

Phenotype diversity of the heterocytous cyanoprokaryotic genus *Anabaenopsis*.

Přehled (fenotypová diversita) heterocytosního cyanoprokaryotního rodu *Anabaenopsis*.

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Abstract

Taxonomic review of the filamentous, nostocacean, heterocytous cyanobacterial genus *Anabaenopsis* (WOŁOSZYŃSKA) MILLER 1923 is presented in the article, with respect to diversity of natural populations. The specific development of heterocytes is the main traditional generic character of *Anabaenopsis*. This genus is delimited by both phenotypic and molecular criteria according to the modern cyanobacterial classification, but the infrageneric diversity is problematic. Morphological characters are discussed and the ecological data are included. A list of *Anabaenopsis*-taxa from natural habitats with their basic characters should serve as a background for identification and morphological evaluation of diversity of this biologically and ecologically important genus. – The study was supported by the grants GA AS CR no. IAA6005308 and KSK6005114.

Introduction

The cyanobacterial filamentous, heterocytous genus *Anabaenopsis* (WOŁOSZYŃSKA) MILLER 1923, is satisfactorily defined by its morphological, biological and molecular characters. It belongs to traditional order Nostocales. However, the infrageneric diversity is unclear. Each population differs only slightly from other ones, and transitional forms occur between almost all described species. The following review of the phenotypic characters and all described morphospecies from natural habitats should yield summarised data about phenotypic diversity for the next taxonomic, ecological and experimental studies.

Short history

The first taxa from this generic entity were described by G.S.WEST (1907) as planktic members of the genus *Anabaena* (*Anabaena flos-aquae* var. *circularis*, *A. tanganyikae*) from large lakes of Eastern Africa. In 1912, WOŁOSZYŃSKA studied similar populations from Indonesia (Java) and recognized their special strategy of heterocyte development. She established therefore a new “section *Anabaenopsis*” for

this group of species inside of the morphologically similar genus *Anabaena*. Habitually, the species of *Anabaenopsis* resemble really other planktic *Anabaena*-species, but the heterocyte development is specific. The WOŁOSZYŃSKA's section was transferred therefore to the generic status by MILLER (1923), with the new described species *Anabaenopsis elenkinii*, which was designated as a type species. Numerous species were described later mainly from plankton of reservoirs and lakes with more or less salty or mineralised waters, mostly from Africa and warm regions of Eurasia, but their natural diversity is not solved yet.

A special type of heterocyte formation is the main diagnostical character of the genus *Anabaenopsis* (Fig. 1). Recently, the genus was confirmed also by 16S rRNA sequencing (ITEMAN & al. 2002, RAJANIEMI & al. 2005; Fig. 2). In 1985, the new genus *Cyanospira* FLORENZANO & al. was described (with the type species *C. rippkae*), also from plankton of salty lakes in Eastern Africa, which corresponded morphologically also to *Anabaenopsis*, and also the molecular analyses supported the identical classification of both genera (Fig. 2). From about 33 species (and more than 50 taxa) were described up to now, but 15 taxa do not correspond to the generic diagnosis, and were transferred to other genera (see Excludenda, p. 32). All other taxa are mentioned in the review.

Generic description

Anabaenopsis (WOŁOSZYŃSKA) MILLER, Arch. Soc. Russ. Protistol. **2**: 125, 1923.

Anabaena sect. *Anabaenopsis* WOŁOSZ., Bull. Acad. Cracovie, Ser. B, p. 679, 1912.

Cyanospira FLORENZANO, SILI, PELOSI et VINCENZINI, Arch. Microbiol. **140**: 305, 1985; incl.

- Cyanoprokaryotic, free-floating filaments (trichomes), occurring solitary or entangled in small, microscopic clusters, free-floating, arcuated or irregularly circular, spirally or screw-like coiled, rarely almost straight, without firm sheaths, sometimes enveloped by fine, mucilaginous diffuent and colourless envelopes. Trichomes uniseriate, not branched, usually with terminal solitary and doubled intercalary heterocytes, more or less of the same width along the whole length, or slightly narrowed towards the ends, with metameric structure; usually constricted at cross-walls, rarely (one species) unconstricted."
- Cells cylindrical, barrel-shaped up to almost spherical, usually longer, rarely isodiametric or shorter than wide; several species are characteristic by diverse length of cells in one trichome. Occurrence of aerotopes (groups of gas vesicles) is facultative, they develop in majority of morphospecies occasionally, and populations almost completely without aerotopes can occur.
- Heterocytes develop intercalary, metamerically, in twos, after the mirror-like asymmetrical division of two neighbouring vegetative cells in a trichome. They are unipored, with pores on sides oriented to the sister vegetative cell (= main generic character; Fig. 1,3). Form of final heterocytes: spherical, widely oval or ovoid. All stages of the process of heterocyte formation are usually recognizable in trichomes in well developed populations. Trichomes often disintegrate between two intercalary heterocytes; from this process arise common trichomes and fragments of trichomes with terminally situated, secondary solitary heterocytes. Double-pored heterocytes occur exceptionally.
- Akinetes develop intercalary, usually distant from heterocytes, very exceptionally aside heterocytes; after trichome disintegration, they can occur in terminal position. They are solitary, in twos, in several species serially arranged up to 5 in a row. The shape: cylindrical, oval, broadly oval up to almost spherical, with smooth, usually colourless or yellowish or yellow epispore.
- Reproduction: Cell division perpendicular to the trichome axis, disintegration of trichomes, after hibernization by germination of akinetes.
- Type species: *Anabaenopsis elenkinii* MILLER 1923.
- Related genera: The morphologically most similar genera are *Cylindrospermopsis* (asymmetrical cell division before heterocyte formation) and planktic *Anabaena* (trichome morphology, cells with aerotopes). According to molecular sequencing, the most related genus to *Anabaenopsis* is *Nodularia* (Fig. 2).

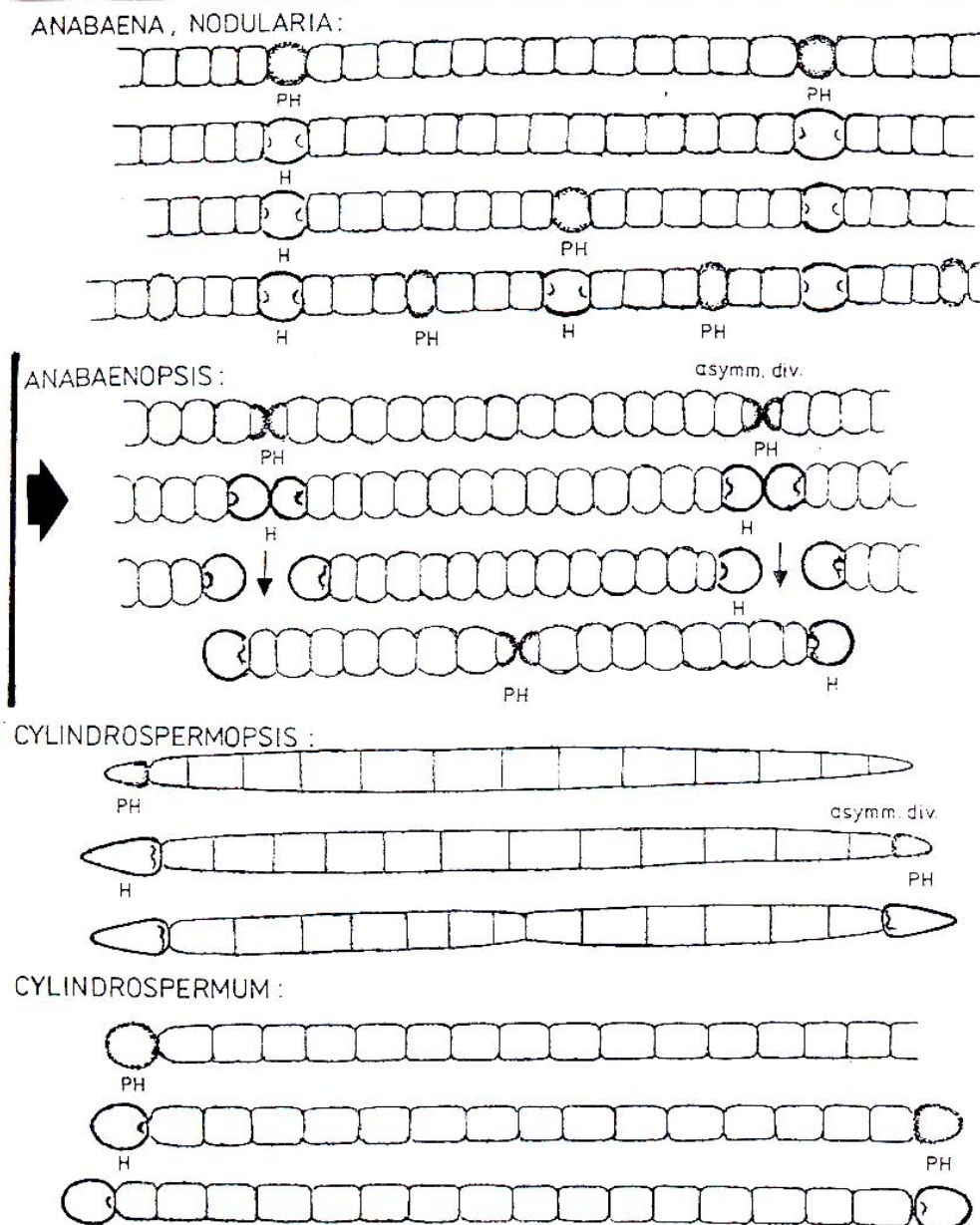


Fig. 1: Typical heterocyte development in the genus *Anabaenopsis*, in comparison with *Anabaena*, *Nodularia*, *Cylindropermopsis* and *Cylindropermum*; PH = proheterocytes, H = heterocytes. (After KOMÁREK & ANAGNOSTIDIS 1989).

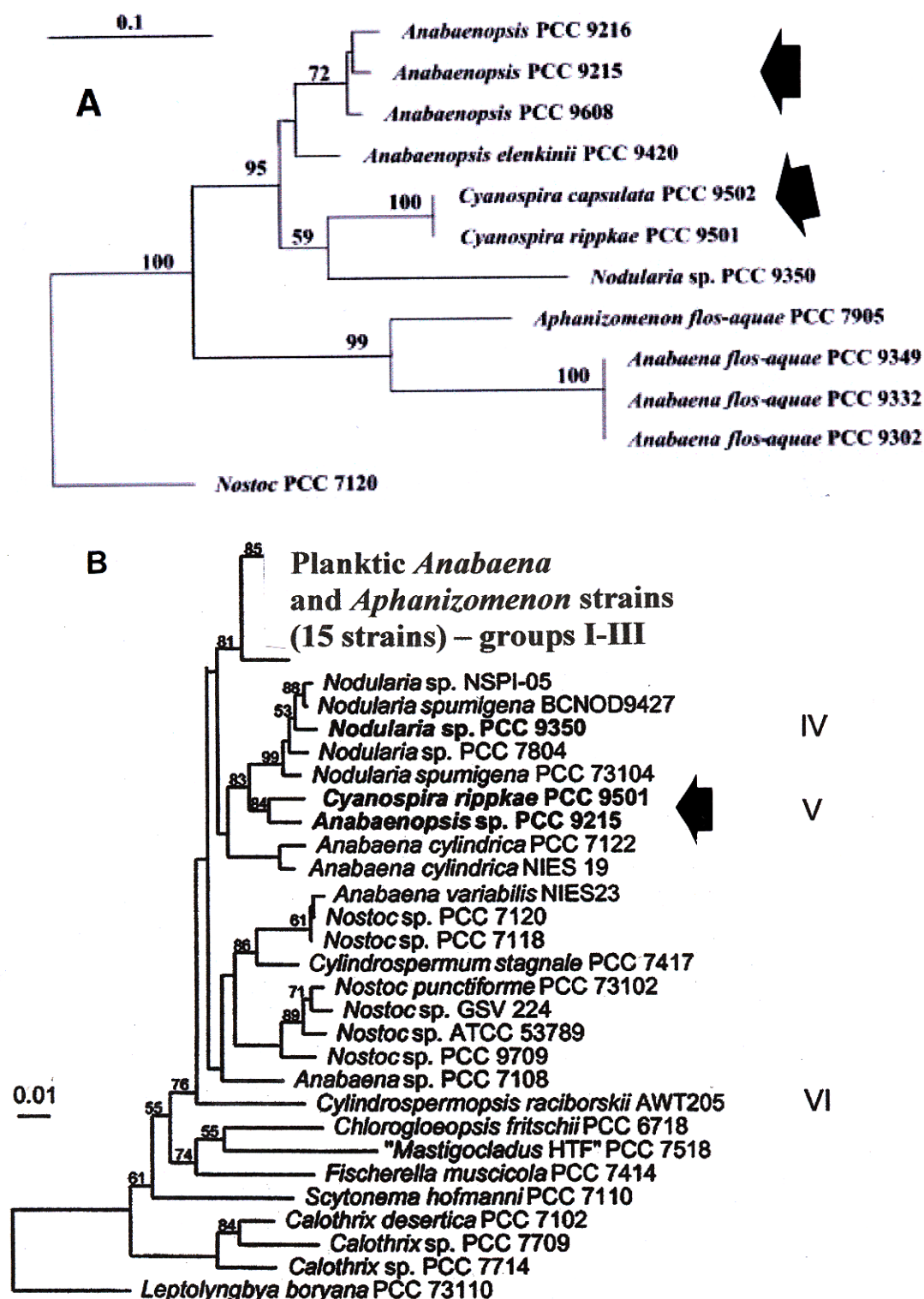


Fig. 2: **A** - Dendrogram constructed from RFLP analysis of 16S rDNA amplicons of 12 strains (after ITEMAN & al. 2002); **B** – phylogenetic tree based on 16S rDNA sequences showing the relationships between selected heterocytous cyanobacteria (after RAJANIEMI & al. 2005); arrows = position of the genus *Anabaenopsis* in phylogenetic trees.

