

The cyanobacterial genus *Macrospermum*

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Abstract: This small tropical cyanobacterial group, containing *Anabaena volzii* LEMMERMANN and a few related species (*A. fuellebornii* SCHMIDLE, *A. unispora* GARDNER, *A. mysorensis* GONZALVES & KAMAT), differs substantially phenotypically from all other planktic or benthic *Anabaena* types, mainly by the subsymmetric structure of the trichomes, type of akinete formation and restricted ecology. The taxonomic uniformity of all other *Anabaena*-like clusters (typical benthic *Anabaena*, planktic *Anabaena* subg. *Dolichospermum*, *Trichormus*, *Aphanizomenon*, *Cuspidothrix*) was already supported by molecular analyses. All of them also have their typical morphological markers, which are clearly different from the “*Anabaena volzii* – cluster”. Therefore, this group can not be classified in any of the mentioned revised genera and must be described as a separate generic entity of heterocytous cyanobacteria (although they have not been sequenced to date). The new genus *Macrospermum* is therefore defined in my article with 4 related, morphologically distinguishable species. The generic name is selected according to the unusually large akinetes.

Key words: Cyanobacteria, taxonomy, *Anabaena*, *Macrospermum*, pantropical genus, akinete formation

Introduction

SCHMIDLE (1902) described a cyanobacterial species *Anabaena fuellebornii* from Africa. This metaphytic species was later found from several localities in tropical Africa (Chad, Guinea, Tanzania – COMPÈRE 1967, 1974, BOURRELLY 1975), tropical Asia (Burma – SKUJA 1949) and America (Brazil, Cuba – KOMÁREK 2005, orig. data). In 1904, LEMMERMANN described *Anabaena volzii*, having a similar trichome structure, from plankton and benthos in Singapore. This species was found also in numerous localities over the whole tropical region in Asia (S. China, India, Indonesia, Singapore – GEITLER 1932, JAO 1948, FRITSCH 1949, GUPTA 1956, DESIKACHARY 1959), Africa (Chad, Guinea, Mozambique, Tanzania – BOURRELLY 1975, RINO 1972) and Central America, particularly in the Caribbean district (Cuba, Guadeloupe, Venezuela – BOURRELLY & MANGUIN 1952, YACUBSON 1974, KOMÁREK 1984, 2005). The number of similar species was enlarged by *Anabaena unispora* GARDNER 1927 known in typical form from Puerto Rico and Cuba, and also by *Anabaena mysorensis*, described by GONZALVES & KAMAT (1959) from India (Mysore State). All of these species have a unique, very specific

morphology, which is different from all other *Anabaena* species. The filaments are nearly symmetric, uniserial, unbranched and isopolar, with two heterocytes localized in the subapical portions of the trichomes, slightly distant from the terminal parts. One central, third heterocyte, localised \pm in the centre of a trichome, sometimes occurs in fully developed trichomes. Unusually large, solitary, oval or ellipsoid akinetes (very exceptionally occurring in pairs) develop after fusion of several vegetative cells joined to the heterocyte on the external side of the heterocyte. The filaments have a typical symmetrical or subsymmetrical structure (in the second case the heterocytes are a little shifted from the central or subterminal positions). Exceptions from this trichome structure can occur, but they are very rare (Fig. 1). Of course, the asymmetry appears after trichome disintegration and in developing filaments.

The cluster of “*Anabaena volzii*”-like species contains now four tropical species. The only non-confirmed record from the temperate zone is “*A. unispora*” from Michigan, recorded by PRESCOTT (1962), but with several unclear features. The species of this cluster differ from one another by the form of the cells (particularly

in the apical parts of trichomes), and the form and colour of akinete episporos. *Anabaena volzii* f. *recta* KISELEV 1931, characterised by straight trichomes, and *A. volzii* var. *crassa* (RAO) FRITSCH 1949 seem to be in the variation range of the

typical species. All transitions between straight, waved and coiled filaments occurred in our studied populations; also, the dimensions in all described populations only slightly deviated and overlapped with all transient forms (Tab. 1).

