Studies on the cyanophytes (*Cyanobacteria*, *Cyanoprokaryota*) of Cuba 11. Freshwater *Anabaena* species

Studie o sinicích (*Cyanobacteria*, *Cyanoprokaryota*) Kuby. 11. Sladkovodní druhy rodu *Anabaena*

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Nineteen traditional *Anabaena* morphospecies were found in freshwater habitats in Cuba. Their taxonomic identification is discussed and variation in natural populations described. Seven species are known only from tropical countries (*A. ambigua, A. fuellebornii, A. iyengarii, A. oblonga, A. orientalis, A. recta, A. volzii*), four from tropical America (*A. manguinii, A. portoricensis, A. torques-reginae, A. unispora*), one was originally described from southern Africa (*A. austro-africana*) and one from central Asia (*A. turkestanica*). Two taxa are recognized as new species (*A. hatueyi, A. jeejiae*) and two remain unidentified (*Anabaena* spp.) because of a shortage of material. Only two species, *A.* cf. *reniformis* and *A.* cf. *bornetiana*, may occur also in the temperate zone (Europe or North America) and as special morphotypes in Cuba.

K e y w o r d s : *Anabaena*, central America, *Cyanobacteria*, *Cyanoprokaryota*, distribution, ecology, phenotype, taxonomy

Introduction

This review is the next in a series of studies on the cyanobacterial microflora of tropical America (Komárek 1984, 1989, 2003, Komárek & Komárková-Legnerová 2002). Nineteen freshwater *Anabaena* morphospecies were found during our studies of the cyanoprokaryotic flora of Cuba (five of them are published in Komárek 1984 and 1989). All species are listed in Table 1. The generic characters of these species (mainly their trichome structure) are discussed particularly in respect to the genera *Aphanizomenon* and *Trichormus*. This review includes all the species corresponding to the traditional generic diagnosis of *Anabaena*. Species, which were included in previous studies, are mentioned only briefly.

Of the recorded *Anabaena* species, two are not yet validly described and two need to be re-evaluated and taxonomically re-combined. All other species belong to tropical, or, at least to subtropical species, with two exceptions, *A.* cf. *reniformis* and *A.* cf. *bornetiana,* described and known from central and eastern Europe and North America, respectively. The modern classification of cyanoprokaryotes is based on a combined evaluation of molecular and phenotypic markers. However, a morphological description of specimens from natural populations is important for determining phenotypic variation and studying the ecology of particular species. The rejection of papers that include only morphological or ecological descriptions is as serious a mistake as rejecting of molecular studies of strains that lack careful description of their phenotypic variation. The isolation of strains from

Table 1. – List of freshwater *Anabaena* species recorded from Cuba, distinguished by using traditional methods.

Species	Number of studied populations	Ecology	Distribution	References
A. cf. *reniformis* Lemm. 1898	1	planktic (solitary coiled trichomes; aerotopes)	Germany, Ukraine; Cuba: Oriente	Hollerbach et al. 1955
A. torques-reginae Komárek 1984	3	planktic (solitary coiled trichomes; aerotopes)	tropical America: Brazil, Cuba, San Salvador	Komárek 1984
A. austro-africana Cronberg et Komárek 2001	4	planktic (solitary or in small clusters; aerotopes)	pantropical?; Brazil, Cuba, Southern Africa	Cronberg & Komárek 2001, Komárek et al. 2001
A. turkestanica (Kisel.) comb. nova	1	metaphytic (facultatively planktic?; clustered trichomes)	Central Asia; Cuba	Elenkin 1938 Hollerbach et al. 1955
Anabaena sp. 1	1	metaphytic (small clusters, second. planktic; faculatively aerotopes)	Cuba: Pinar del Río	
A. cf. recta Geitl. 1935	4	planktic (solitary straight trichomes; aerotopes)	probably pantropical (Cuba, Indonesia)	Geitler & Ruttner 1935 Komárek 1984
A. manguinii (Bourr.) comb. nova	2	planktic (solitary ± straight trichomes; aerotopes)	Caribbean region (Cuba, Guadeloupe, Mexico); Brazil (Pernambuco)	Bourrelly & Manguin 1952 Komárek 1984
A. hatueyi spec. nova	1	planktic (solitary straight trichomes; aerotopes)	Cuba	Komárek 1984
Anabaena sp. 2	1	metaphytic	Cuba	
A. orientalis Dixit 1936	4	metaphytic	pantropical	Desikachary 1959
A. iyengarii Bharadw. 1935	5	metaphytic	pantropical	Desikachary 1959
A. oblonga De-Wild. 1897	2		pantropical	Komárek 1989
A. cf. *ambigua* Rao 1937	3	facultatively planktic (solitary or clustered trichomes; facultatively aerotopes)	pantropical (Cuba, India)	Desikachary 1959
A. volzii Lemm. 1906		metaphytic, sec. free floating (without aerotopes)	pantropical	Desikachary 1959 Komárek 1984
A. fuellebornii Schmidle 1892	4	metaphytic	pantropical	Desikachary 1959
A. unispora Gardn. 1927	5	metaphytic in pools and swamps	Caribbean region (Cuba, Puerto Rico)	Gardner 1927 Geitler 1932
A. cf. *bornetiana* Collins 1896	1	floating clusters (almost straight trichomes; granules in cells)	N and central America (wider distribution?)	Smith 1920 Geitler 1932
A. jeejiae spec. nova	1	metaphytic	Cuba	
A. portoricensis Gardn. 1927	2	metaphytic (on submersed plants and in detritus)	Caribbean region (Cuba, Puerto Rico)	Gardner 1927 Geitler 1932

Cuba (studied more than 20 years ago) was not possible; nevertheless, the morphological description of their populations gives an indication of the diversity of nostocalean cyanobacterial species in Caribbean region.

Methods

The samples of cyanoprokaryotes collected from different freshwater habitats in Cuba from 1980–1982 were studied by optical microscopy. The morphology of Cuban populations was described and documented by means of drawings. In those cases, where the Cuban populations do not agree exactly with other morphotypes, the designation "sp." or "cf." (confer) is used. The morphological and ecological characters of the populations are reviewed in Tables 1 and 2.

Results

1. Planktic species with gas vesicles and coiled trichomes

Anabaena cf. *reniformis* Lemmermann, Bot. Centralbl. 76 (5–6): 155, 1898. Figs 1–2

D e s c r i p t i o n : Planktic and metaphytic species. Trichomes solitary, free floating, intensely irregularly, more or less screw-like or spirally coiled, without distinct mucilaginous envelopes, not attenuated at the ends, slightly constricted at cross walls. Cells barrel-shaped, more or less isodiametrical or slightly longer than wide, (3.2–) 3.6 (–4.0) μm wide, with distinct, usually elongated aerotopes within cells; apical cells not different from other cells, rounded at the ends. Heterocytes oval to barrel-shaped, ± 4.5 × 3.4–4.0 μm. Akinetes spherical or subspherical, solitary, at heterocytes, about 10 μm in diameter, with a hyaline epispore.

Planktic and among submerged water plants, found in a pool polluted by cattle, about 5 km NE from Mayarí Arriba, Oriente, coll. on 8 July 1981; green water bloom.

Morphologically almost identical species was recorded by Aptekar' (1927; cited according to Elenkin 1938, Fig. 225, p. 766–769; Hollerbach et al. 1955, Fig. 164: 3, p. 277–278) from the Ukraine (cells 6.0–8.0 × 4.0–5.5 μm, akinetes 8.5–11.0 μm in diameter) under the name "*Anabaena reniformis* Lemm.". However, Lemmermann's species, described in 1898 from Germany, without akinetes, has ± spherical heterocytes and cells 7–8 × 4 μm. The studied specimens represent a distinct species, but their identity with Lemmermann's and Aptekar's specimens is uncertain.

Anabaena torques-reginae Komárek, Acta Bot. Cubana 19: 14, 1984. Fig. 3

This species, originally described from Cuba, is found in Brazil and San Salvador. For a description and figures of this characteristic planktic species with coiled trichomes and spherical akinetes at heterocytes (populations from Cuba: see Komárek 1984b, p. 14–16, Fig. 10).

Table 2. – Comparison of benthic *Anabaena* morphospecies (excl. morphologically distinct and typical planktic species) from Cuba. HTC – heterocytes, AK – akinetes; (+) – rarely present.

	Trichome ends narrowed	Trichome ends cylindrical	Cells barrel-shaped	Cells cylindrical	Facultative aerotopes	HTC spherical	HTC cylindrical	AK at HTC	AK distant from HTC	AK cylindrical	AK oval	AK widely oval	Coloured exospore	Endospore
A. austro-africana	+		+		+	+		+				+	–	
A. turkestanica	+		+			+	(+)	+				+	–	
A. ambigua	(+)		+		+	+		+				+	–	
A. orientalis	+			+			+	+			+		(+)	brown
A. iyengarii		+	+			+	+	+		+	+	+	–	–
Anabaena sp. 1	(+)		+			+		+			+		–	
A. oblonga	+		+				+		+	+			–	
A. bornetiana		+	+			+			+	+			–	
Anabaena sp. 2	(+)		+			+			+		+		dark	

2. *Planktic species with gas vesicles, ± straight trichomes and akinetes on both sides of heterocytes*

Anabaena austro-africana Cronberg et Komárek, Nova Hedwigia 78 (1–2): 74, 2004. Fig. 4

D e s c r i p t i o n : Trichomes are straight or slightly curved (indistinctly coiled), constricted at cross walls, 3.6–5.8 (6.2) μm wide, at the ends distinctly successively narrowed, up to 2 μm wide, but the cells are only exceptionally slightly elongated, of the same inner structure as in the middle. End cell is conical or cylindrical and rounded. Cells are barrel-shaped, subspherical, more or less isodiametrical, pale blue-green, with or without subspherical, irregular, or slightly elongated aerotopes (some parts of trichomes with and sometimes without aerotopes). Heterocytes almost spherical, (5.0–) 7.3 (–8.0) μm in diameter (sometimes a little narrowed and only 3.2–6.5 μm in diameter), up to 5 in one trichome, in metameric position. Akinetes widely oval, on one side ("inner") of a heterocyte or on both sides, with more or less homogeneous contents, (9.8) 10.8–12.6 (18.0) × (7.2) 9.0–12.4 μm and with colourless exospore.

This species is common in Cuba, known from several localities. Populations from six pools in pastures (about 5 km northern from Mayarí Arriba, Oriente, coll. 8 October 1981) and a small lake (near Pinares Mayarí, Oriente, coll. 20 August 1981) were evaluated.

