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Authors: Alwathnani, Hend, and Johansen, Jeffrey R.

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CYANOBACTERIA IN SOILS FROM A MOJAVE DESERT ECOSYSTEM

Hend Alwathnani[1] and Jeffrey R. Johansen[2]

ABSTRACT.—The Fort Irwin National Training Center in the Mojave Desert of California contains soils that represent a diversity of disturbance regimes, including some soil sites that have been protected from anthropogenic disturbance for many years. Previous studies of the soils of this military installation discussed biogeography and ecology of the crusts but did not conduct detailed study of the species present. In this study, we selected 6 sites in and around the Fort Irwin Training Center to be the subject of intensive isolation efforts. These sites contained at least some development of microbiotic soil crust. Out of the more than 90 cyanobacterial isolates characterized, only 23 distinctive morphospecies were differentiated. Of these, only 13 were identified to a previously described species, the others being comparable to previously described aquatic species (cf.) or so dissimilar to described taxa that they were given numbers as identification. *Leptolyngbya* was the most species rich and also the most commonly isolated genus. Twelve filamentous genera were found; no coccoid representatives occurred in our samples. All taxa are described and illustrated. This study is significant as it is the first since the 1960s to examine cyanobacterial taxonomy of Mojave Desert soils in a systematic fashion. Our unidentified taxa are very likely new species but will require molecular sequence analysis before they can be named.

Key words: taxonomy, floristics, phycology, microbiotic crusts, cyanobacteria, Mojave Desert.

Microbiotic crusts, also known as biological soil crusts, are major components of most desert ecosystems in the world. In North America, microbiotic crusts appear to be less developed in the hottest and driest deserts, such as the Mojave Desert or Sonoran Desert, but they are typical in that they are colonized by many filamentous species of cyanobacteria (Johansen et al. 2001, Flechtner et al. 1998). As noted in previous studies, species of *Microcoleus, Nostoc*, and *Schizothrix* are the most prevalent cyanobacteria in both arid and semiarid lands (Johansen et al. 1981, Ashley et al. 1985, Johansen et al. 1985, Flechtner et al. 1998, Johansen et al. 2001) and are possibly the species most important in developing the appearance of the soil surface (Johansen 1993). In most cases, the dominant genera of filamentous cyanobacteria in hot desert soils are *Microcoleus, Phormidium, Plectonema, Schizothrix, Nostoc, Tolypothrix*, and *Scytonema* (Cameron 1960, Durrell 1962, Shields and Drouet 1962). However, taxonomic work in the hot deserts of North America has not been conducted recently, and our understanding of the cyanobacteria of Mojave Desert soils is particularly weak.

Johansen et al. (2001) conducted an extensive study of the distribution and abundance of microbiotic soil crusts in a large area of the Mojave Desert within and near the Fort Irwin National Training Center, San Bernadino County, California. Fort Irwin encompasses more than 2500 km^2 of desert valley and mountains. Johansen et al. (2001) examined valley areas receiving frequent training use, where no microbiotic crusts could be found; valley areas receiving infrequent to minimal training, where some crusts were present; and valley areas outside of National Training Center boundaries that were being considered as expansion sites and that had poorly to well-developed crusts. The undisturbed expansion sites are now within the boundaries of the training center. This study focuses on the taxonomy of the cyanobacteria isolated from the least disturbed, best crusted sites of that earlier study. We will report original descriptions and illustrations of the taxa present based upon our cultured material from those sites.

METHODS

Site Descriptions

A subset of 6 sites in Johansen et al. (2001) were chosen for detailed taxonomic work. These samples contained the most well-developed

[1]Department of Botany and Microbiology, King Saud University, Box 2455 Riyadh 11451, Saudi Arabia. E-mail: wathnani@ksu.edu.sa
[2]Department of Biology, John Carroll University, University Heights, OH 44118. E-mail: johansen@jcu.edu

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microbiotic crusts. Site photographs, soil chemistry, and cover categories of vascular plants, lichen crusts, moss crusts, algal crusts, and rock and bare soil are given in that paper and so will not be reported here. Only minimal descriptions of the sites necessary for understanding the content of this paper will be given below.

RPL1 is located just outside the boundaries of the National Training Center within sight of Red Pass Lake (a playa), at 35°1.695′N, 116° 19.079′W. While undisturbed, the site shows only minimal crust development. The site is sparsely vegetated with *Ambrosia dumosa* and *Larrea tridentata.* RPL2 is located just within the boundaries of the National Training Center slightly north of Red Pass Lake, at 35° 17.011′N, 116°19.504′W. RPL2 shows evidence of off-road vehicle disturbance and has very little shrub cover (<3% cover of *Ambrosia dumosa* and *Larrea tridentata*). However, it has good algal crust development (55% cover). The third Fort Irwin site, FISS, is in the southeastern corner of the National Training Center at 35°07.607′N, 116°29.716′W in an area protected from disturbance because of the presence of the protected desert tortoise. Shrub cover is again low (3.5%), with *Ambrosia dumosa, Lycium* sp., and *Larrea tridentata* present, whereas algal crust cover is high (69%).

SV2-1 is in the Silurian Valley, east of the National Training Center and north of Baker, located at 35°28.909′N, 116°07.335′W (this area has since been annexed to Fort Irwin). Dominant vascular plants are *Ambrosia dumosa* and *Larrea tridentata,* and algal crust is common (53% cover).

PR2 and PR3 are to the west of the National Training Center at Fort Irwin in an area known as Paradise Range (this area has since been annexed to Fort Irwin). PR2 is a gentle south-facing slope dominated by *Ambrosia dumosa* and minimal algal and moss crust cover, at 35°09.524′N, 116°52.201′W. The second Paradise Range site (PR3) is below PR2, at 35°09.954′N, 116°52.368′W, in a broad dry wash. Its shrub composition is very different from all other sites and includes *Ephedra californica, Senna armata,* and *Hymenoclea salsola.* Algal crust (with both lichens and mosses) has 57% cover in this site.

All sites have soils classified as loamy sands.

Isolation and Culture

Samples used in this study were all collected in 1997–1998. Soil samples were composites of ten 5-g samples from systematically placed quadrats within each site. Soil samples were crushed and mixed to produce homogenous samples. Subsamples (1.0 g) were dilution plated in triplicate on agar-solidified Z-8 medium (Carmichael 1986), as described in Flechtner et al. (1998), and were incubated at 20 °C under fluorescent light (200 $\mu E \cdot s^{-1}cm^{-1}$) with a 16 h light/8 h dark photoperiod until good growth was obtained (3–6 weeks).

Morphological Characterization

All cyanobacterial isolates were examined using a high-resolution Olympus photomicroscope equipped with Nomarski DIC optics to study cellular features. Colony morphology was examined using a stereomicroscope. For all the strains examined in this study, morphological characteristics were noted, such as sheath type, presence or absence of false branching, cell and trichome dimensions, types of thylakoid arrangement, constrictions at cross-walls, shape of end cells, presence or absence of meristematic zones, presence or absence of necridia, and pigmentation. In addition to descriptive notes on morphological characteristics, color slides of all strains were taken at 400X or 1000X for future reference. Drawings were made from the slides (drawn from projections) of representative specimens from selected strains. Voucher specimens of surviving cultures were prepared by drying material onto glass fiber filters as well as by preserving the culture in 4% formaldehyde in glass bottles. These materials will be housed in the Herbarium for Nonvascular Cryptogams (BRY) in the Monte L. Bean Life Science Museum, Provo, Utah.

RESULTS

We isolated over 90 strains of cyanobacteria from soils at the 6 sites. The most commonly isolated genus was *Leptolyngbya,* a difficult and problematic taxon. Originally we had nearly a dozen different "taxa" in this genus, but after further study these were collapsed into only 6 taxa, including *L. foveolarum, L. nostocorum, L. tenuis,* and 3 unnamed morphospecies. *Nostoc* and *Scytonema* were also commonly isolated.

We identified 23 morphospecies in 12 genera (Table 1) based on Geitler (1930–1932),

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TABLE 1. Species and their distribution for 6 selected sites in the Mojave Desert.

Species	RPL1	RPL2	FISS	SV2-1	PR2	PR3
Pseudanabaenales						
Arthronema cf. *africanum*		X			X	
Leptolyngbya foveolarum	X	X	X	X	X	X
Leptolyngbya nostocorum		X	X			X
Leptolyngbya tenuis					X	
Leptolyngbya sp. 1		X			X	X
Leptolyngbya sp. 2					X	
Leptolyngbya sp. 3					X	
Trichocoleus sp. 1					X	X
Oscillatoriales						
Pseudophormidium hollerbachianum		X				
Phormidium cf. *kuetzingiana*		X		X		
Phormidium sp. 1		X	X	X		
Symploca muscorum				X		
Microcoleus steenstrupii	X			X		X
Microcoleus vaginatus	X				X	X
Nostocales						
Nostoc indistinguenda			X		X	X
Nostoc desertorum	X		X		X	
Nostoc punctiforme				X	X	
Calothrix cf. *fusca*		X				
Scytonema javanicum			X			X
Scytonema cf. *obscurum* var. *terrestre*				X		
Scytonema hyalinum			X			
Hassallia byssoidea			X			
Tolypothrix cf. *camptylonemoides*			X			X
Total species richness	4	7	10	5	12	10

Desikachary (1959), and the modern classification scheme of Komarek and Anagnostidis (1986, 1989, 1999, 2005). There was little difference in the number of species that occurred in each site. PR2 in Paradise Range was the most diverse site, with a total of 12 species, but FISS and RPL3 were almost as diverse, with 10 species each (Table 1). RPL2 was the only site that had *Calothrix* species, but it only had a total of 7 cyanobacterial species. FISS was the only site containing *Pseudophormidium.* Among all studied sites, RPL1 had the lowest diversity (4 species). SV2-1 in the Silurian Valley was also low in diversity (5 species). These latter 2 sites were both undisturbed but were geologically aged, with extensive desert pavement and sparse shrub development.