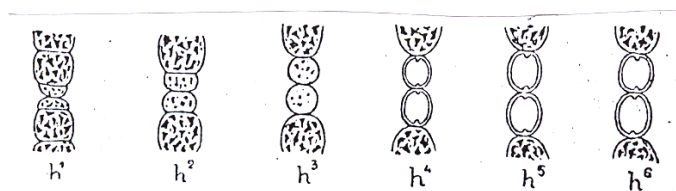


Fig. 3: Heterocyte development in *Anabaenopsis arnoldii* (after APTEKAR' 1926).

Ecology and distribution

All *Anabaenopsis* species are planktic (with exception of the very unclear *A. sturmiæ*, which belongs evidently to another genus), living in solitary, coiled, rarely straight filaments, or in small clusters of several filaments. Gas vesicles and

aerotopes occur facultatively in cells, but just this phenomenon is very variable, and populations with plenty aerotopes and also quite without visible aerotopes can occur. Majority of species can develop water-blooms.

Anabaenopsis species occur in lakes and ponds, mainly in tropical and “warm” parts of temperate regions, usually in summer seasons. Eleven species were described and almost 90% of localities were registered from tropical zone, and all the other from temperate zone with hot summer season (Pannonian region – 2 species; central Asia, mainly Turkmenistan and Caspian Sea – 7 species; Japan – 1 species; Southern European Russia and Ukraine – 2 species). Only few floristic data are from summer seasons from central Europe (Czech Republic, northern Germany, Denmark), central Japan, Great Lakes Area in North America, and from the vicinity of Buenos Aires in Argentina. The regions with most common species and numerous floristic data are Eastern Africa (mainly in large and mineral lakes), India, Pannonian region, warm central Asia and Philippines. The whole genus can be designated therefore as thermophilic, preferring habitats with average temperature over (20) 25°C.

All species are known from mesotrophic to eutrophic reservoirs (pools, ponds, lakes), one species was described from paddy fields in India. About 50% of species (9) were described from mineral (e.g., soda-) or salty lakes, both inland and coastal. Numerous species have also the main areas of distribution in regions with plenty of salty or mineral lakes, as Eastern Africa, Pannonian region, central Asia, Caspian Sea, and several coastal localities (Fig. 4).

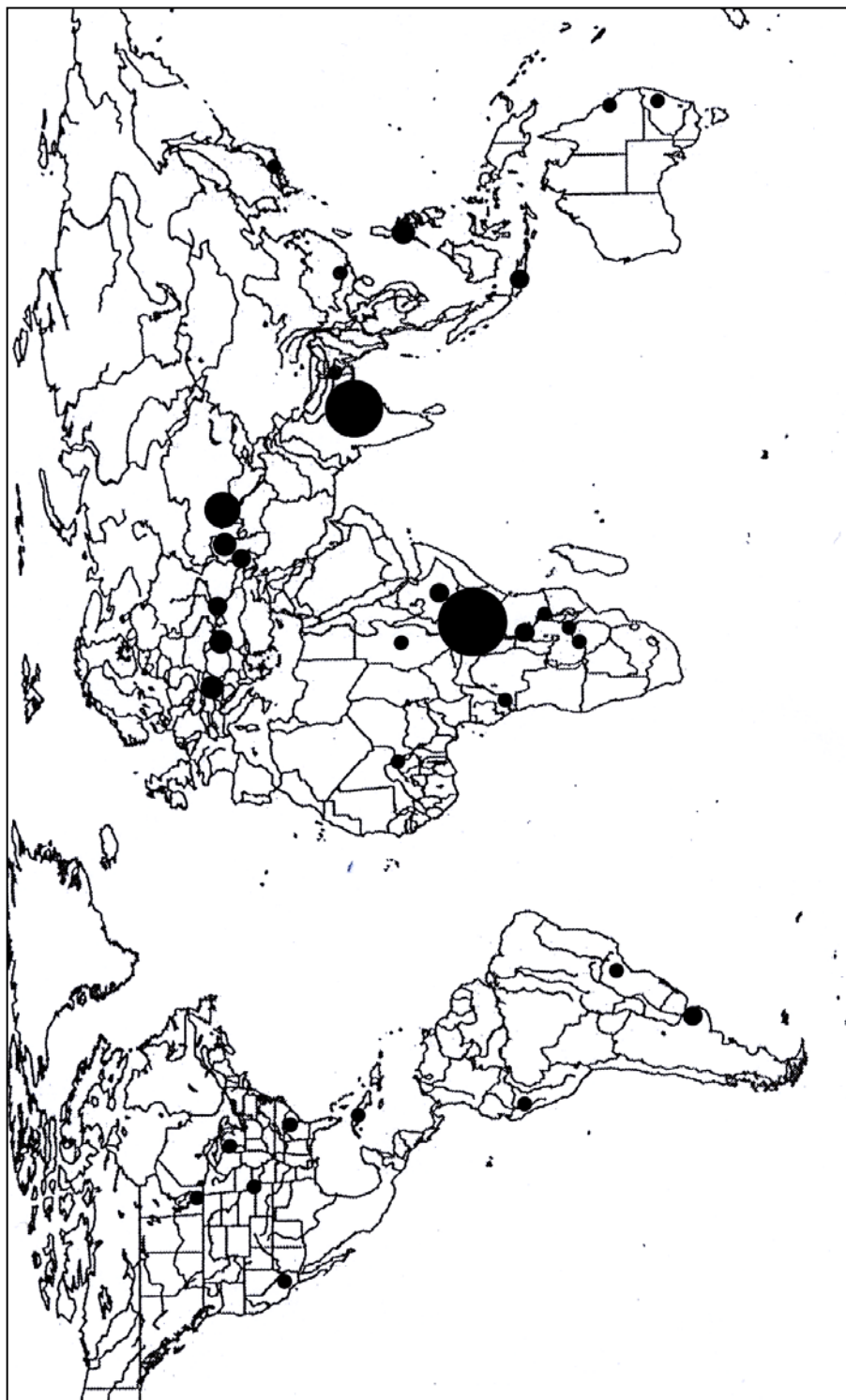


Fig. 4: Distribution of *Anabaenopsis*-species. The diameter of black points corresponds approximately with the number of recorded localities.

Key to the identification of morphospecies:

The clear morphological limits do not exist between different species. Shape of cells (Fig. 5), dimensions and type of coiling are considered as the main diacritical features.

- 1a** Trichomes always $\pm$ straight or slightly curved **2**
- 1b** Trichomes mainly coiled, exceptionally almost straight (solitary in populations of coiled trichomes) **3**
- 2a** Cells distinctly longer than wide, $-16.4 \times 2-3.8 \mu\text{m}$, akinetes cylindrical (6)8-10(16) $\times 3-4 \mu\text{m}$ **2. A. cunningtonii**
- 2b** Cells isodiametric or maximally 2x longer than wide, $2-7 \times 2.4 \mu\text{m}$, akinetes oval, $6-10 \times 5-7.5 \mu\text{m}$ **3. A. ambigua**
- 3a** Trichomes cylindrical, not constricted at cross walls **1. A. tanganyikae**
- 3b** Trichomes always constricted at cross walls **4**
- 4a** Cells cylindrical with $\pm$ straight sides **5**
- 4b** Cells with $\pm$ convex sides **8**
- 5a** Cells $\pm 2.5 \mu\text{m}$ wide; in trichomes usually 2-4, maximally 6 cells **5. A. hungarica**
- 5b** Cells (2.5)3-6 μm wide; trichomes usually with more 4 cells **6**
- 6a** Heterocytes oval; cells $3.5-3.6 \mu\text{m}$ wide **4. A. circularis**
- 6b** Heterocytes $\pm$ spherical **7**
- 7a** Cells $3.1-3.5 \mu\text{m}$ wide; heterocytes $2.8-4 \mu\text{m}$ in diameter **4a. A. woltereckii**
- 7b** Cells $4-5 \mu\text{m}$ wide; heterocytes $8-8.5 \mu\text{m}$ in diameter **10. A. rippkae**
- 8a** Cells in average distinctly longer than wide **9**
- 8b** Cells spherical or barrel-shaped, isodiametric or (often) shorter than wide **14**
- 9a** Cells typical barrel-shaped **10**
- 9b** Cells rather spindle-like with “cut” ends, slightly narrowed to their ends **12**
- 10a** Heterocytes $\pm$ spherical **11**
- 10b** Heterocytes mainly oval, ovoid, rarely almost spherical; long coiled trichomes with numerous cells **13. A. teodorescui**
- 11a** Cells $3.3-4 \mu\text{m}$ wide; trichomes usually with few cells, tightly coiled together **6. A. nadsonii**
- 11b** Cells (4)6.4-9.9 μm wide **9. A. milleri**
- 12a** Heterocytes spherical or only very little elongated; cells (3)4-9(12.9) $\times$ (2.8)4-6(7.5) μm , akinetes $8.1-16.8 \times 5.5-10.7 \mu\text{m}$ **7. A. elenkinii**
- 12b** Heterocytes mainly distinctly oval, ellipsoid or ovoid **13**
- 13a** Cells $3.5-5 \mu\text{m}$ wide, akinetes $9.5-15 \times 6-8 \mu\text{m}$ with colourless epispore; central Asia **7a. A. kelifii**

- 13b** Cells 5.2-7.5 μm wide, akinetes 12.2-16.2 x 8.1-9.7 μm , with yellow epispor; Philippines **7b. A. luzonensis**
- 14a** Trichomes irregularly screw-like or almost spirally coiled; cells $\pm$ spherical or regularly barrel-shaped **15**
- 14b** Trichomes very densely irregularly coiled; cells asymmetrically barrel-shaped **20**
- 15a** Cells variable in one trichome, 4-5(5.4) μm wide; akinetes $\pm$ kidney-shaped **8a. A. intermedia**
- 15b** Cells in one trichomes $\pm$ unified (only with variable length after cell division), 5-8-11 μm wide **16**
- 16a** Cells 5-8(9) μm wide, akinetes with smooth, not striated epispor **17**
- 16b** Cells 7.6-11.4 μm wide, akinetes oval, with striated epispor **14. A. magna**
- 17a** Heterocytes $\pm$ slightly elongated; akinetes slightly asymmetrical, 9.5-11.4 x 7.6-9.5 μm **8b. A. venkataramanii**
- 17b** Heterocytes $\pm$ spherical, akinetes oval, with striated epispor **18**
- 18a** Akinetes develop in trichomes solitary or in pairs, with colourless epispor; mainly in freshwater inland lakes **19**
- 18b** Akinetes develop in trichomes in rows of 1-5, with yellowish epispor; mainly in salty lakes **12. A. knipowitschii**
- 19a** Heterocytes often narrower than vegetative cells; akinetes 15-18 x 12-14 μm **8. A. doliiformis**
- 19b** Heterocytes usually wider than vegetative cells; akinetes 11.5-14.5 x 10.4-11.5 μm **11. A. arnoldii**
- 20a** Cells 4.5-5 x 5.4-7 μm , heterocytes 8.5-10.8 μm in diameter; central Asia **15. A. issatschenkoi**
- 20b** Cells 6-12 x 4-8 μm , heterocytes 6-10 μm in diameter; Etiopia **16. A. abijatae**

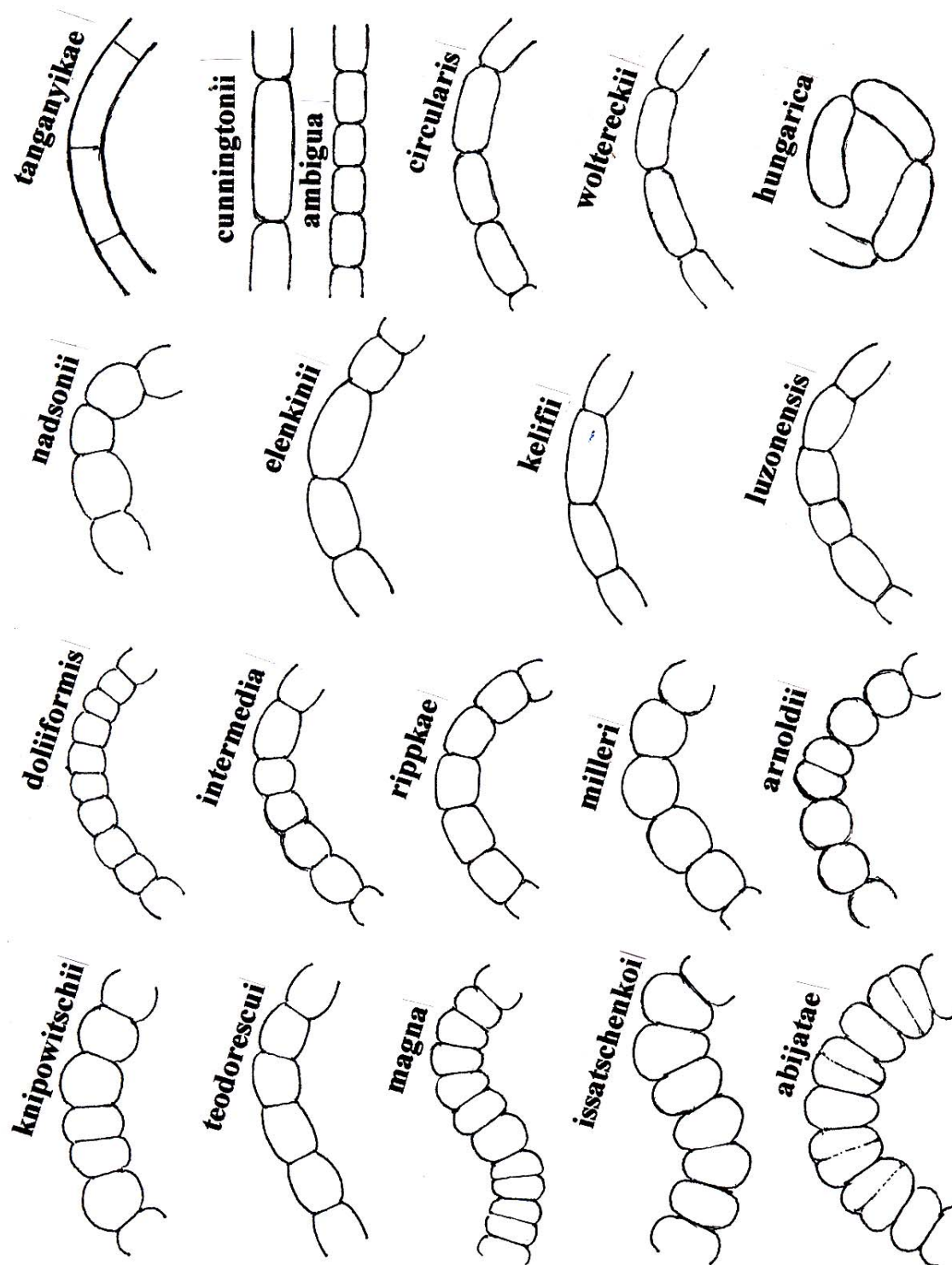


Fig. 5: Typical shape of cells of different *Anabaenopsis*-species.

