritical features:
- form of trichomes
- dimensions
- position and form of akinetes

Variability: Not studied.

Distribution: Halophilic, known only from Caspian Sea.

← ad *A. circinalis*

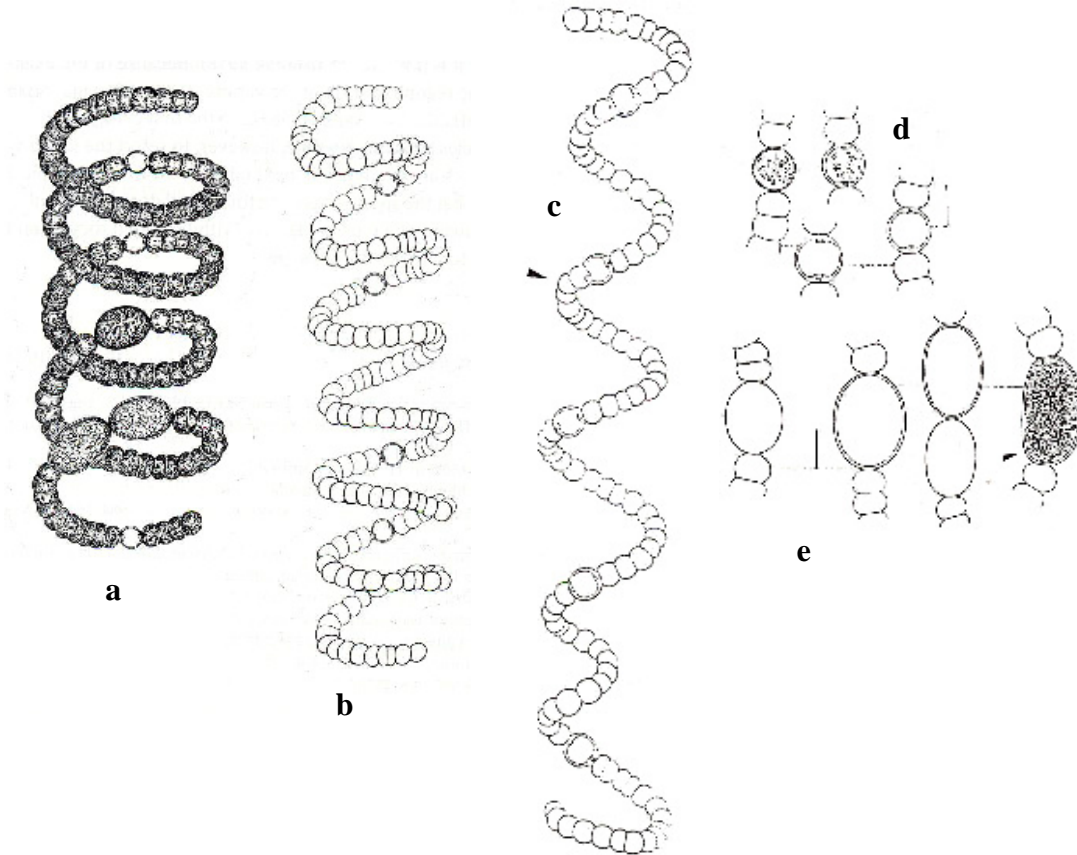
Population from the Czech Republic



16. *Anabaena crassa* (LEMMERMANN) KOMÁRKOVÁ-LEGNEROVÁ et CRONBERG, *Algological Studies* 67: 24–25, 1992.

Synonym: *Anabaena spiroides* var. *crassa* LEMMERMANN 1898.

Fig. 16. After KOMÁRKOVÁ-LEGNEROVÁ & CRONBERG 1992 and KOMÁREK 1958.



Shape of vegetative cells: **spherical to barrel-shaped**

Width of trichomes: **(8)10–15 µm**

Shape of akinetes: **oval, rarely slightly kidney-shaped**

Size of akinetes: **15–42 x 13–25 µm**

Position of akinetes: **solitary or in pairs,
distant from heterocytes**

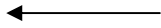
Diacritical features:

- regular coils (spirals 0.5–2 : 1;
40–70 µm wide, 30–55 µm high)
- dimensions
- size and position of akinetes

Variability: Loosening of trichome coiling and filament straightening can be observed under culture conditions. Trichomes are almost always regularly coiled, irregularities in coiling occur rarely during the cultivation. Transient forms occur sometimes between *A. crassa* and *A. circinalis*, both types differ mostly by the type of coiling.