SPECIES ACCOUNTS

Pseudanabaenales

Pseudanabaenaceae

Arthronema cf. *africanum* (Schwabe) Komárek et Lukavský

(Figs. 1, 2, 47)

Filaments with one trichome per sheath, with no false branching evident, 3.0–3.5 μm wide. Sheaths thin, firm, open, colorless. Trichomes slightly flexuous, untapering, slightly constricted at the cross-walls, without evident meristematic zones or necridia, 2.5–3.5 μm wide. Cells yellowish green in color, granular, with thylakoids peripheral along the outside walls and cross-walls, mostly longer than wide, but with asymmetric cell division, 3.0–12.0 μm long. Involution cells are only slightly wider and slightly more irregular than normal cells. End cells bluntly rounded, not differing otherwise. Few-celled hormogonia rare.

Arthronema is distinguished from *Leptolyngbya* both by the presence of involution cells and the presence of asymmetrical cell division. Our strains had fairly indistinct involution cells compared to other described species but clearly had the asymmetrical cell division. This taxon is similar to the broadly defined *A. africanum,* a form which lives in saline-wetted desert localities in North Africa. It differs by having longer cells (3–12 versus 1–7) and smaller involution cells and by living in low salt conditions and occupying dry soils.

Phylogenetic analyses of Pseudanabaenaceae that include *Arthronema africanum* and *A. gygaxiana* Casamatta et Johansen (Casamatta

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et al. 2005) indicate that *Arthronema* is closely related to putative *Leptolyngbya* and *Limnothrix* taxa and may not be monophyletic. Further work in this genus is needed to see if the diacritical characters of involution cells and asymmetric cell division define a monophyletic cluster of taxa within the family. Our strains likely belong to a distinctive species different than *A. africanum* but should not be described until the status of *Arthronema* is determined through molecular methods.

Leptolyngbya foveolarum
(Rabh. ex Gom.) Anag. et Kom.
(Figs. 3–8, 46, 50)

Filaments with single trichome per sheath, with single false branching evident, rarely slightly tapering, 2.0–3.0 μm wide. Sheaths thin, open, colorless, firm to soft. Trichomes slightly flexuous, untapering, unconstricted to slightly constricted at the cross-walls, with meristematic zones, with thin translucent necridia, 1.5–2.0 μm wide. Hormogonia few-celled, evidently constricted at the cross-walls, and lacking sheath material. Cells light blue green to yellowish, nongranular or with central granule, with thylakoids along the cross-walls and outside walls, generally shorter than wide to quadrate, 1.0–2.0(4) μm long. End cells bluntly rounded, sometimes tapered.

This morphospecies was common in our sites (Table 1). It is very similar to another form seen on San Nicolas Island (Flechtner et al. 2008) and given the same name. While we question the identification of desert soil forms as European soil forms, our taxon fits the species and has the features associated with *Leptolyngbya* sensu stricto: cells shorter than wide, with distinct peripheral thylakoids, necridia, false branching, and rounded end cells. We saw considerable variability associated with the life cycle. The thinnest trichomes (Figs. 3, 4, 7, 8) are most like the published descriptions of the species (Komárek and Anagnostidis 2005). The widened trichomes with very short cells (meristematic zones) have a very different appearance (Figs. 5, 6), but were seen in multiple isolates. This group of *Leptolyngbya* needs further work.

Leptolyngbya nostocorum
(Bornet ex Gom.) Anag. et Kom.
(Figs. 15, 16)

Filaments with single trichome per sheath, with no false branching, 2.0–2.5 (3.0) μm wide. Sheaths thin, open, colorless, soft. Trichomes slightly flexuous, not tapering, very constricted at the cross-walls, without meristematic zones, without necridia, 2.0–2.5 μm wide. Hormogonia few-celled, evidently constricted at the cross-walls, and lacking sheath material. Cells blue green, becoming yellowish to washed-out brown with age, rarely with a small central granule, with thylakoids not visible in light microscopy, generally isodiametric, 2.0–2.5 (4.0) μm long. End cells slightly conical to bluntly rounded.

This is a widely reported taxon from soils and was named for the bead-like cells in the trichome, similar to what is seen in many *Nostoc* species. Komárek and Anagnostidis (2005) report that the trichomes are only feebly constricted, and Flechtner et al. (2008) show specimens also from California soils that are clearly constricted but not as bead-like as what we saw in the Fort Irwin area. This is a cosmopolitan taxon that molecular analysis may show contains many cryptic species.

Leptolyngbya tenuis (Gom.) Anag. et Kom.
(Figs. 19, 51)

Filaments with one trichome per sheath, with no false branching evident, 2.5 μm wide. Sheath thin, open, colorless. Trichomes slightly flexuous, often arranged in parallel fascicles, tapered, slightly constricted at the cross-walls, no evidence of meristematic zones or necridia, 1.5–2.0 μm wide. Cells pale green in color, no granules, longer than wide, 2.0–5.0 μm long. End cells elongated, tapering.

This morphospecies was present only in PR2. *Leptolyngbya tenuis* has been reported from soils, stagnant salty waters, and thermal springs. Given the breadth of physiology and biogeography reported, it is likely a cluster of cryptic species. *Leptolyngbya tenuis* is based on *Phormidium tenue* (Menegh.) Gom. ex Gom., which has been reported from other desert soils (Johansen et al. 1982, 1993). *Phormidium tenue* belongs in the subgenus *Protolyngbya,* which differs from subgenus *Leptolyngbya* by having cells longer than wide and no necridia.

Leptolyngbya sp. 1
(Figs. 9, 10, 49)

Filaments generally with one trichome per sheath, rarely with 2–3 trichomes in a common sheath, with single and double false branching evident, 2.5–3.0 μm wide. Sheaths thin, open,

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colorless. Trichomes slightly flexuous, slightly tapering, unconstricted at the cross-walls, with no evidence of meristematic zones, with thin translucent necridia, 2.0–3.0 μm wide. Cells green to yellowish green to washed-out brown, nongranular to slightly granular, with thylakoids peripheral along the cross-walls and outside walls, 0.75–2.0 times as long as wide, 1.5–4.0 μm long, rarely longer. End cells bluntly rounded. Hormogonia result through production of necridia.

This taxon was isolated multiple times from the Paradise Range (both PR2 and PR3). These strains are distinguished by having double false branching, no constrictions, and no meristematic zones. The cells are often longer than wide, but not so much as to identify the strain to the subgenus *Protolyngbya.*

Leptolyngbya sp. 2

(Figs. 11, 12, 48)

Filaments with one trichome per sheath, with double false branching evident, 4.0 μm wide. Sheaths firm, open, colorless. Trichomes slightly flexuous, not tapering, unconstricted at the cross-walls, without meristematic zones, with thin translucent necridia, 2.0–3.0 μm wide. Cells washed-out brown in color, with 1 or 2 large granules at the cross-walls, generally shorter than wide or quadrate, 1.5–4.0 μm long. End cells bluntly rounded.

This taxon was found only in PR2. It has double false branching similar to *Leptolyngbya* sp. 1 but differs by the presence of 2 large granules straddling each cell cross-wall and by the evident, widened, very firm sheath. Trichomes can become doubled in the sheath (Fig. 12), a fairly distinctive feature.

Leptolyngbya sp. 3

(Figs. 17, 18, 55).

Filaments with one trichome per sheath, with no false branching evident, 3.0 μm wide. Sheaths thin, firm, open, colorless. Trichomes slightly flexuous, tapering toward apices, slightly constricted at the cross-walls, without meristematic zones, mostly 2.0–2.5 μm wide. Cells yellowish green in color, often with 2 large granules positioned near the cross-wall, with thylakoids not visible in the light microscope, usually longer than wide, 2.5–5.5 μm long. End cells bluntly rounded. Few-celled hormogonia rare to common.

This taxon was represented by 3 isolates from PR2 in the Paradise Range. This *Leptolyngbya* is distinct from the species in subgenus *Protolyngbya* catalogued in Komárek and Anagnostidis by its larger diameter. Most *Protolyngbya* do not exceed 2.0 μm in diameter. The granules at the cross-walls are an unusual feature for the genus. This taxon bears a resemblance to some *Geitlerinema* species, which can be similarly granulated at the cross-walls. However, we saw no motility in our populations, and the single soil species of *Geitlerinema* (*G. tenuius* [Stockmayer] Anag.) is not granulated at the cross-walls.

Schizotrichaceae

Trichocoleus sp. 1

(Figs. 13, 14).

Filaments with 1 to 2 trichomes per sheath, without false branching, 2.5–3.0 (4.0) μm wide. Sheaths thin, open, colorless, firm, becoming diffluent. Trichomes slightly flexuous, tapering, slightly constricted at the cross-walls, meristematic zones not common, without necridia, 2.0–3.0 μm wide. Hormogonia few-celled, evidently constricted at the cross-walls, and lacking sheath material. Cells blue green, becoming olive to washed-out brown with age, rarely granular, with thylakoids peripheral along the outside wall, mostly isodiametric but both shorter and longer than wide, 1.5–3.5 (7) μm long. End cells acutely conical, sometimes longer than other cells, up to 5.0 μm long.

Several strains of this species were isolated from soils in the Paradise Range. The occurrence of multiple trichomes in an open sheath is characteristic of the genus *Trichocoleus.* Our trichomes frequently had cells shorter than wide, a characteristic more reminiscent of *Leptolyngbya* than *Trichocoleus*, which typically has cells longer than wide. Flechtner et al. (2008) reported *Trichocoleus* cf. *delicatulus* from San Nicolas Island, California, but their strain had narrower trichomes and longer cells. Both their strain and ours have conical end cells, but the 2 forms likely represent different species. Our strain is also very similar to *Schizothrix arenaria* Gomont but differs in the sheath characteristics and in the cells which can be shorter than wide. Molecular work on this complex is needed, as the genus *Trichocoleus* currently has no known sequences, and its identity may be confused with *Leptolyngbya* and *Schizothrix.*

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Oscillatoriales

Phormidiaceae

Pseudophormidium hollerbachianum (Elenkin) Anag.

