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Streptosarcina costaricana var. *goloustica* var. nov. (Klebsormidiophyceae, Charophyta) from soils of Baikal mountains, Russia

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Abstract: The charophyte algae of the genus *Streptosarcina* (Hormidiellales) are quite rare terrestrial protists, according to current knowledge. The genus consists of two species, *S. arenaria* and *S. costaricana*, which are isolated in Eastern Europe and Central America, respectively. Only five strains of the genus have been studied using microscopy and/or molecular methods, based on published data. Here, we examined two strains, IRK–A 417 and 448, isolated from the chestnut soils of the Primorsky Range at the southwestern shore of Lake Baikal. The combination of molecular (18S rDNA, ITS, rbcL) and microscopy data (LM and TEM) was used to determine the taxonomic and phylogenetic position of the studied plants. It is established that they are most similar to the filamentous *Streptosarcina* species from Central America. IRK–A strains represent a new genetic lineage of the genus. The description of the new variety, *S. costaricana* var. *goloustica*, is proposed.

Key words: algae distribution, biodiversity, Hormidiellales, integrative approach, morphology, phylogeny, terrestrial green microalgae

Introduction

Klebsormidiophycean algae are an essential part of the world terrestrial algal flora. They are mainly filamentous and sarcinoid microorganisms with a largely unknown diversity. Recently, the new members of this class have been described: new genus *Streptosarcina* Mikhailyuk et Lukešová (Mikhailyuk et al. 2018), and new species of the genera *Interfilum* Chodat emend. Mikhailyuk et al. (Mikhailyuk et al. 2008) and *Klebsormidium* P.C.Silva et al. (Novis 2006; Samolov et al. 2019). The position of another new genus, *Streptofilum* Mikhailyuk et Lukěsová (Mikhailyuk et al. 2018), in the system of this class is debatable (Glass et al. 2023; Bierenbroodspot et al. 2024; Žárský & Eliáš 2024; Glaser et al. 2025). Potentially new lineages of the Klebsormidiophyceae from terrestrial habitats may be characterized (e.g., Kulichová et al. 2014; Samolov et al. 2020; Rybalka et al. 2023; *Interfilum* in GBIF Secretariat 2023). Ideas about the status, size, and structure of this taxonomic group and subordinate taxa are evolving and changing (e.g., Sluiman et al. 2008; Rindi et al. 2008, 2011; Mikhailyuk et al. 2018; McCourt et al. 2022; Glass et al. 2023; Bierenbroodspot et al. 2024; Glaser et al 2025). Some algae of the class are widespread and can occur in large numbers on surfaces of soil or different natural or artificial terrestrial substrates. For example, the amount of *Klebsormidium* cells (as *Chlorhormidium* Fott) in virgin mountain soil of Asian Russia varied between 3.9×10^6–6.1×10^6 per $1cm^3$ (Perminova et al. 1989), and in arable soil of European Russia it was up to 5.9×10^6 per $1cm^2$ (Domracheva & Shtina 1985). The estimated biomass of *K. montanum* (Hansg.) Shin. Watan. (as *Hormidium montanum* (Hansg.) Skuja) in a grey forest soil in a meadow community of West Siberia reached 2.68 $g.m^{-2}$ (Shushuyeva 1980). At technogenic dumps of the coal mining industry in West Siberia, the absolutely dry biomass of *K. montanum* varied from 1.2 to 22.9 $g.m^{-2}$ in different measurement periods, and the dry biomass of *K. nitens* (Kütz.) Lokhorst (as *Hormidium nitens* Mengh.) was 0.02–0.12 $g.m^{-2}$ (Shushuyeva 1977). Functional roles of the klebsormidiophyceans in terrestrial ecosystems are unclear in many aspects. It has a role in biogeochemical cycling, primary production (e.g., Shushuyeva 1977; Perminova et al. 1989; Karsten et al., 2016; Lie et al. 2016; Xu et al. 2021), and food chains in soil and/or terrestrial substrates (Domracheva & Shtina 1985; cyt. by Lukešová & Frouz 2007). They are photosynthetic participants in associations with other cryptogames (e.g., Zauer 1956; Büdel et al. 2016; Videv et al. 2017; Mukhin et al. 2018) and vascular plants (e.g., Handa et al. 1991; Gärtner 1994; Lemes–da–Silva et al. 2010; Kireeva et al. 2011; Kulichová et al. 2014). The belonging of klebsormidiophyceans to the Charophyta causes increased interest among researchers. Study of this phylum is important for understanding the evolution

of embryophytes and the ways of terrestrialization of organisms (Wodniok et al. 2011; Hori et al. 2014; Wickett et al. 2014; de Vries & Archibald 2018; Morozov & Solovyev 2019, etc.).