Distribution: Eutrophic waters in temperate zones of both hemispheres, up to subtropical regions.

ad *A. crassa*

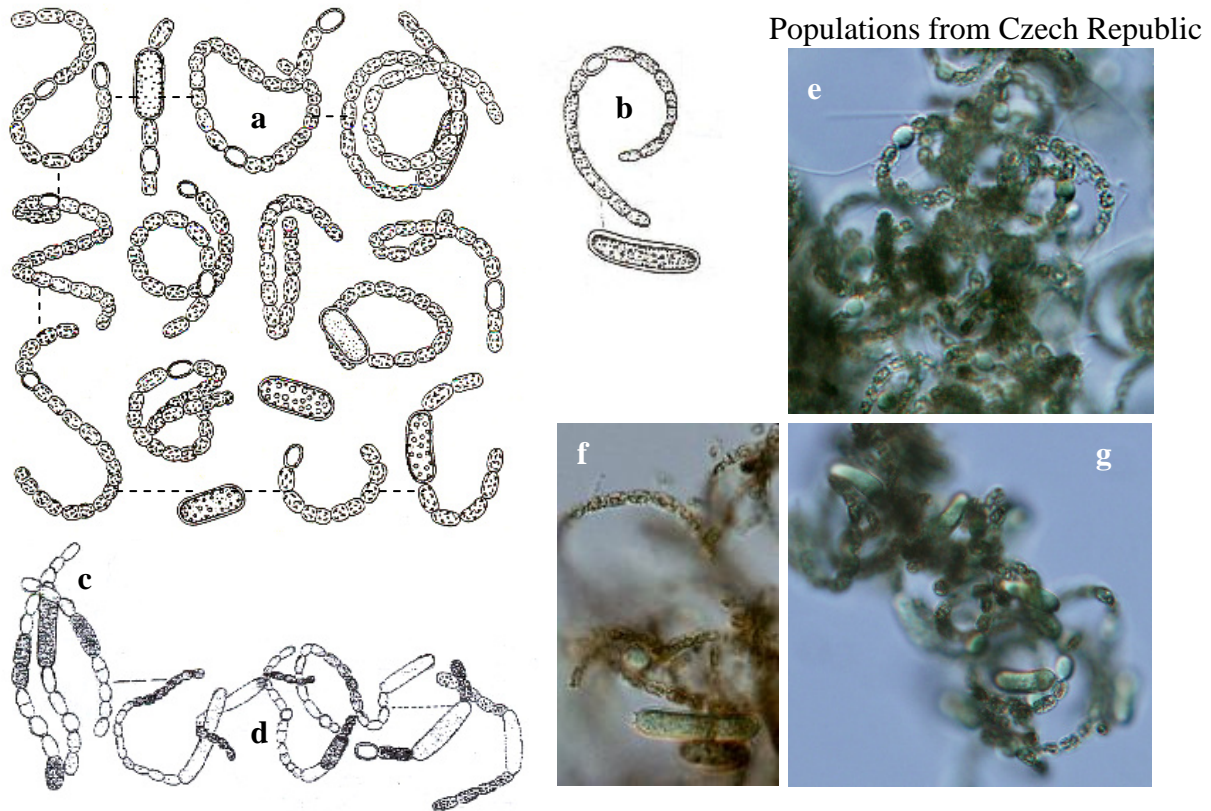


Populations from the Czech Republic



17. *Anabaena sigmoidea* NYGAARD, Kong. Danske Vidensk. Selsk. Biol. Skr. 7(1): 199, 1949.Synonym: *Anabaena circinalis* [KÜTZING] HANSGIRG ex LEMMERMANN 1907.

Fig. 17. After NYGAARD 1949, LEMMERMANN in KONDRATEVA 1968 and G.M. SMITH 1920.