(Figs. 20. 21, 52)

Filaments with one to few trichomes per sheath, with false branching evident, sheath sometimes widened, 4–10 μm wide. Sheaths firm, open, colorless. Trichomes untapered, constricted at the cross-walls, necridia sometimes present, 3.0 μm wide. Cells blue green in color, nongranular, with thylakoids parietal along outside walls and cross-walls, cells mostly shorter than wide, 1.5–2.0 (4) μm long.

Pseudophormidium hollerbachianum is a soil species originally observed in Russia but found widely. Our specimens fit this species well. *Pseudophormidium hollerbachianum* is easily confused with *Leptolyngbya;* indeed, the genus *Pseudophormidium,* as currently conceived, is likely a polyphyletic assemblage containing species in both the Pseudanabaenaceae and Phormidiaceae. It was observed in FISS, a relatively undisturbed site in Fort Irwin.

Phormidium cf. *kuetzingianum* (Kirchner) Anag. et Kom.

(Figs. 24–25, 53)

Filament with solitary trichome in firm open sheath, 5–7 μm wide. Trichomes straight or slightly curved, solitary. Untapering to slightly tapering, sometimes constricted though generally not constricted at the cross-walls, with no evident meristematic zones and necridia, cells 3.5–6.0 μm wide. Cells green in color, granular with large granules, irregular thylakoids, mostly longer than wide or quadrate, 4–11 μm long. End cells mostly bluntly rounded.

This morphospecies was found in Silurian Valley (CSV2-1) and Red Pass Lake (FI2). Our strains differ from *P. kuetzingianum* in that they have a wider diameter range. On average, they are 5.0 μm wide, whereas *P. kuetzingianum* has a diameter of 3–4 μm (Komárek & Anagnostidis 2005).

Phormidium sp. 1

(Figs. 22, 23, 56)

Filaments with solitary trichome in firm, thick, colorless sheaths, 3.5–6.0 μm wide. Trichomes slightly flexuous, not tapering, slightly constricted at the cross-walls, with evident meristematic zones and necridia, cells 3.5–5.0 μm wide. Hormogonia short and numerous. Cells green in color, not granular, isodiametric or shorter than broad, 1.5–3.5 (6.0) μm long. End cells bluntly rounded.

This species is also similar to *P. kuetzingianum,* but the constricted cross-walls, smaller size, and abundant hormogonia indicate that it is different than the taxon we call by that name.

Symploca muscorum (Ag.) Gomont.

(Figs. 26–27, 54)

Filaments with one trichome per sheath, with no false branching evident, 5.0–6.5 μm wide. Sheaths firm, colorless. Trichomes slightly flexuous, unconstricted at the cross-walls in rapidly growing cultures, becoming constricted with age, without evident meristematic zones, 4.0–5.5 μm wide. Cells green in color, nongranular or at times with 1–2 granules near the cross-walls, with bluish granules in the centroplasm, with thylakoids not visible in the light microscope, longer than wide, 3–10 (15) μm long. Cells not tapering or slightly tapering toward the ends. End cells bluntly rounded to rarely tapered.

This taxon was identified based on cellular dimensions, sheath characteristics, and habitat preference. We did not see the upright bundles characteristic of the genus in our culture material. The trichomes were constricted in aged cultures.

Microcoleus steenstrupii

(Figs. 28–29, 60)

Filaments with one trichome per sheath, 6.5–7.0 μm wide. Sheaths firm, open, colorless. Trichomes slightly flexuous, arranged in parallel fascicles, tapering, unconstricted to slightly constricted at the cross-walls, lacking calyptra, with necridia, 4.5–6.5 μm wide. Cells pale green to yellowish green, nongranular to granular, shorter than broad to quadrate, 2.5–4.5 (6.0) μm long. End cells bluntly rounded after fragmentation, becoming attenuated toward the ends when mature.

This morphospecies was discussed extensively in Boyer et al. 2002. Our strains were typical of the species, and clearly differed from *Microcoleus vaginatus* by the type of cell-type division and the characteristics of the end cell, which is elongated and has no calyptera. In culture it is typical to lose the characteristic multitrichome filaments.

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Microcoleus vaginatus
Goment ex Goment

(Figs. 30–31, 57)

Filaments with one trichome per sheath, with calyptera, 6.0–10.5 μm wide. Sheaths firm, open, colorless. Trichome slightly flexuous, narrowed at the ends, unconstricted at the cross-walls, with no necridia observed, 4–7 μm wide. Cells pale yellowish brown in color, cells very granular at the cross-walls, cells shorter than wide or quadrate, 2.0–6.5 μm long. End cells bluntly rounded after fragmentation, becoming tapered to as small as 3.5 μm wide, calyptrate.

Our strains were very typical for this taxon (Boyer et al. 2002). In culture, only one trichome per sheath was evident.

Nostocales

Nostocaceae

Nostoc indistinguendum
Řeháková et Johansen

(Figs. 32–33, 61)

Colonies are microscopic, spherical to oval when very young, becoming irregular and elongated oval when larger, with trichomes densely arranged in firm, colorless sheaths. Mucilage generally colorless, rarely becoming yellowish brown, without individual sheaths on the trichomes. Trichomes generally so compact that they cannot be discerned but are discernable in old, large colonies, pale green to darker yellowish green, distinctly constricted at the cross-walls, 3.5–7.5 μm wide, with the production of hormogonia (3.75–4.0 μm wide) and germling filaments (up to 7.5 μm wide). Vegetative cells are shorter than broad to quadrate, 2.0–7.5 μm long. Akinetes are rare with slightly granular contents. Heterocytes apical on colonies, 3.5–7.5 μm wide, 3.5–5.5 μm long.

This species was recently described by Řeháková et al. (2007) from the Clark Mountains in California, a locality east of Fort Irwin. Our specimens were a close morphological fit.

Nostoc desertorum
Řeháková et Johansen

(Figs. 34–35, 62)

Colonies are microscopic, spherical to irregular, with cells compact in unrecognizable trichomes. Colonial mucilage firm, colorless to yellowish brown, with individual sheaths around groups of cells in the colony. Germling filaments one to several cells wide, apparently growing from a uniseriate series into elongate colonies. Trichomes so compact that they cannot be discerned, very constricted at the cross-walls, dark green to yellowish, with the production of germling filaments, 2.5–6.5 μm wide. Vegtative cells are longer than broad to quadrate, 3–8 μm long. Akinetes are rare with slightly granular contents. Heterocytes apical, 4–7 μm wide, 4.0–6.5 μm long.

This species is characterized by the dark yellow color of the firm sheath as well as the clear individual sheaths that develop around the cells of mature colonies. It was also described from the nearby Clark Mountains (Řeháková et al. 2007).

Nostoc punctiforme Kütz. ex Hariot

(Figs. 58, 59)

Colonies microscopic, mostly spherical, but occasionally irregularly subspherical or elongated, with trichomes densely arranged in mucilage. Colonial mucilage firm, thin, with a firm outer layer, yellowish to colorless, with individual sheaths around the trichomes not evident. Trichomes so compactly arranged as to generally not be visible as trichomes in the colonies, distinctly constricted at the cross-walls, with the production of hormogonia and germling filaments, blue green to yellowish, 3.0–6.5 μm wide. Vegetative cells quadrate to longer than broad, 2.5–8.0 μm long. Akinetes are rare with slightly granular contents. Heterocytes intercalary, 4–6 μm wide, 3–7 μm long.

This species was restricted to the Paradise Range. This is a commonly reported species which may actually represent young populations of *N. indistinguendum.*

Rivulariaceae

Calothrix cf. *fusca* Born. et Flah.

(Figs. 36–37, 66).

Filaments heteropolar with a widened, often bulb-like basal part, unbranched, not tapering to a hair, 7.5–13.0 μm wide at the widest part, 6.5–9.5 μm wide in the middle, becoming as narrow as 3.5 μm wide at the apex. Sheath firm, thin, unlamellated, smooth, colorless to yellowish. Trichome distinctly constricted at the cross-walls, sometimes with necridia. Cells olive green to yellowish, minutely granular, shorter than wide at the base, becoming elongated toward the ends, 3.5–16.0 μm long. End cells tapered. Heterocytes basal, solitary, 4.5–7.5 wide, 2–7 μm long. Akinetes absent.

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This species was found only in RPL2. Our strains most closely resemble *C. fusca*, but differ from that taxon (and others) by never tapering to a hair and by ecophysiology (*C. fusca* is found in the mucilage of aquatic algae).

Scytonemataceae

Scytonema javanicum Bornet et Thuret ex Bornet et Flahault.

(Figs. 38–39, 67)

Filaments growing upright, isopolar, with mostly double false branching, with some single false branching, with single trichome per sheath, 10.5–14.0 μm wide. Sheath firm, thin, unlamellated, colorless to dark brownish yellow. Trichomes not constricted at the cross-walls, sometimes slightly tapered towards apices, 9.2–12.8 μm wide. Cells blue green to olive green, minutely to coarsely granular, shorter than wide, 2.4–7.6 μm long. End cells rounded. Necridia present. Heterocytes 9.2–11.6 μm wide, 6.8–9.2 μm long.

This species was found in 2 undisturbed sites (Table 1). Our specimens fit the description of *S. javanicum*. *Scytonema javanicum* is a reportedly cosmopolitan terrestrial species but was originally described from wet soils, not desert soils.

Scytonema cf. *obscurum* var. *terrestre* Hansgirg

(Figs. 40–41, 63)

Filaments growing upright, with double false branching, with single trichome per sheath, 11 μm wide. Sheath thin, firm, unlamellated, colorless. Trichomes constricted to not constricted at the cross-walls, occasionally producing necridia, 8.5–11.0 μm wide. Cells minutely to coarsely granular, dull olive green, shorter than wide, 3–6 μm long. End cell bluntly conical, longer than wide, nongranular. Heterocytes 8.5–11.0 μm wide, 8.5 μm long.

This species bears some resemblance to *Scytonema javanicum*, but it has shorter cells, thinner trichomes, and other minor differences. It is similar to the terrestrial taxon *Scytonema obscurum* var. *terrestre*, except that its cells are generally longer than reported for that taxon (ours are 1/2–1/3 as long as broad, compared to 1/3–1/5 as long as broad reported for the species).