Review of morphospecies

1. *Anabaenopsis tanganyikae* (G.S.WEST) MILLER 1923

Anabaena tanganyikae G.S.WEST, J. Linn. Soc. Bot. 38: 171, 1907.

Anabaena flos-aquae var. *circularis* G.S.WEST, J. Linn. Soc. Bot., 38: 170, 1907, p.p. (excl. typo).

Anabaena (*Anabaenopsis*) *circularis* (G.S.WEST) WOŁOSZYŃSKA, Bull. Int. Acad. Sci. Cracovie, Cl. mat.-nat., ser. B, 1912: 681, 1912, p.p. (excl. typo).

Anabaenopsis tanganyikae (G.S.WEST) MILLER, Arch. Russk. Protistol. Obšč. 2: 125, 1923.

Anabaenopsis circularis (G.S.WEST) MILLER, Arch. Russk. Protistol. Obšč. 2: 125, 1923, p.p. (excl. typo).

Anabaenopsis circularis f. *tanganyikae* (G.S.WEST) USAČEV in PROŠKINA-LAVRENKO & MAKAROVA, Vodor. Plankt. Kasp. Morja, p. 104, 1968.

Trichomes coiled, circular or irregularly screw-like with 1-2(3) coils, short, solitary, without sheaths and mucilaginous envelopes, cylindrical, not constricted at cross-walls.

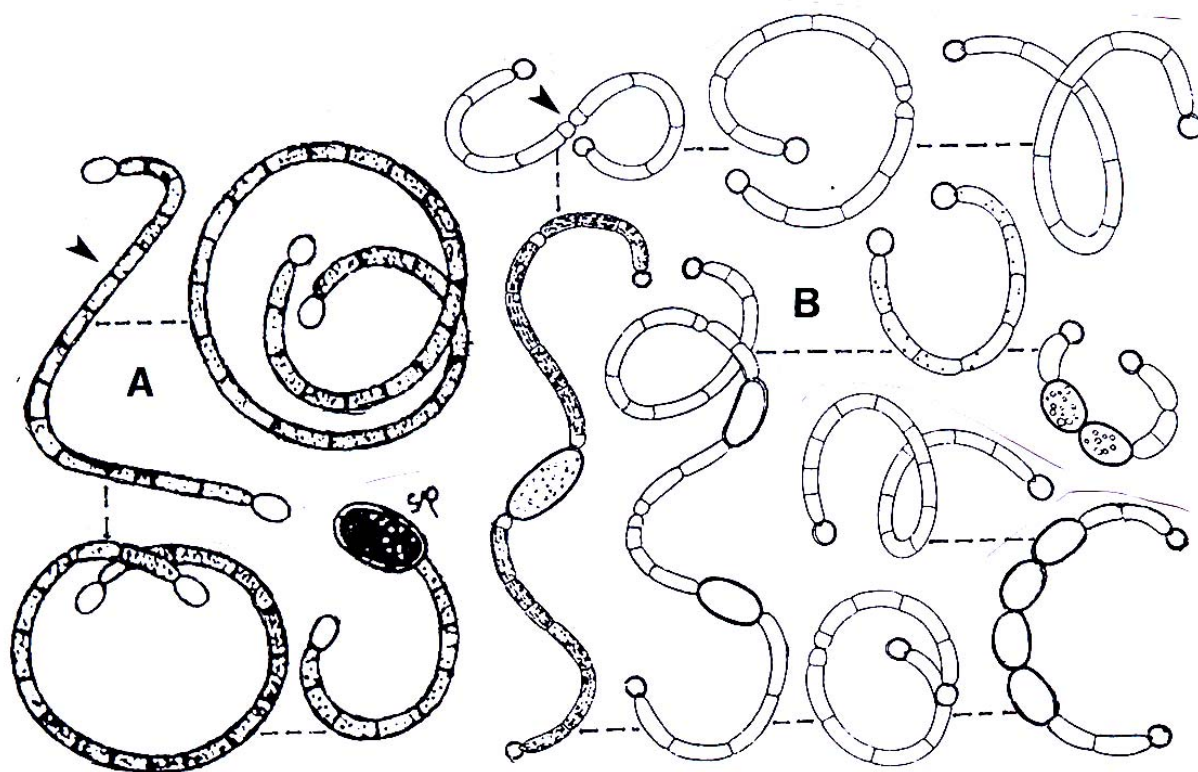
Cells cylindrical, pale blue-green, with solitary granules, aerotopes occur only rarely, (1.5)2-3(5)x longer than wide, (2)3.8-10(15) x (2)2.4-3(3.5;3.9?) μm .

Heterocytes broadly oval or ellipsoidal; (3.2)3.8-7.9 x 3-5.2 μm .

Akinetes ellipsoidal or oval, develop solitary or in series up to 4 in a row, with colourless episporic; 8-15 x 4-7 μm .

Distribution: Planktic in large lakes and reservoirs, described from Tanganyika lake; common in lakes in E. Africa, Caspian Sea, Chad, Cuba, Greece, India, Kenya, SW. Slovakia, Sudan, Tanzania, Uganda, Zaire.

Fig.: A = after G.S.WEST (1907); B = after HINDÁK (1988) and HINDÁK & MOUSTAKA (1988).



2. *Anabaenopsis cunningtonii* TAYLOR 1932

Anabaena flos-aquae var. *circularis* G.S.WEST, J. Linn. Soc. Bot. 38: 170, 1907, p.p.

Anabaena (*Anabaenopsis*) *circularis* (G.S.WEST) WOŁOSZYŃSKA, Bull. Int. Acad. Sci. Cracovie, Cl. mat.-nat., ser. B, 1912: 681, 1912.

Anabaenopsis circularis (G.S.WEST) MILLER, Arch. Russk. Protistol. Obšč. 2: 125, 1923.

Anabaenopsis cunningtonii TAYLOR, Amer. J. Bot. 19: 457, 461, 1932.

Anabaenopsis circularis f. *recta* FUKUSHIMA, Sci. Res. Ozegahara Moor, p. 624, 1954.

Anabaenopsis raciborskii WOŁOSZYŃSKA sensu MICHEEVA, Acta Univ. Carol., Biol., 1967: 257-258, 1967.

? *Anabaenopsis* sp. sensu PROŠKINA-LAVRENKO & MAKAROVA, Vodor. Plankt. Kasp. Morja, Fig. 24: 16-17, 1968.

Trichomes $\pm$ straight or slightly arcuated, short, composed usually from 4-12 cells, maximally 340 μm long, solitary, without sheaths or envelopes, cylindrical, distinctly or slightly constricted at cross walls.

Cells $\pm$ cylindrical, pale blue-green, usually without visible aerotopes, sometimes slightly granulated; usually 3-4 x longer than wide, 6.6-16.4 x 2-3.8(4.5) μm .

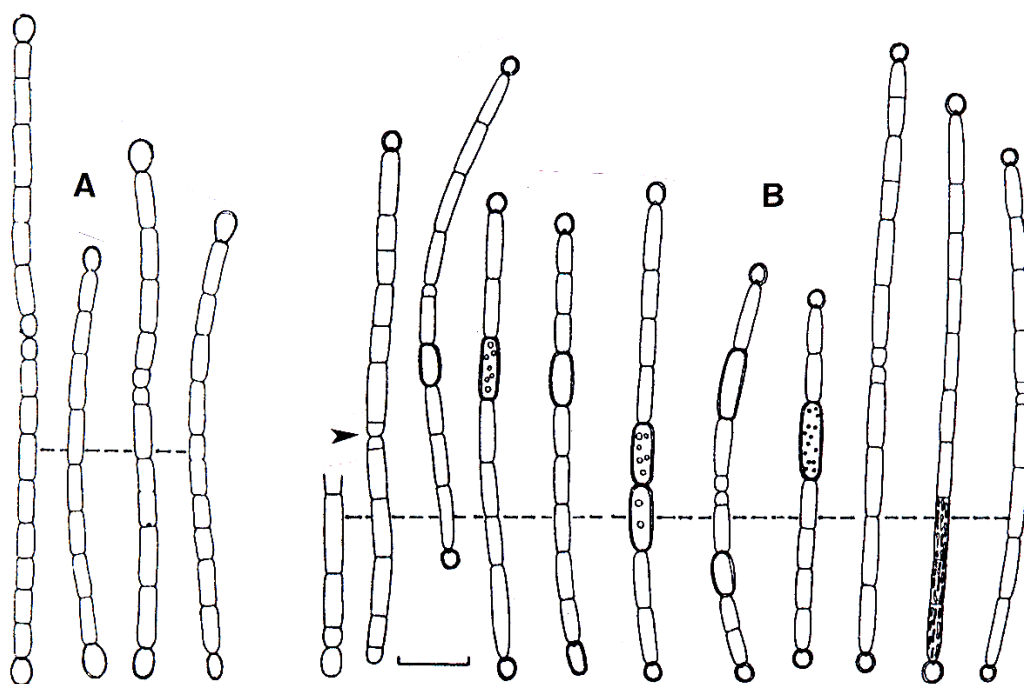
Heterocytes ellipsoid or ovoid, sometimes with thickened terminal part of a cell-wall; (3.3)6.6-10.3(15?) x (3.3)4.7-6.6 μm .

Akinetes cylindrical to oval (less frequently), solitary or in pairs, epispore?; 6-10 x 3-4 μm .

Distribution: Planktic in large lakes and reservoirs, described from the lake Tanganyika; Belorussia, Caspian Sea, N. Germany, India, Japan ?, SW. Slovakia, Tanzania.

Note: Morphologically slightly different population (larger dimensions, e.g., akinetes 11-16 x 4.4-8.2 μm) was described by PROŠKINA-LAVRENKO & MAKAROVA (1968) from Caspian Sea, and MICHEEVA (1967) from Belorussia (akinetes – 12 x 7.5 μm).

Fig.: **A** = after TAYLOR (1932); **B** = after HINDÁK (1988).



3. *Anabaenopsis ambigua* PANDEY et MITRA 1962

? *Anabaenopsis arnoldii* var. *recta* ROLL, Ann. Protistol. 1(4): 164, 166, 1928.

? *Anabaenopsis arnoldii* f. *recta* (ROLL) ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 801, 1938.

Anabaenopsis ambigua PANDEY et MITRA, N. Hedwigia 4(3-4): 345, 1962.

Trichomes usually straight, rarely irregularly bent, sometimes in microscopic fascicles, parallelly arranged, enveloped by colourless, diffuent individual sheaths, short, up to 150 μm long, distinctly constricted at cross-walls.

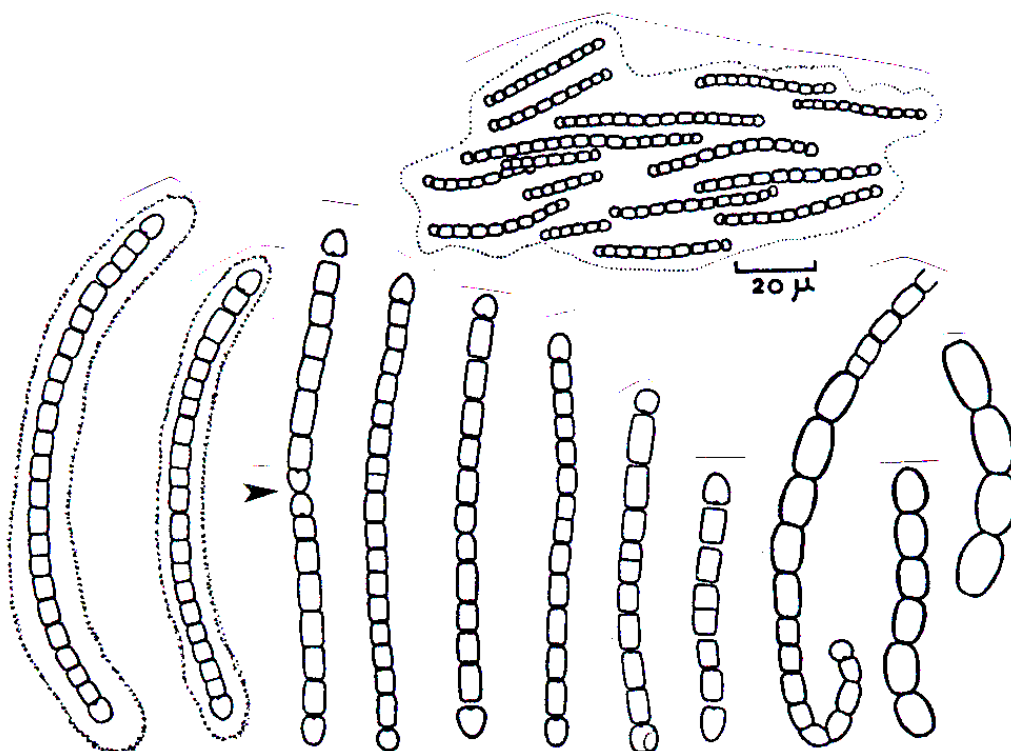
Cells $\pm$ cylindrical, blue-green with facultatively occurring aerotopes, $\pm$ isodiametric or slightly (up to 2x) longer than wide; (2)3-6.5(7) x (2)2.5-3.5(4) μm .