Metaphytic and planktic species, occurring in shallow water-bodies with vegetation, swamps and small ponds in warm countries (Brazil, South Africa).

	length : width ratio		Cell width	Heterocytes: dimensions	Akinetes: dimensions
cells	HTC	AK	[µm]	[µm]	[µm]
± 1:1	0.8–1.6:1	1.3–1.5:1	3.6–6.2	5.0–8.0 × 3.2–6.5	9.8–18.0 × 7.2–12.4
0.4–1.3:1	0.9–1.1:1		3.6–4.8	3.2–4.8 × 4.6–5.0	
0.4–0.8:1	0.8–1.2:1	1.1–1.4:1	5.9–9	6.0–11.2 × 7.0–12.8	13.2–15.0 × 10.6–12.0
0.8–1.4:1	1.4–1.9:1	1.9–2.3:1	3–5.4	5.8–14.3 × 5.8–7.6	13.0–24.0 × 9.2–14.3
0.4–1.0:1	0.9–1.4:1	1.2–2.5 :1	3.5–5	5.6–9.6 × 5.6–7.2	12.0–21.4 × 9.2–10.8
0.7–1.2:1	1.2–1.5:1	1.1–1.8:1	5.2–6.2	5.6–7.2 × ± 8.0	
1–1.5:1	1.2–1.8:1	2–4:1	4.5–5	7.0–9.6 × 6.2–7.3	
0.6–1:1	0.9–1.1:1	3.6–4.9:1	7–7.3	7.0–9.5 (diameter)	17.8–24.0 × 7.2–9.2
0.6–1.4:1	1–1.3:1	±1.9–2:1	6.4–6.8	7.8–9.6 (diameter)	±20.0 × 11.2

Anabaena turkestanica (A. Kiselev) Komárek, **comb. nova** Fig. 5

B a s i o n y m : *Anabaena oscillarioides* var. *turkestanica* A. Kiselev, Trudy Sredne-Aziatsk. Gosud. Univ., ser.12a, Geogr., 9: 74, 1931.

D e s c r i p t i o n : Filaments in mats on soil in paddy fields, ± straight or slightly coiled, trichomes attenuated gradually towards ends, clearly constricted at cross walls, 3.6–4.8 µm wide, ends narrow to ± 2 µm, heterocytes spherical, 3.2–4.8 × 4.6–5.0 µm, akinetes widely oval, on both sides of heterocytes, with colourless epispor (ripe?). – From paddy fields near Guanamon de Herrera (prov. Habana, coll. 14 April 1981) and old paddy fields and pools with *Azolla* near Laguna del Pesquero (prov. Pinar del Río, coll. in December 1980). It grows periphytically and metaphytically, usually among submerged water plants.

Similar to *A. austro-africana*, but lacks gas vesicles and lives in benthic habitats. It was originally described as a variety of *Anabaena oscillarioides* (periphytic species from paddy fields in Tourkmenistan forming mats and always without aerotopes). Trichomes sometimes arranged more or less in parallel in mucilage, later they become solitary. The solitary trichomes float in the water, rarely in small clusters. The benthic clusters are morphologically almost identical with the description given by Kiselev (1931). Another small difference is the narrowed terminal cells. Kiselev describes "conical or bluntly triangular" end cells. Both these differences are part of the range in variation of this taxon, which is distinct from the typical *A. oscillarioides.* The separation of this taxon from the type is therefore acceptable.

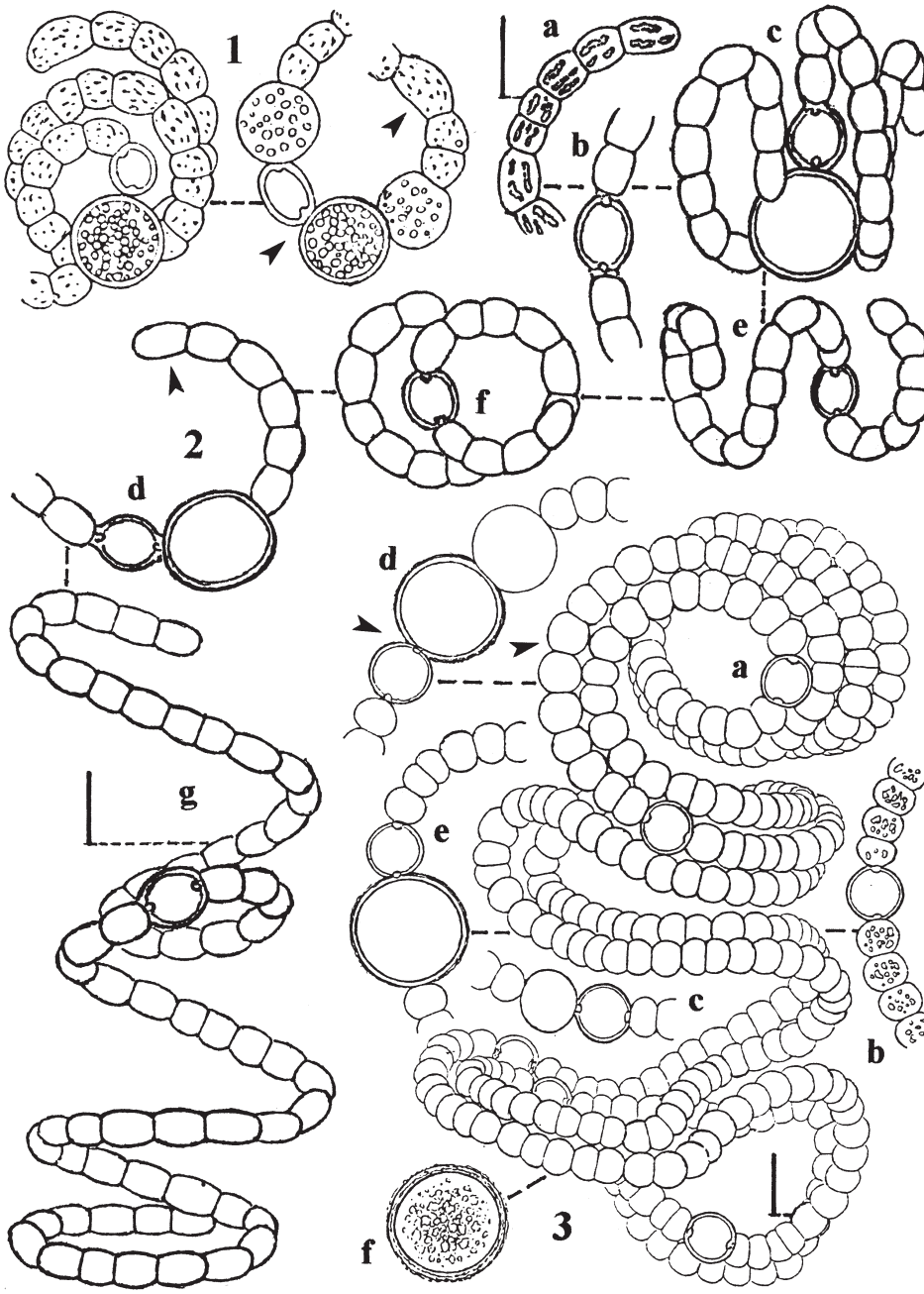

Fig. 1. – *Anabaena* cf. *reniformis*: after Aptekar' 1927 under "*A. reniformis* Lemm." Note on all figures: scale bar = 10μm.

Fig. 2. – *Anabaena* cf. *reniformis*: orig. from Mayarí Arriba; a – detail of terminal cells with aerotopes, b – detail of a heterocyte, c–d – trichomes with akinetes, e–g – trichomes.

Fig. 3. – *Anabaena torques-reginae* : after Komárek 1984, from Cuba; a – coiled filament, b–c – details of heterocytes, d–f – detail of an akinete.

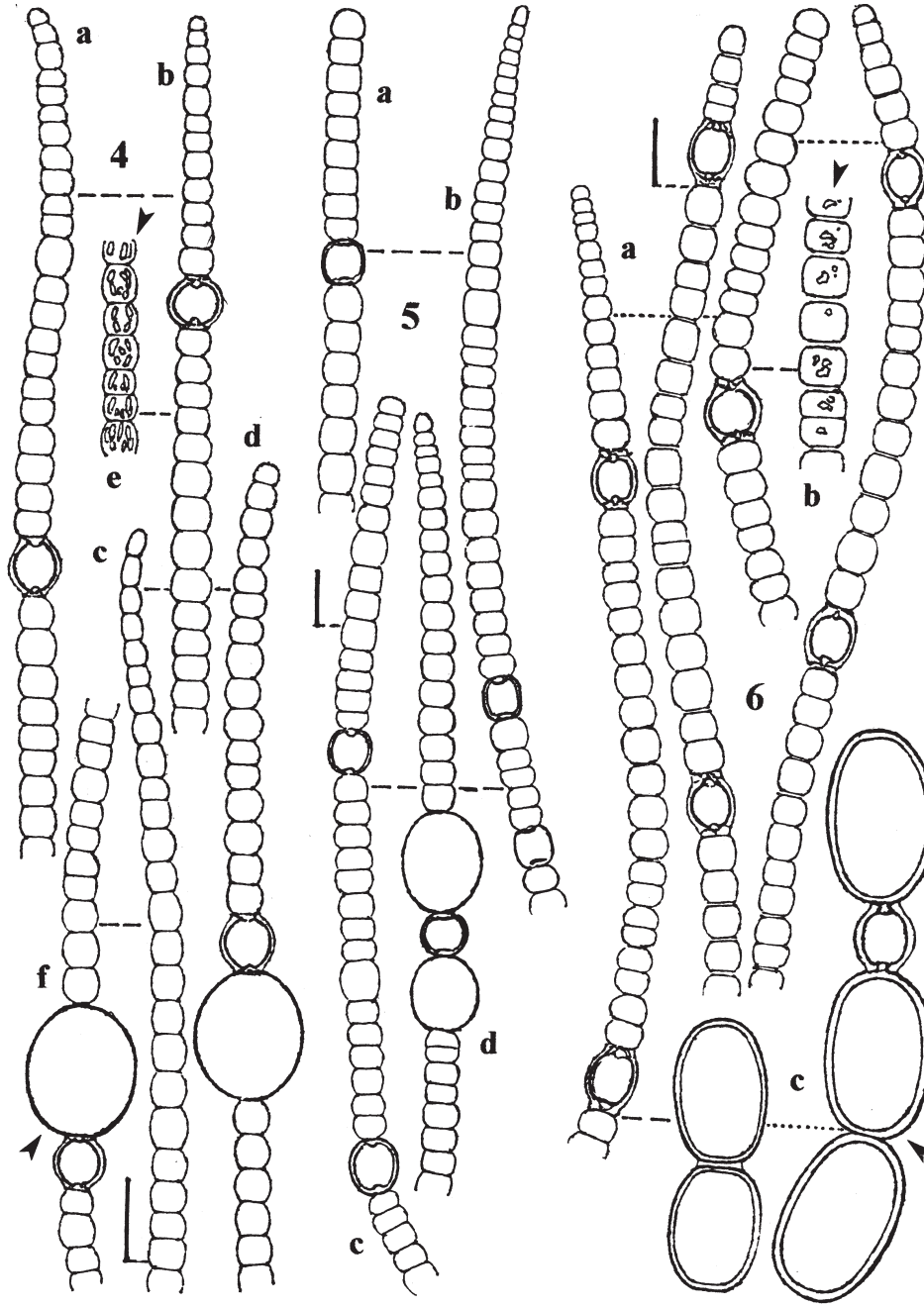

Fig. 4. – *Anabaena austro-africana*: orig. from Cuban localities, metaphytic or planktic with aerotopes in cells; a–d – ends of trichomes with intercalar heterocytes and akinetes, e – detail of cells with aerotopes, f – detail of a trichome with one akinete.