Shape of vegetative cells: **barrel-shaped**Width of trichomes: **(2.5)3–4(5.3) μm** Shape of akinetes: **cylindrical,**
sometimes slightly arcuateSize of akinetes: **(12)16–22.6(27.4?) x (5.7?)6.8–8.5 μm** Position of akinetes: **solitary, distant from heterocytes****Diacritical features:**

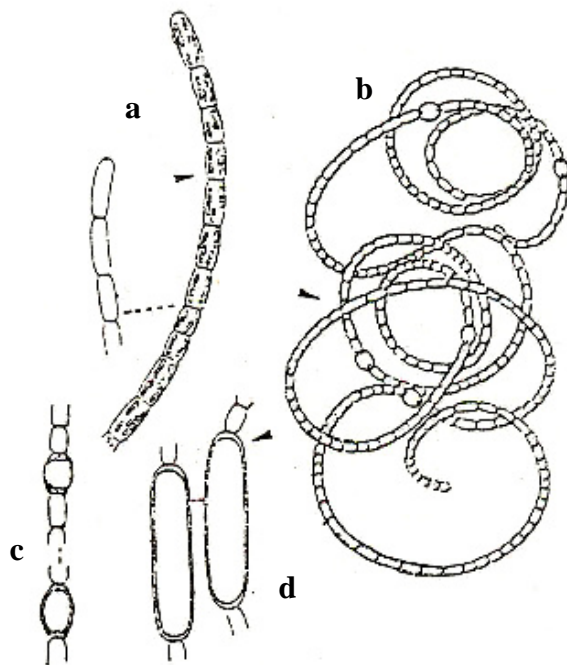
- coiling
- shape and size of cells
- shape, position and size of akinetes

Variability: Variability of morphological features is not very wide when natural populations are compared. Trichomes are usually irregularly coiled, forming clumps of various sizes. Tendency to fragmentation. Loosening of trichome coiling up to entirely straight trichomes can occur under culture conditions. Both regularly and irregularly coiled filaments can be observed in the same strain during the cultivation. Variability of length:width ratio of vegetative cells is high in culture. The diacritical characters are not very clear to *A. mendotae*.

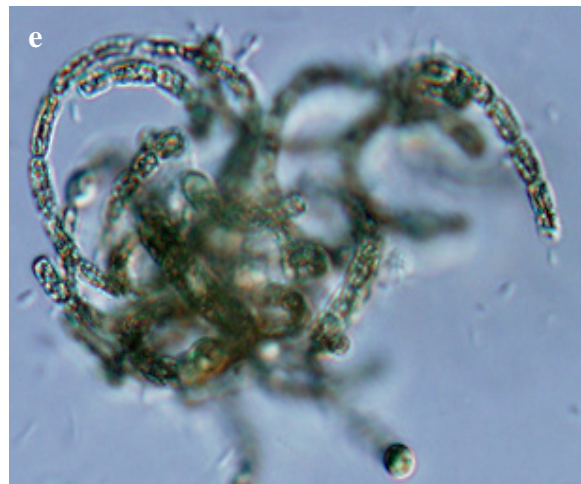
Distribution: Common in water blooms in plankton of eutrophic reservoirs, usually with higher pH; temperate zone particularly in Eurasia.

18. *Anabaena mendotae* TRELEASE, Trans. Wisconsin Acad. Sci. 7: 123, 1889.Synonym: *Anabaena flos-aquae* var. *treleasei* BORNET et FLAHAULT 1888.

Fig. 18. After KOMÁREK 1958.



Populations from the Czech Republic



Shape of vegetative cells: **cylindrical**
 Width of trichomes: **2.5–4.5(5.0?) μm**
 Shape of akinetes: **long, cylindrical**
 Size of akinetes: **(13.5)16–30(45?) x**
(4.5)5.4–7.8(8.5?) μm
 Position of akinetes: **solitary, distant from**
heterocytes

Diacritical features:

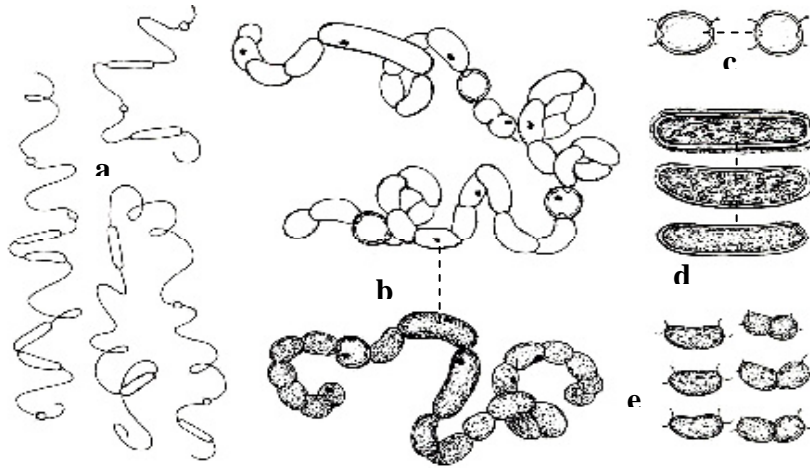
- shape of cells
- shape, size and position of akinetes
- dimensions

Variability: Trichomes usually irregularly coiled, forming free clumps of various sizes. Tendency to fragmentation. Loosening of trichome coiling up to entirely straight trichomes can occur under culture conditions. Both regularly and irregularly coiled filaments can be observed in the same strain during the cultivation. Variability of length:width ratio of vegetative cells is high under culture conditions. Sometimes occur populations with transitions to *A. sigmoidea*.