Heterocytes subspherical or elongated obovoid; 3-5 x 3-4.5(5) μm .

Akinetes ellipsoidal, solitary or serially arranged up to 5 in rows, episporic?; 6-8.5(10) x 5-7.5 μm .

Distribution: Free floating in paddy fields; India.

Fig.: After PANDEY & MITRA (1962).



4. *Anabaenopsis circularis* (G.S.WEST) WOŁOSZYŃSKA et MILLER in MILLER 1923

Anabaena flos-aquae var. *circularis* G.S.WEST, J. Linn. Soc. Bot. 38: 170, 1907 (p.p. typico).

Anabaena (*Anabaenopsis*) *circularis* (G.S.WEST) WOŁOSZYŃSKA, Bull. Int. Acad. Sci. Cracovie, Cl. mat.-nat., ser. B, 1912: 681, 1912 (p.p. typico).

Anabaenopsis circularis (G.S.WEST) WOŁOSZYŃSKA et MILLER in MILLER, Arch. Russk. Protistol. Obšč. 2: 125, 1923.

Anabaenopsis circularis (G.S.WEST) MILLER sensu TAYLOR, 1932.

Anabaenopsis nadsonii sensu PROŠKINA-LAVRENKO & MAKAROVA, 1968.

? *Anabaenopsis tanganyikae* sensu GUARRERA & al., 1972.

Anabaenopsis elenkinii f. *circularis* (G.S.WEST) JEEJI-BAI, Algolog. Stud. 18: 23, 1977.

Trichomes slightly arcuated or screw-like coiled (1-1.5 coils), short, solitary, without mucilaginous envelopes, cylindrical, constricted at cross-walls.

Cells ± cylindrical (and usually slightly arcuated), pale blue-green, often with solitary, distinct granules, and/or facultative aerotopes; 4-10.6(15?) x (2)4-6.5(8?) µm.

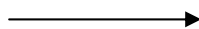
Heterocytes ± spherical to widely oval; 5-8.4 x (3?)3.5-7.5(8) µm.

Akinetes widely oval, solitary or in pairs; 7-12 x 4-7 µm.

Distribution: Planktic in lakes and reservoirs, mainly with tropical distribution, but also in warm areas (in summer seasons) in Europe and temperate South America; described from lake Tanganyika, known from Argentina (near Buenos Aires), Bulgaria, Chad, Hungary, SW. Slovakia, Tanzania and from other more localities in E. Africa.

Note: The population described by RICH (1933) from the east African lakes Edward, Nakuru and Kaianda lagoon, has cells up to 3-4 x longer than wide (4-15 x 4-5 µm), heterocytes only 3-5 µm wide and akinetes 10-11 x 7-8 µm. To this type belongs probably also "*A. tanganyikae*" sensu GUARRERA & al. 1972 (p. 198), from Buenos Aires, Argentina.

Fig.: **A** = after RICH (1933), **B** = after HINDÁK (1988), **C** = after TAYLOR (1932).



4a. *Anabaenopsis woltereckii* BEHRE 1956

Anabaenopsis woltereckii BEHRE, Arch. Hydrobiol., Suppl. 23(1): 27, 1956.

Trichomes coiled, circular, short, maximally with 12 cells, without gelatinous envelopes, $\pm$ cylindrical, constricted at cross-walls.

Cells cylindrical, with grey-blue, $\pm$ homogeneous or slightly granular content; 2-3(4) x longer than wide, 7-10.5(14) x 3.1-3.5 μm .

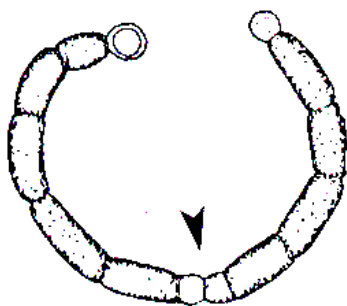
Heterocytes spherical, 2.8-3.2(3.6) μm in diameter.

Akinetes not known.

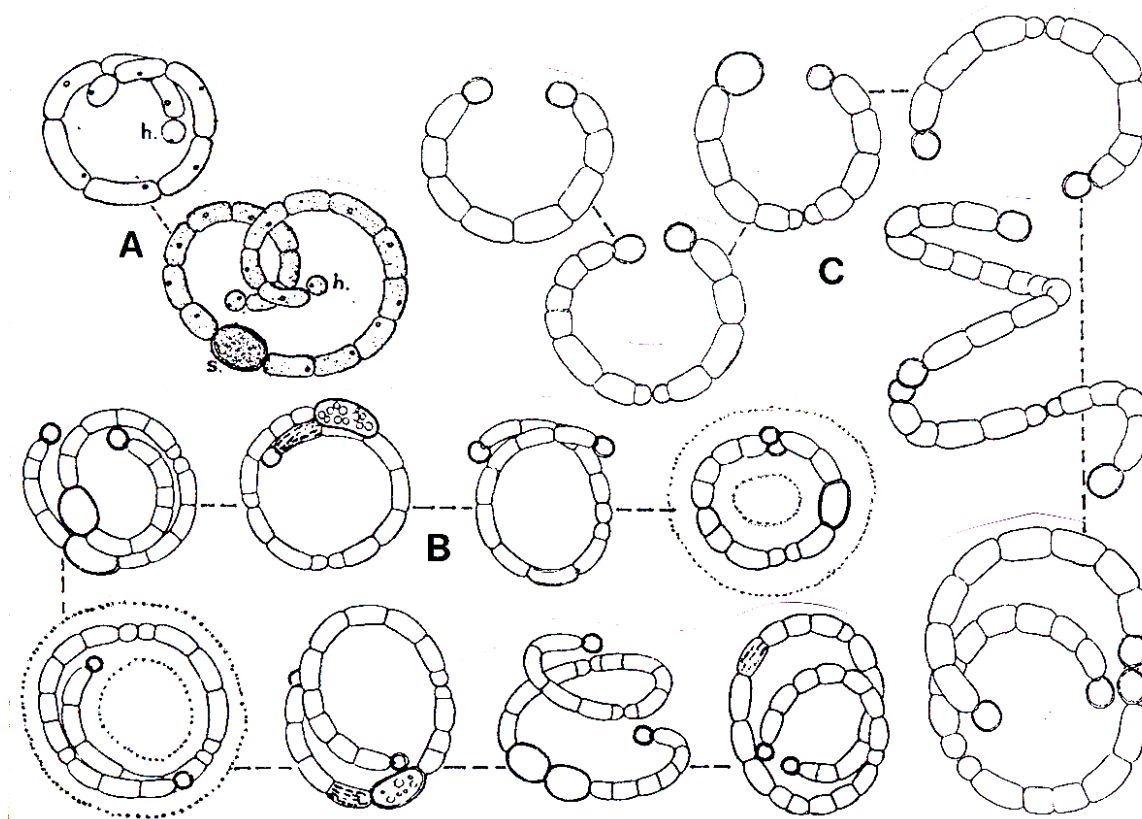
Distribution: Described from plankton of two lakes in Philippines (Luzon).

Note: Very similar to *A. circularis*.

Fig.: After Behre (1956).



A. circularis



5. *Anabaenopsis hungarica* HALÁSZ 1939

Anabaenopsis hungarica HALÁSZ, Borbásia 1(1): 69, 1938.

? *Anabaenopsis circularis* var. *indica* NAIR, Hydrobiologia 30: 146-147, 1967.

Anabaenopsis elenkinii f. *hungarica* (HALÁSZ) JEEJI-BAI, Algolog. Stud. 18: 23, 1977.

? *Anabaenopsis elenkinii* f. *indica* (NAIR) JEEJI-BAI, Algolog. Stud. 18: 23, 1977.

Trichomes tightly and intensely, irregularly coiled, circular or shortly screw-like, short, composed usually from (2)4(6?) cells, constricted at cross-walls.

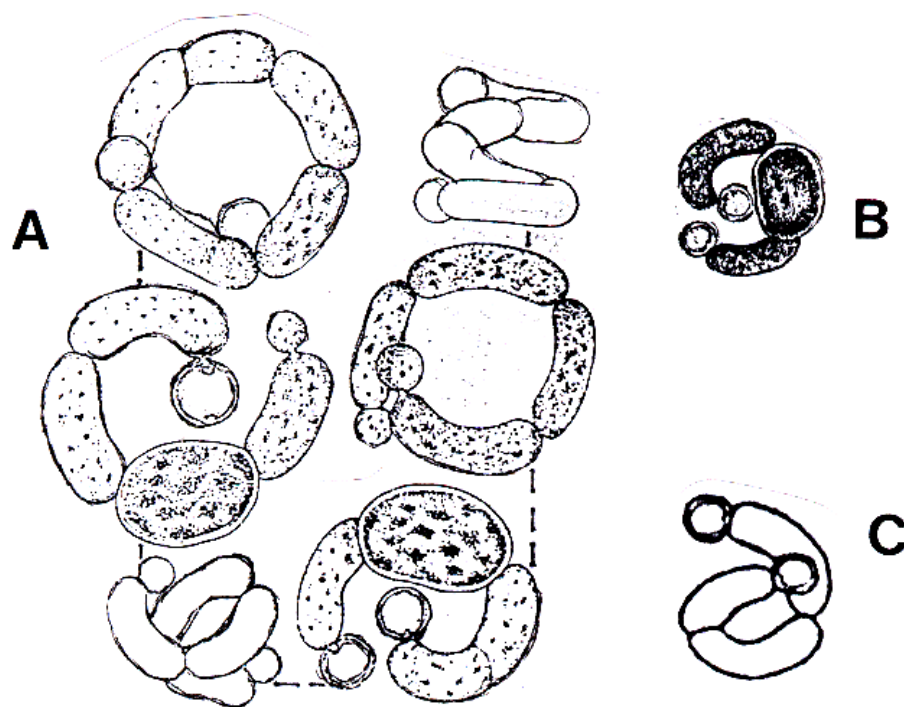
Cells cylindrical, sometimes with few aerotopes, arcuated; always longer than wide, $\pm 7.5 \times 2.5 \mu\text{m}$.

Heterocytes spherical, $\pm 2.5\text{-}3 \mu\text{m}$ in diameter.

Akinetes solitary, widely oval, slightly asymmetrical (kidney-shaped); $5.5\text{-}9.5 \times 2.6\text{-}4.2 \mu\text{m}$.

Distribution: Described from mineralised lake Valencze (Hungary), found also in small coastal salt lake in Albania.

Fig.: **A** = after HALÁSZ (1939); **B** = after HALÁSZ (1940); **C** = after SCHMIDT (1975).



6. *Anabaenopsis nadsonii* VORONICHIN 1929

Anabaenopsis nadsonii VORONICHIN, Izv. glavn. bot. Sada 1929: 35, 1929.

? *Anabaenopsis arnoldii* var. *natrophila* KOL, Arch. Protistenk. 66(3): 519, 1929.

Anabaenopsis kulundinensis VORONICHIN in ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 793, 1938.

? *Anabaenopsis peruviana* TUTIN, Trans. Linn. Soc. London, Ser. 3, 1: 201, 1940.

? *Anabaenopsis* sp. sensu NIEMI & HÄLLFORS, 1974.

Trichomes solitary, circular or coiled, shortly screw-like, with 1-4(-6) tight coils; coils (13(16)-19(32) μm wide, 3.2-4.8(13) μm high; distinctly constricted at cross-walls. In populations occur also solitary, $\pm$ straight trichomes.

Cells barrel-shaped, (3)4.8-6.4(?13.2) $\times$ 3-4.8(5.2) μm , only rarely with aerotopes.

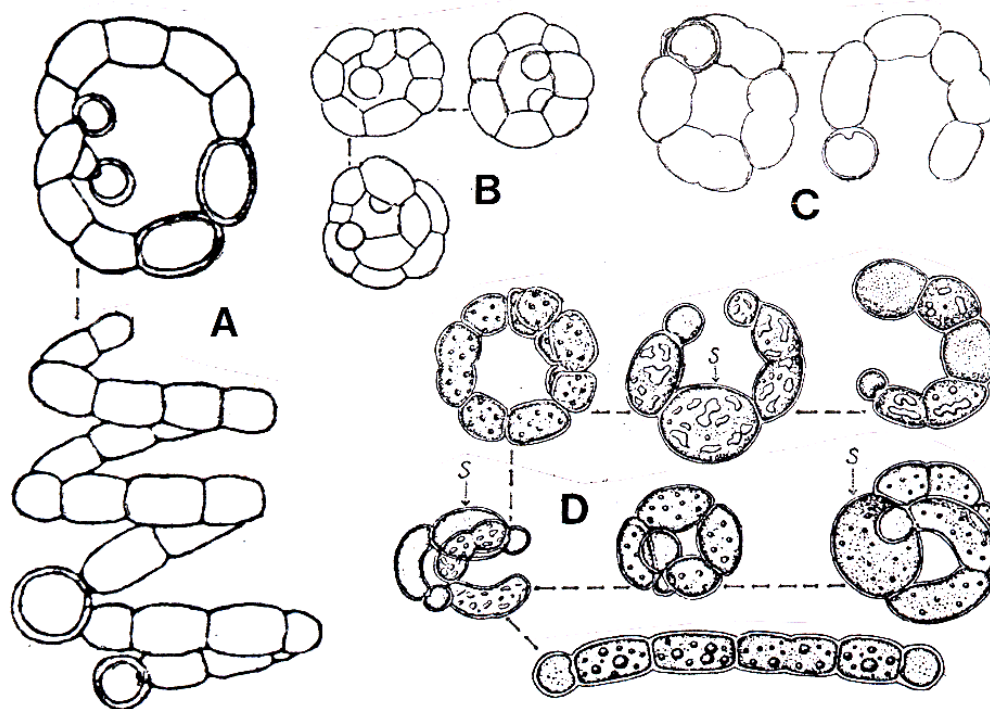
Heterocytes spherical or only exceptionally slightly elongated (widely oval), (3)3.2-4.7(5.2) μm in diameter (often narrower than vegetative cells).