In Algaebase, to date, there are some taxa at the genus level: *Closteriospira* Reverdin, *Elakatothrix* Wille, *Entransia* E.O.Hughes*, Hormidiella* M.O.P.Iyengar et Kanth. emend. Mikhailyuk et Lukešová, *Interfilum, Klebsormidium, Maithea* Purn.Srivastava et S.Kumar, *Streptosarcina,* and *Streptofilum,* which are listed within the class Klebsormidiophyceae (Guiry & Guiry 2025). The ultrastructural and molecular genetic data supported that the representatives of genera *Entransia, Hormidiella*, *Interfilum, Klebsormidium, Streptosarcina,* and, putative *Streptofilum* belong to the class Klebsormidiophyceae within the Charophyta (e.g., Stewart & Mattox 1975; Karol et al. 2001; Turmel et al. 2002; Sluiman et al. 2008; Mikhailyuk et al. 2018; Glass et al. 2023; Bierenbroodspot et al. 2024). The members of these genera were studied by light and electron microscopy, as well as methods of molecular genetics, physiology, and biochemistry (e.g., Cook 2004; Karsten & Holzinger 2012; Karsten et al. 2014; Mikhailyuk et al. 2014, 2015; Herburger et al. 2016; Kondo et al. 2016; Blaas & Holzinger 2017; Pierangelini et al. 2019; Hartmann et al. 2020). In Russia, studies of klebsormidiophyceans are still scarce in comparison with some other charophytes, such as algae of the classes Charophyceae (e.g., Romanov et al. 2015; Sviridenko & Sviridenko 2016; Chemeris & Filippova 2017; Vishnyakov & Philippov 2018; Romanov & Glazkova 2024) or Zygnemophyceae (e.g., Kossinskaya 1960; Rundina 1998; Anissimova & Philippov 2018; Anissimova & Luknitskaya 2021). The findings of the members of *Klebsormidium, Interfilum, Hormidiella,* and *Streptosarcina* were recorded. *Klebsormidium* has been most often found in terrestrial habitats from polar to subtropical ecosystems of Russia and also in aquatic biotopes (e.g., Gollerbakh 1936; Matvienko 1956; Dorogostaiskaya & Sdobnikova 1973; Aleksakhina & Shtina 1984; Sdobnikova 1986; Perminova 1990; Ilchibaeva et al. 2018). There are some studies devoted to algae of this genus (Gaysina et al. 2009; Purina & Kabirov 2009). *Interfilum* has been examined mainly in floristic works based on the morphology. This genus is registered in different habitats on earth surfaces or in soils (e.g., Aleksakhina & Shtina 1984; Moshkova & Gollerbakh 1986; Egorova et al. 2020; Novakovskaya et al. 2020). Algae, registered as *Hormidiella* and *Streptosarcina*, have been found in biological soil crusts in the northwestern part of Russia (Davydov & Redkina 2021).

In this paper, we focus on the representatives of the genus *Streptosarcina*, isolated from the soil of the Primorsky Range (Baikal mountain land, Asian Russia). The genus was erected in 2018 (Mikhailyuk et al. 2018). It contains two species, *S. arenaria* Mikhailyuk et Lukešová (type species of the genus) and *S. costaricana* Mikhailyuk et Lukešová, known from soils of Eastern Europe and Central America, respectively (Mikhailyuk et al. 2018). The key morphological character used to recognize species of *Streptosarcina* is the type of a morphological structure of the thallus (mainly sarcinoid for *S. arenaria* and filamentous for *S. costaricana*). We examined two filamentous strains deposited in the culture collection of algae IRK–A, 417 and 448, using culturing, microscopic (LM and TEM), and molecular techniques (18S rDNA–ITS, and *rbc*L phylogeny). This study has the objectives (i) to determine the morphological and life cycle features of the strains IRK–A, (ii) to explore phylogenetic relationships of studied strains with other known *Streptosarcina* species. Based on the obtained data, we describe the new variety, *S. costaricana* var. *goloustica* var. nov. This study provides new data on the reproduction, morphology, diversity, ecology, and geography of *Streptosarcina* algae.

Materials and Methods

Area and sampling. During long–term research on soil and terrestrial algal diversity and ecology in the Baikal Region, two filamentous *Streptosarcina*–like strains were isolated from the surface layers of soils at the Primorsky Range, in the vicinity of the village Bolshoye Goloustnoye, the Irkutsk Region, Russia (Fig. 1, 2; Table 1). Soil specimens were sampled from two different plant communities in early August 2021. The studied plant communities were situated nearby (Fig. 2; Table 1).