Fig. 5. – *Anabaena turkestanica*: orig. from old paddy fields near Guanamo de Herrera, forming benthic and periphytic mat; a–c – terminal part of trichomes with heterocytes, d – terminal part of a trichome with heterocyte and akinetes.

Fig. 6. – *Anabaena* sp. 1: orig. from a pool near lake Laguna del Pesquero, forming periphytic mats; a – terminal part of trichomes with heterocytes, b – detail of cells with granules, c – details of akinetes.

Anabaena sp. 1 Fig. 6

Description: Metaphytic and periphytic species, usually forming small, free clusters. Trichomes almost straight or slightly sinuate or arcuate, clearly constricted at cross-walls, sometimes slightly narrowed towards ends, 5.2–6.2 μm wide. Cells short barrel-shaped, rarely isodiametric, pale blue-green, with or without aerotopes. Heterocytes solitary, ± regularly situated on trichomes (up to 11 per trichome), ± spherical or shorter than wide, 5.6–7.2 × ±8.0 μm. Akinetes on both sides of heterocytes, oval, with colourless exospore and (ripe) usually distinctly granular contents.

Found in Pinar del Río, in a pool near laguna del Pesquero ("arrozal viejo"), with rich growth of *Azolla*, coll. 18 December 1980.

This morphotype belongs to the group of periphytic and metaphytic *Anabaena*-species with akinetes on both sides of heterocytes, to which other similar morphospecies found in Cuban freshwater habitats belong (e.g. *A. turkestanica, A. iyengarii, A. oblonga*). The studied population from Pinar del Río does not correspond exactly to any described species, but it is possible, that molecular evaluation will reveal that these similar species are very closely related.

Anabaena cf. *recta* Geitler in Geitler et Ruttner, Arch. Hydrobiol., Suppl. 14 (Trop. Binnengew. 6): 459, 1935. Fig. 7

Planktic species with solitary, more or less straight trichomes with narrow ends and cells with aerotopes. Descriptions of Cuban populations are in Komárek (1984b) under the name "*Aphanizomenon* cf. *aphanizomenoides*". As at that time akinetes had not been described in Cuban material, identification was not easy. Its narrow trichome ends also resulted in this species sometimes being classified as an *Aphanizomenon.* However, the terminal parts of filaments of numerous planktic as well as periphytic *Anabaena* species narrow, including those of *Anabaena recta* and *Anabaena aphanizomenoides* (syn. *Aphanizomenon aphanizomenoides*). But the apical cells of these Anabaenas are usually not characteristically elongate and hyaline, as is typical of the *Aphanizomenon* species with "cut" (*A. flos-aquae, A. flexuosus*, etc.) or pointed (*A. issatschenkoi, A. tropicale*) apical cells. The trichomes of these *Anabaena*-species also probably have a metameric trichome structure.

The taxonomic position of *Anabaena* species with narrow trichome ends is therefore not yet resolved as all morphological transitions between types and species with attenuated ends and strictly cylindrical trichomes (not attenuated at ends) are known. Several species from this *Anabaena*-group were described as species of *Aphanizomenon* (e.g. *A. ovalisporum* Forti, *A. manguinii* Bourrelly, *A. chinense* Negoro), but the main diagnostic, *Aphanizomenon*-generic features are elongate and hyaline end-cells, tendency to form fascicles of filaments, trichomes with subsymmetrical structure, and planktic type of life (gas vesicles always present). Thus, their classification within the genus *Anabaena* seems to be more appropriate. The genus *Aphanizomenon* includes those species that have elongate (sometimes also slightly narrowed or widened) and hyaline terminal cells. This type of terminal "hair"-like cells is probably associated with a special metabolism of filamentous cyanoprokaryotes, as in *Rivulariaceae* (Whitton 1987). In this case, the difference between "narrowed" ends and endings with cytomorphologically changed cells is associated with a specific metabolism and should be taxonomically respected.

Anabaena recta has probably a pantropical distribution because it is known from Cuba, Indonesia, and South Africa.

Anabaena manguinii (Bourrelly) Komárek, **comb. nova** Fig. 8

B a s i o n y m : *Aphanizomenon manguinii* Bourrelly in Bourrelly et Manguin, Alg. Eau Douce Guadel. Dépend. 1: 155, 1952.

Planktic *Anabaena* species with solitary, straight trichomes, which are sometimes sharply curved at heterocytes and narrowed towards the ends. This attenuation is gradual, and sometimes at the ends there are slightly elongate cells of the same structure and contents as the vegetative cells. Cuban populations were described by Komárek (1984b: 19–22) under the name *Aphanizomenon manguinii.*

Anabaena manguinii was originally described from the Caribbean district of Guadeloupe by Bourrelly (in Bourrelly & Manguin 1952) who commented on the narrowed ends. This species is still known only from central, subtropical and tropical America (Cuba, tropical Brazil, Mexico). Komárek (1984b) tried to evaluate the structure of the trichomes (only 3–4 heterocytes commonly occur on filaments) and describes a subsymmetrical scheme of trichomes. However, in other populations there are up to 5 (6) heterocytes per trichome and the metameric structure of the trichomes is evident. "*Aphanizomenon manguinii*" therefore belongs to the group of planktic straight Anabaenas with narrowed ends, which includes several morphospecies described under the generic name *Aphanizomenon*.

Anabaena hatueyi Komárek, **spec. nova** Fig. 9

D i a g n o s i s : Trichomata solitaria, libere natantia, plus minusve recta vel leviter irregulariterque circinata, ad septa constricta, in media parte ad 10.8 μm lata, ad apices attenuata et ad 2 μm lata. Cellulae barriliformes, plus minusve isodiametricae, protoplasmate subtiliter granulares cum aliquot aerotopis minutis; 1–(4) cellulae terminales leviter elongatae, paucim hyalinae; cellula apicalis plus minusve acuminata. Heterocytae intercalares, sphaericae vel breve ovales, 7.0–8.5 × ± 7.2 μm. Akinetes intercalares, solitariae, ovales, ab heterocytis remotae, 15.2–16.2 × 7.5–9.0 μm, cum episporio fusco. – Typus (holotypus – iconotypus)**:** figura nostra 9. – Habitatio: Planktice in lacubus stagnisque, in aquis dulcis mesotrophicis; locus classicus: Cuba, provincia Ciudad de la Habana, Cubanacán, piscina El Laguito, 10–11–1964 coll. – Etymologia: species ad memoriam Hatueyi, heroi tribu originali in Cuba, nominata.

D e s c r i p t i o n : Solitary, straight or very slightly coiled trichomes, free floating, clearly constricted at cross walls, 3.8–4.6 μm wide, with usual short narrow or widened ends; 1–3-several cells at the ends are narrow and elongate, or short, round and slightly wider compared to the vegetative cells; narrowed apical cells are up to 2 μm wide, widened end cells up to 10.8 μm wide; 1–3 end cells rarely almost hyaline and pointed at the apex. Vegetative cells are barrel-shaped or cylindrical-barrel-shaped, isodiametrical or a little longer than wide (only after division shorter than wide), with gas vesicles (visible as small, point-like or granular-like aerotopes). Heterocytes spherical or slightly oval, 7.0–8.5 × ±7.2 μm. Akinetes develop solitary, distinct from heterocytes, cylindrical-oval with rounded ends, 15.2–16.2 × 7.5–9.0 μm, with brownish exospore.

This species rarely occurs in water blooms (together with *Cylindrospermopsis raciborskii*) in eutrophic, but not polluted ponds and water reservoirs as an accessoric species. Found in several localities in the provinces of Ciudad de la Habana and Habana in central Cuba.