Akinetes almost spherical or widely oval, 6.4-11(14) $\times$ 4.5-8.3(9) μm , solitary or in pairs, with smooth, colourless epispore.

Distribution: Planktic in slightly salty lakes (up to 10.5‰), at temperature over 18°C forming sometimes water blooms; described and known from several localities in central Asia (Russia, Turkmenistan, northern part of Caspian Sea), but recorded also from Denmark (GRØNTVED 1960), Hungary (HORTOBÁGYI 1959), Romania (PÉTERFI 1964), India (HORTOBÁGYI 1969) and Argentina (GUARRERA & al. 1972).

Note: Morphologically similar to *A. milleri*, which has larger dimensions.

Fig.: **A** = after VORONICHIN (1929); **B** = after PÉTERFI (1964); **C** = after HORTOBÁGYI (1969); **D** = after HORTOBÁGYI (1959).



7. *Anabaenopsis elenkinii* MILLER 1923

Anabaenopsis elenkinii MILLER, Arch. Soc. Russ. Protistol. 2: 125, 1923.

? *Anabaenopsis circularis* (G.S.WEST) MILLER sensu TIFFANY, 1934.

Anabaenopsis elenkinii f. *curta* DEDUS.–ŠČEGOL., Bot. Mat. Otd. Spor. Rast. Bot. Inst. Komarova AN SSSR 12: 45, 1959, incl.

Anabaenopsis elenkinii f. *ovalispore* DEDUS.–ŠČEGOL., Bot. Mat. Otd. Spor. Rast. Bot. Inst. Komarova AN SSSR 12: 44, 1959, incl.

Anabaenopsis circularis f. *caspica* USAČEV in PROŠKINA-LAVRENKO & MAKAROVA, Vodor. Plankt. Kasp. Morja, p. 107, 1968, pro synon.

Trichomes solitary, irregularly screw-like coiled, with 0.5-2.5(5) coils, which are (9)18-33(50) μm wide and 16.5-20 μm high, up to 100 μm long, constricted at cross-walls; between heterocytes maximally 8 cells.

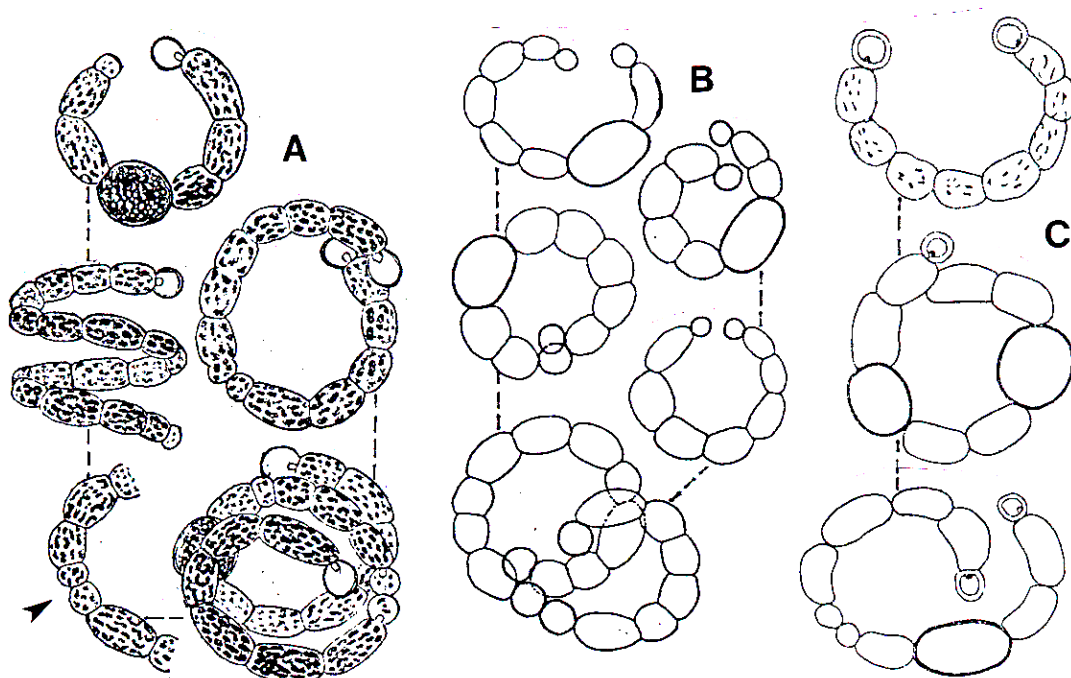
Cells long ellipsoid (spindle-like with “cut” ends), 1.2-4 x longer than wide, usually with aerotopes, (3)4-9(12.9) x (2.8)4-6(8) μm .

Heterocytes spherical or slightly elongated (widely oval); (2.8)3-7(10) μm in diameter.

Akinetes solitary, rarely in pairs, almost spherical up to widely oval, with colourless or yellowish epispor, solitary or rarely in pairs, (8.1)9.3-15(16.8) x (5.5)8-10.7(13.7) μm .

Distribution: Planktic (also water-bloom forming) in different eutrophic reservoirs (over 18°C), sometimes slightly halophilic; widely distributed (but not common) in warmer areas of the temperate zone, central Asia, Turkmenistan, Caspian Sea, Czech Republic, Hungary, southern and central Russia, Ukraine, recorded also from Lake Erie (USA).

Fig.: **A** = after MILLER (1923); **B** = after HEGEWALD et al. (1975); **C** = after DEDUSENKO-ŠČEGOLEVA from KONDRATEVA (1968).



7a. *Anabaenopsis kelifii* KOGAN 1962

Anabaenopsis kelifii KOGAN, Bot. Mat. Otd. Spor. Rast. 15: 12-13, 1962.

Anabaenopsis elenkinii f. *kelifii* (KOGAN) JEEJI-BAI, Algolog. Stud. 18: 22, 1997.

Trichomes solitary, rarely joined into clusters with 2-3 trichomes, circular or spirally or screw-like coiled with 3/4-1.5 coils, constricted at cross-walls; width of coils 30-39 μm .

Cells cylindrical with slightly convex sides, with aerotopes, 5-14 x 3.5-5 μm .

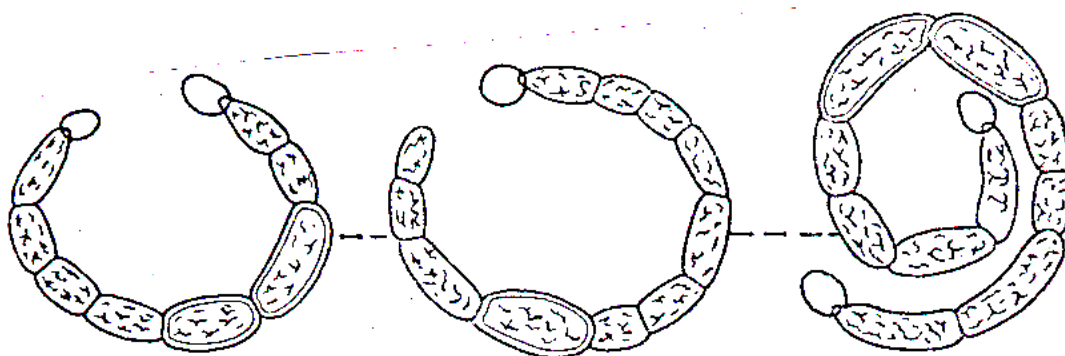
Heterocytes $\pm$ widely ellipsoid.

Akinetes ellipsoid or long ellipsoid, sometimes slightly asymmetrical, solitary or in pairs, with colourless epispore, 9-15 x 6-8 μm .

Distribution: Known only from plankton of lakes in Turkmenistan.

Note: Morphological very similar to *A. elenkinii*.

Fig.: After KOGAN from KONDRATEVA (1968).



7b. *Anabaenopsis luzonensis* TAYLOR 1932

Anabaenopsis luzonensis TAYLOR, Amer. J. Bot. 19: 460, 462, 1932.

Anabaenopsis elenkinii f. *luzonensis* (TAYLOR) JEEJI-BAI, Algolog. Stud. 18: 23, 1977.

Trichomes circular, arcuated up to irregularly screw-like coiled with up to 3.5 coils, constricted at cross-walls, often joined together with pairs of heterocytes, sometimes slightly narrowed towards ends; coils 28-45 μm in diameter.

Cells barrel-shaped, almost without aerotopes, 5.6-10.5 x 5.2-7.5 μm .

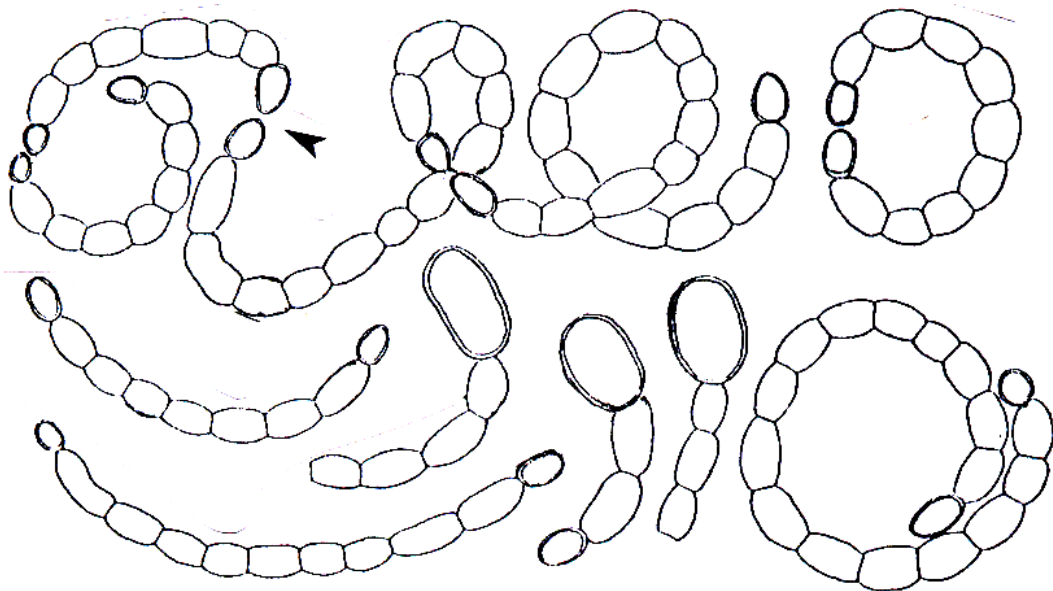
Heterocytes oval or ovoid; 4.5-9.6 x 3.7-7.5 μm .

Akinetes oval or slightly asymmetrical, solitary, with smooth, yellow epispore; 12.2-16.2 x 8.1-9.7 μm .

Distribution: Described from plankton of lakes in Philippines.

Note: Similar to *A. elenkinii*, but without visible aerotopes and more oval heterocytes.

Fig.: After TAYLOR (1932).



8. *Anabaenopsis doliiformis* NODA 1963

Anabaena (*Anabaenopsis*) *circularis* var. *javanica* WOŁOSZYŃSKA, Bull. Acad. Sci. Cracovie, mat.-nat., ser. B, 1912: 680, 1912, p.p., excl. typo.

Anabaenopsis circularis var. *javanica* WOŁOSZYŃSKA in ELENKIN, Not. syst. Inst. Crypt. Horti bot. Petropolit. 2, 5: 77, 1923.

Anabaenopsis arnoldii var. *javanica* (WOŁOSZYŃSKA) TAYLOR, Amer. J. Bot. 19: 458, 1932.

Anabaenopsis arnoldii f. *javanica* (WOŁOSZYŃSKA) TAYLOR in ELENKIN, Monogr. Alg. Cyanoph., P. spec., 1: 800, 1938.

Anabaenopsis doliiformis NODA, J. Fac. Sci. Niigata Univ., ser. 2, 4(3): 121, 1963.

Trichomes circular with 1-3 coils, constricted at cross-walls.

Cells shortly barrel-shaped, $\pm$ isodiametric or slightly shorter or longer than wide, blue-green, without visible aerotopes; 4.5-9 μm wide.