The study area is located within the Baikal mountain land, in the southeastern part of the Primorsky Range. The altitudes of the Primorsky Range here are up to 900–1200 m above sea level. The southern part of the ridge is composed of Upper Proterozoic strongly metamorphosed carbonate–silicate formations (dolomites, limestones, conglomerates, etc.) (Baikal. Atlas 1993). The peculiarities of the geological and geomorphological conditions of the territory near Lake Baikal determine the specifics of ecoclimatic conditions. The Primorsky Range acts as an orographic barrier in the way of air masses carrying precipitation. Most of them fall on its western macroslope (up to 600–700 mm per year). The climate of the eastern macroslope and coast of the lake is drier (264 mm of precipitation per year; the air masses that have crossed the ridge have already been dried up), relatively warm (the average air temperature in January is –18.2 °C, in July +14.1 °C), with a long frost–free period, up to 80–90 days (Kartushin 1969). The low atmospheric moisture contributes to the formation of herbaceous plant communities at the foot of the mountains, including steppes with *Stipa baicalensis* Roshev. Coniferous forests with a predominance of pine (*Pinus sylvestris* L.) and larch (*Larix sibirica* Ledeb.) are developed on mountain slopes (Fig. 2).

In an area of steppe and forest–steppe communities developed on chestnut soils, two combined surface soil samples were taken per 10–15 m^2. Chestnut soils or Kastanozems (by IUSS Working… 2022) belong to the type of soils that forms mainly in conditions of dry steppes or semi–deserts, on carbonate loess–like loams and clays, as well as on clayey–loamy eluvial–deluvial formations of bedrock. These soils are usually chestnut–brown in color (Zech et al. 2022). A feature of chestnut soils is the presence in the soil profile of the humus horizon (mollic), the carbonate horizon (calcic) located

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at a depth of <50 cm from the lower boundary of the humus horizon (mollic), and the saturation of the entire soil profile with bases (pH ≥ 7) (cyt. by Pankova & Yamnova 2019). More detailed descriptions of this type of soils can be found in the literature (e.g., Tsybzhitov 1991; Shishov et al. 2004; Zech et al. 2022). The combined surface soil samples consisted of ten individual samples. Each individual sample was about 5–10 cm^2 in size and 1–2 cm thick. They were collected in sterile paper bags. Soil samples were also taken to determine some physicochemical parameters (Table 1). In the laboratory, sample preparation, establishing of cultures, and isolation of strains were carried out as we described earlier (Egorova et al. 2023). Two unialgal cultures from different locations (Table 1) have been obtained. They were stored under numbers 417 and 448 in the IRK–A culture collection of algae of the Siberian Institute of Plant Physiology and Biochemistry (SIPPB) of the Siberian Branch of the Russian Academy of Sciences. Herbarium vouchers of air–dried material (a drop of unfixed cells on watercolor paper or cellulose membrane filter), holotype, isotypes, and paratypes, were stored in the herbarium at SIPPB (IRK), Irkutsk. Also, several isotypes were deposited in the Algological Herbarium of Komarov Botanical Institute RAS (LE), Saint–Petersburg, Russia.

Cultivation and microscopy. We used different media and conditions to get actively grown cultures. Most observations were obtained for the studied strains grown on various modifications of the Bristol media, N and 3N BBM, according to Bold (cyt. by Chantanachat & Bold 1962 and Starr et Zeikuss 1993). The strains were grown in a liquid and

Fig. 1. The map shows the location of the sampling area (pink circle). The circled line indicates the location of the Bolshoye Goloustnoye village.

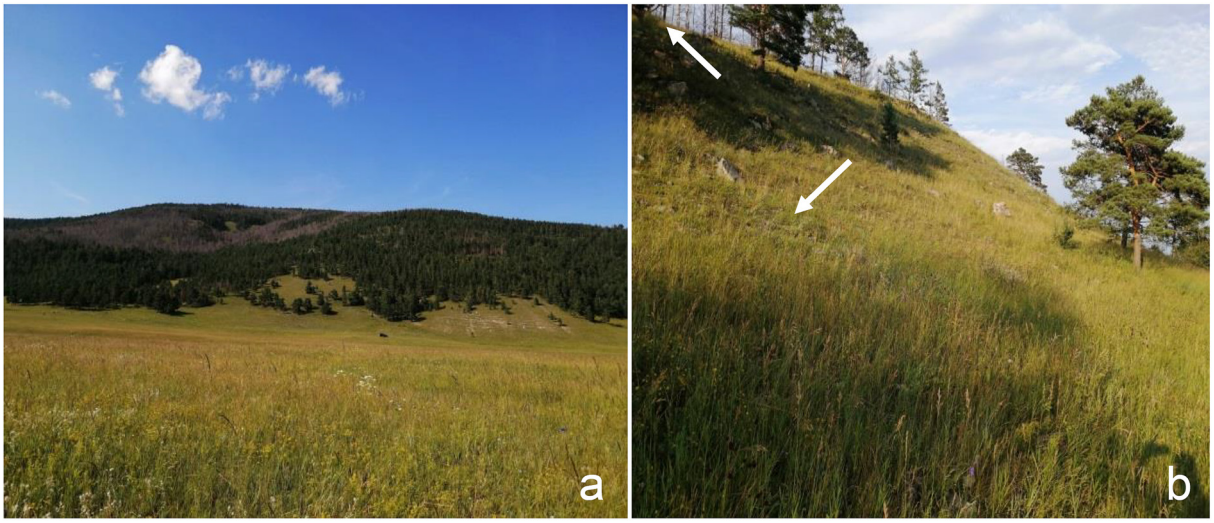

Fig. 2. (a) overview of the eastern macroslope of the Primorsky Range; (b) sampling sites (marked by white arrows).