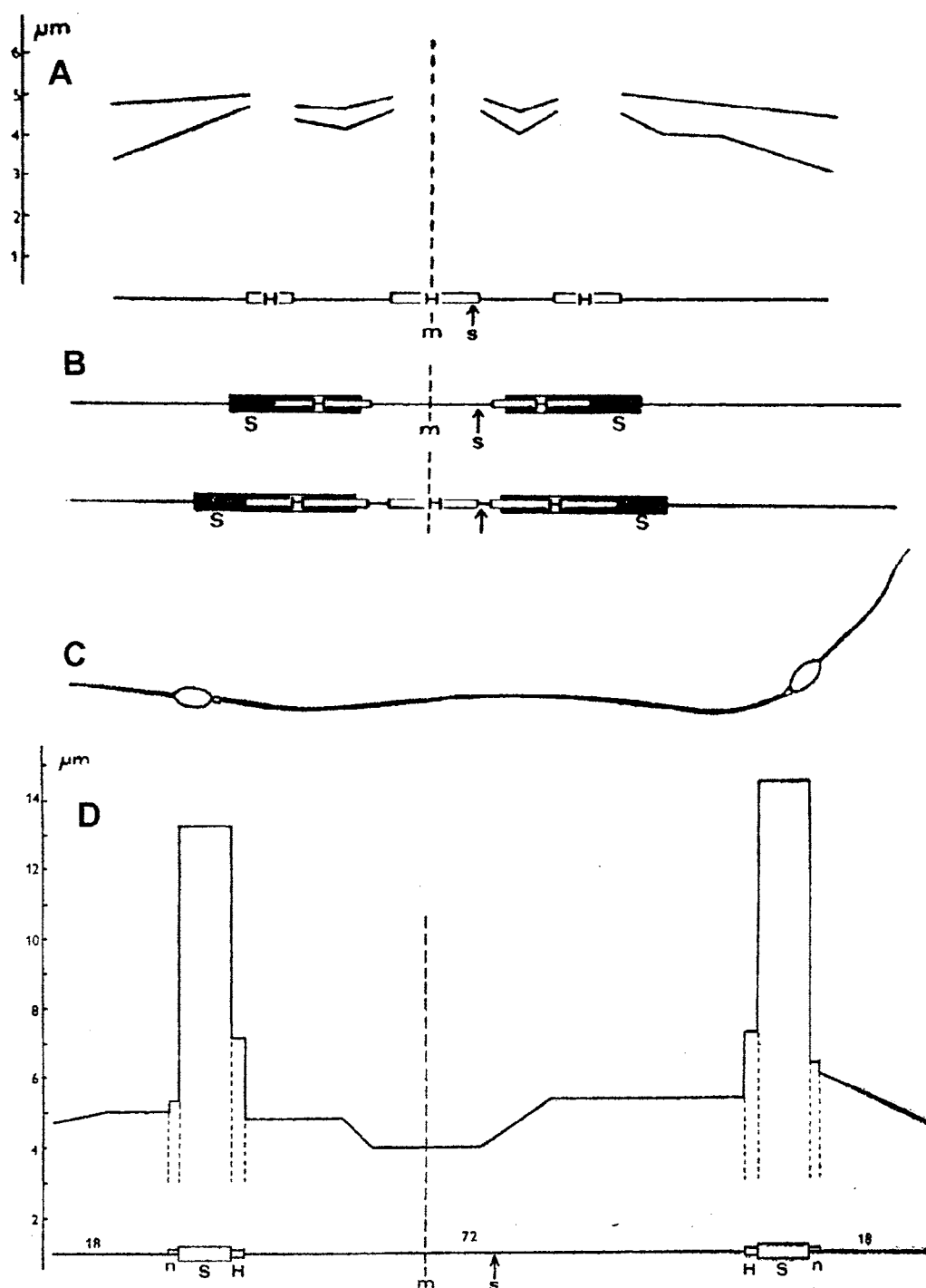


Fig. 1. Scheme of the slightly subsymmetric to symmetric trichomes of "*Anabaena/Aphanizomenon*" (= *Macrospermum*) *volzii* (populations from Cuba) and their development: A – variability of cell width in trichomes and position of heterocytes (H) in filaments; B – variability (average limits from 48 filaments) in the position of heterocytes (H) and akinetes (S) in trichomes with two (48 measurements) and three (14 measurements) heterocytes; C – typical filament with two heterocytes and two akinetes at low magnification; D – scheme of a typical filament with fully developed akinetes and average width of vegetative cells, necridic cells (n), akinetes (S), heterocytes (H) and with the number of cells in corresponding segments of trichomes; m = morphological centre of a trichome, s = geometrical centre of a trichome. (After KOMÁREK 1984, sub *Aphanizomenon volzii*.)