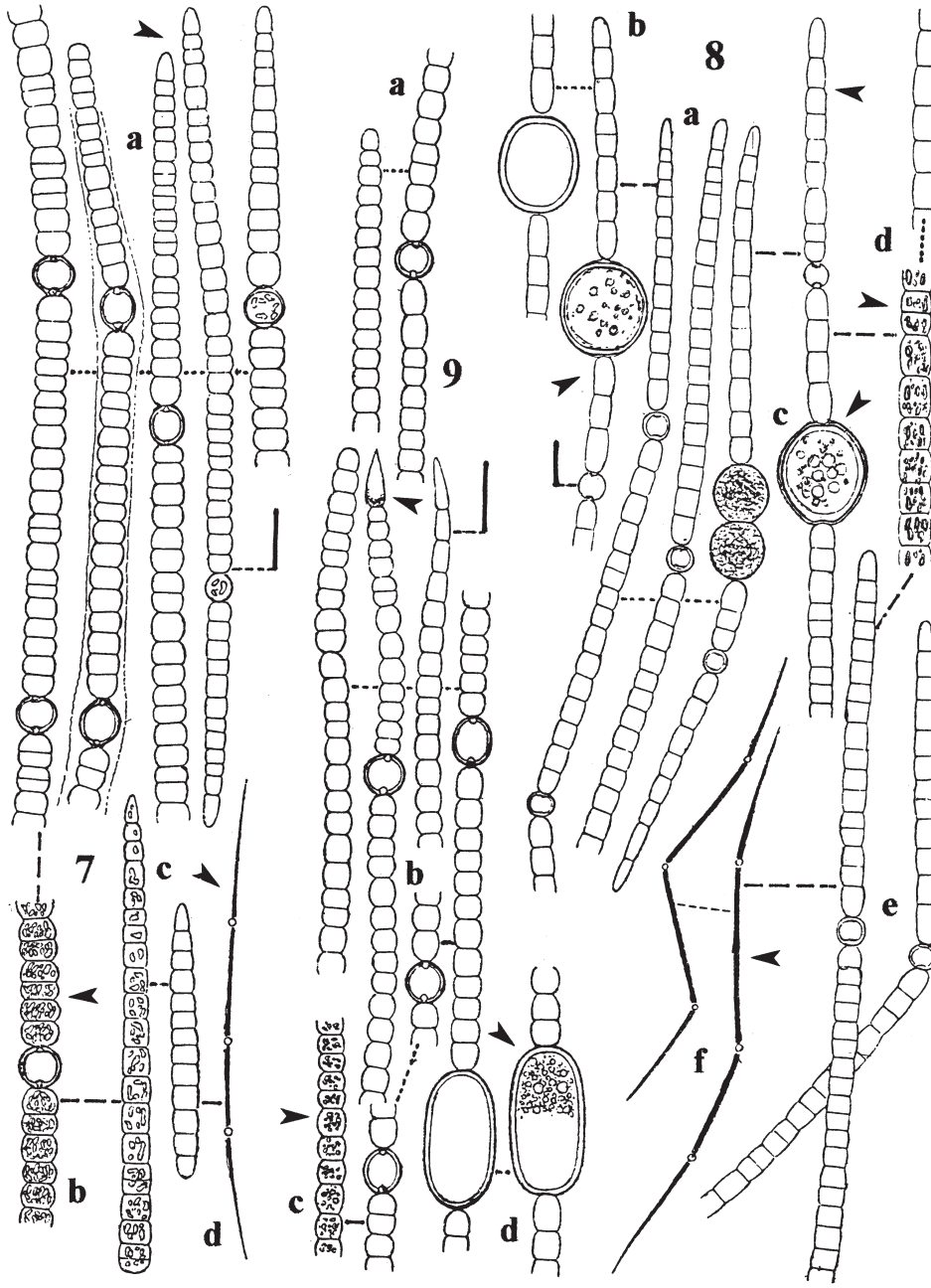

Fig. 7. – *Anabaena recta*: after Komárek 1984, planktic, from Cuba, sub "*Aphanizomenon* cf. *aphanizomenoides*?"; a – details with heterocytes, b – detail of cells with aerotopes, c – hormogonia, d – structure of a trichome.

Fig. 8. – *Anabaena manguinii*: after Komárek 1984, planktic from lakes in Cuba, sub "*Aphanizomenon manguinii*"; a – terminal parts of trichomes, b–c – details of akinetes, d – details of cells with aerotopes, f – structure of trichomes.

Fig. 9. – *Anabaena hatueyi*: after Komárek 1984, planktic from Cuba, sub "*Aphanizomenon* sp.".

Anabaena hatueyi is a planktic species related to *A. manguinii* as it has straight trichomes and narrow ends. Its relation to *Aphanizomenon* is more relevant than that of the previous species, because sometimes (in old trichomes) the 1–3 end cells not only appear to narrow but are also slightly elongate and almost hyaline. Rarely is the apical cell enlarged and pointed. That is, the morphology of end cells in this species is different and this variable cell morphology is characteristic also of trichomal cells. Sometimes more rounded and wider cells occur between normal barrel-shaped vegetative cells. This phenomenon, however, also occurs in other species, such as *A. levanderi, A. manguinii,* etc. (G. Cronberg & J. Komárková-Legnerová, in preparation, J. Komárek, unpublished). Hyaline cells are also sometimes present in planktic *Anabaena* species that lack narrow ends.

This species was first described from Cuba as *Aphanizomenon* (*Anabaena*?) sp. (Komárek 1984b, p. 23–24), but after a study of further samples and the literature, it cannot be identified as another *Aphanizomenon* or *Anabaena* species. For these reasons, explained when discussing *Anabaena recta*, it is taxonomically defined as a new species of *Anabaena* although its generic classification is still doubtful.

3. Mainly metaphytic species with akinetes distant from heterocytes

Anabaena sp. 2 Fig. 10

D e s c r i p t i o n : Trichomes gathered in small clusters, coiled, slightly attenuated at the ends, clearly constricted at cross walls, 6.4–6.8 μm wide, at the ends only 4.8 μm wide. Cells barrel-shaped, usually wider than long, only old cells or before division almost isodiametrical or indistinctly longer than wide, with dark blue-green, homogeneous content. Heterocytes spherical or shortly oval, 7.8–9.6 μm in diameter. Akinetes develop singly, distant from heterocytes, oval, ± 20.0 × 11.2 μm (few measurements), with finely granular contents and dark, almost blackish exospore.

Our population was found in old paddy fields near lake Pesquero, prov. Pinar del Río, coll. in December 1980.

This species is morphologically and ecologically similar to *A. turkestanica*, but aerotopes were never observed, the dimensions of all types of cells are slightly larger and (mainly) the akinetes are distant from heterocytes. However, as only one population was studied, in which only few ripe akinetes were found, the taxonomic classification of this species cannot be solved with certainty.

Anabaena orientalis S. C. Dixit, Proc. Indian Acad. Sci., B, 3: 101, 1936. Fig. 13

D e s c r i p t i o n : Trichomes slightly coiled, arranged in small, thin mat-like clusters, cylindrical, attenuated at the ends (in developed filaments), constricted at cross walls, 3–5.4 μm wide. Cells cylindrical, more or less isodiametrical, or slightly (up to 1.8 ×) longer than wide, with pale blue-green, finely granular contents. Heterocytes intercalar, solitary, oval to cylindrical, with bluish-hyaline contents, 5.8–12.0 (–14.3) × (5.0–) 7.0–7.6 (–8.0) μm. Akinetes oval, arise on both sides of heterocytes, singly or in pairs (rarely up to 3 in a series), with smooth surface, brownish endospore and colourless or very slightly brownish exospore, finely or roughly granulated contents, 13.0–18.0 (–24) × 9.2–10.8 (–14.3) μm.

Anabaena orientalis is common in Cuba. It differs from the original description mainly in its indistinct dimensions (width of akinetes). For this study four populations from the

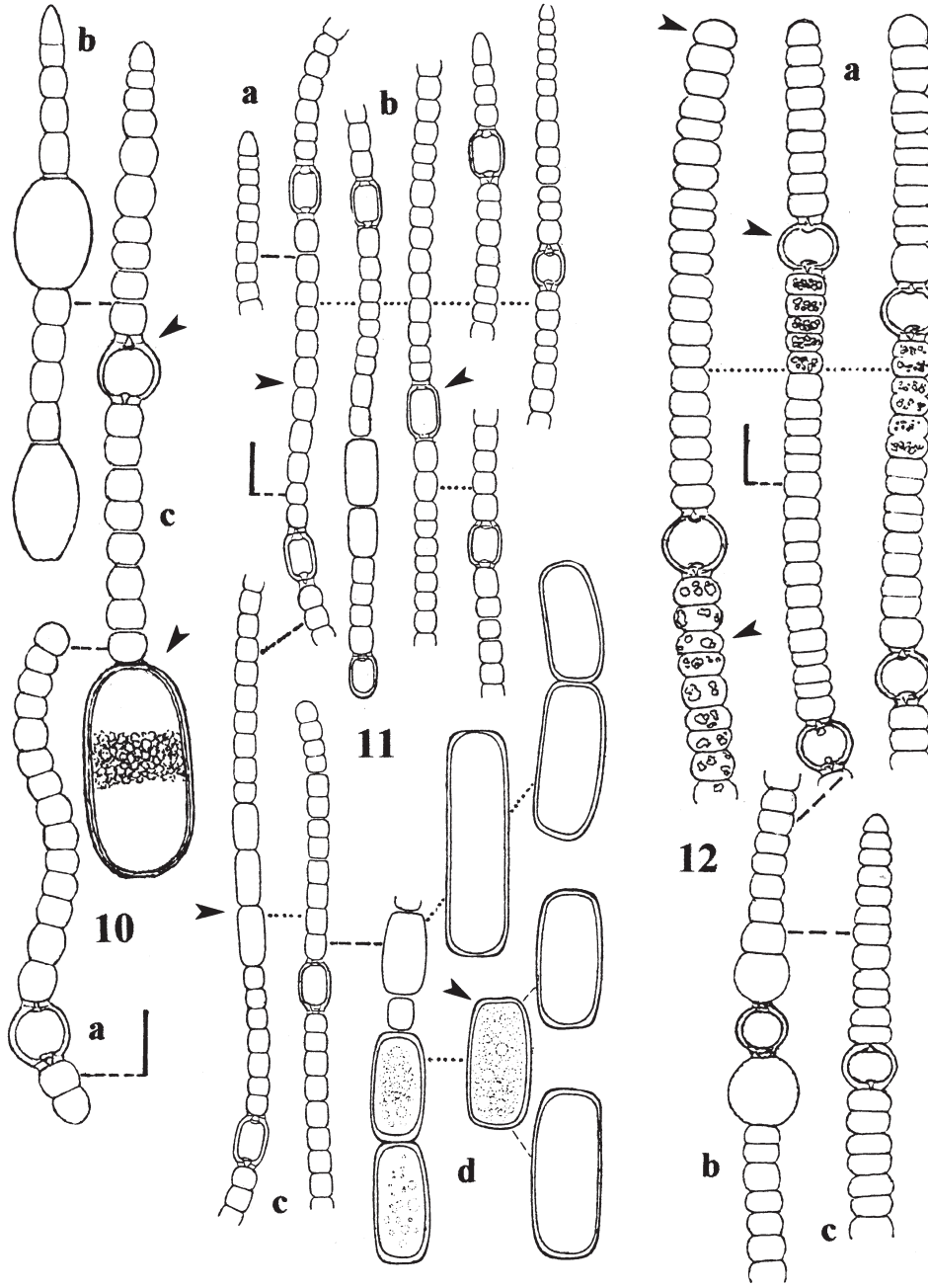

Fig. 10. – *Anabaena* sp. 2: orig, metaphytic and benthic from paddy fields near lake Laguna del Pesquero, Pinar del Río; a – young trichome with heterocyte, b – short trichome with young akinetes, c – part of trichome with heterocyte and akinete.