agar–solidified media with different salt concentrations, pH, and with or without vitamins (B1 and B12). In cultures with vitamins and neutral and alkaline pH, the strains grew better. In acidic pH, they did not grow. Regimes of illumination and temperature were as previously described (Egorova et al. 2023). To obtain motile reproductive cells, we used actively growing three– to fourteen–day cultures. These were typically cultures that had undergone third or fourth passages within two to three weeks after initial seeding. Motile cells were obtained by transferring IRK–A 417 and 448 onto an agar–solidified medium in an Eppendorf flask using distilled water and then keeping the flasks overnight in the dark at room temperature. The next morning, samples were examined for motile cells. This technique was chosen based on the personal commentary of V. M. Andreyeva and the work of Farooqui (1969) to obtain some green microalgae zoospores. In stationary growth phases or rare replanting, the studied strains did not produce motile cells. For morphological observations, AxioScope.A1 microscope, equipped with a color digital camera, ICc5 (Carl Zeiss, Germany), was applied. To assess the presence of mucilage and the structure of cell walls, cells were stained in vivo with 0.1% gentian violet and China ink. For descriptions of the studied alga, the morphological terminology was taken according to published works (Ettl 1988; Sluiman et al. 1989; Cook 2004; Mikhailyuk et al. 2014, 2018). Information about other strains within the genus, including their names, strain numbers, collection acronyms, and origin is obtained from published sources (Mikhailyuk et al. 2018; Bierenbroodspot et al. 2024), and from GenBank. For transmission electron microscopy (TEM), 7–10–day cells of IRK–A 417 and IRK–A 448 cultures were fixed at 4 °C with a standard l fixation protocol (2.5% glutaraldehyde, 1% OsO_4, culturing medium), dehydrated in an acetone series, and enclosed in an epon–araldite resin mixture, according to Egorova et al. (2023). Sections for TEM were prepared with an LKB III ultramicrotome (Sweden) and glass knives. The ultrathin sections were counterstained on grids with 3% lead citrate for 10 min. Cells were examined at 120 kV with a Libra 120 Plus electron microscope (Carl Zeiss, Germany).

PCR amplification and sequencing. DNA was isolated from the living (agar medium) strains IRK–A 417 and 448 using the Vector–Best DNA/RNA extraction kit C–8896 (Novosibirsk, Russia). The cystron 18S rDNA–ITS2 was amplified and sequenced with conditions and primers described by Egorova et al. (2023). The rbcL gene was amplified with primers published by Little et al. (2003) and Schuettpelz et al. (2007). A comparison search for nearest homologues was performed using Blast (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Nucleotide sequences were assembled and edited with the BioEdit 7.0.5.3 program (Hall 1999) and aligned with Mafft v.7 (Katoh 2019). The nucleotide sequences of 18S rDNA–ITS and rbcL of the studied strains were submitted to the GenBank database with accession numbers PQ535701–PQ535702 and PQ553565–PQ553566, respectively.

Phylogenetic reconstruction and ITS2 secondary structure analysis. The phylogenetic relationships of the studied strains were inferred from the 18S rDNA–ITS data. A maximum likelihood (ML) tree was reconstructed in IQtree v.1.6.12 (Nguyen et al. 2015) with ultrafast bootstrap support (Hoang et al. 2018). The best substitution model was selected using ModelFinder implemented in IQtree (Kalyaanamoorthy et al. 2017). The best–fit model of nucleotide substitutions, TNe+I+G4, was chosen according to BIC. Bootstrap tests were run for 1000 replicates. FigTree 1.4.4 was applied as a graphical viewer of phylogenetic trees (Rambaut 2010). The 18S rDNA–ITS sequence of *S. costaricana* SAG 2653 was assembled from genome data using metaSPAdes (Nurk et al. 2017) on the Galaxy platform (https://usegalaxy.org/) from the SRA archive SRR26030664. The GenBank accession numbers of sequences used in the analyses are listed in Supplementary Table S1. The genetic distances, based on Kimura two–parameter (K2P model, were calculated in Mega 11.08 (Tamura et al. 2021).