Distribution: In large lakes and water reservoirs, in the whole temperate zone, not very common.

19. *Anabaena farcimiformis* CRONBERG et KOMÁRKOVÁ-LEGNEROVÁ, *Algological Studies* 50–53: 278, 1988.

Fig. 19. After CRONBERG & KOMÁRKOVÁ-LEGNEROVÁ 1988.



Shape of vegetative cells: **cylindrical** (“sausage-like”)

Width of trichomes: **4.3–5.7 μm**

Shape of akinetes: **cylindrical, slightly arcuated**

Size of akinetes: **22.8–30 x 7.1–8.6 μm**

Position of akinetes: **distant from heterocytes**

Diacritical features:

- form of cells

- form and size of akinetes

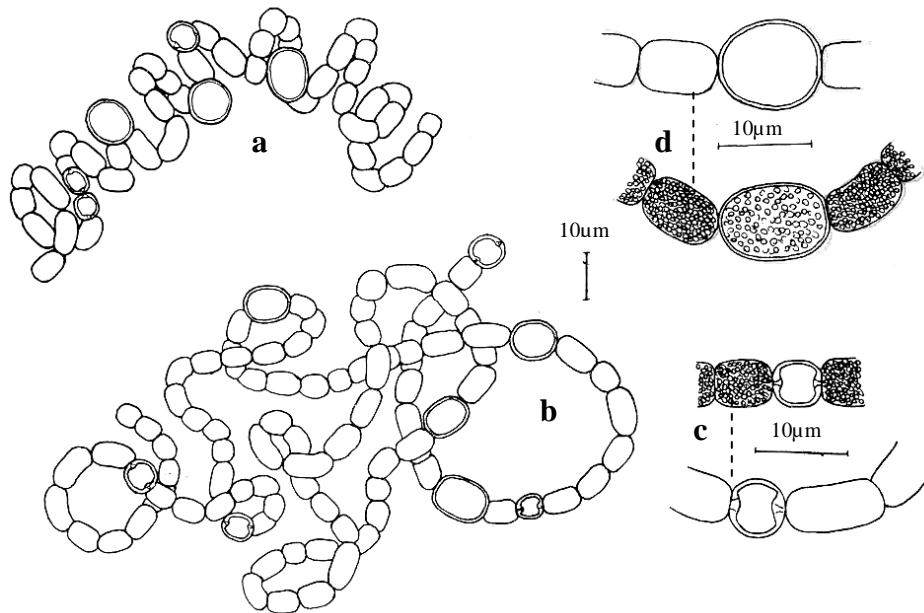
Variability: Not studied.

Distribution: In plankton of small ponds and pools, known only from south Sweden.

20. *Anabaena longicellularis* (PANKOW) KOMÁRKOVÁ-LEGNEROVÁ et ELORANTA, Algological Studies 67: 125, 1992.

Synonym: *Anabaena spiroides* var. *longicellularis* PANKOW 1965.

Fig. 20. After PANKOW 1965.



Shape of vegetative cells: **cylindrical to barrel-shaped**
(l:w = 1–1.5x)

Width of trichomes: **5–6 µm**

Shape of akinetes: **widely oval**

Size of akinetes: **9–12 x 8–11 µm**

Position of akinetes: **distant from heterocytes**

Diacritical features:

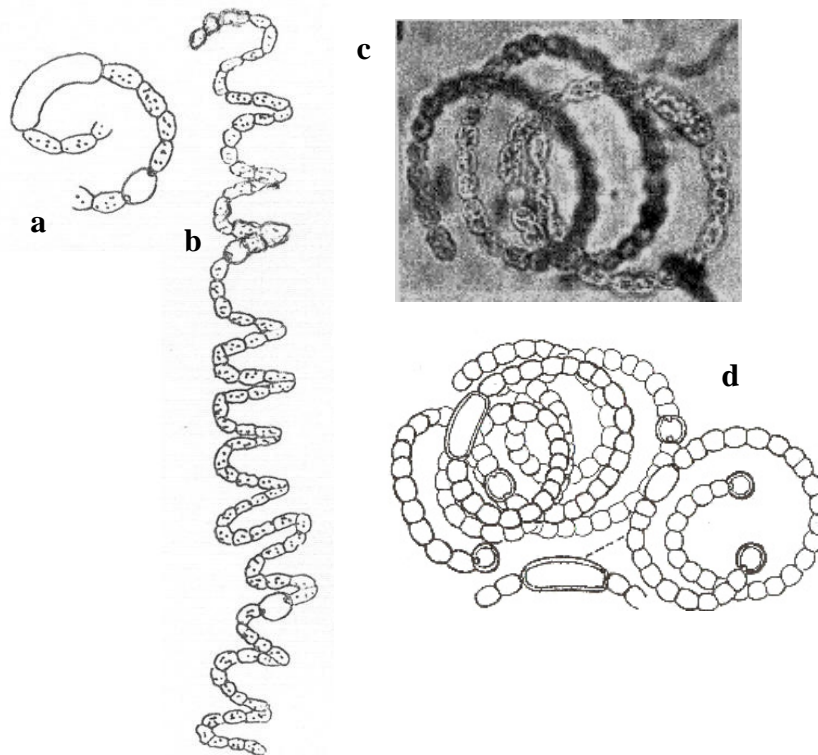
- dimensions
- shape of cells and akinetes

Variability: Not studied.

Distribution: Small eutrophic and slightly saline reservoirs, known from North Poland (delta of Visla river) and Southern Finland.

21. *Anabaena helicoidea* BERNARD, Protococc. & Desmid. d'Eau Douce, p. 52, 1908.Synonym: ?*Anabaena bonariensis* SECKT 1922.

Fig. 21. After BERNARD 1908, WERNER orig., KOMÁREK & KOMÁRKOVÁ-LEGNEROVÁ 2002.



Shape of vegetative cells: **barrel-shaped**
 Width of trichomes: **(3.0)3.5–7.0(7.5) μm**
 Shape of akinetes: **cylindrical, slightly arcuate**
 Size of akinetes: **15.2–25.0 x 5.0–9.5 μm**
 Position of akinetes: **solitary, distant from heterocytes**

Diacritical features:

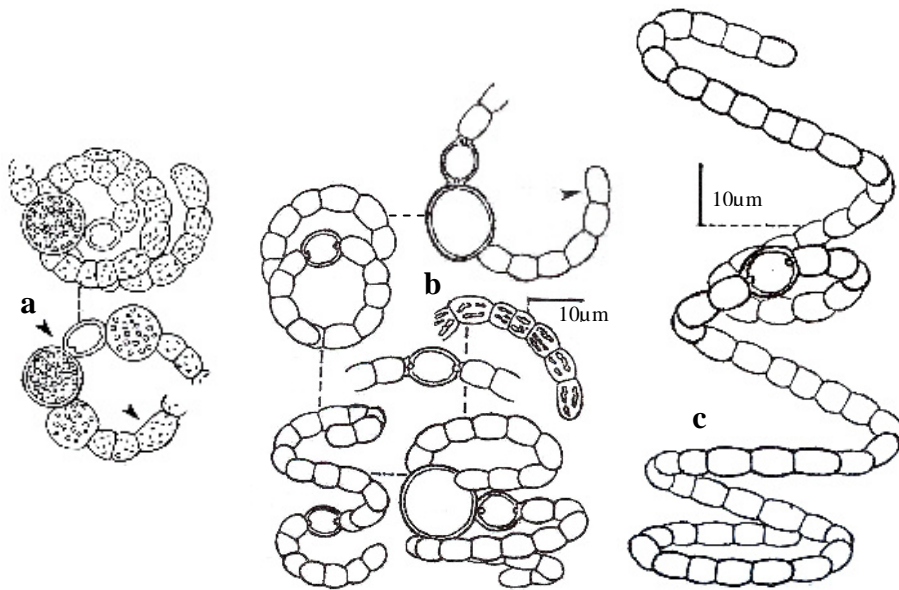
- coiling
- position and shape of akinetes
- dimensions

Variability: Little known tropical species with large variability in the width of trichomes (different types?). Populations, recently designated as *A. helicoidea* differ slightly from the original description by coiling, shape of akinetes and width of trichomes (cf. **a,b** vs. **c,d**).