Fig. 11. – *Anabaena oblonga*: after Komárek 1984, from benthic mats in shallow road puddles; a – end of a trichome, b–c – details of trichomes with heterocytes and young akinetes, d – details of akinetes.

Fig. 12. – *Anabaena* cf. *ambigua*: orig., periphytic on submerged plants, near La Fé, Pinar del Río; a–c – details of trichomes with heterocytes, granules in cells and young akinetes (b).

provinces of Habana (growing in detritus and in metaphyton near the outflow of the reservoir "Niña Bonita" on Rio Jaimanitas, coll. in October 1980) and Pinar del Río (among water plants in pools with plenty of vegetation near lake Pesquero, coll. in December 1980) were used.

Described from India, not well known, but probably has a pantropical distribution. It is easily distinguishable from the more widely distributed *A. iyengarii* (the next species) by the usually clearly narrowed ends of the trichomes and by cylindrical cells.

Anabaena iyengarii Bharadwaja, Proc. Indian Acad. Sci., B, 2: 105, 1935. Fig. 14

D e s c r i p t i o n : Filaments joined into metaphytic aggregations and clusters, which later float among water plants; trichomes are sometimes enveloped by a colourless mucilage. Trichomes slightly curved or coiled, cylindrical, not attenuated towards ends, distinctly constricted at cross walls, 3.5–5.0 μm wide. Cells barrel-shaped, usually shorter than wide (after division only 0.5 times longer than wide) to isodiametrical (rarely slightly longer than wide before division), with olive-green content; apical cells widely rounded. Heterocytes spherical, slightly elongated-spherical to barrel-shaped or almost cylindrical, with flattened poles, (5.6) 7.0–9.6 × (5.6) 7.0–7.2 μm. Akinetes arise on both sides of heterocytes, singly or in pairs, with smooth and almost colourless cell walls, of very variable shape: the ripe akinetes can vary from almost cylindrical (with l:w up to 2.5: 1) to almost spherical or wide oval (l:w = approximately only 1.2: 1); akinete dimensions: 12.0–21.4 × 9.2–10.8 μm.

Anabaena iyengarii was recorded from small pools and puddles, rice fields, swamps and littoral zones of ponds and lakes with plenty of vegetation. For this study I used populations from the provinces of Habana (freshwater pools near El Cayuelo, coll. in 1977; reservoir "Niña Bonita", coll. in 1980; pools near Managua, coll. in 1980), Pinar del Río (lake Pesquero, coll. in 1980) and Las Villas (small pond on the northern slopes of Sierra Escambray, coll. in 1981).

Commonly occurring pantropical species, described from India and widely distributed in Cuba. The species is very variable, as indicated by the numerous varieties and forms. This wide variation is also present in Cuban populations. The material corresponds almost exactly with the descriptions from India. It differs from *A. orientalis* mainly in having cylindrical trichomes without narrowed ends and barrel-shaped cells.

Anabaena oblonga De Wildeman, Ann. Jard. Bot. Buitenzorg, Suppl. 1: 50, 1897. Fig. 11

D e s c r i p t i o n : Our population from Cuba, found in shallow road-puddles, was described by Komárek (1989). This species occurs also in the littoral zone of ponds and lakes, forming mats on various substrates (plants, stones, detritus). The following description is based on material from one of these lake populations (lake Pesquero, prov. Pinar del Río, coll. in December 1980): Trichomes coiled, 4.5–5.0 μm wide, narrowed towards ends (up to 3 μm), end cell rounded. Cells barrel-shaped, ± isodiametrical, with pale yellow-green contents, without aerotopes. Heterocytes ± cylindrical, isodiametrical or elongated, 7.0–9.6 × 6.2–7.3 μm. Akinetes arise far from heterocytes, singly or in pairs, and are cylindrical, with more or less suddenly flatten ends (almost "upright cut"). *A. oblonga* appears to be an exclusively tropical species with cylindrical akinetes.

Anabaena oblonga was included along with *A. laxa* and *A. californica* by Geitler (1932) in *A. inaequalis*; Desikachary (1959) accepted this proposal, but under the name

A. laxa. However, the populations from Cuba correspond with the original description of De Wildeman (1897) of material from Indonesia, but not with that of *A. inaequalis* (which is well known from European localities). It is possible that all these species are identical even though features are very variable, but a comparative study with an abundance of material, including that of numerous other species, which possess similarly variable characters, is needed (see Discussion).

Anabaena cf. *ambigua* C. B. Rao, Proc. Indian Acad. Sci., B, 5: 101, 1937. Fig. 12

D e s c r i p t i o n : Trichomes aggregated in fine mats, long, slightly sinuate, cylindrical or indistinctly and shortly narrowed at the ends, clearly constricted at cross walls, with terminal cells widely rounded, (5.9–) 7.2–9.0 µm wide. Cells shorter than wide, to almost isodiametric, barrel-shaped, with pale blue-green, slightly granulated contents. Cells sometimes contain many aerotopes, but this is a very transient phenomenon in this species. Heterocytes are more or less spherical, or a little shorter than wide, solitary, in a metameric position, (6.0–) 7.1–8.3 (–11.2) × (7.0–) 9.0–9.5 (–12.8) µm. Akinetes widely oval, arise on both sides of heterocytes, usually with granular contents, 13.2–15.0 × 10.6–12.0 µm and colourless exospore.

Three populations from the western part of Pinar del Río (small ponds near La Fé, coll. 17 December 1981) and old paddy fields and ponds near the lake Pesquero, coll. 18 December 1980), were studied.

Periphytic species living in solitary trichomes or forming mats on submerged plants in tropical swamps, littoral zone of lakes and in unpolluted shallow water of different kinds. Described from India, but probably has a pantropical distribution. This species could be related to the previous species; I have never found it floating in solitary trichomes, but it is possible. The most important difference of possibly taxonomic value is their size. However, the specimens differ from the original description in being a little larger, which may only indicate wide variation in this feature. Both these species are ad interim separated, but further study of their variation is needed. *Anabaena ambigua* and *A. turkestanica* belong to the facultatively floating (planktic) species, which occasionally develop gas vesicles in their cells, but they mainly grow on and around submerged water plants in shallow water.

4. Metaphytic (mat-forming) species with extremely large akinetes aside heterocytes

Anabaena volzii Lemmermann, Abh. Naturwiss. Vereine Bremen 18: 153, 1906. Fig. 15

Common and characteristic pantropical species, which is common also in Cuban waters. Originally a periphytic species, but later sometimes found in plankton in unpolluted lakes (usually shallow) with rich littoral and submerged vegetation. Solitary aerotopes occur very rarely in floating trichomes. Species, in which the aerotopes appear only in a part of the vegetation cycle (see also *A. turkestanica* and *A. ambigua*), are ecologically different from the obligatoric planktic species that have aerotopes during the whole vegetation period and originated as planktic species.

The rich Cuban populations of *A. volzii* were described by Komárek (1984a). In this paper the subsymmetrical type of trichomes was also discussed as a diagnostic feature according to which *A. volzii* belongs rather to the genus *Aphanizomenon*. However, the end cells are only narrow (and sometimes only slightly elongate) and have the same cell con-

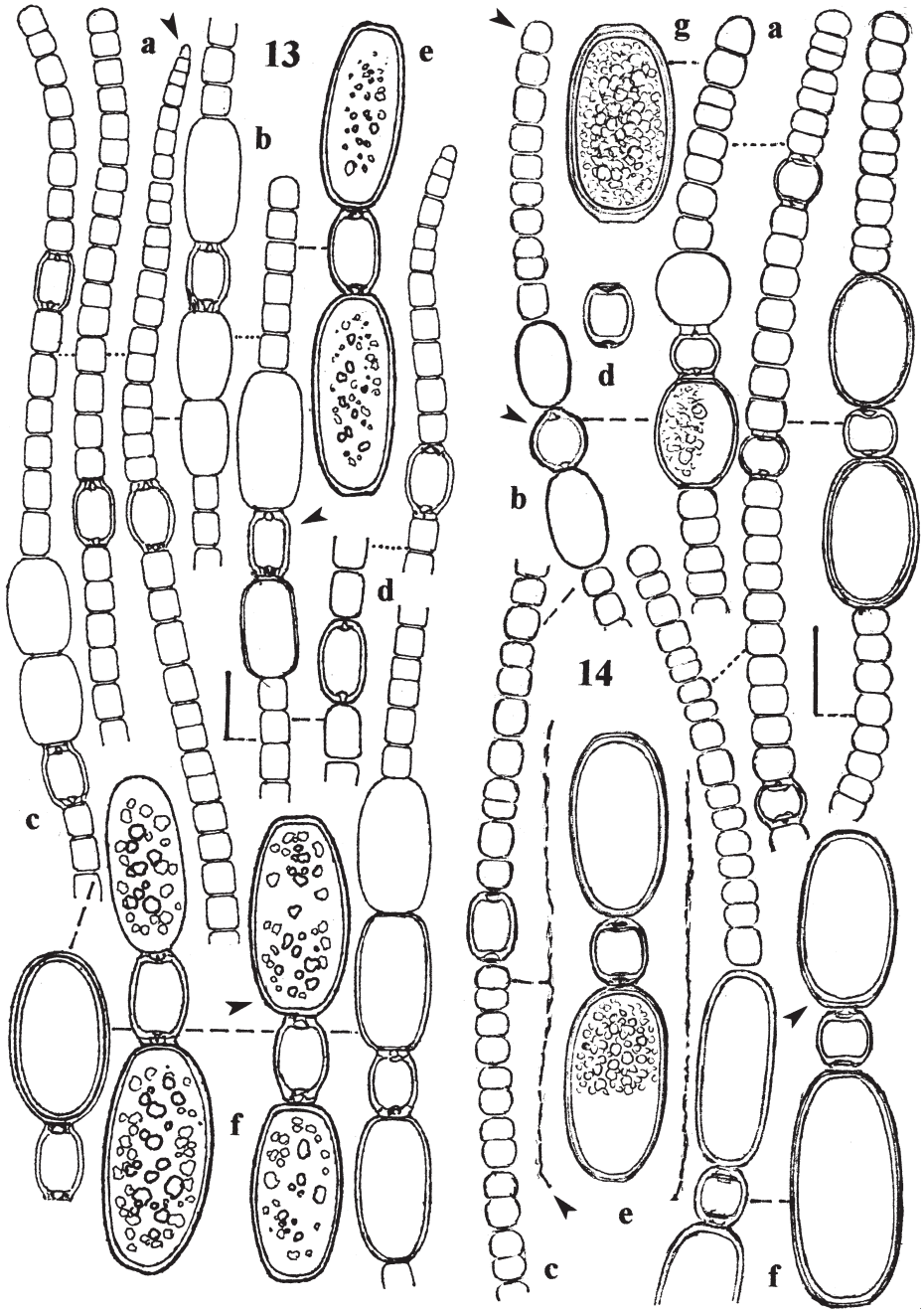

Fig. 13. – *Anabaena orientalis*: orig., metaphytic clusters among water plants from various Cuban localities (see text); a – apical part of trichomes with heterocytes, b–c – part of trichomes with young akinetes, d – details of heterocytes, e–f – details of akinetes.