For the ITS2 secondary reconstruction, the ITS2 Database (Ankenbrand et al. 2015) and Mfold web server (Zuker 2003) (default parameters) were applied for *Streptosarcina* strains IRK–A 417, IRK–A 448, SAG 36.98, SAG 2560, SAG 2562, and WH 1312 except for the strain SAG 2653 (with the nucleotide uncertainties in ITS2). The secondary structures were visualized with Pseudoviewer 3.0 (Byun & Han 2009). The program 4SALE with default settings was used for secondary structure alignments (Seibel et al. 2008). The compensatory base changes (CBC) were searched with the CBCAnalyzer tool (Wolf et al. 2005). Hemi–CBCs, deletion, mismatches, and unpaired bases were assessed visually. The nucleotide alignments used in the study are available in Supplementary Files S2–S4.

Results

Morphological observations

In liquid mixed/enrichment or unialgal cultures, the algae could form a superficial layer of hydro repellent thalli. In agar solid cultures, the plant mass may look shiny, wet, or velvety green. The two studied strains, IRK–A 417 and 448, exhibited a similar morphology during their life cycles and had morphology similar to the filamentous *Streptosarcina* species (Figs 3–5;

Table 1. Characteristics of sampling sites of the studied *Streptosarcina* strains at the Primorsky Range, Russia.

Strain	Habitat, pH_{H20}(pH_{KCl})	Vegetation	Date of sampling	Coordinates	Altitude, m above s.l.
IRK–A 417	chestnut soil 8.3(7.9)	mountain forest–steppe	04 August 2021	52.05531°N, 105.40131°E	~ 490
IRK–A 448	chestnut soil 7.6(7.1)	mountain steppe	04 August 2021	52.05490°N, 105.40176°E	~ 475

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Table 2). No morphological differences were observed between the studied strains. Usually, the algae formed short filaments, consisting of two to four or six cells (Fig. 3). The filaments were able to branch. They were uniseriate, sometimes biseriate, or only parts of the filaments were biseriate (Figs 3, 4). The biseriate regions resembled sarcinoid packages, but they never had a regular three–dimensional shape (Fig. 4). The branches could be short or long and located in different planes. The complex branching thalli could be formed. Sometimes, the algae produced *Klebsormidium*– or *Hormidiella*–like filaments, but without gelatinous sheath or a stalk.

The cells were homo– or heteropolar. They had a variable shape, ranging from broadly ellipsoidal to ovoid or cylindrical, elongated, angular, and/or swollen, to globose and semi–globose (Figs 1, 2). The length of the cells could exceed the width by 2–10 times (Table 2). During the life cycle, the shape of cells could change significantly. As a result of swelling or bulging, a part of a cell or the entire cell can take a spherical or irregular shape (Fig. 3h–j). Such cells reached large sizes in diameter or width (Table 2). They were capable of division

Table 2. Morphology of known *Streptosarcina* representatives.

Morphological traits	**Members/strain**		
	S. arenaria **SAG 2560*,1**	***S. costaricana*** **SAG 36.98*,1**	***S. costaricana* var. *goloustica,* var. nov.** **IRK–A 417 and 448*,2**
Type of thallus	sarcinoid, packet–like, can be disintegrating to short filaments, cell diads and unicells	short filaments, cell diads and unicells, with a tendency to true branching	short filaments, cell diads and unicells, branched, filamentous branching complexes
Shape of vegetative cells	wide–ellipsoid, hemispherical	ellipsoid, cylindrical, elongated cylindrical	ellipsoid, wide–ellipsoid, cylindrical, elongated cylindrical, hemispherical, globose, swollen, angular
Length × width, µm	14.2–15.5 × 8.7–10.3(11.9)	13.2–30.0(41.9) × (7.0)7.7–8.6	(6.5)10–50(82.2) × 5.3–10(30)
Cell wall	smooth	smooth, with H–like fragments	smooth, with H–like fragments
Chloroplast	parietal, plate–shaped, with waved or dissected margin	parietal, plate–shaped, with waved or dissected margin	parietal, plate–shaped, with waved or dissected margin
Pyrenoid	one, with layers of starch grains	one in young cells, and several in old elongated cells, with layers of starch grains	one in young cells, and several in old elongated cells, with layers of starch grains
Nucleus	one	one	one
Reproduction			
cell division, and fragmentation of thalli	present	present	present
Spores			
Zoospores	present	not observed	present
The shape	ellipsoid	–	ellipsoid, ovoid, globose, irregular
Cell wall	without	–	without
Flagella	two equal subapical	–	two equal subapical
Stigma	without	–	without
Length × width, µm	–	–	7.3–14.2 × 6.0–9.2
Aplanospores	not observed	not observed	present
Number of spores per cells	one	–	one

Note. * – a reference strain. 1 – by Mikhailyuk et al., 2018; 2 – this study. "–" data are not available.