Distribution: Eutrophic reservoirs, probably pantropic (tropical Asia, South and Central America).

22. *Anabaena reniformis* LEMMERMANN, Bot. Centralbl. 76(5–6): 155, 1898.

Fig. 22. After APTEKAR' 1927 and KOMÁREK 2005.



Shape of vegetative cells: **barrel-shaped**
 Width of trichomes: **(3.2)3.6–5.5 µm**
 Shape of akinetes: **almost spherical**
 Size of akinetes: **8.5–11 µm in diameter**
 Position of akinetes: **from both sides of heterocytes**

Diacritical features:
 - shape and size of cells
 - shape, size and position of akinetes

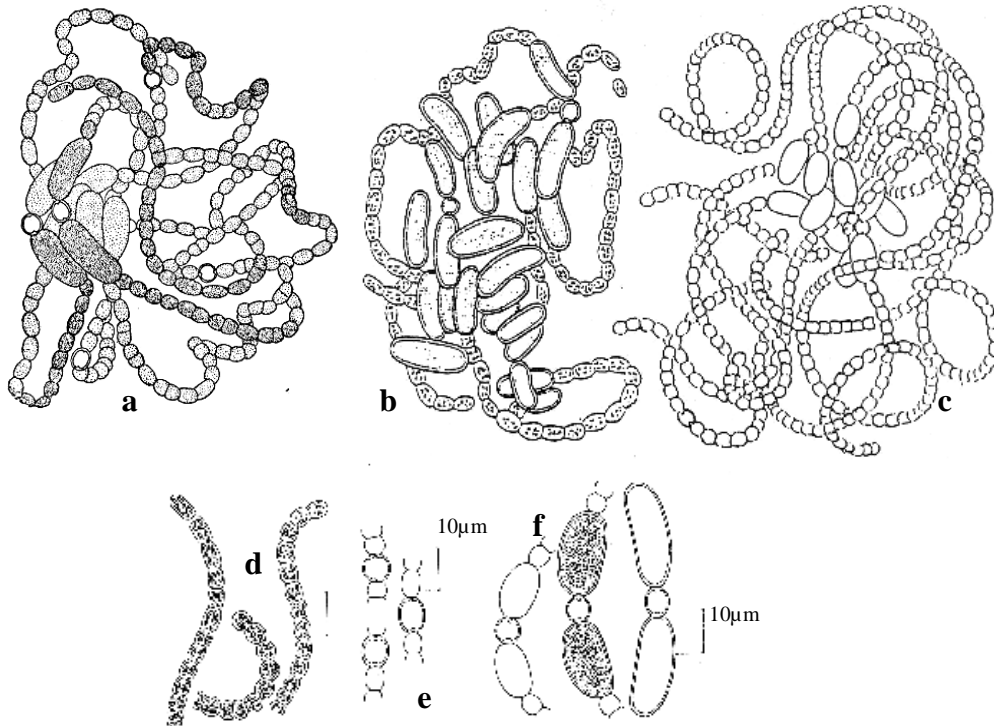
Variability: Not studied.

Distribution: Sporadically in very distant localities (Ukraine, Germany, Cuba, Japan).

23. *Anabaena lemmermannii* RICHTER in LEMMERMANN, Forschungsber. Biol. Stat. Plön 10: 153, 1903.

Synonym: *Anabaena utermoehlii* GEITLER 1925.

Fig. 23. After G.M. SMITH 1920, KOSINSKAJA in KONDRATEVA 1968 and KOMÁREK 1958.



Shape of vegetative cells: **barrel-shaped**

Width of trichomes: **(2.5)4–6.9 µm**

Shape of akinetes: **kidney-shaped**

Size of akinetes: **(13)15–25.6 x (6.3)7.9–11(13.3?) µm**

Position of akinetes: **at both sides of heterocytes;
clusters of aggregated akinetes
at the end of vegetation period**

Diacritical features:

- shape and size of colonies; coiling
- shape of cells
- position and form of akinetes
- life cycle

Variability: Variability of morphological features is wide when various natural populations are compared, especially length, width and length:width ratio of vegetative cells. There were described two varieties/forms according to length of cells which do not differ substantially in ecology (KOMÁRKOVÁ 1988). Trichomes irregularly coiled, forming clumps of various sizes. Akinetes usually occur as big aggregations in the center of clumps together with heterocytes. - Sequencing of 16S rRNA showed that *A. lemmermannii* is diversified at the molecular level (GUGGER et al. 2002a, b). Detailed study both on molecular and morphological level would be necessary to clarify the situation within the morphotype. - Loosening of trichome coiling can be observed under culture conditions. Position of akinetes at both sides of heterocytes is stable.