Scytonema hyalinum Gardner

(Fig. 68)

Filaments isopolar, with single and double false branching, with a single trichome per sheath, 12–16 μm wide. Sheath firm, thin, unlamellated, colorless to yellowish brown. Trichomes not constricted to slightly constricted at the cross-walls, 10–14 μm wide. Cells olive green, minutely to coarsely granular, shorter than wide, 2.8–7.2 μm long. End cell with a cap. Necridia present. Heterocytes 10.4 μm broad, 2.4 μm long.

This taxon is distinguished by its apical cap. Geitler (1930–1932) questions the taxonomic value of the cap and suggests this species may actually be *S. javanicum.* We consider the apical cap to have taxonomic value.

Microchaetaceae

Hassallia byssoidea Hass. ex Bornet et Flahault

(Figs. 42–43, 65)

Filaments heteropolar, with mostly single false branching, with some double false branching, 8–12 μm wide. Sheath evident, moderately wide but thinner than the trichome, rough, colorless. Trichomes usually slightly constricted at the cross-walls, sometimes not constricted, dirty blue green to brownish, with subapical meristematic regions, with abundant necridia, 8–10 μm wide. Cells shorter than broad, 1.6–4.0 μm long. Heterocytes with a single polar nodule, 6.4 μm wide, 3.6 μm long.

Hassallia has recently been reseparated from *Tolypothrix* based on constricted trichomes, short disk-like cells, tendency to branch to 1 side, and predominance in soils and subaerial habitats.

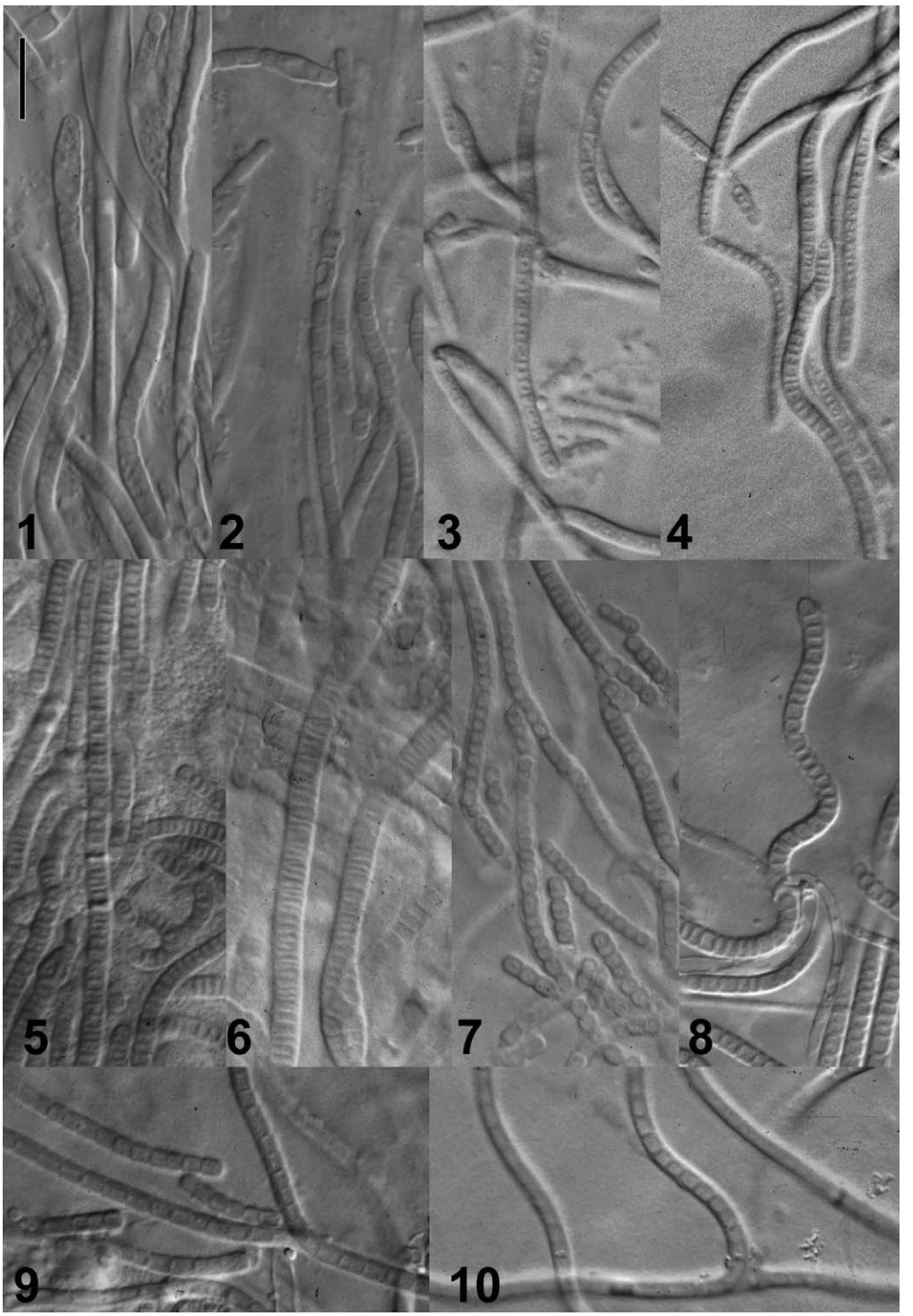
Tolypothrix cf. *camptylonemoides* Ghose

(Figs. 44–45, 64)

Filaments heteropolar, with rare single false branching, mostly breaking into individual short filaments following heterocyte formation, 7.0–9.5 μm wide. Sheath thin, smooth, colorless. Trichomes usually not constricted at the cross-walls, sometimes slightly constricted, blue green to yellowish green, without meristematic zones, with necridia, 5.0–8.5 μm wide. Cells slightly granular, shorter than wide, 3–6 μm long. End cells rounded to bluntly conical. Heterocytes with a single polar nodule, 6.5–10.0 μm wide, 5.5–10.0 μm long.

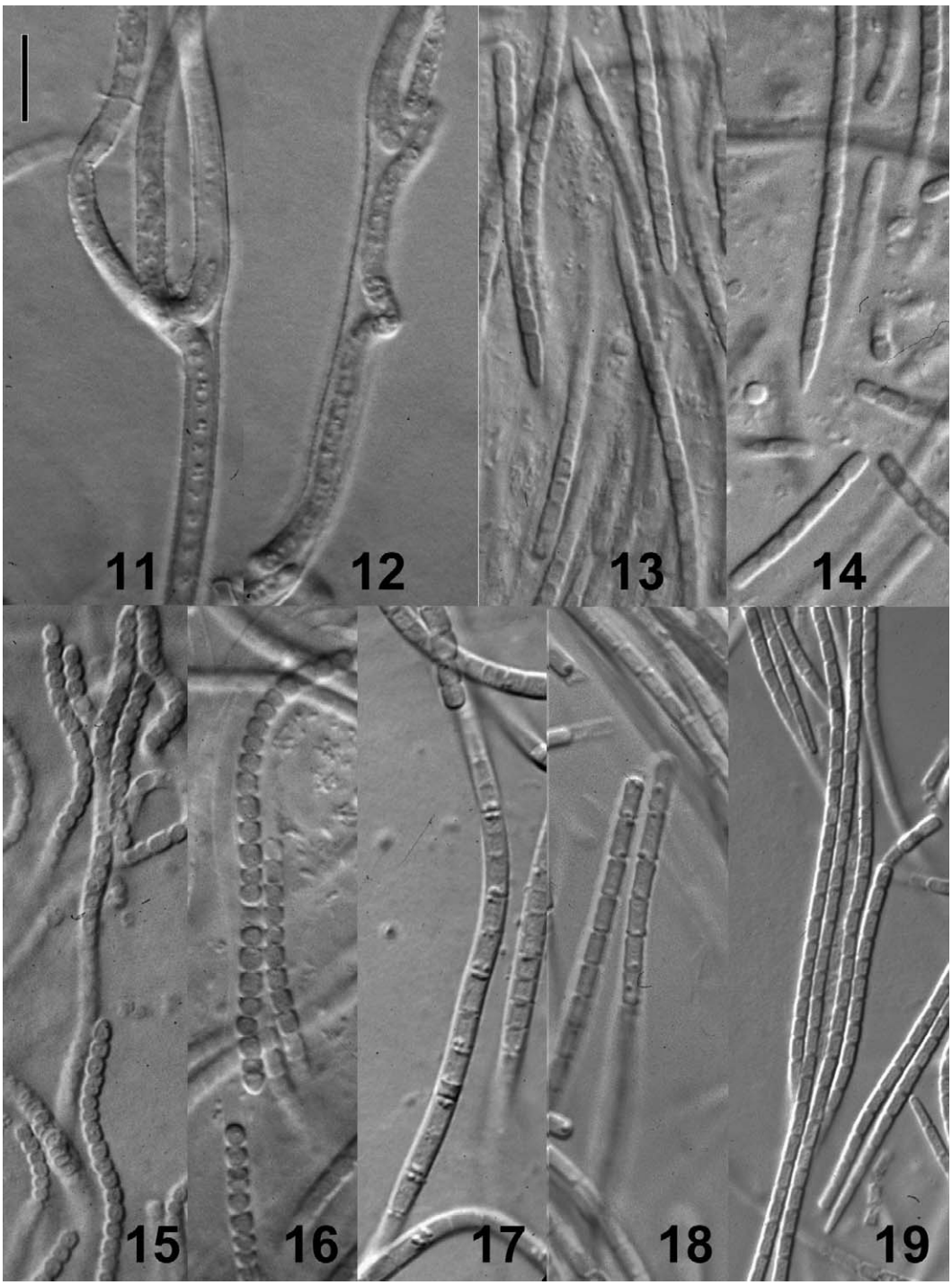
This taxon was present only in very undisturbed sites. Although our form fits the dimensions of *T. camptylonemoides*, it is considerably less constricted than illustrations of that taxon (Geitler 1930–1932, Fig. 467). It shares the terrestrial habit of that taxon and also repeatedly fragments to form hormogonia.