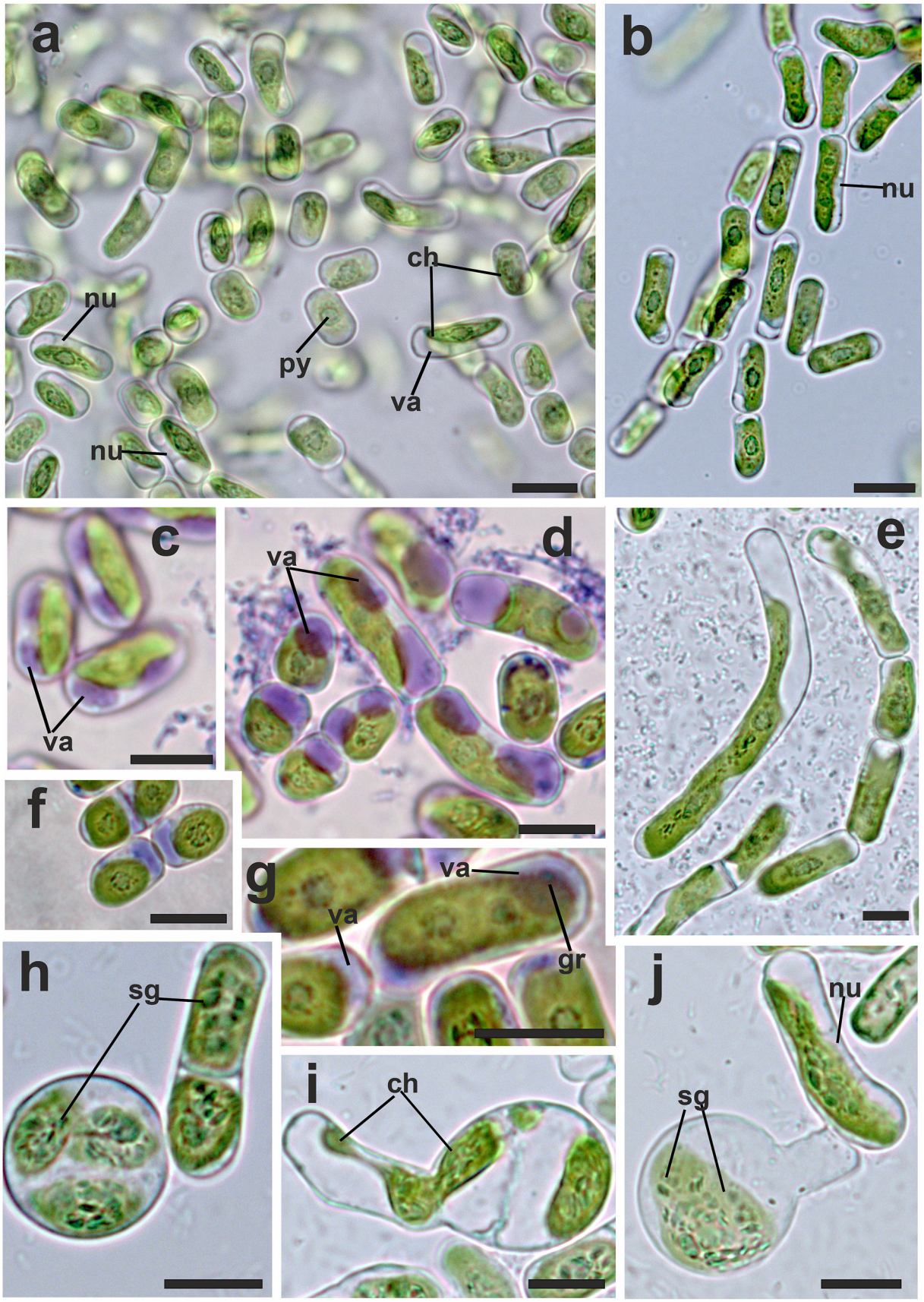

Fig. 3. Morphology of single cells and filaments of *Streptosarcina costaricana* var. *goloustica*, var. nov.: (a–j) the cells of different shape and sizes, (a, b, d–i) filamentous thalli from two to four cells, (h–j) the globular and swollen cells, (c, d, f, g) colored with gentian violet. Designating: chloroplast (ch), granule (gr), nucleus (nu), pyrenoid (py), starch grain (sg), vacuole (va). Scale bar 10 µm.