Distribution: Common in plankton of eutrophic reservoirs in whole temperate zone (distinct water blooms); never found in tropical regions.

24. *Anabaena skujae-laxa* comb. and nomen novum

Synonym (basionym): *Anabaena flos-aquae* var. *laxa* SKUJA, N. Acta R. Soc. Sci. Upsal., Ser. 4, 16(3): 78, 1956.

Fig. 24. After SKUJA 1956.



Shape of vegetative cells: **long barrel-shaped**
Width of trichomes: **5–6 µm**
Shape of akinetes: **cylindrical**
Size of akinetes: **20–35 x 7–9.5 µm**
Position of akinetes: **at both sides of heterocytes**

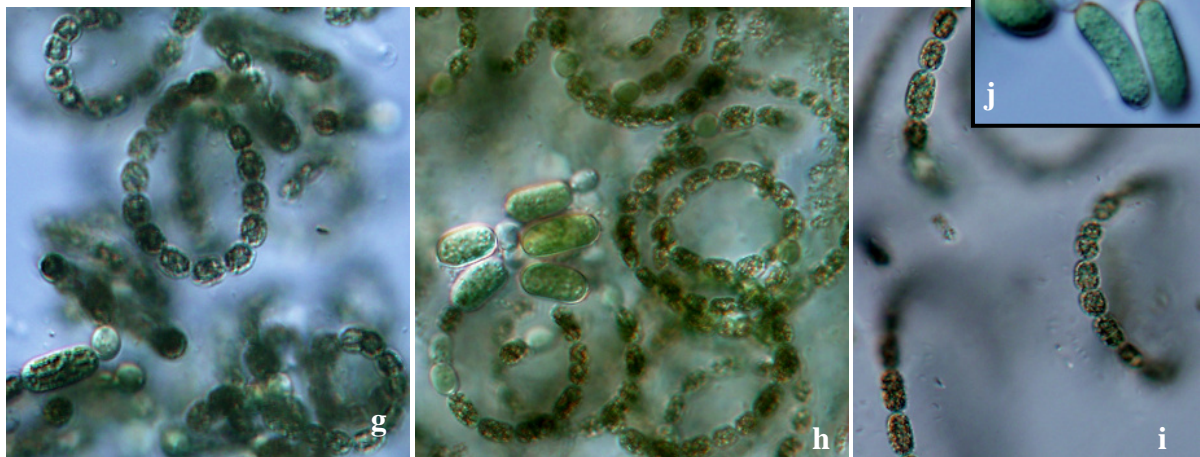
Diacritical features:
- free coiling
- mucilaginous envelopes
- form, size and position of akinetes

Variability: Not studied.

Distribution: Plankton of slightly eutrophized reservoirs, known from northern part of temperate zone in Europe.