Fig. 14. – *Anabaena iyengarii*: orig., mats, metaphytic from pools with many water plants, specimens from a few localities in prov. Habana; a–c – parts of trichomes with heterocytes and akinetes, d – detail of a heterocyte, e–g – details of akinetes.

tents as other vegetative cells (as in other *Anabaena* species with narrow trichomes ends). The generic position of this species and others with transient features needs to be resolved. This species and the two following morphospecies possibly represent a special generic entity.

Anabaena fuellebornii Schmidle, Engler's Bot. Jahrb. 32: 61, 1892 Fig. 17

D e s c r i p t i o n : Filaments in clusters or mats, without distinct, visible gelatinous envelopes, slightly and irregularly coiled, constricted at cross walls, 4.8–7.4 μm wide, sometimes slightly narrowed towards ends. Cells barrel-shaped to cylindrical, isodiametrical or longer than wide, end cells conically rounded. Cell contents blue-green, ± homogeneous or finely, evenly granulated. Heterocytes more or less cylindrical, isodiametrical or elongated, 7.1–11.6 (–16.0) × 6.8–9.8 μm, with hyaline, yellow-brownish contents. Akinetes arise on both sides of heterocytes, solitary or in pairs, widely or elongate oval, with colourless (rarely slightly brown), but granular-punctulate exospore (ripe!), and brownish endospore. Cell wall of young akinetes colourless, smooth. Akinetes with finely granulated contents, sometimes with solitary large granules, 25.0–45.0 × (14.3–) 16.5–19.0 (–21.6) μm (ripe); around akinetes a very narrow, hyaline, gelatinous envelope is sometimes discernable.

Anabaena fuellebornii was found in Cuba in unpolluted, shallow tropical swamps, where it grows among submerged and littoral water plants or on *Azolla*. For the description three populations from pools and old rice fields near lake Pesquero (prov. Pinar del Río, coll. repeatedly in 1980 and 1981) and swamps near La Fé (Isla de Pinos – Isla de la Juventud, coll. in January 1981) were used.

Anabaena fuellebornii differs from other *Anabaena*-species that have large single akinetes, which arise aside of the heterocytes, by the surface sculpture of their akinete exospores. It is a tropical and well defined species, in spite of the doubts of several authors. Compared with other reports, the Cuban specimens are a little larger, but their specific identity is certain.

Anabaena unispora N. L. Gardner, Mem. New York Bot. Garden 7: 59, 1927. Fig. 16

D e s c r i p t i o n : Fine micro- up to macroscopic, brownish clusters of filaments or mats, growing freely on submerged vegetation or among water plants in clear, alkaline pools and swamps. Trichomes slightly irregularly coiled, cylindrical, only rarely very slightly narrowed towards ends, or in the middle of trichomes (as in *A. volzii*), slightly constricted at cross walls, 4.0–5.4 μm wide. Cells cylindrical, ± isodiametrical up to twice as long as wide with widely rounded or flattened-rounded tops; cell contents pale greyish blue-green, without granulation or with fine or distinct granules. Heterocytes oval to cylindrical, intercalar, localized singly, (9.0–) 10.0–13.0 (–17.0) × (5.4–) 6.0–9.0 μm. Akinetes wide oval, arising on one, rarely both sides of heterocytes, very rarely with two akinetes in a row, with smooth cell walls and colourless or slightly brownish exospore and brown endospore, (18.0–) 20.0–40.0 (–43.0) × (8.0–) 12.5–20.5 μm; contents of ripe akinetes distinctly granular.

Originally described as growing among algae and debris in a pool in Puerto Rico (Gardner 1927); in Cuba found several times in metaphyton among submerged water plants in alkaline swamps in Ciénaga de Lanier (Isla de Pinos – Isla de la Juventud, coll. in January 1981 and in October 1981), in swamps between Nueva Gerona and Aeropuerto (Isla de Pinos – Isla de la Juventud, coll. in January 1981) and in the province Matanzas

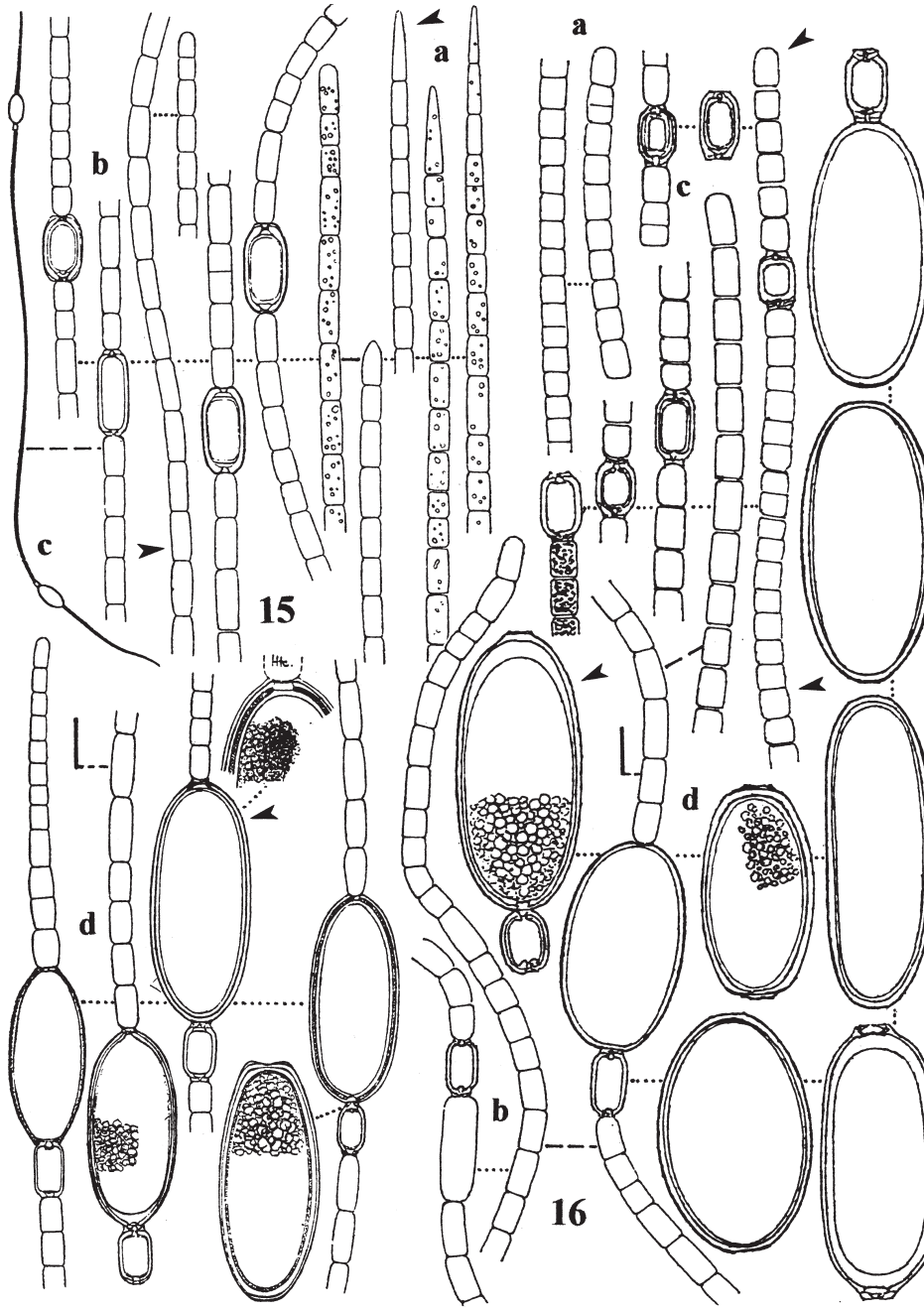

Fig. 15. – *Anabaena volzii*: after Komárek 1984, from Cuban localities; a – ends of trichomes, b – parts of trichomes with heterocytes, c – structure of a trichome, d – development and details of akinetes.

Fig. 16. – *Anabaena unispora:* orig., metaphytic cluster among water plants, from alkaline swamps in Ciénaga de Lanier (Isla de Pinos – Isla de la Juventud); a–b – parts of trichomes, c – parts of trichomes and details of heterocytes, d – variability of akinetes.

(Zapata peninsula, particularly in pools between Laguna del Tesoro and Playa Larga, coll. in February 1964). The Cuban populations only very slightly differ from the original Gardner's material from Puerto Rico in having a wider range of cell size.

Anabaena unispora, like *A. volzii* and *A. fuellebornii*, has a single (very rarely two) large akinete at heterocytes, which is many times larger than the vegetative cells.

5. Floating Anabaena-species that form fascicles and have granules in the cells

Anabaena cf. *bornetiana* Collins, Erythrea 4: 120, 1896. Fig. 18

D e s c r i p t i o n : Growing metaphytically among water plants, later in floating clusters. Trichomes straight or very slightly arcuate, without distinct mucilaginous envelopes, not attenuated towards ends, clearly constricted at cross walls. Cells shortly barrel-shaped, almost always shorter than wide, rarely isodiametrical, 7.0–7.3 μm wide, with bright blue-green and slightly granular contents, without gas vesicles, sometimes with several larger, prominent granules; apical cells widely rounded. Heterocytes almost spherical or very slightly longer or shorter than wide, wider than vegetative cells, (7.0–) 8.4 (–9.5) μm in diameter. Akinetes solitary, distant from heterocytes, containing large granules, cylindrical with rounded ends, with colourless, smooth epispore, 17.8–24.0 × (7.2–) 8.3–9.2 μm.