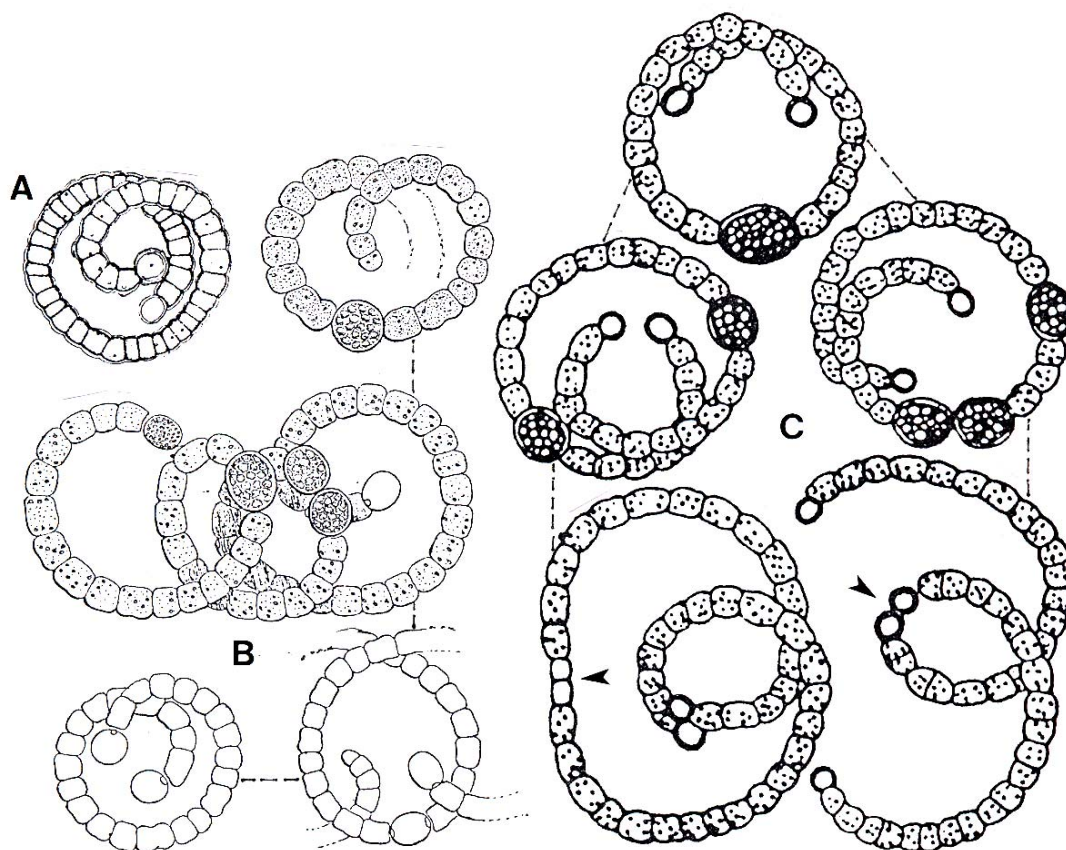
Heterocytes spherical, sometimes smaller than vegetative cells, up to 3.7-9 μm in diameter.

Akinetes solitary, rarely in pairs, ellipsoidal to widely oval, 13-18 x (11)12-14 μm , with colourless epispor.

Distribution: In lakes and ponds (alkaline, pH = $\pm$ 9); China, India, Indonesia (Java), Japan, Philippines, large lakes in E. Afrika (Tanzania); probably also in Argentina (GUARRERA & al. 1949, 1968, 1972 sub "*A. arnoldii*"?; from Buenos Aires).

Note: The smaller form cited by BEHRE (1956) from Philippines belongs probably to another genotype.

Fig.: **A** = after NODA (1963); **B** = after RICH (1932); **C** = after WOŁOSZYŃSKA (1912).



8a. *Anabaenopsis intermedia* KOGAN 1967

Anabaenopsis intermedia KOGAN, Nov. Syst. Plant. non Vascul. 1967: 6, 1967.

Trichomes solitary, slightly arcuated up to circular or irregularly screw-like contorted, constricted at cross-walls, with 1-2 coils, short, to 100 μm long; coils 18-27 μm wide.

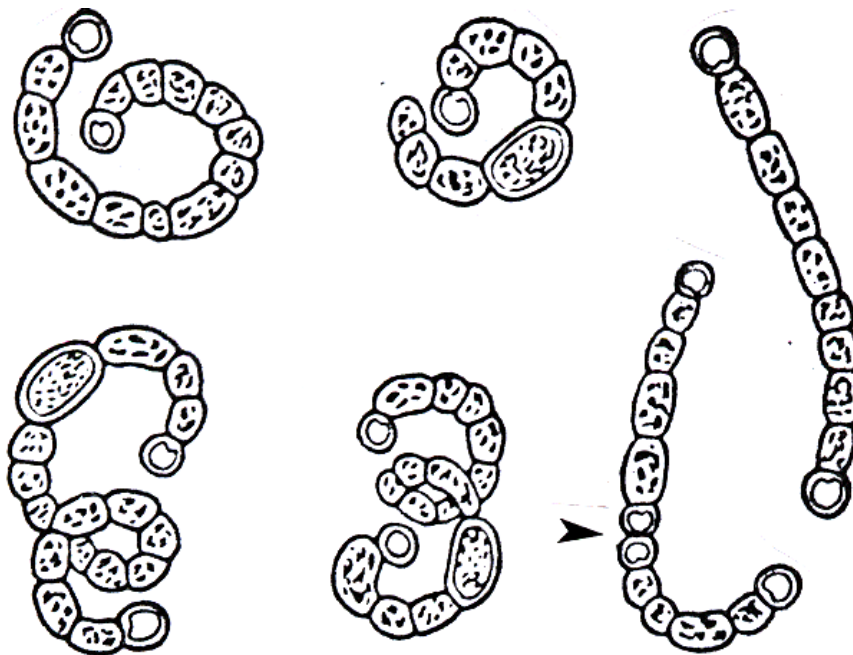
Cells shortly barrel-shaped, $\pm$ isodiametric or slightly shorter or longer than wide, with aerotopes; 4-8(12) $\times$ 4-5.4 μm .

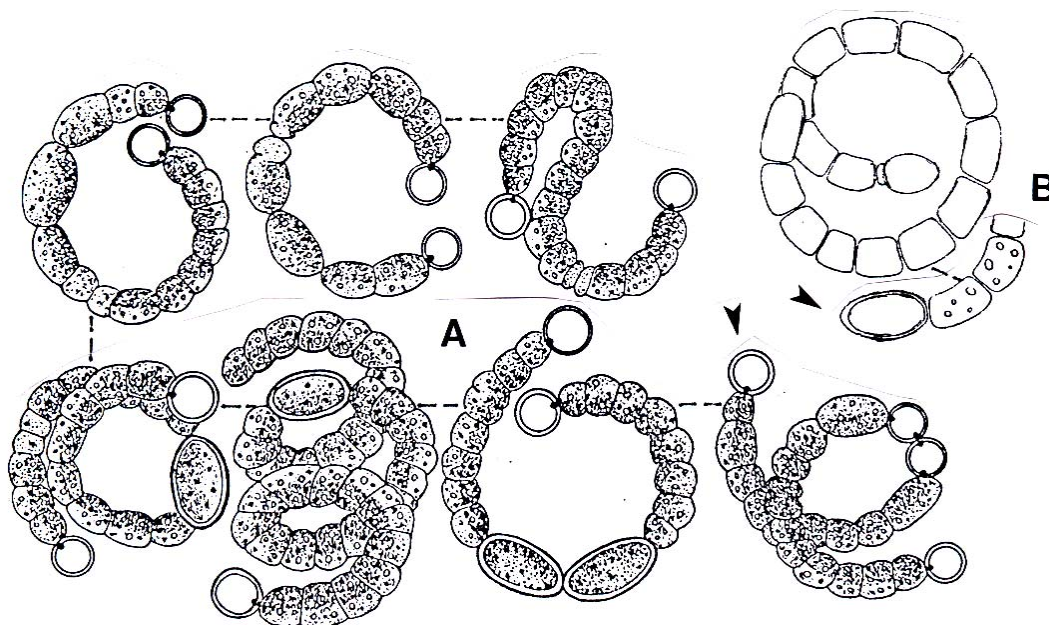
Heterocytes spherical, 3-5.4 μm in diameter.

Akinetes oval or slightly asymmetrical, solitary, 8.1-12.6 $\times$ 5.7-8.5 μm , with colourless episporium.

Distribution: Described from summer or autumn plankton (over 25°C) of a channel in Turkmenia.

Fig.: After KOGAN (1967).



8b. *Anabaenopsis venkataramanii* CHANDHYOK 1966*Anabaenopsis venkataramanii* CHANDHYOK, Hydrobiologia 27(3-4): 323, 1966.**Trichomes** circular or irregular screw-like coiled, with 0.5-3 coils, constricted at cross-walls; coils 12.8-28.8 μm wide.**Cells** barrel-shaped, $\pm$ isodiametric, or longer (up to 1.5x) or shorter than wide, with blue-green protoplast with aerotopes; 5.7-9.6 x 5.7-6.8 μm .**Heterocytes** spherical, (3)5.7-7.6 μm in diameter.**Akinetes** single or rarely in pairs, ellipsoidal, 9.5-11.4 x 7.6-9.5 μm .**Distribution:** Planktic in reservoirs, India.**Note:** Similar population without akinetes was described by HORTOBÁGYI (1969) from Jamuna river, India, but with smaller dimensions (cells 3-6.3 x 2.8-3.2 μm), but with elongated heterocytes (4.7-7 x 3-3.8 μm) on one end of trichomes!?Fig.: **A** = after CHANDHYOK (1966); **B** = after HORTOBÁGYI (1969), heterocytes!?

9. *Anabaenopsis milleri* VORONICHIN 1929

Anabaenopsis milleri VORONICHIN, Izv. Glavn. bot. Sada 1929: 34-35, 1929.

Trichomes solitary, irregularly screw-like coiled with up to 6(-7) coils, which are 24-27 μm wide and 2-4.8 μm high, constricted at cross-walls; often joined together with pairs of heterocytes.

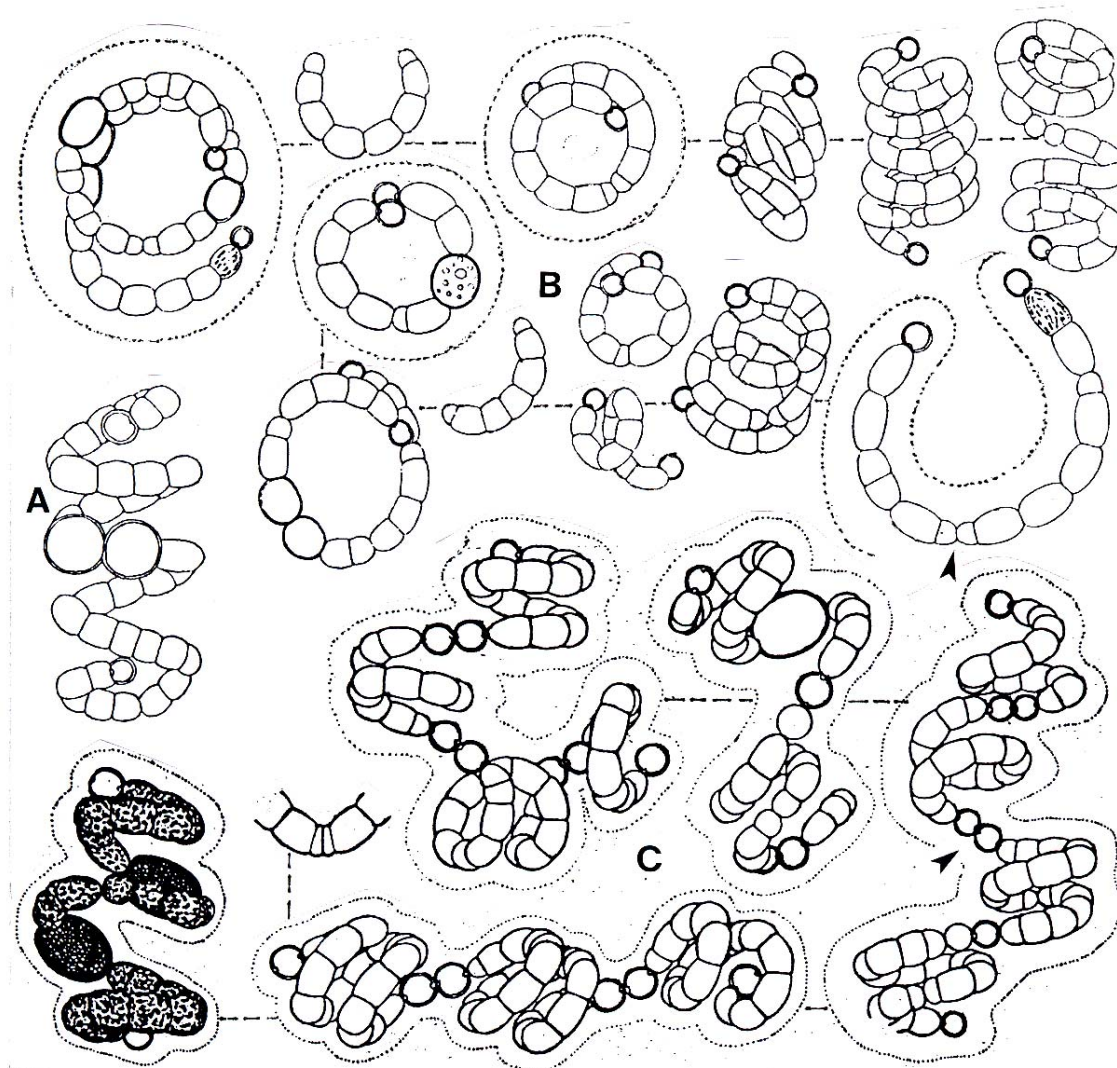
Cells widely barrel-shaped, with aerotopes, (3)4-8(11) x 4.6-8.8(9.9) μm .

Heterocytes spherical or widely oval, (3)4-8(11) x (3)4.8-8 μm .

Akinetes spherical or little longer than wide, widely oval, solitary or in pairs, (5?)8-12(15) x (5?)6-9.6(12) μm , with colourless epispor.

Distribution: Planktic in ponds and lakes, sometimes halophilic; described from central Asia (W. Siberia), rarely occurs also in Czech Republic, Hungary, Romania, and Slovakia.

Fig.: **A** = after VORONICHIN (1929); **B** = after HINDÁK (1988); **C** = after CYRUS (1952).



10. *Anabaenopsis rippkae* (FLORENZANO et al.) comb. nova

Cyanospira rippkae FLORENZANO, SILI, PELOSI et VINCENZINI, Arch. Microbiol. **140**: 305, 1985, (basionym).

Trichomes solitary, circular with up to 6 coils, constricted at cross-walls, without mucilaginous envelopes.