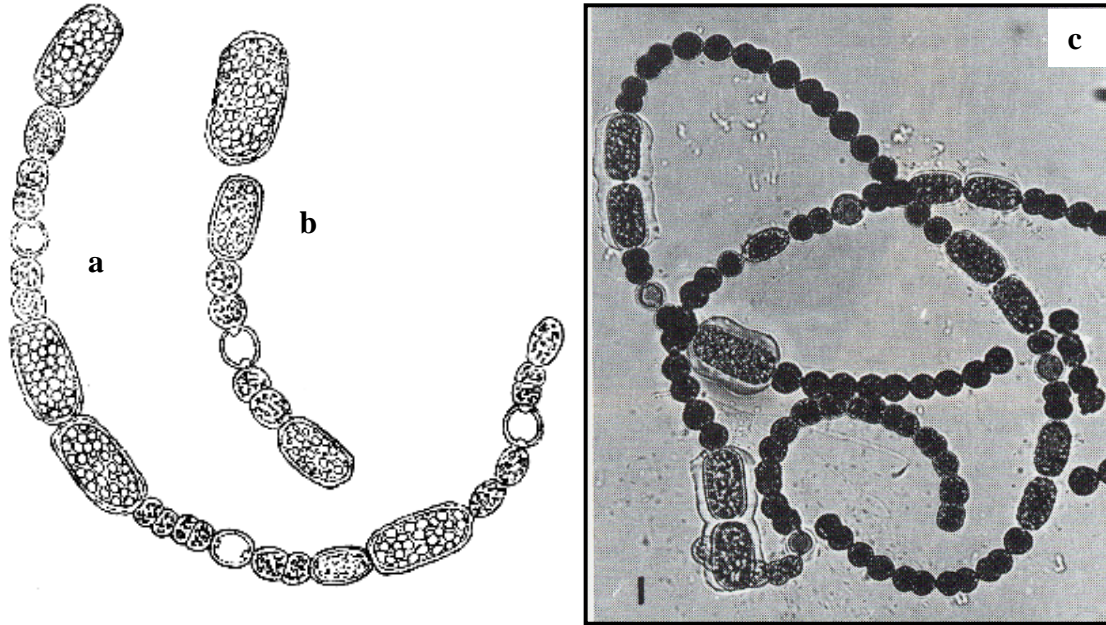
← ad *A. lemmermannii*

Populations from the Czech Republic



25. *Anabaena berezowskii* USAČEV, Tr. Sibir. Naučn. Ribochoz. Stan. Krasnojarsk 3(2): 32, 1928.

Fig. 25. After USAČEV from HOLLERBACH et al. 1953 and KOMÁRKOVÁ-LEGNEROVÁ & ELORANTA 1992.



Shape of vegetative cells: **shortly to elongated barrel shaped**

Width of trichomes: **5–7(10) μm**

Shape of akinetes: **cylindrical with rounded ends**

Size of akinetes: **18–25(30) x 8–12(13) μm**

Position of akinetes: **solitary or two together, distant from heterocytes**

Diacritical features:

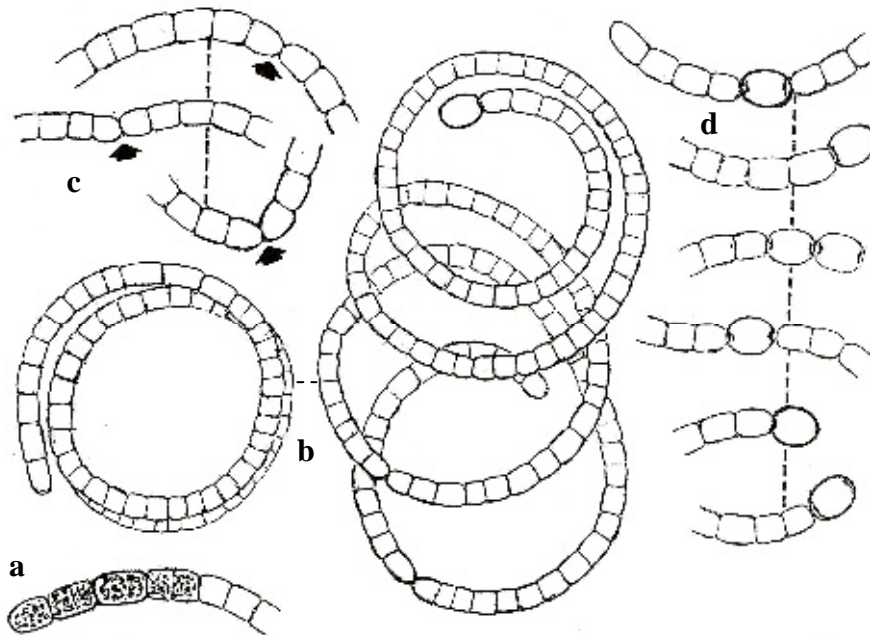
- arcuate or sigmoid trichomes
- form of cells
- position, form and size of akinetes

Variability: Not studied.

Distribution: Known only from north Asia (Siberia) and northeast Europe (Estonia, Latvia, northern Finland).

26. *Anabaena fallax* KOMÁREK et KOMÁRKOVÁ-LEGNEROVÁ, Preslia 74: 223. 2002.

Fig. 26. After KOMÁREK & KOMÁRKOVÁ-LEGNEROVÁ 2002.



Shape of vegetative cells: **cylindrical to slightly barrel-shaped**

Width of trichomes: **5.2–6 μm**

Shape of akinetes: **akinetes unknown**

Size of akinetes: no data

Position of akinetes: no data

Diacritical features:

- coiling
- shape of cells
- structure of trichomes
- shape and position of heterocysts

Variability: Not studied. Akinetes are not known, but the morphology of trichomes (shape of cells, type of fragmentation of trichomes) is specific.

Distribution: Known only from eutrophic reservoirs in central Mexico.

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