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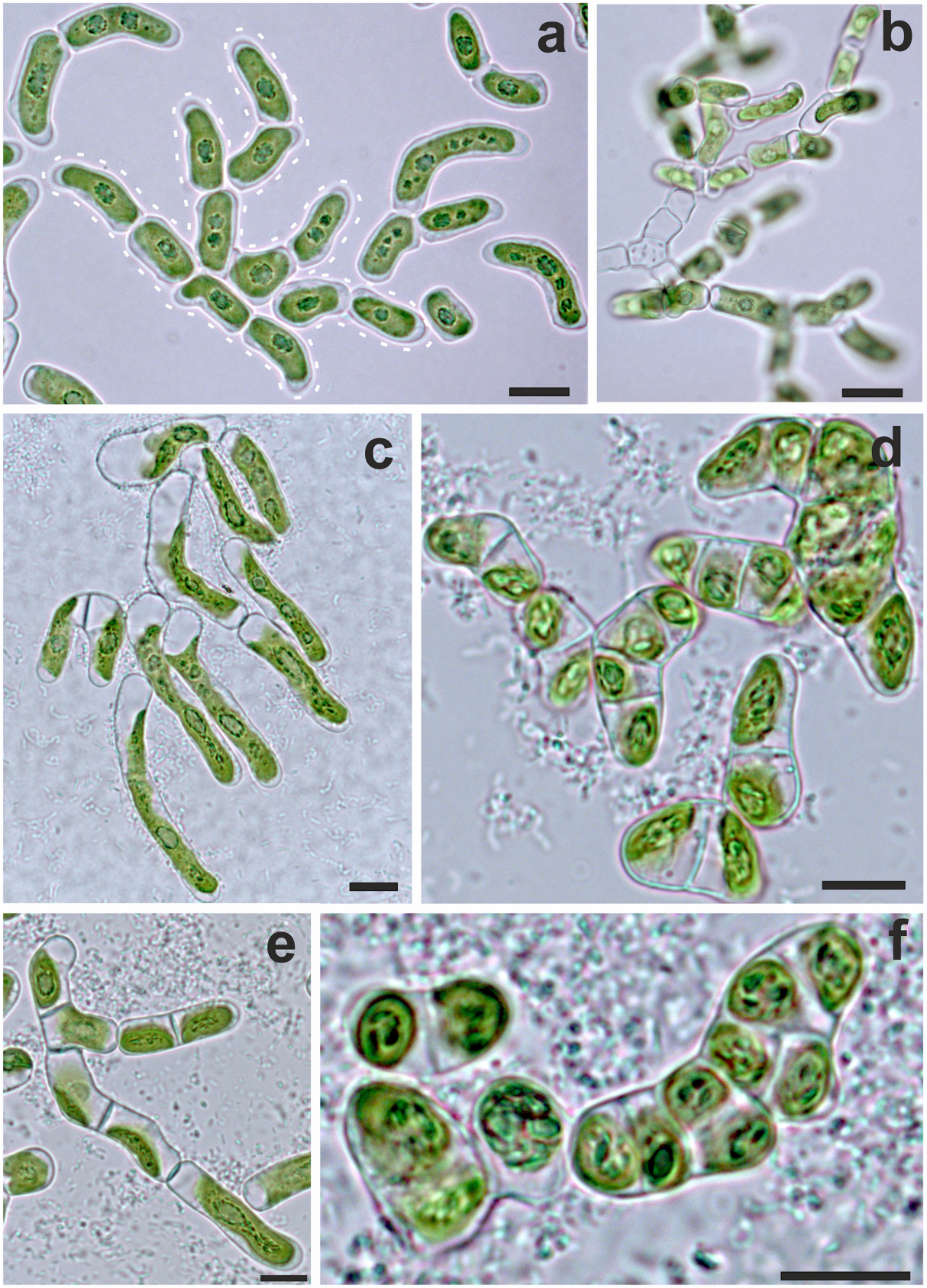

Fig. 4. Cell complexes of *Streptosarcina costaricana* var. *goloustica* var. nov.: (a–e) branching, (d, f) formation of double–row sections of filaments. The dotted line indicates a complex of cells. Scale bars 10 µm.

(Fig. 3h, j). If a swelling cell was part of a filament, then such filaments were often heteropolar (Figs 3j; 4c, d). The cell wall was devoid of mucus. The chloroplast was a single per cell, parietal, with one or more pyrenoids in aging cells. Usually, there were two large vacuoles in the cell lumen (Fig. 3a, c, d, g).

The reproduction was by cell division, fragmentation of the thalli, and/or by the production of asexual reproductive cells (zoo– and aplanospores) (Fig. 5). One mother cell produced one spore. Spore was released through a small hole in the cell wall (Fig. 5c, d). The shape of zoospores was ellipsoid, globose, elongated, and sometimes irregular. After a short period of motility, they stopped moving and became round. Young cells originating from zoospores were spherical or ellipsoid in shape (Fig. 5c, e). It was not observed that they immediately germinated. As a rule, a small number of zoospores were formed. Also, a large number of cells originated from motile spores were registered (Fig. 5e). Aplanospores were observed more often (Fig. 5f–i). Their release from the mother cell was slow. Often, one end of the aplanospore remained in the mother cell, while the reproductive cell began to divide (Fig. 5f, c). Aplanospores had a different shape; they could be homo– or heteropolar. Filaments, germinated from them, were also homo– or heteropolar. The sexual reproduction was not observed. Old cells may contain numerous inclusions (Fig. 5j–l), which resemble oil droplets. The contents of old cells were granular or homogeneous. More information on the morphology obtained by LM is given in Table 2 and the section "Taxonomic Result."