Thus, the *Anabaena volzii*-type differs from the other *Anabaena*-like species (both planktic or benthic) by the specific trichome structure (in all *Anabaena*-types is strictly metameric), from *Aphanizomenon* and *Cuspidothrix* by the morphology of cells, type of life (formation of mats), position and form of akinetes, and form of colonies. This type also differs from other nostocalean genera by the special subsymmetric structure of the trichomes and the position of the heterocytes and akinetes (Fig. 2). No species from the whole described *Anabaena volzii* cluster has been isolated in culture up to now, nor have they yet been sequenced. However, their morphology and life form differ substantially from all genera, as shown by generic analyses and confirmed by the corresponding phenotypic markers (*Anabaena*, *Aphanizomenon*, *Cylindrospermum*, *Cylindrospermopsis*, *Cuspidothrix*, *Trichormus*, *Anabaenopsis*, and others – cf. e.g., GUGGER & al. 2002a, b, RAJANIEMI et al. 2005, etc). Because the generic classification of this characteristic morphological group into any existing genus is not possible, the description of a new generic entity is necessary (e.g., for the prepared monographic elaboration of the heterocytous cyanobacteria for Süsswasserflora von Mitteleuropa).

Results

The main generic phenotypic diacritical feature of the new genus *Macrospermum* is the structure of the trichomes: The trichomes are isopolar with a nearly symmetric or subsymmetric structure (KOMÁREK 1984). The heterocytes develop in the apical parts of trichomes, slightly distant from the ends. The third heterocyte develops in old trichomes \pm in the centre, or slightly shifted from the geometric middle of a trichome. Akinetes develop after fusion of several vegetative cells, attached to a marginal heterocyte, usually on the side towards the ends of a trichome, exceptionally at both sides of marginal heterocytes. The akinete was never observed at the central heterocyte. Trichome width in *Anabaena* (= *Macrospermum*) *volzii* is always a little greater in parts with heterocytes, while being slightly narrowed between heterocytes and towards the ends (Fig. 1).

Usually, only two akinetes develop in a trichome, very rarely in pairs. They are formed after fusion of few neighbouring vegetative cells and are extremely large (oval or ellipsoidal) in

comparison with akinetes of other genera. The epispore is smooth or sculptured; differences in surface structure of akinetes is considered as differential feature between morphospecies.

All described species are distributed in tropical regions (with one exception – see discussion; PRESCOTT 1962). They appear in aquatic habitats, marshes, ponds, the littoral of lakes and in paddy fields. They form free colonies (disintegrating fine mats) on water plants, or small floating clusters in the metaphyton. Solitary trichomes or small groups of filaments can occur less frequently and secondarily also in the plankton. Facultatively rare aerotope-like inclusions occur in cells of *Anabaena* (*Macrospermum*) *volzii*.

Formal description of the genus *Macrospermum*: Cyanobacterial, heterocytous, filamentous genus. Filaments are free-living, solitary, in small irregular clusters or in fine macroscopic mats. Trichomes have symmetric to subsymmetric structure with two subapical heterocytes and sometimes with one \pm central heterocyte; they are nearly straight or irregularly coiled with fine, colourless, diffuent and indistinct slime, uniseriate, unbranched, \pm cylindrical, constricted at cross-walls, sometimes narrowed to the ends and in distinct central parts. Cells cylindrical or slightly barrel-shaped, \pm isodiametric or rather longer than wide, with blue-green, homogeneous content with scarce granules and facultatively with solitary aerotopes; terminal cells are rounded, conical or narrowed and bluntly pointed. Heterocytes always solitary, intercalary, cylindrical, usually wider than vegetative cells, usually two in subapical position in a trichome, or with the third heterocyte \pm in the middle of a trichome. Akinetes widely oval, developing from several neighbouring cells, large, solitary, rarely in pairs, always attached to outer heterocytes; in one trichome develop usually only two akinetes, outside from heterocytes, rarely also at the “inner” side of a heterocyte. Reproduction by fragmentation of trichomes and by akinetes. Type species: *Macrospermum volzii* (LEMMERMANN) comb. nova (= *Anabaena volzii* LEMMERMAN 1904). This species was selected as the type-species instead of the older “*Anabaena fuellebornii*” (1902), because it is the best known and most distributed species from the whole new genus.