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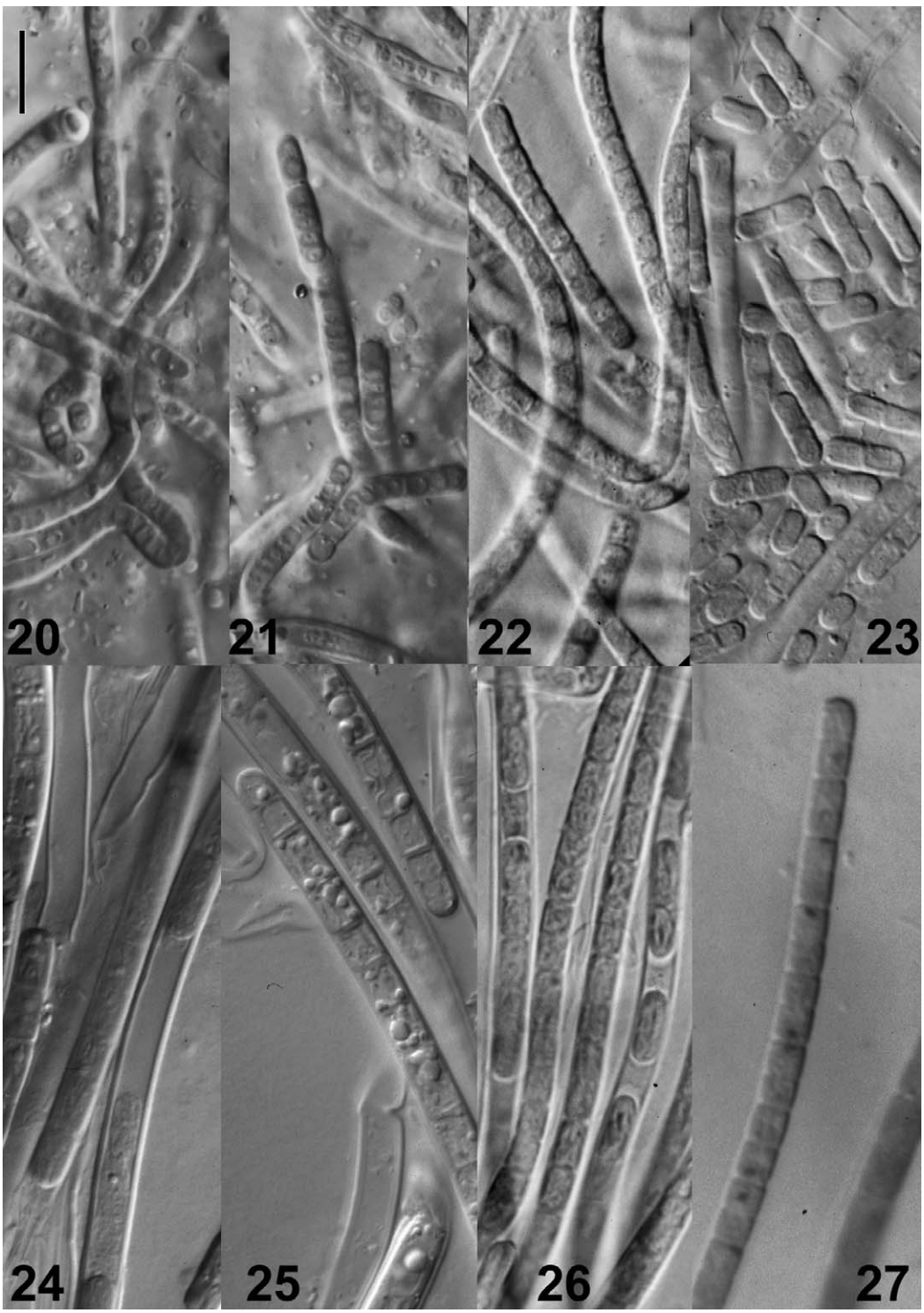
Figs. 1–10. Pseudanabaenaceae in Mojave Desert soils: **1–2,** *Arthonema* cf. *africanum,* showing variability of trichome width and apical involution cells; **3–8,** *Leptolyngbya foveolarum,* showing trichome and cell variability associated with the life cycle. Note meristematic zones and necridia (Fig. 5), false branching (Figs. 6–7); **9–10,** *Leptolyngbya* sp. 1 showing single false branching. Scale = 10 μm.

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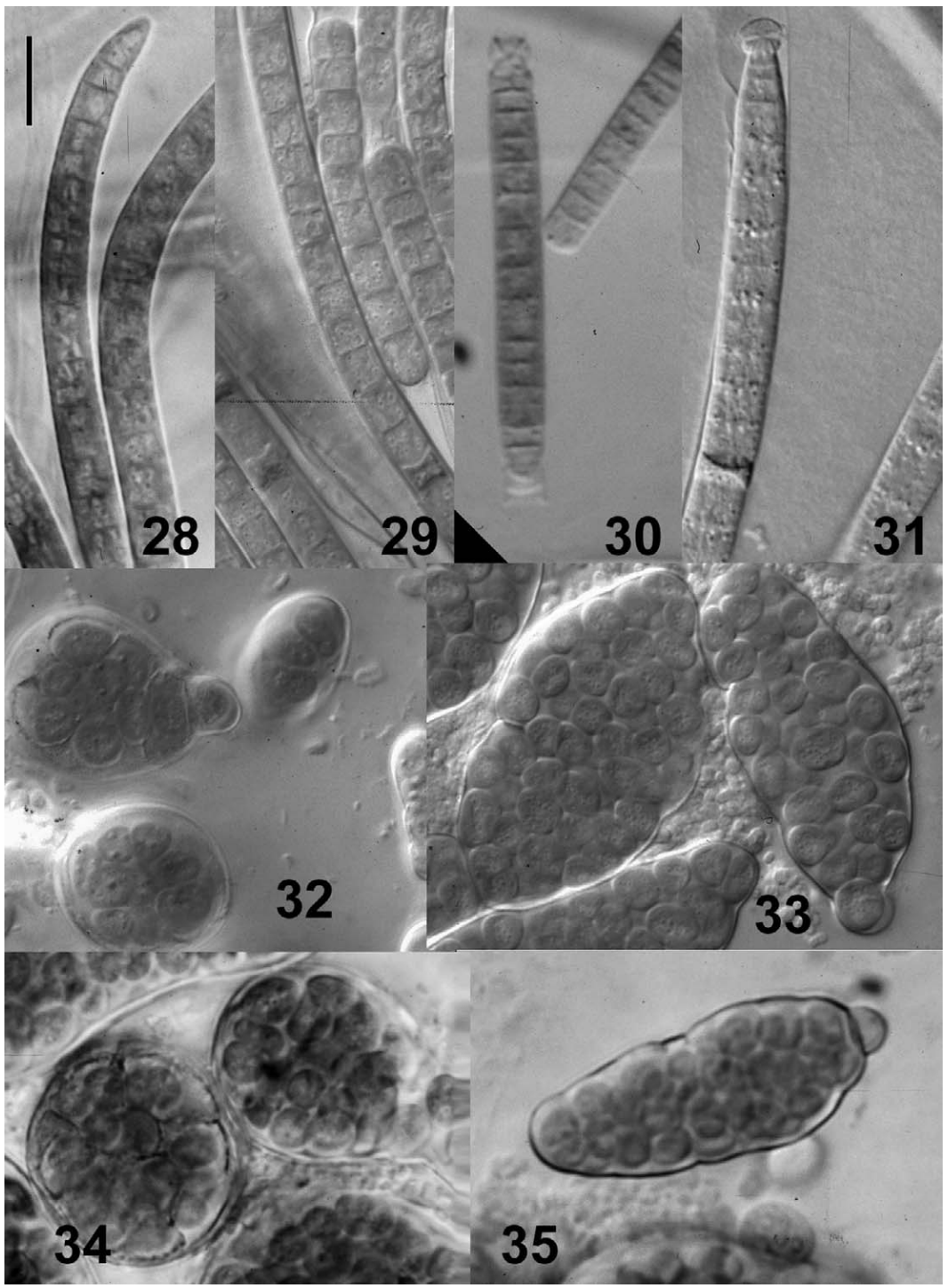
Figs. 11–19. Pseudanabaenaceae and Schizotrichaceae in Mojave Desert soils: **11–12,** *Leptolyngbya* sp. 2 showing double false branching with very firm sheath; **13–14,** *Trichocoleus* sp. 1; **15–16,** *Leptolyngbya nostocorum.* Note the very constricted cross-walls; **17–18,** *Leptolyngbya* sp. 3. Note large granules positioned near the cross-walls; **19,** *Leptolyngbya tenuis* showing trichomes with elongated end cells arranged in parallel fascicles. Scale = 10 μm.