Found in floating macroscopic clusters with detritus and among submerged plants in the littoral zone (near the outflow) of the artificial reservoir Niña Bonita (Rio Jaimanitas, prov. Habana), coll. repeatedly in October 1980.

The filaments of this species are very similar to those of the planktic *A. planctonica*, but differ in having cylindrical akinetes, lacking aerotopes (but usually with prominent brownish granules in the cell), and in growing in clusters in metaphyton and secondary floating at the water surface, not in plankton. *Anabaena bornetiana* is usually treated following the concept of Smith (1920), because according to Collins' description (based on material from brooks in Massachusetts, USA) the akinetes are adjacent to the heterocytes. The studied material also differs from G. M. Smith's in its small size (Smith 1920 gives trichomes ± 12 μm wide, akinetes 50–90 × 15–20 μm). However, it is the nearest species, and the taxonomy of this group must be more accurately defined on the basis of more samples and cultures.

6. Fine metaphytic species with akinetes with structured exospore

Anabaena jeejiae Komárek, **spec. nova** Fig. 19

D i a g n o s i s : Trichomata tegetes mucilaginosas, amorphas, tenues formantia, brevia, leviter circinata, ad septa valde constricta, cylindrica, ad apices non-attenuata, 2.8–3.8 μm lata; mucilago sine colore, diffusus. Cellulae cylindricae vel barriliformes, plus minusve isodiametricae vel breviores quam latae, 1.5–5.0 μm longae, contentu plus minusve homogeneo, pallide griseo-aeruginoso, tenue granulari, aerotopis carentes; cellulae apicales rotundatae. Heterocytae ovales ad cylindricae, 6.5–7.5 × 4.6–5.2 μm. Akinetes solitariae, intercalares, ab heterocytis remotae, ovales ad cylindricae, cum lato, radiatim structurato exosporio, lutescente episporio, contentu granulari, 17.6–28.5 × 13.6–19.2 μm. – Typus (holotypus – iconotypus)**:** figura nostra 19. – Habitatio: Metaphytice priphyticeque in fossis et stagnis, inter plantas aquaticas; locus classicus: Cuba, provincia Habana, lacus artificialis Presa de Abra, 11–09–1980 coll. – Etymologia: Species ad honorem phycologi indici Dr N. Jeeji-Bai (Madras, India), nominata.

D e s c r i p t i o n : Filaments forming clusters and small gelatinous mats, attached to a substrate (usually floating mosses, remains of plants, detritus, etc.); around solitary trichomes

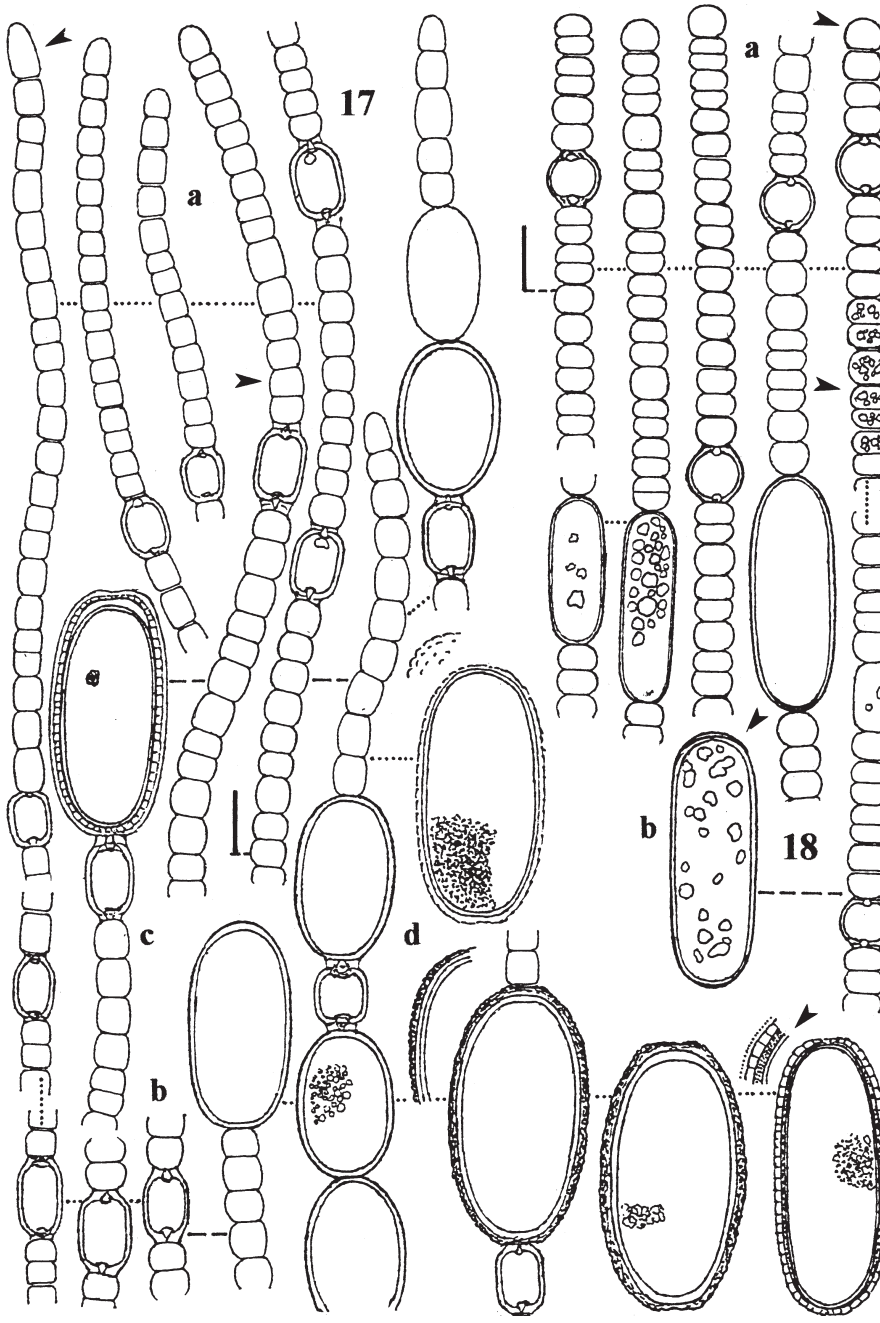

Fig. 17. – *Anabaena fuellebornii*: orig., metaphytic among *Azolla*, from rice fields near lake Laguna del Pesquero, Pinar del Río; a – parts of trichomes with heterocytes, b – details of heterocytes, c – part of a trichome with a heterocyte and akinete, d – development and variability of akinetes.

Fig. 18. – *Anabaena* cf. *bornetiana*: orig., from floating clusters among water plants in littoral zone of artificial reservoir Niña Bonita (prov. Habana); a – trichomes with heterocytes and akinetes, b – details of akinetes.

a fine, diffluent, colourless gelatinous envelope. Trichomes irregularly coiled, often short, cylindrical, clearly constricted at cross walls, not attenuated toward ends, 2.8–3.5 (3.8) μm wide, composed of barrel-shaped, more or less isodiametric, slightly longer or (after division) only 0.5 times longer than wide cells (1.5–5.0 μm long), with pale greyish-blue, homogeneous or finely granular contents, without aerotopes; apical cells widely rounded. Heterocytes barrel-shaped, oval to cylindrical, slightly wider than vegetative cells, 6.5–7.5 × 4.6–5.2 μm. Akinetes oval, arise singly, distant from heterocytes, with smooth cell walls when young, when ripe with wide, radially structured, colourless or yellowish exospore and blue-green, slightly granular contents; dimensions of akinetes: (17.6–) 19.0–25.4 (–28.5) × [8.0–11.0 (–20.0) = inner outline, without exospore] 13.6–16.0 (–19.2) μm. In both samples studied there were numerous very short, 2–7-celled hormogonia, which develop after the disintegration of trichomes without necridic cells and immediately started to grow.

Type material was collected in pools below the dam of the Presa de Abra reservoir, which contained submerged plants and detritus containing rich ferrous precipitates, on 11 September 1980. The species is dedicated to Dr Narendra Jeeji-Bai from Madras, India.

This species cannot be misidentified if the akinetes are developed. I have found only two populations of this species, both in the central part of Isla de Pinos – Isla de la Juventud, but the sculpture on the akinete epispore is very unique within the genus *Anabaena* and justifies the description of a new species.

7. Metaphytic species with spherical akinetes ± in rows

Anabaena portoricensis N. L. Gardner, Mem. New York Bot. Garden 7: 62, 1927 Fig. 20

D e s c r i p t i o n : Trichomes form periphytic and metaphytic clusters and mats on submerged water plants, stones and on bottoms of water bodies. They often occur along with other cyanoprokaryotes and algae, are slightly coiled, not attenuated toward ends, composed of more or less spherical or barrel-shaped cells, (7–) 8–10 μm wide, only after division shorter (up to 4.0–5.6 μm); end cells are spherical. Cells with pale or bright blue-green contents, usually with solitary, dark brown granules. Heterocytes always spherical (rarely a little flattened at poles), (8.0–) 9.0–10.0 (–13.2) μm in diameter, with homogeneous, yellow-green contents. Akinetes arise in rows, sometimes almost all the cells between heterocytes change into akinetes, but in most cases they start to develop on both sides of a heterocyte or irregularly anywhere on a trichome; this species therefore, is classified as *Anabaena* and not *Trichormus.* Akinetes ripen very irregularly and within rows occur akinetes of uneven size. Ripe akinetes are spherical to very wide-oval or barrel-shaped, with dark blue-green, distinctly roughly granular contents, slightly brownish endospore and colourless exospore, 14.5–19.2 × (–13.0) 15.4–18.0 μm.

Well developed colonies (mats) of this species with many akinetes were found in December 1980 in ponds and old paddy fields near lake Pesquero, province of Pinar del Río.

Anabaena portoricensis was originally described by Gardner (1927) from a ditch in Puerto Rico and the studied populations differ from it only slightly in the dimensions (width) of the akinetes. The width of the trichomes of the specimens, also from the Caribbean region, was particularly variable (7.0–8.4, 8.0–9.5, 9.0–10.0 μm). A similar species, *A. leonardii* Comp. 1967, described from Africa, differs in size and slightly in trichome structure.