Diagnosis: *Macrospermum* genus nova – Genus cyanobacteriis heterocytosis. Filamenta

solitaria, libere natantia vel in strata irregularia, macroscopica aggregata, sine vaginis, vel cum muco incolore, tenue, amorpho circumdatae. Trichomata uniseriata, plus minusve recta vel irregulariter flexuosa, not ramosa, symmetrica vel subsymmetrica, ad dissepimenta constricta, ad apices paucim attenuata vel cylindrica, cum heterocytis duobus subapicalis, raro cum heterocyta tertia centrali. Cellulae cylindricae vel paucim barriliformes, plus minusve isodiametricae vel longior quam latae, contentu aerugineo, homoganeo, cum granulis sparsis et aerotopis solitariis facultativis; cellula terminalis cylindrica vel conica, apice rotundata. Heterocytiae intercalares, solitariae, cylindricae, plerumque latior quam cellulae vegetativae, in trichomatibus subapicaliter dispositae, rare plus una heterocyta centralis. Akinetes late ovals, intercalares, cum heterocytis conjunctae, valde ad eos partes externis dispositae, solitariae, rarissime binae, cum episporio laevi vel ornati, praecipue duas in una trichoma. Reproductio trichomatibus fragmentatione et akinetis germinatione. - Typus generis: *Macrospermum volzii* (LEMMERMANN) comb. nova (syn.: *Anabaena volzii* LEMMERMAN 1904).

List of species:

Macrospermum volzii (LEMMERMANN) comb. nova (Fig. 3)

Basionym: *Anabaena volzii* LEMMERMAN Abh. Nat. Ver. Bremen 18(1): 153, 1904.

Syn: *Anabaena volzii* f. *recta* I. KISELEV Tr. Sr.-Aziat. Gos. Univ. (Tashkent), Ser. XIIa, 9: 74, 1931; incl.; *Anabaena unispora* var. *crassa* RAO Proc. Ind. Acad. Sci. 6(6B): 362, 1937; incl.; *Anabaena volzii* var. *crassa* (RAO) FRITSCH J. Ind. Bot. Soc. 28(3): 155, 1949; incl. *Anabaena volzii* var. *unispora* (GARDNER) BOURRELLY sensu BOURRELLY Bull. Inst. France Afr. Nord., ser. A, 19(4): 1049, 1957; incl.; *Aphanizomenon volzii* (LEMMERMANN) KOMÁREK Acta Bot. Cubana 18: 9, 1984.

Diacritical characters: Cells cylindrical, 4.5-14 x 4-5.8 µm; apical cells slightly elongated, narrowed and bluntly pointed; akinetes with smooth, colourless or brownish epispor, (20)32-48 x (13)15-21 µm. With pantropical distribution and in central Asia (E. KISELEVA 1931, I. KISELEV 1931 from ELENKIN 1938).

Macrospermum fuellebornii (SCHMIDLE) comb. nova (Fig. 4)

Basionym: *Anabaena fuellebornii* SCHMIDLE Engler's

Bot. Jahrb. 32: 61, 1892.

Diacritical characters: Cells slightly barrel-shaped, 3.8-8.2 x 4.8-7.4 µm; apical cells slightly narrowed, rounded; akinetes with granular-dotted, brownish epispor, 25-45 x (14.3)16.5-19(21.6) µm. With pantropical distribution.

Macrospermum mysoreense (GONZALVES et KAMAT) comb. nova (Fig. 5)

Basionym: *Anabaena mysorensis* GONZALVES et KAMAT Hydrobiologia 13: 237, 1959.

Diacritical characters: Cells cylindrical, up to twice as long as wide, 6.4-12.3 x 5.8-7.5 µm; apical cells probably cylindrical and rounded (not described in the original diagnosis); akinetes ellipsoidal to oval, having epispor with pointed, up to 3,2-4,5 µm long, spines, 35.8-51,6 x 12.5-19.4 µm. Known only from India (Mysore State).

Macrospermum unisporum (GARDNER) comb. nova (Fig. 6)

Basionym: *Anabaena unispora* GARDNER Mem N.Y. Bot. Garden 7: 59, 1927.

Syn.: *Anabaena volzii* var. *unispora* (GARDNER) BOURRELLY Bull. Inst. Franc. Afr. Nord, Ser. A, 19(4): 1049, 1957.