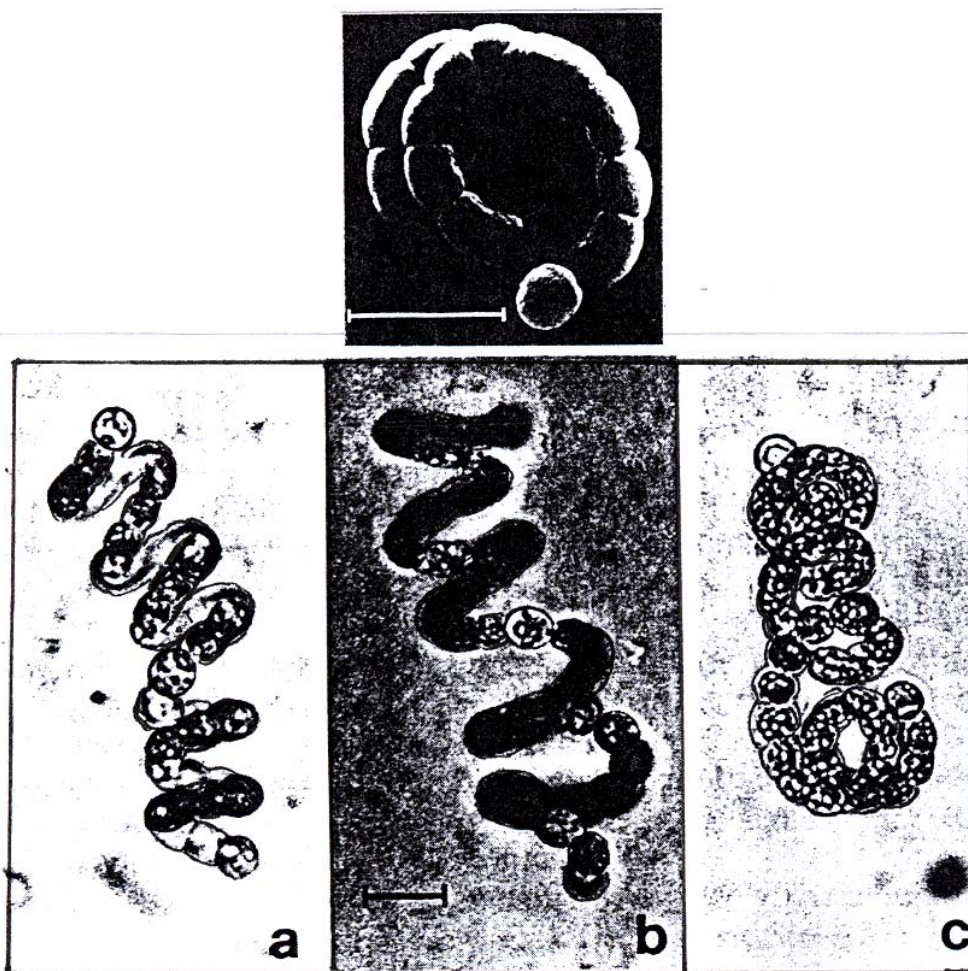
Cells shortly cylindrical, 4-5 μm wide, with aerotopes.

Heterocytes spherical or very slightly elongated and widely oval, wider than vegetative cells, 7-8.5 μm in diameter.

Akinetes almost spherical, solitary or in rows up to 4(5), ± 9 -9.6 μm in diameter.

Distribution: Described and isolated from an alkaline soda-lake in Kenya (planktic).

Fig.: After FLORENZANO et. al. (1985).



11. *Anabaenopsis arnoldii* APTEKAR' 1926

Anabaena flos-aquae var. *circularis* G.S.WEST, J. Linn. Soc. Bot. 38: 170, 1907 (p.p. excl. typo).

Anabaena (*Anabaenopsis*) *circularis* (G.S.WEST) WOŁOSZYŃSKA, Bull. Int. Acad. Sci. Cracovie, Cl. mat.-nat., ser. B, 1912: 681, 1912, (p.p. excl. typo).

Anabaenopsis circularis (G.S.WEST) MILLER, Arch. Russk. Protistol. Obšč. 2: 125, 1923 (p.p. excl. typo).

Anabaenopsis arnoldii APTEKAR', Not. Syst. Inst. Crypt. Horti bot. Princip. URSS 4, 4: 54-55, 1926.

? *Anabaenopsis arnoldii* var. *recta* ROLL, Ann. Protistol. 1(4): 164, 166, 1928, p.p.

Anabaenopsis arnoldii f. sensu KISELEV 1931 incl.

Anabaenopsis arnoldii f. („African form“) sensu TAYLOR 1932 (incl.)

Anabaenopsis arnoldii f. *rossica* APTEKAR' in ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 800, 1938, incl.

Anabaenopsis arnoldii f. *africana* TAYLOR in ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 800, 1938, incl.

Anabaenopsis arnoldii f. *kisseleviana* ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 800, 1938, incl.

Anabaenopsis arnoldii f. *philippinensis* TAYLOR in ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 800, 1938, incl.

? *Anabaenopsis arnoldii* f. *recta* (ROLL) ELENKIN, Monogr. Alg. Cyanoph., P. spec. 1: 801, 1938, p.p.

Trichomes solitary or clustered in small colonies (up to 200 µm in diameter), ± irregularly screw-like coiled, in 0.5-9(12) coils; coils 25-58 µm wide, 7-32 µm high, constricted at cross-walls, with wide, colourless, diffuent mucilaginous envelopes.

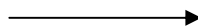
Cells ± spherical or widely barrel-shaped, grey-blue to yellow-green, usually with aerotopes, (4)6-9(11) x (4.8)5-8.5(9.4-?11.4) µm.

Heterocytes ± spherical, rarely widely oval, 5-11 x 5-10.3 µm.

Akinetes solitary or in pairs (rarely in rows?), widely elliptical, with colourless episporium, 10-19(22) x 8-14(19) µm.

Distribution: In plankton of ponds and lakes; eastern Africa, central Asia, China, Czech Republic, Hungary, India, Indonesia, Israel, Philippines, Romania, southern Russia, Ukraine, USA (Lake Erie).

Fig.: **A** = after APTEKAR' 1926; **B** = after HEGEWALD et al. (1975); **C** = after TAYLOR (1932).



12. *Anabaenopsis knipowitschii* (USAČEV) comb. nova

Anabaena knipowitschii USAČEV, Rec. l'honn. Prof. N.M. Knipovič, Moscow, 1885-1925, p. 411, 1927 (basionym).

Trichomes $\pm$ regularly screw-like coiled, up to 200 μm long, with several coils, with gelatinous, diffluent, colourless envelope.

Cells spherical, shortly barrel-shaped or widely elliptical, with aerotopes, 4-9 $\times$ 5-8 μm .

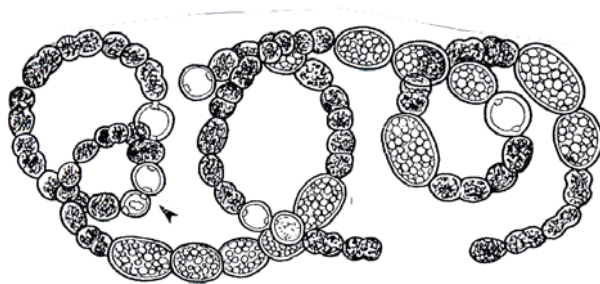
Heterocytes spherical, 8-12 μm in diameter.

Akinetes widely elliptical, solitary up to 4(5) in series, with colourless or slightly yellowish epispore, 12-20(22) $\times$ 10-14 μm .

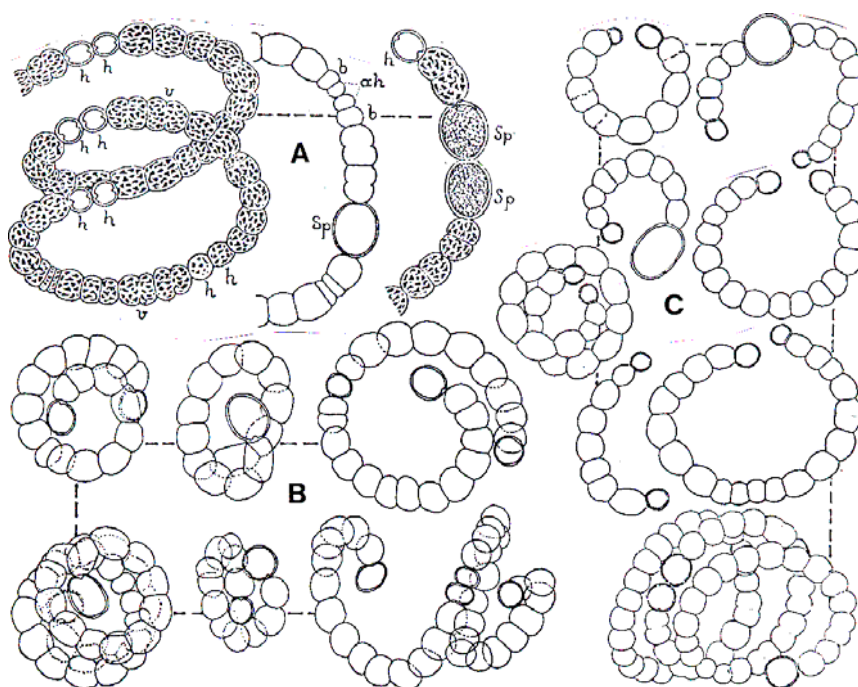
Distribution: In plankton of salty coastal lakes and ponds, forming also water blooms; Romania (Danube estuary), coastal region of Ukraine, southern Russia (Azov Sea).

Notes: Morphologically similar to *A. arnoldii*, but occurring mainly in reservoirs with higher salinity.

Fig.: After USAČEV from KONDRATEVA (1968).



A. arnoldii



13. *Anabaenopsis teodorescui* MORUZI 1960

Anabaenopsis teodorescui MORUZI, Rev. Algal. N.S. 5: 196-197, 1960.

Trichomes solitary, without gelatinous envelopes, screw-like coiled, with 3-10(12) low coils, which are 36-40 μm wide, slightly, but distinctly constricted at cross-walls.

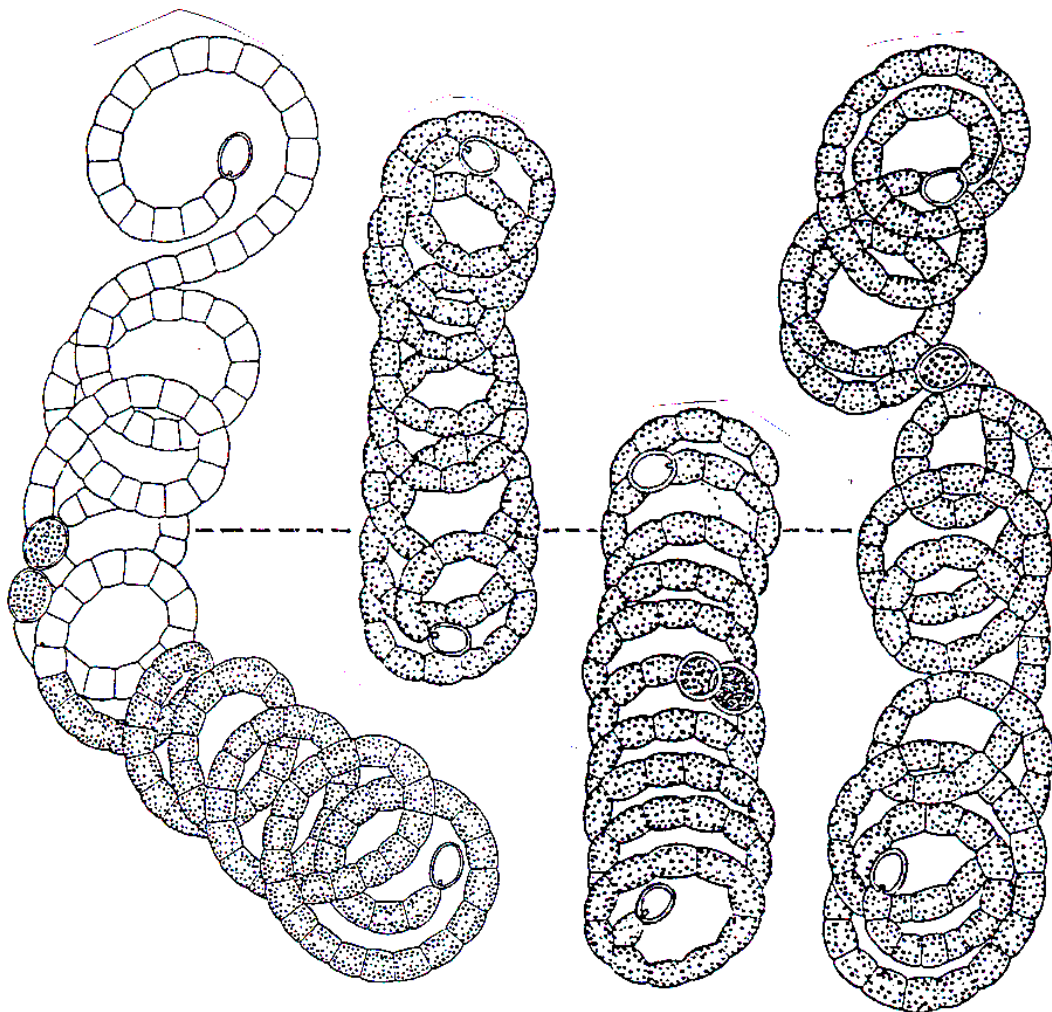
Cells slightly barrel-shaped, with aerotopes, (7)9.8-10 x (6)7-8 μm .

Heterocytes oval, 8-12 x 7-9.6 μm .

Akinetes solitary or in pairs, widely oval or almost spherical, 12-13 x 10-12 μm , with thick, smooth, colourless epispore.

Distribution: Known only from salty, polluted lake in Romania, forming water-bloom.

Fig.: After MORUZI (1960).



14. *Anabaenopsis magna* EVANS 1962

Anabaenopsis arnoldii var. *indica* RAMANATHAN, J. Ind. Bot. Soc. 17: 333-334, 1938.

Anabaenopsis magna EVANS, Hydrobiologia 20: 81-82, 1962.

Trichomes solitary, short or long, screw-like coiled with 0.5 to 16 coils, slightly constricted at cross-walls; coils 30-80 μm wide.