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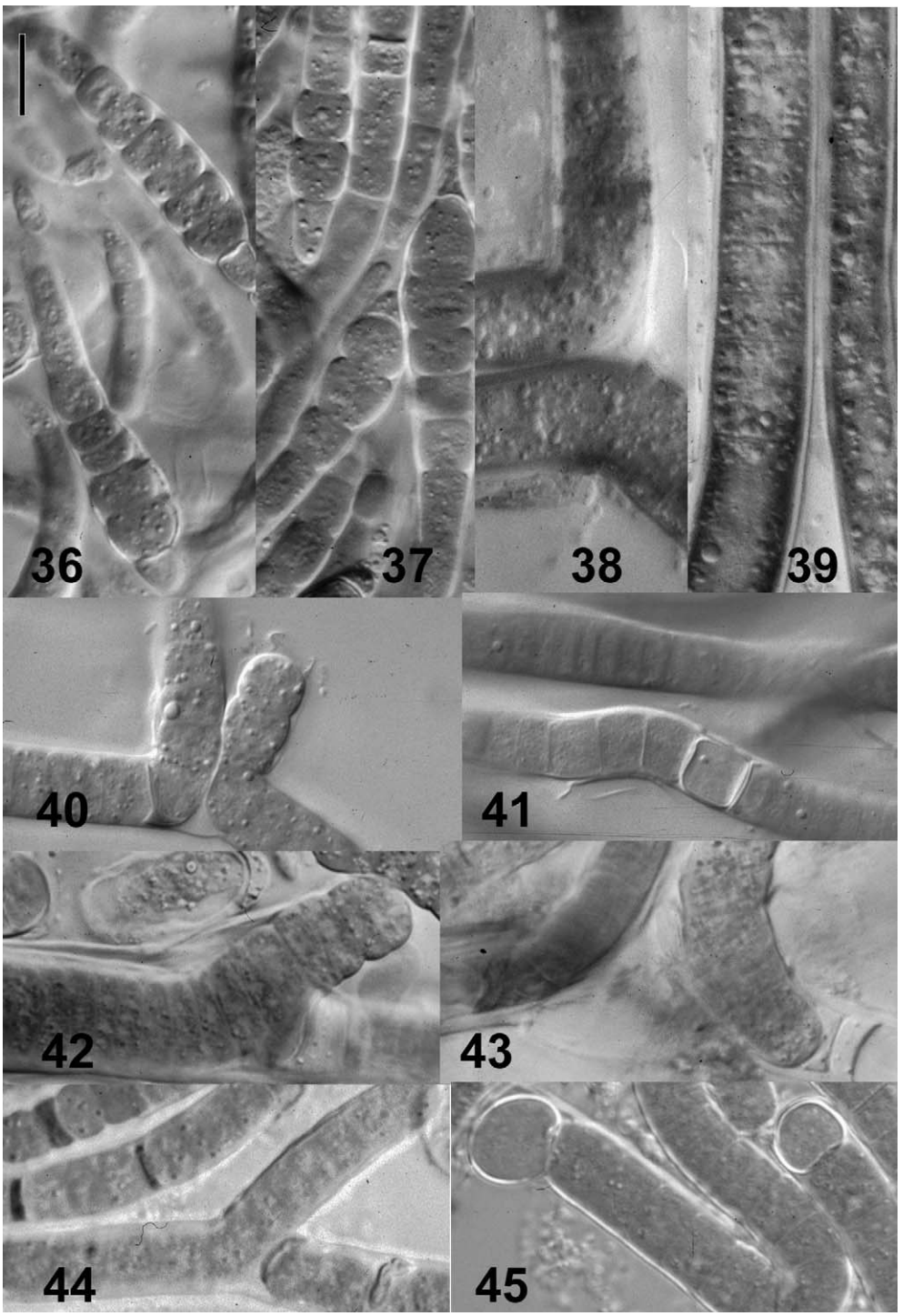
Figs. 20–27. Phormidiaceae in Mojave Desert soils: **20–21,** *Pseudophormidium hollerbachianum;* **22–23,** *Phormidium* sp. 1. Note the numerous short hormogonia; **24–25,** *Phormidium* cf. *kuetzingianum;* **26–27,** *Symploca muscorum.* Note dark granules (blue in color) in the centroplasm. Scale = 10 μm.

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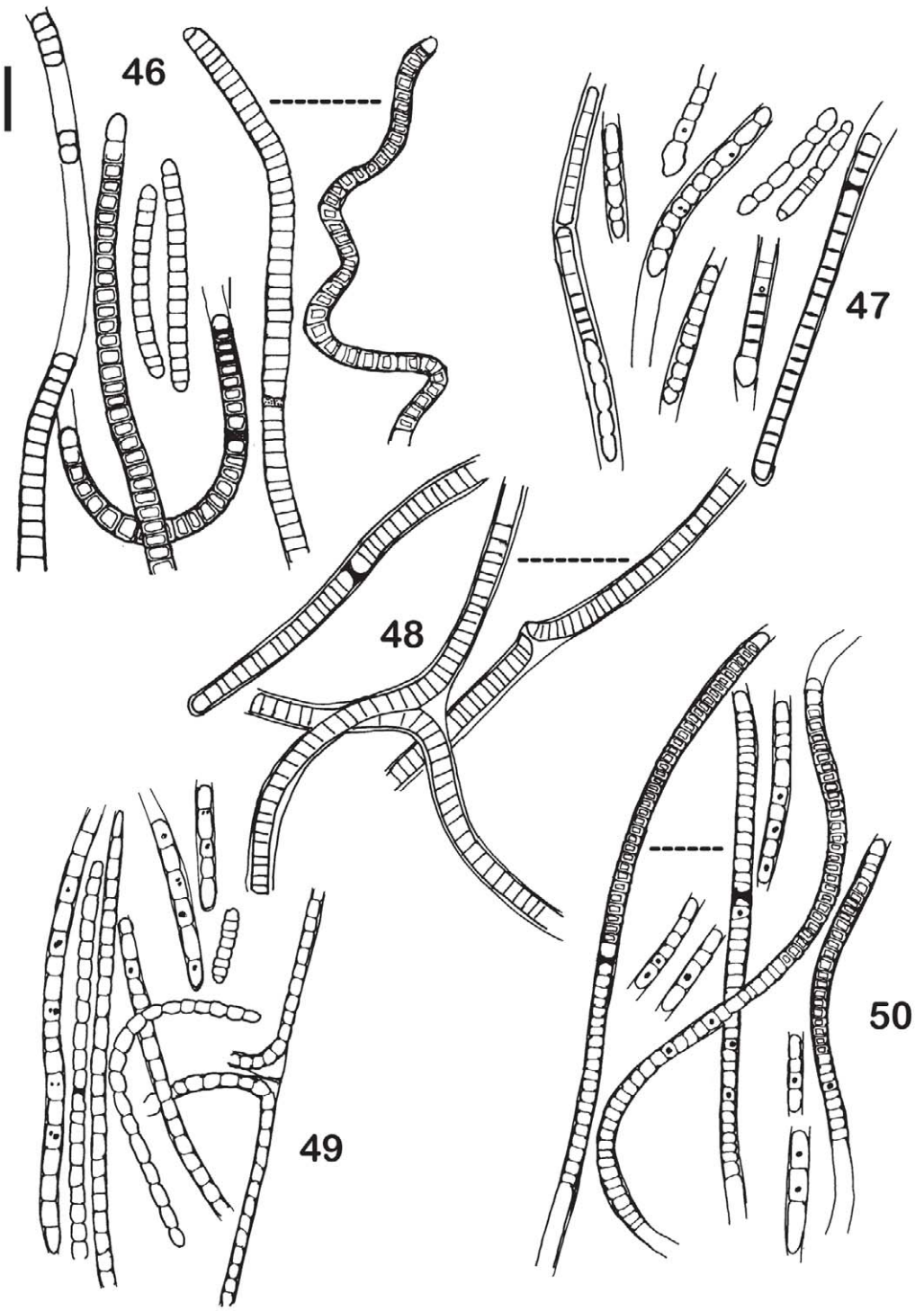
Figs. 28–35. Phormidiaceae and Nostocaceae in Mojave Desert soils: **28–29,** *Microcoleus steenstrupii* showing trichomes arranged in parallel fascicles and noncalyptrate, elongated, tapering end cell; **30–31,** *Microcoleus vaginatus.* Note shortened calyptrate end cells; **32–33,** *Nostoc indistinguendum;* **34–35,** *Nostoc desertorum.* Note compartmentalized sheath (Fig. 34, left colony). Scale = 10 μm.

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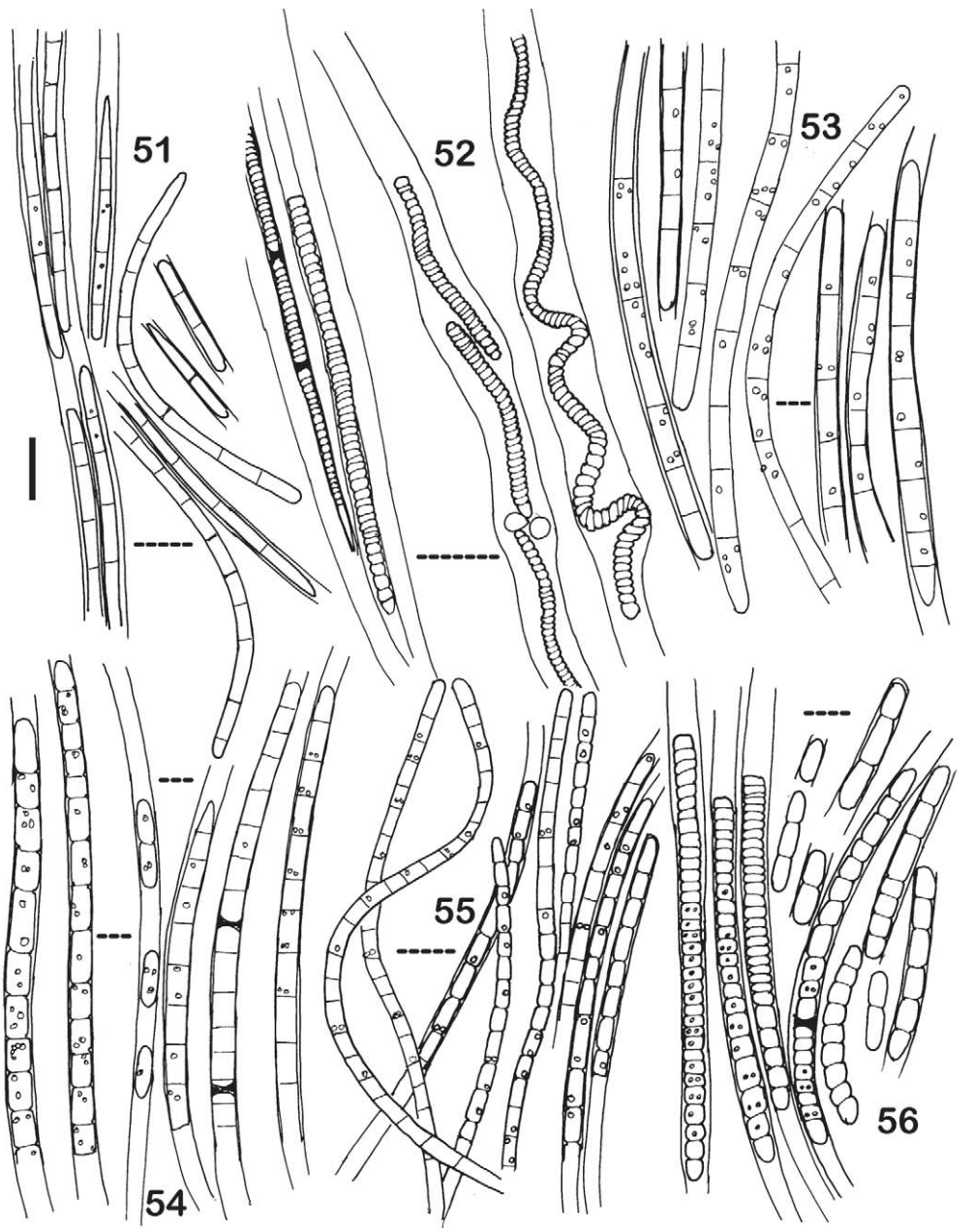
Figs. 36–45. Rivulariaceae, Scytonemataceae and Microchaetaceae in Mojave Desert soils: **36–37,** *Calothrix* cf. *fusca;* **38–39,** *Scytonema javanicum.* Sheath was clearly yellowish brown; **40–41,** *Scytonema* cf. *obscurum;* **42–43,** *Hassallia byssoidea.* Note cells distinctly shorter than wide; **44–45,** *Tolypothrix* cf. *camptylonemoides.* Scale = 10 μm.