Diacritical characters: Cells cylindrical, mostly isodiametric, infrequently up to twice as long than wide, 4-10.2 x 4-5.4 µm; apical cells ± cylindrical, rounded; akinetes with smooth, brown epispor, (18)20-40(43) x (8)12.5-20.5 µm. Known from tropical America, particularly from the Caribbean district (Cuba, Puerto Rico); the records from Michigan (PRESCOTT 1950) need confirmation.

The key to the species identification:

1a Ripe akinetes with smooth epispor **2**
1b Ripe akinetes with sculptured epispor **3**

2a Vegetative cells isodiametric or (usually) longer than wide, apical cells elongated, narrowed, end cell bluntly pointed ***M. volzii***

2b Vegetative cells commonly isodiametric or only slightly longer than wide, apical cells cylindrical, not narrowed, end cell cylindrical and rounded ***M. unisporum***

3a Surface of akinetes granular-dotted (brownish), cells ± isodiametric, end cells cylindrical to slightly barrel-shaped, apical cells conical rounded ***M. fuellebornii***

3b Surface of akinetes with pointed spines, cells cylindrical, longer as wide (up to twice), apical cells

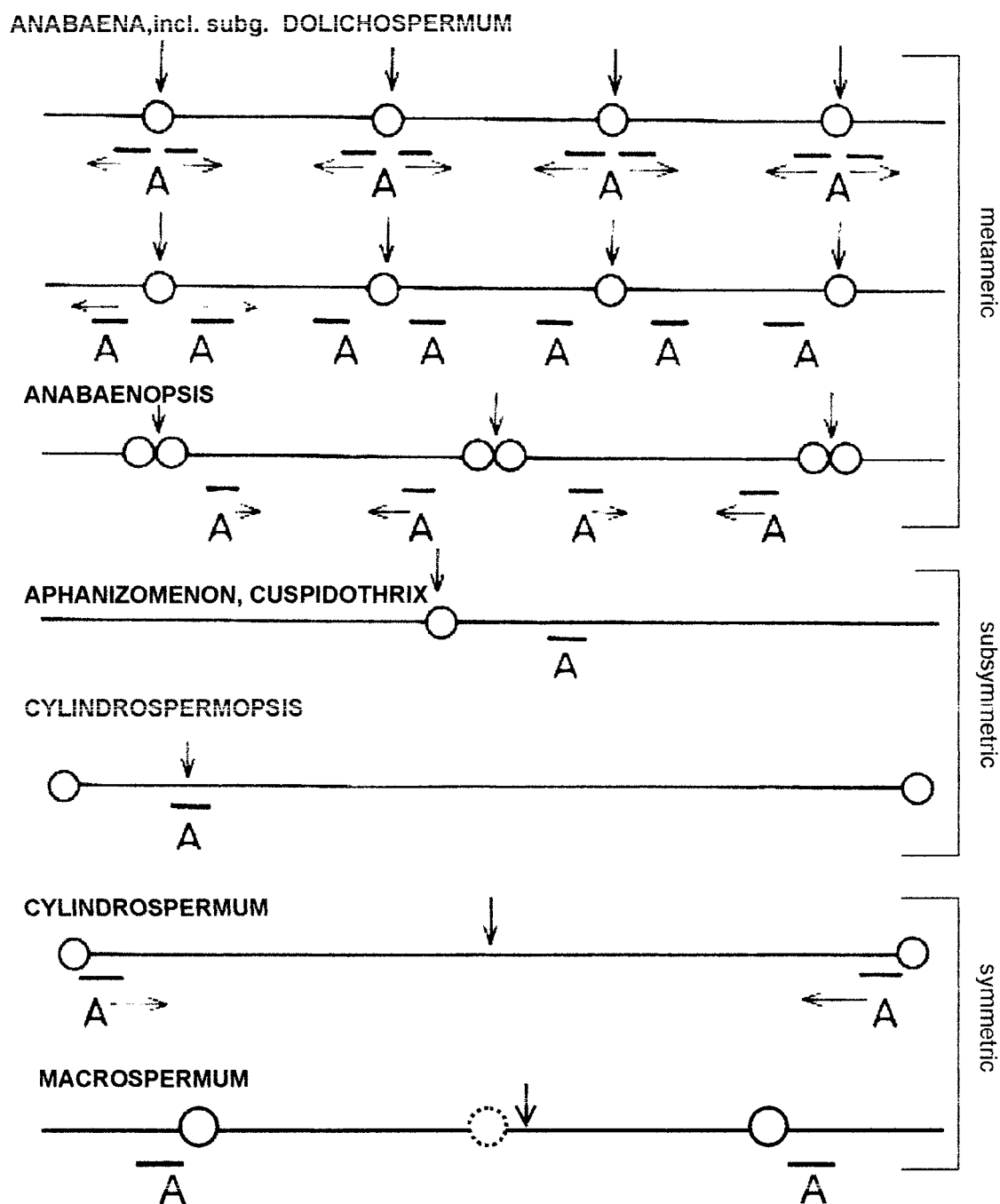


Fig. 2. Scheme of the trichome structure of *Macrospermum* in comparison with other nostocalean genera with paraheterocytic origin of akinetes; circles indicate the places of heterocyte origin: A = place of akinete development. (Partly from KOMÁREK & ANAGNOSTIDIS 1989.)

cylindrical rounded (?) *M. mysorensis*

Discussion

The modern taxonomy of cyanobacterial genera is based primarily on molecular sequencing, joined with a combined evaluation of phenotypic, biochemical and ecological markers. However, typical characteristic phenotype markers were found in all generic units, being defined and supported

by phylogenetic studies. The groups of genera, which evidently do not belong to clusters already revised by molecular sequencing and which morphologically evidently belong beyond the range of morphological variation of complexly revised generic entities remain taxonomically problematic. The group of the genus *Macrospermum* is just a typical case of such clusters. The various species were described as members of the traditional