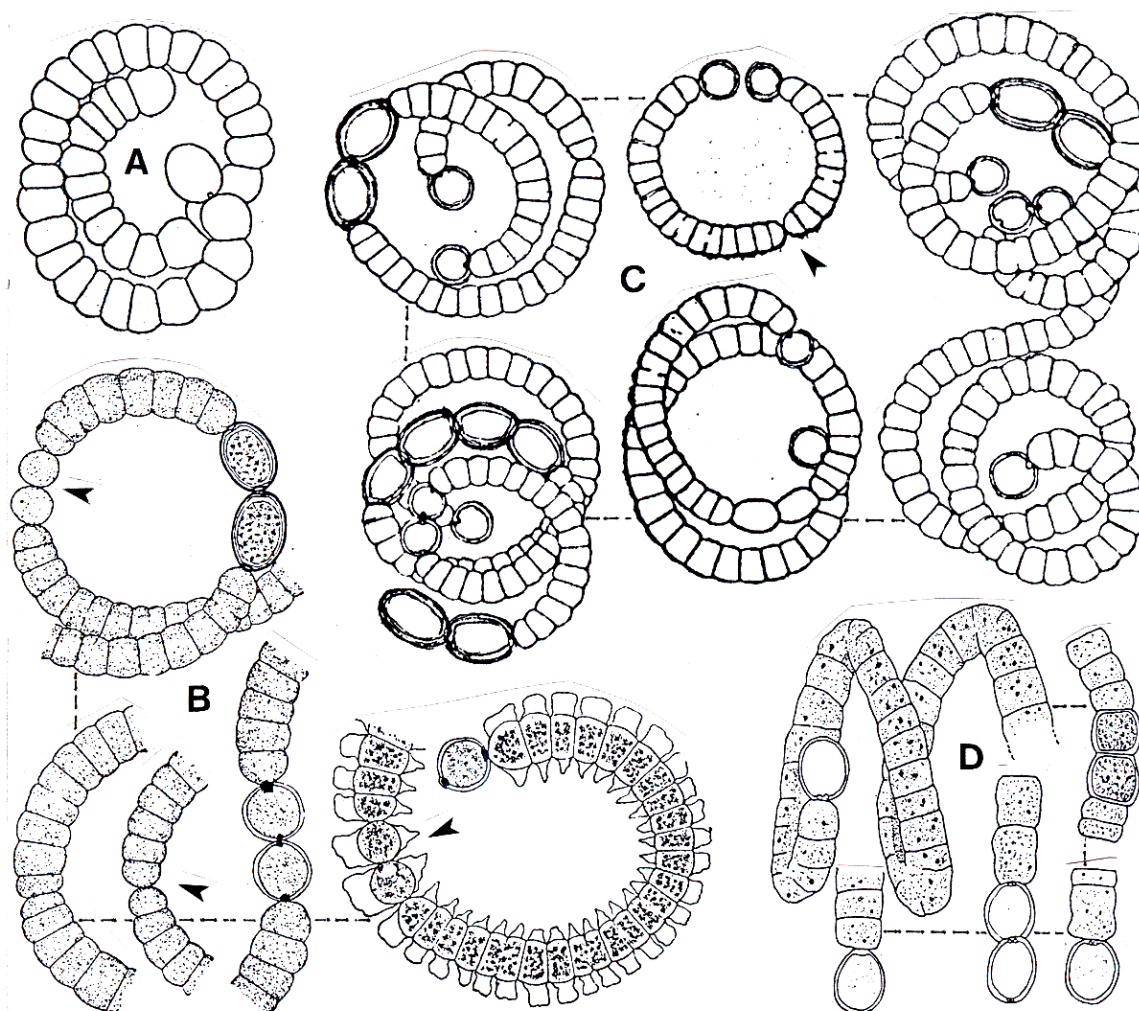
Cells almost cylindrical to slightly barrel-shaped, $\pm$ isodiametric or shorter than wide, without visible aerotopes or with few aerotopes, blue-green, with finely granular content, 5.7-12 x 7.6-11.4 μm .

Heterocytes almost spherical or slightly oval, 9.5-17.1 μm in diameter (longer axis).

Akinetes rarely solitary, usually in pairs, barrel-shaped to widely oval, with slightly striated episporium, 10-22.8 x 11-19 μm .

Distribution: Planktic in large rivers and lakes (near shore); India, Kenya, Peru.

Fig.: A = after JEEJI-BAI et al (1977); B-C = after RAMANATHAN (1938); D = after EVANS (1962).



15. *Anabaenopsis issatschenkoi* VORONICHIN 1934

Anabaenopsis issatschenkoi VORONICHIN, Exp. Koulandine Acad. Sci. URSS, Tr. Sov. Izv. Priro. Res., ser. Sibirsk. 8: 182-183, 1934.

Trichomes densely, irregularly coiled, forming clustered colonies up to 100 µm in diameter, with slightly visible mucilaginous envelopes, distinctly constricted at cross-walls; coils $\pm$ 27 µm wide, between coils spaces up to 3.6 µm wide.

Cells shortly, asymmetrically barrel-shaped, always shorter than wide, without visible aerotopes, 4.5-5 x 5.4-7 µm.

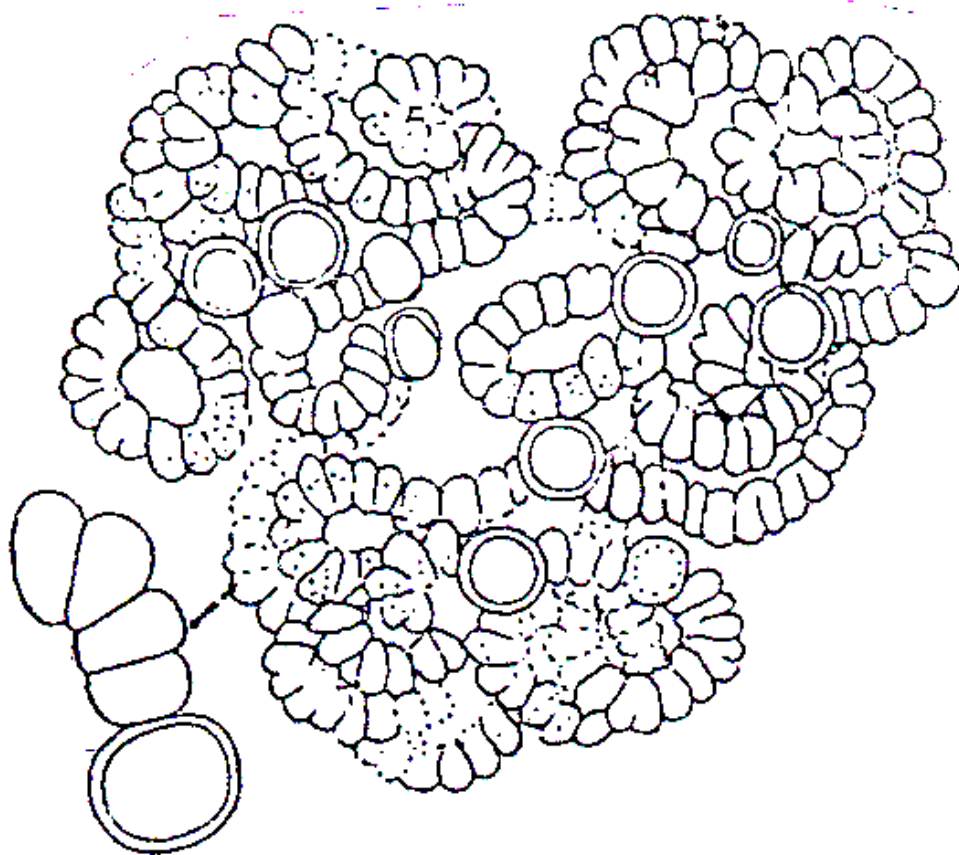
Heterocytes spherical or widely elliptical, 8.5-9.5(12.6) x 8.5-10.8 µm.

Akinetes not known.

Distribution: Planktic in mineralised (natron) shallow waters, sometimes forming water-blooms; described and known only from SW. Siberia, Russia.

Notes: The generic identification is not clear.

Fig.: After VORONICHIN from HOLLERBACH et al. (1953).



16. *Anabaenopsis abijatae* KEBEDE et WILLÉN 1996

Anabaenopsis abijatae KEBEDE et WILLÉN, Algolog. Stud. **80**: 3, 1996.

Trichomes very densely and irregularly coiled (in loops) and packed to compact, $\pm$ spherical clusters, up to 200 μm in diameter, enveloped by distinct slime, distinctly constricted at cross-walls.

Cells short, asymmetrically barrel-shaped, often shorter than wide up to almost subspherical, with aerotopes, 6-12 x 4-8 μm .

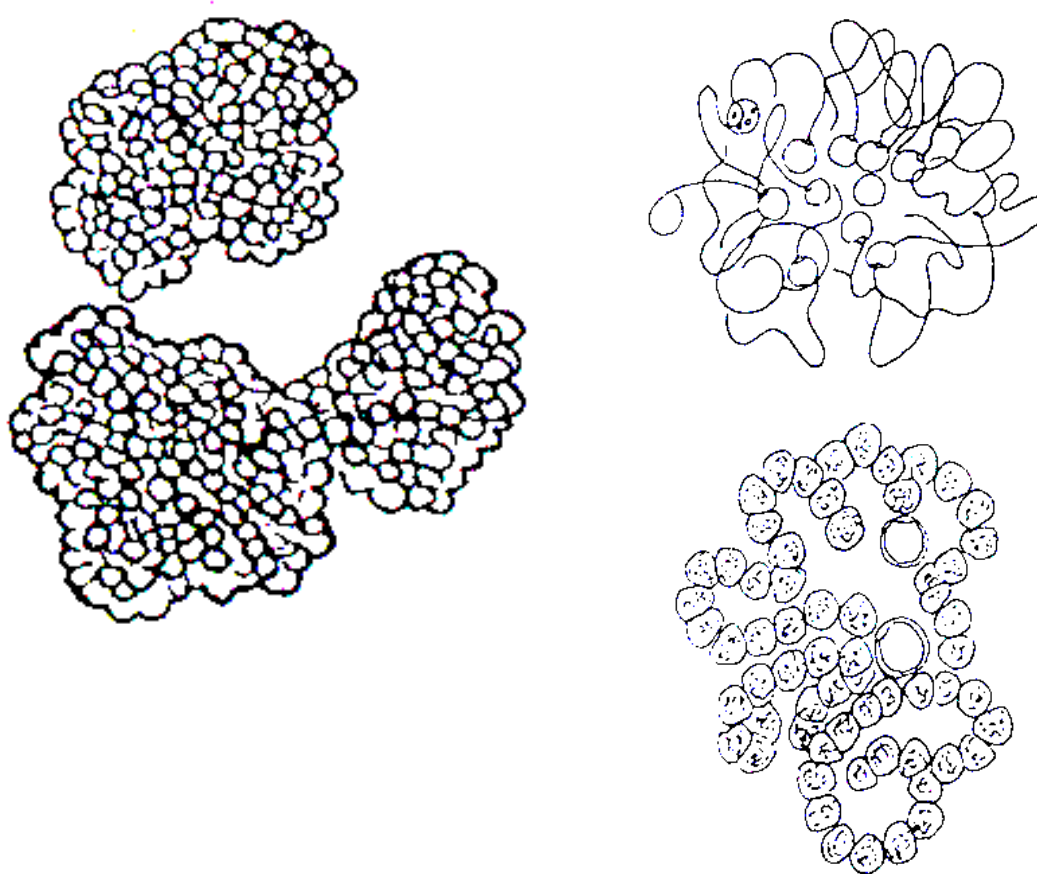
Heterocytes spherical to slightly widely oval, 7-12 x 6-7(10) μm .

Akinetes $\pm$ spherical, solitary or rarely in pairs, 12-14 x 8-10(14) μm .

Distribution: Planktic in eutrophic, mineralised lakes; Ethiopia.

Notes: Generic confirmation is necessary.

Fig.: After KEBEDE & WILLÉN (1996).



Excludenda

- Anabaenopsis raciborskii* WOŁOSZ. 1912 p.p. (sine typo) = *Cylindrospermopsis philippinensis* (TAYLOR) KOM. 1984
- Anabaenopsis raciborskii* (WOŁOSZ.) ELENK. 1923 = *Cylindrospermopsis raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis cuatrecasasii* GONZ.–GUERR. 1928 = *Cylindrospermum majus* KÜTZ. ex BORN. et FLAH. 1888
- Anabaenopsis hispanica* GONZ.–GUERR. 1928 (incl. var. *luteola*) = ? *Cylindrospermum licheniforme* KÜTZ. ex BORN. et FLAH. 1888
- Anabaenopsis philippinensis* TAYLOR 1932 = *Cylindrospermopsis philippinensis* (TAYLOR) KOM. 1984
- Anabaenopsis sturmieae* VORONICH. 1934 = probably *Trichormus*; solitary heterocytes develop from both terminal and intercalar cells, akinetes develop serially between heterocytes
- Anabaenopsis raciborskii* var. *lyngbyoides* GEITL. 1935 = *Cylindrospermopsis* cf. *raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis raciborskii* var. *longiscellula* SZALAI 1942 = *Cylindrospermopsis* cf. *raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis tanganyikae* var. *longiscellula* SZALAI 1942 = *Cylindrospermopsis* sp.
- Anabaenopsis seriata* PRESC. et ANDREWS 1955 s. str. = *Cylindrospermopsis raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis woloszynskae* CLAUS 1961 = ? *Cylindrospermopsis raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis koganii* OBUCH. 1964 = *Cylindrospermopsis raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis maksimilianii* OBUCH. 1964 = *Cylindrospermopsis raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis wustericum* OBUCH. 1964 = *Cylindrospermopsis raciborskii* (WOŁOSZ.) SEENAYYA et SUBBA-RAJU 1972
- Anabaenopsis gangetica* NAIR 1967 = Prior name of *Cylindrospermopsis curvispora* M. WATANABE 1995

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