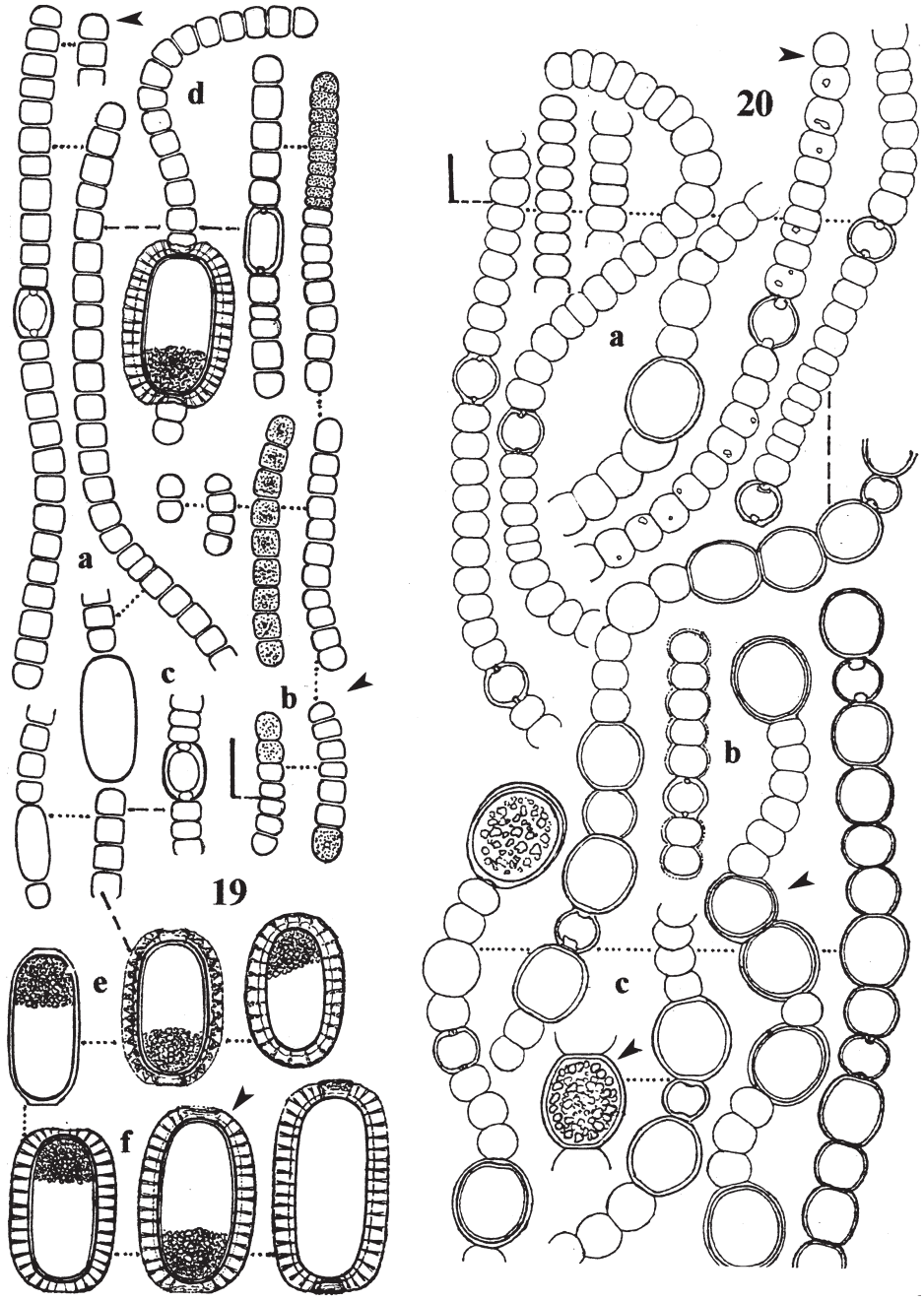

Fig. 19. – *Anabaena jeejiae*: orig., from gelatinous mats attached to floating mosses in pools near the reservoir Presa de Abra; a – terminal parts of a trichome, b – hormogonia, c – detail of a heterocyte, d – part of a trichome with akinete, e – development and variability of akinetes.

Fig. 20. – *Anabaena portoricensis*: orig., from old paddy fields near lake Laguna del Pesquero, Pinar del Río; a – parts of trichomes with heterocytes and developing akinetes, b – hormogonium with a heterocyte, c – parts of trichomes with heterocytes and akinetes.

Discussion

The genus *Anabaena* is a very diverse and variable genus of cyanoprokaryotes. Numerous morphospecies were described, which differ in a few (sometimes transient) characters and further studies are needed to establish their identity. Stulp & Stam (1984a, b) found in 16 cultures eight species determinable by traditional cytomorphological criteria, but with almost identical mo1% GC-complex of DNA (39.0–42.6), indicating the close genetic relatedness of these species and the uniformity of the genus. Gugger et al. (2002a, b) and Rajaniemi et al. (2005) studied planktic strains (morphotypes) of *Anabaena*, which differ in genotype from benthic *Anabaena, Trichormus, Cylindrospermum* and *Nostoc*-morphotypes. The planktic Anabaenas are very closely related to *Aphanizomenon*-species. However, in nature there is rather wide morphological variation within *Anabaena* and *Aphanizomenon* (Hindák 1992, Horecká & Komárek 1979, Komárek & Kováčik 1989), and stable morphologically distinct units (traditional species) repeatedly occur in a limited number of habitats and can be cultured. The stability of morphological characters in different clusters of the planktic *Anabaena/Aphanizomenon* complex must be confirmed by method another than 16S rRNA sequencing. For example, Li & Watanabe (1998) showed that various species of *Aphanizomenon* are genetically distinct. Therefore, the traditional system was used in this study and changes were only accepted if confirmed by modern methods.

The great morphological complexity of Anabaenacean types means that there are more cytomorphological features for studying the relations between populations or strains, and determining the variation in the ranges of morphological characters. Therefore, they could be model system for such studies and the description of natural populations could be used to evaluate the existence of very broad, plastic species, or limited, stabilized morphotypes (see Castenholz 1992).

This list of Cuban freshwater, free living *Anabaena* species is a preliminary one. It contains only those species, which were recorded from Cuba up till 1982. Interesting is the absence of temperate zone, particularly planktic species. Cuba is situated on an important bird migration route, therefore, the presence of planktic species from the temperate zone was expected. However, the number of samples is still too small for evaluating the similarities in planktic cyanoprokaryotic species occurring in Cuba and elsewhere.

None of the Cuban freshwater species of *Anabaena* has a cosmopolitan distribution. Of the 19 recorded morphospecies, seven are known only from tropical countries, several only from Africa, India or central Asia (*A. austro-africana*, *A. ambigua*, *A. orientalis)* but could have a pantropical distribution. On the other hand, four species, that were originally described from the Caribbean (Guadeloupe, Puerto Rico) and are now known to occur in Cuba (*A. portoricensis, A. unispora*, *A. manguinii*, and *A. torques-reginae*), could occur in other tropical areas.

Species that have a wide distribution (e.g. pantropical) always occur in several different morphotypes. For this reason, the Cuban populations are described and compared with original diagnoses of recorded species.

Several species are well distinguished and definitely characterized (*A.* cf. *reniformis*, *A. torques-reginae*, *A. manguinii*, *A. jeejiae* and others). On the other hand, in the studied material there are groups of related species, the delimitation of which is difficult. For example, one such group consists of three very similar species, characterized by large, oval, singly developed akinetes aside on heterocytes, usually many times larger than the vegetative cells *(A. volzii*, *A. unispora*, *A. fuellebornii).* The existence of different species within

this cluster was sometimes discussed (Geitler 1932, Desikachary 1959). In my samples all these types are distinguishable and are kept ad interim as separate species.

Difficulties in taxonomic evaluations exist in other groups of metaphytic *Anabaena* species with a wide variation in almost all features but very similar or identical ecology (Table 2). Wide variation in metaphytic species is common and in the studied material all populations differed slightly from one another with the values for the majority of their characters overlapping. For evaluation 22 well developed populations were selected, for which all types of cells, including ripe akinetes, were available for studies. Seven species were recognized among them. The first traditional criterion, which is stable in many *Anabaena* species, is the origin of the akinetes on the trichomes. Three species with akinetes distant from the heterocytes could be determined by cell dimensions, form of akinetes and morphology of trichome ends *(A. oblonga*, *A. cylindrospora*, *Anabaena* sp.).

The taxonomic classification of the next cluster of populations with akinetes usually on both sides of the heterocytes and with narrowed trichome ends, in which there are many transient forms, is also difficult (Table 2). The evaluation of species is uncertain. The majority of them are originally periphytic or metaphytic and their relatedness is evident. Several morphospecies in this group were recognized, based on literary descriptions: *A. austro-africana*, *A. turkestanica*, *A. ambigua*, *A. orientalis* and *A. iyengarii,* but all are very plastic and their delimitation must be confirmed. Five of these species have narrow trichome ends, but this character is facultative and common to almost all *Anabaena* species of this type.

Gas vesicles and aerotopes occasionally occur in *A. austro-africana*, *A. ambigua* and several other types. This feature could be diagnostic if the ability to form gas vesicles is found characteristic of these species, and absent in others. The traditional distinguishing features in benthic *Anabaena*-morphotypes (barrel-shaped and cylindrical cell form, cell size, differences in length/width ratios of vegetative and prominent cells, morphology of apical cells) were also used in the evaluation, but further study of variation in these types may affect their taxonomic designation.

Acknowledgements

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Souhrn

V sladkovodních stanovištích Kuby bylo zjištěno 19 tradičních, morfologicky definovaných druhů rodu *Anabaena*. V článku je diskutována jejich taxonomie a popsána variabilita jejich přírodních populací. Sedm druhů je známo pouze z tropických zemí (*A. ambigua, A. fuellebornii, A. iyengarii, A. oblonga, A. orientalis, A. recta, A. volzii*), čtyři z tropické Ameriky (*A. manguinii, A. portoricensis, A. torques-reginae, A. unispora*), jeden byl původně popsán z jižní Afriky (*A. austro-africana*) a jeden ze střední Asie (*A. turkestanica*). Dva druhy jsou nově popsány (*A. hatueyi, A. jeejiae*), dva nebyly identifikovány kvůli nedostatku materiálu. Pouze dva druhy, *A.* cf. *reniformis* and *A.* cf. *bornetiana*, se vyskytují i v temperátní zóně Evropy nebo Severní Ameriky a na Kubě představují speciální morfotyp.

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