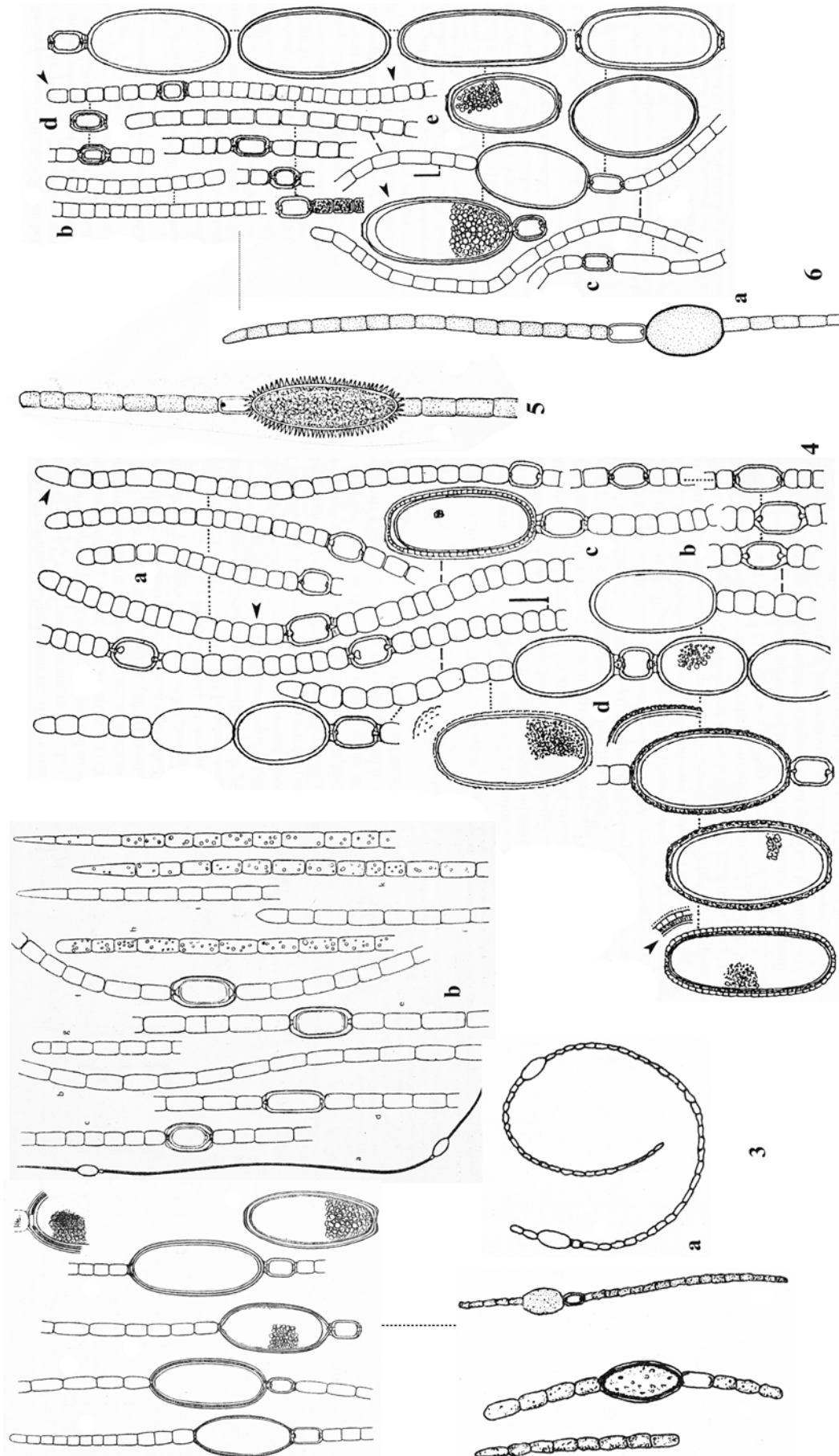


Fig. 3. *Macrospermum fuellebornii*: a – original drawing after LEMMERMANN (1904, sub *Anabaena volzii*); b – populations from Cuba after KOMÁREK (1984, sub *Aphanizomenon volzii*); Fig. 4. *Macrospermum fuellebornii*: a – ends of trichomes; b – variability of heterocysts; c – position of a heterocyst with joined akinete; d – variability of akinetes (from KOMÁREK 2005, sub *Anabaena fuellebornii*); Fig. 5. *Macrospermum mysorensis* (after GONZÁLEZ & KAMAT 1959 from India – Mysore, sub *Anabaena mysorensis*); Fig. 6. *Macrospermum unisporea*: a – original drawing after GARDNER (1927) from Puerto Rico; b-e – variability of trichome ends, heterocysts and akinetes from the Cuban population, after KOMÁREK (2005), (all sub *Anabaena unisporea*).

genus *Anabaena*, but their morphology is substantially different (subsyzmetric structure of trichomes) from the updated and revised metameric *Anabaena*-like clusters. This includes typical benthic *Anabaena* species, based on the type-species *A. oscillarioides* BORY ex BORNET et FLAHAULT 1888, planktic *Anabaena* subg. *Dolichospermum* with the type-species *A. flos-aquae* (LYNGBYE) BRÉBISSEON ex BORNET et FLAHAULT 1888, as well as the genus *Trichormus* with apoheterocytic formation of akinetes with type species *T. variabilis* (KÜTZING ex BORNET et FLAHAULT) KOMÁREK et ANAGNOSTIDIS 1989 (sooner “*Anabaena variabilis*” KÜTZING ex BORNET et FLAHAULT 1886).