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Figs. 46–50. Pseudanabaenaceae from Mojave Desert soils: **46,** *Leptolyngbya foveolarum;* **47,** *Arthonema* cf. *africanum;* **48,** *Leptolyngbya* sp. 2; **49,** *Leptolyngbya* sp. 1; **50,** *Leptolyngbya foveolarum.* Scale = 10 μm.

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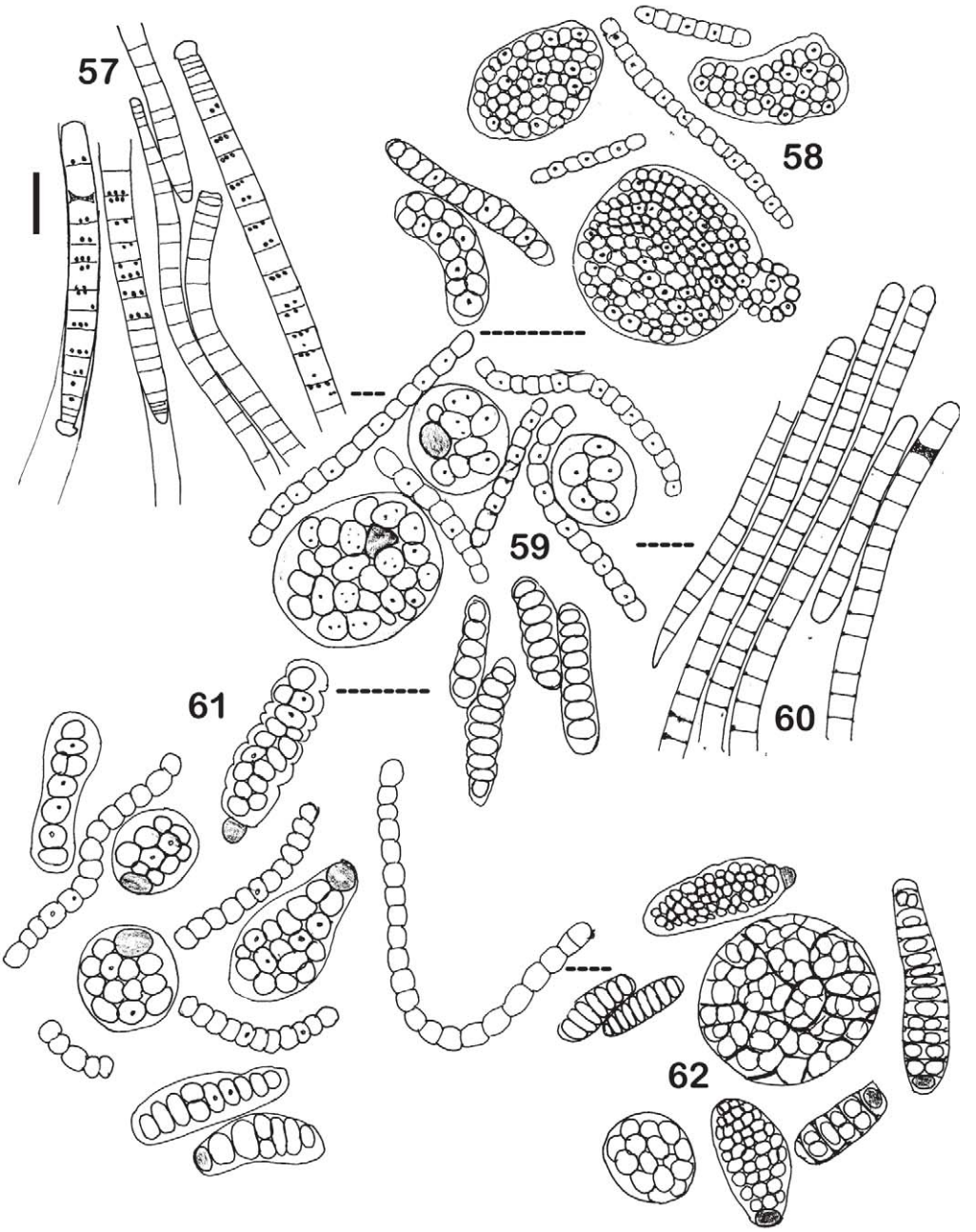


Figs. 51–56. Pseudanabaenaceae and Phormidiaceae in Mojave Desert soils: **51,** *Leptolyngbya tenuis;* **52,** *Pseudophormidium hollerbachianum;* **53,** *Phormidium* cf. *kuetzingianum;* **54,** *Symploca muscorum;* **55,** *Leptolyngbya* sp. 3; **56,** *Phormidium* sp. 1. Scale = 10 μm.

DISCUSSION

In this study we had representatives of 3 subclasses of cyanobacteria: Synechococcophycidae (Pseudanabaenaceae, Schiztrichaceae), Oscillatoriophycidae (Phormidiaceae), Nostocophycidae (Nostocaceae, Rivulariaceae, Scytonemataceae, Microchaetaceae. The flora was more depauperate than that found recently on the San Nicolas Islands (Flechtner et al. 2008), which had 32 cyanobacteria in 19 genera. Notably, we did not have any coccoid taxa; nor

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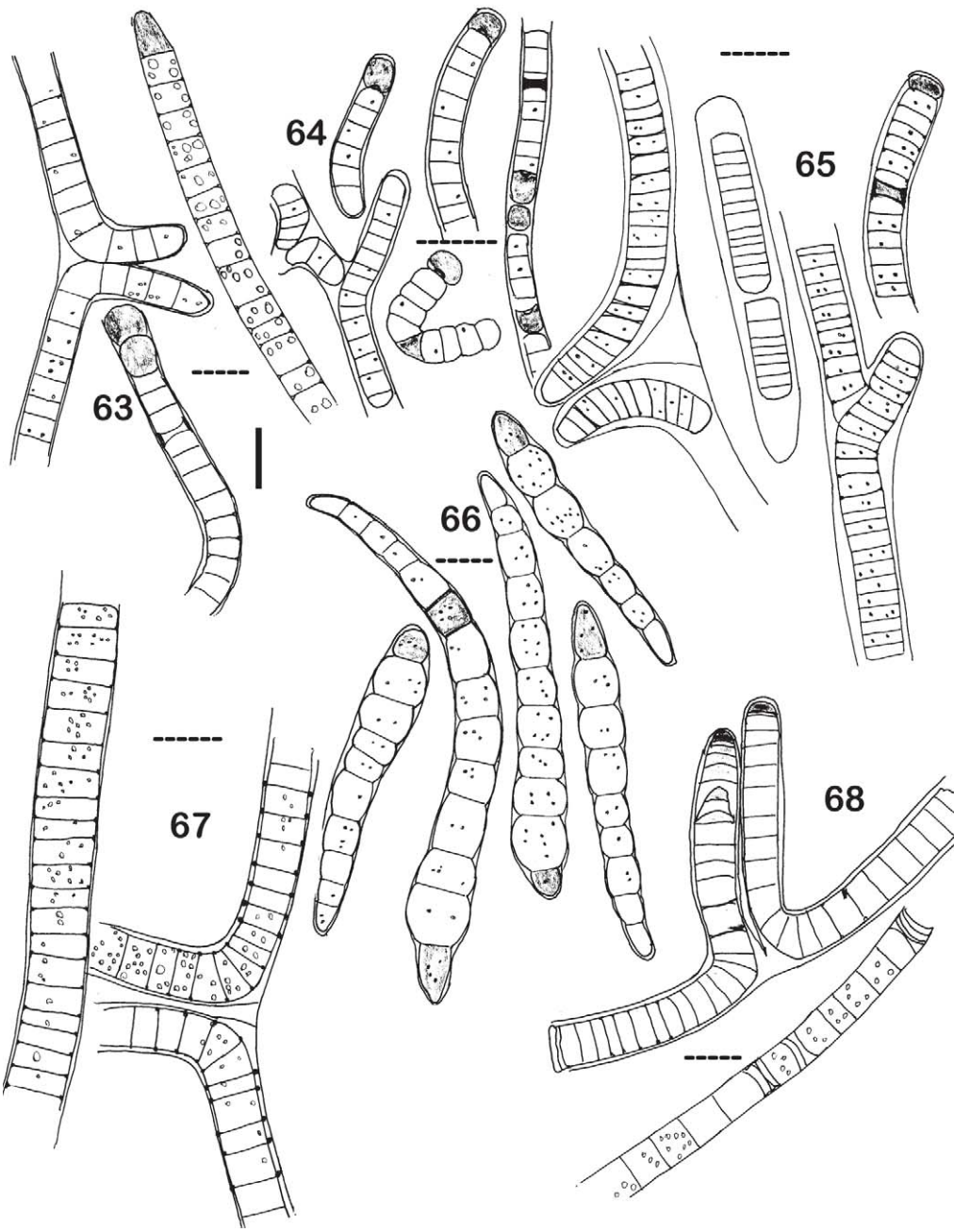


Figs. 57–62. Phormidiaceae and Nostocaceae in Mojave Desert soils: **57,** *Microcoleus vaginatus;* **58–59,** *Nostoc punctiforme;* **60,** *Microcoleus steenstrupii;* **61,** *Nostoc indistinguendum;* **62,** *Nostoc desertorum.* Scale = 10 μm.

did we have the diversity of taxa in the Microchaetaceae that Flechtner et al. (2008) found in their sites. The Mojave Desert is especially arid and has poorly developed crusts even in undisturbed areas (Johansen et al. 2001). We are not surprised to see fewer taxa here than in the soils of the maritime climate off the coast of California.