Macrospermum, by having a symmetric or subsyzmetric structure of trichomes is similar mainly to the genera *Cylindrospermum*, *Aphanizomenon*, *Cuspidothrix* and *Cylindrospermopsis* (cf. Fig. 2). *Cylindrospermum* and *Cylindrospermopsis* differ by the development of heterocytes from terminal cells, *Aphanizomenon* and *Cuspidothrix* by the type of akinete formation and the life form. However, the phylogenetic position of *Macrospermum* seems to be rather near this group of genera than to the *Anabaena*-like clusters, to which all the *Macrospermum* species were traditionally classified.

All of the species morphologically congruent with the genus *Macrospermum* are described from aquatic biotopes in tropical regions. To this can be added also the rice fields in Tadzhikistan near Samarkand (central Asia; see KISELEV in HOLLERBACH & al. 1953 and DESIKACHARY 1959). The only exception is “*Anabaena unispora*” recorded by PRESCOTT (1962) from Michigan, USA. However, this specimen has cells up to twice as long than the type and the akinetes develop “near the middle of the filaments, with the dimensions 20–34 x 11–15 µm”. The identity of these populations with typical *Macrospermum unisporum* is therefore problematic and should be confirmed.

Thus, the genus *Macrospermum* is described, because the group of “*Anabaena volzii*” remained out of any generic classification after molecular confirmation of the most related anabaenacean genera.

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