It was interesting to note that 2 of the recently described species from the Clark Mountains, *Nostoc desertorum* and *Nostoc indistinguendum,* were also present in our soils. These

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Figs. 63–68. Rivulariaceae, Scytonemataceae, and Microchaetaceae in Mojave Desert soils: **63,** *Scytonema* cf. *obscurum;* **64,** *Tolypothrix* cf. *camptylonemoides;* **65,** *Hassallia byssoidea;* **66,** *Calothrix* cf. *fusca;* **67,** *Scytonema javanicum;* **68,** *Scytonema hyalinum.* Scale = 10 μm.

taxa were identified primarily on molecular evidence with only limited morphological differences from *Nostoc punctiforme* (Řeháková et al. 2007). Our ability to recognize them based on morphology alone helps to justify ex post facto the description of these species. The Clark Mountains are less than 200 km from Fort Irwin.

We had 6 *Leptolyngbya* species, the same as in the San Nicolas Islands, but in mostly

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different species. *Leptolyngbya foveolarum* and *L. nostocorum* were present in both sites. The Pseudanabaenales are currently in need of more intensive study. *Leptolyngbya* is clearly a polyphyletic taxon (Johansen et al. 2008, 2011), and most of the genera are separated by sheath characteristics, a feature known to be plastic and unreliable for higher level taxonomy. *Leptolyngbya, Pseudanabaena, Trichocoleus, Pseudophormidium,* and *Schizothrix* all need molecular definition. Presently we have clear molecular resolution of *Leptolyngbya* sensu stricto, which includes *L. boryana* (the generitype), *L. angustata,* and *L. tenerrima. Leptolyngbya foveolarum* is a typical soil species with very similar morphology to *L. boryana,* and it is possible these 2 taxa have been confused in culture collections, as the names are often applied irrespective of ecology (*L. boryana* was desribed from aquatic habitats) and morphology (*L. boryana* has false branching; *L. foveolarum* does not). Our strains—which are in soil but still have false branching—do not fit either taxon well.

Microcoleus vaginatus (Vauch.) Gomont is considered the most dominant species in soil (Johansen 1993, Evans and Johansen 1999), and data collected from other studies indicated that *Microcoleus vaginatus, Microcoleus steenstrupii,* and *Schizothrix calcicola* were the most abundant species in Fort Irwin sites, while *Scytonema* was the least abundant taxon (Johansen et al. 2001). The morphological characterization used in this study revealed 5 putative new species in the Pseudanabaenales based on the most recent revision of Komarek and Anagnostidis (2005). *Leptolyngbya* was the dominant group in Fort Irwin sites and had highest frequencies in the PR2 and RPL2 sites. This study contained some rare taxa which were found only in a single site, such as *Leptolyngbya* sp. 2, *Leptolyngbya* sp. 3, *Leptolyngbya tenuis, Calothrix* cf. *fusca, Scytonema* cf. *obscurum* var. *terrestre, Scytonema hyalinum, Hassallia byssoidea,* and *Tolypothrix* cf. *camptylonemoides.*

Even though the Fort Irwin cyanobacteria species showed similarities to other floras of western North America (Johansen et al. 1981, 1984, 1993, Ashley et al. 1985, Flechtner et al. 1998, 2008), it contained a number of species that have minor differences in continuous characters within strains. We consider it inadvisable to identify a soil isolate using descriptions of aquatic taxa as reported in Geitler (1930–1932) or Desikachary (1959). Geitler's descriptions are primarily from European aquatic habitats and were based on field material without culturing. It is likely that many new species exist in desert soils, and problems associated with delimitation of cryptic species need to be the subject of future studies.

LITERATURE CITED

ASHLEY, J., S.R. RUSHFORTH, AND J.R. JOHANSEN. 1985. Soil algae of cryptogamic crusts from the Uintah Basin, Utah, USA. Great Basin Naturalist 45:432–442.

BOYER, S.L., J.R. JOHANSEN, AND V.R. FLECHTNER. 2002. Phylogeny and genetic variance in terrestrial Microcoleus (Cyanophyceae) species based on sequence analysis of the 16S rRNA gene and associated 16S-23S ITS region. Journal of Phycology 38:1222–1235.

CAMERON, R.E. 1960. Communities of soil algae occurring in the Sonoran Desert in Arizona. Journal of the Arizona Academy of Science 1:85–88.

CARMICHAEL, W.W. 1986. Isolation, culture, and toxicity testing of toxic freshwater cyanobacteria (blue-green algae). Pages 1249–1262 *in* V. Shilov, editor, Fundamental research in homogenous catalysis. Volume 3. Gordon & Breach, New York, NY.

CASAMATTA, D.A., J.R. JOHANSEN, M.L. VIS, AND S.T. BROADWATER. 2005. Molecular and morphological characterization of ten polar and near-polar strains within the Oscillatoriales (Cyanobacteria). Journal of Phycology 41:421–438

DESIKACHARY, T.V. 1959. *Cyanophyta.* Indian Council Agricultural Research, New Delhi. 686 pp.

DURRELL, L.W. 1962. Algae of Death Valley. Transactions of the American Microscopical Society 81:267–278.

EVANS, R.D., AND J.R. JOHANSEN. 1999. Microbiotic crusts and ecosystem processes. Critical Reviews in Plant Sciences 18:183–225.

FLECHTNER, V.R., J.R. JOHANSEN, AND J. BELNAP. 2008. The biological soil crusts of the San Nicolas Island: enigmatic algae from a geographically isolated system. Western North American Naturalist 68:405–436.

FLECHTNER, V.R., J.R. JOHANSEN, AND W.H. CLARK. 1998. Algal composition of microbiotic crusts from the central desert of Baja California, Mexico. Great Basin Naturalist 58:295–311.

GEITLER, L. 1930–1932. *Cyanophyceae.* Koeltz Scientific Books, Königstein, Germany. 1196 pp.

JOHANSEN, J.R. 1993. Cryptogamic crusts of semiarid and arid lands of North America: minireview. Journal of Phycology 29:140–147.

JOHANSEN, J.R., J. ASHLEY, AND W.R. RAYBURN. 1993. The effects of rangefire on soil algal crusts in semiarid shrub-steppe of the Lower Columbia Basin and their subsequent recovery. Great Basin Naturalist 53:73–88.

JOHANSEN, J.R., C. BRITTON, T.C. ROSATI, L. XUESONG, L.L. ST. CLAIR, B.L. WEBB, A.J. KENNEDY, AND K.S. YANKO. 2001. Microbiotic crusts of the Mojave Desert: factors influencing distribution and abundance. Nova Hedwigia, Beiheft 123:339–369.

JOHANSEN, J.R., L. KOVACIK, D.A. CASAMATTA, K. FUČÍKOVÁ AND J. KAŠTOVSKÝ. 2011. Utility of 16S-23S ITS sequence and secondary structure for recognition of

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intrageneric and intergeneric limits within cyanobacterial taxa: *Leptolyngbya corticola* sp. nov. (Pseudanabaenaceae, Cyanobacteria). Nova Hedwigia 92: 283–302.

JOHANSEN, J.R., C.E. OLSEN, R.L. LOWE, K. FUČÍKOVÁ, AND D.A. CASAMATTA. 2008. *Leptolyngbya* species from selected seep walls in the Great Smoky Mountains National Park. Algological Studies 126:21–36.

JOHANSEN, J.R., AND S.R. RUSHFORTH. 1985. Cryptogamic soil crusts: seasonal variation in algal populations in the Tintic Mountains, Juab County, Utah, USA. Great Basin Naturalist 45:14–21.

JOHANSEN, J.R., S.R. RUSHFORTH, AND J.D. BROTHERSON. 1981. Subaerial algae of Navajo National Monument, Arizona. Great Basin Naturalist 41:433–439

JOHANSEN, J.R., AND L.E. SHUBERT. 2001. Algae in soils. Nova Hedwigia 123:297–306.

JOHANSEN, J.R., L.L. ST. CLAIR, B.L. WEBB, AND G.T. NEBEKER. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. Bryologist 87:238–243.

KOMÁREK, J., AND K. ANAGNOSTIDIS. 1986. Modern approach to the classification system of cyanophytes. 2: Chroococcales. Algological Studies 43:157–226.

_____. 1989. Modern approach to the classification system of cyanophytes. 4: Nostocales. Algological Studies 56:247–345.

_____. 1999. Cyanoprokaryota 1. Teil: Chroococcales, Süsswasserflora von Mitteleuropa, Bd. 19/1, Gustav Fisher Verlag, Jena, Germany. 548 pp.

_____. 2005. Cyanoprokaryota 2. Teil Oscillatoriales, Süsswasserflora von Mitteleuropa, Bd. 19/2, Gustav Fisher Verlag, Jena, Germany. 900 pp.

ŘEHÁKOVÁ, K., J.R. JOHANSEN, D.A. CASAMATTA, L. XUESONG, AND J. VINCENT. 2007. Morphological and molecular characterization of selected desert soil cyanobacteria: three species new to science including *Mojavia pulchra* gen. et sp. nov. Phycologia 46:481–502.

SHIELDS, L.M., AND F. DROUET. 1962. Distribution of terrestrial algae within the Nevada Test Site. American Journal of Botany 49:547–554.

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