TEM examination

Cell walls covered the vegetative cells of both strains almost evenly (Fig. 6a–d). They were relatively thin and looked fibrillar (Fig. 6b, c). The fibrils were parallel to the cell surface. Local dark areas have been seen mainly in the outer part of cell walls (Fig. 6c). The plasmalemma had predominantly wavy contours (Fig. 6a–h, k). The chloroplast was almost completely filled with large packs of relatively long thylakoids, numbering about 10 units per pack. Packed thylakoids converged in the periphery and diverged inside the chloroplast (Fig. 6c–e, i). Sometimes, presumably in just divided cells, thylakoid packs were smaller and contained 3–7 units per pack (6h, f, k). The pyrenoid was immersed in the chloroplast and occupied a central place in it (Fig. 6d). Its sheath was formed by several relatively large starch plates (Fig. 6d, i,). The matrix was dense and penetrated by one or two thylakoids (Fig. 6d, i, l), which entered

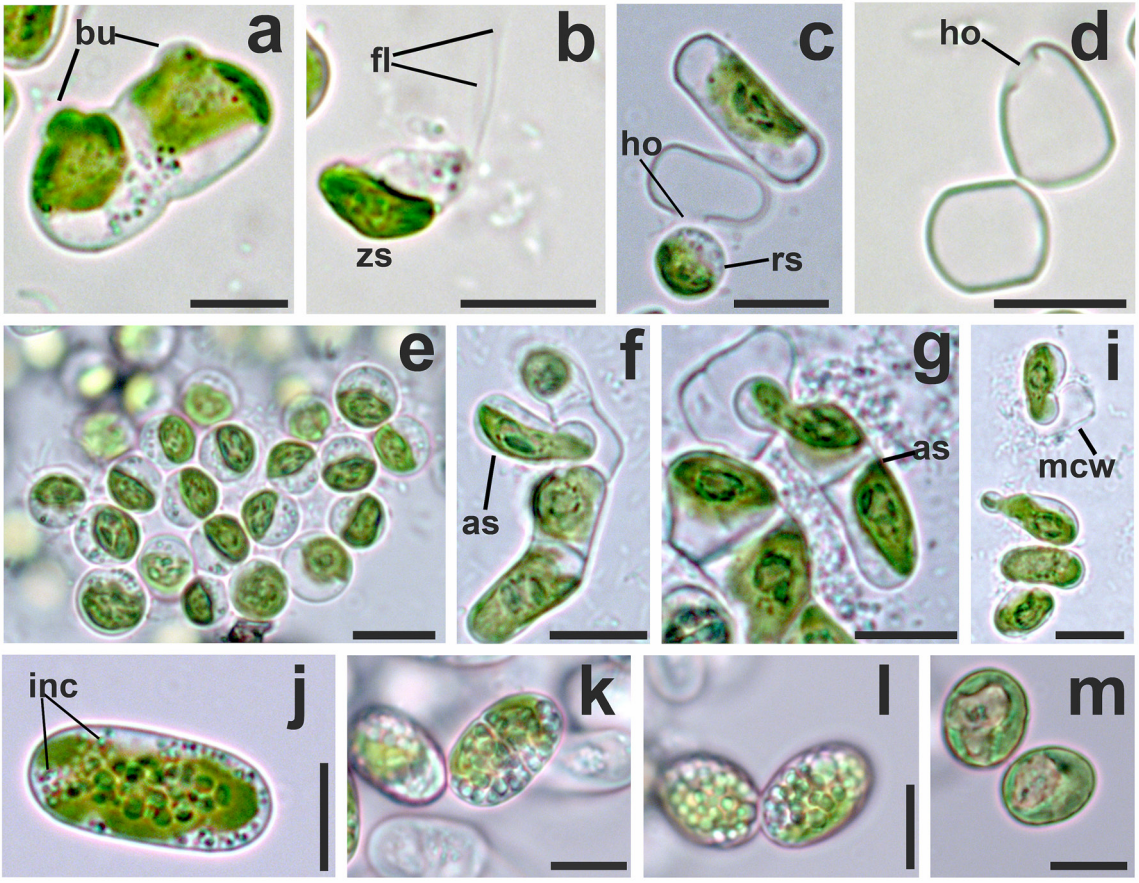

Fig. 5. The reproductive and aging cells of *Streptosarcina costaricana* var. *goloustica* var. nov.: (a) the bulging (bu) of the cell wall prior to the release of spores, (b) zoospore (zs) with two flagella (fl), (c, e) rounded spores (rs), (c, d, f–i) maternal cell walls (mcw) with holes (ho) from which spores are released, (f–i) aplanospores (as), (j–m) aging cells, (j–l) cells with inclusions (inc). Scale bars 10 μm.

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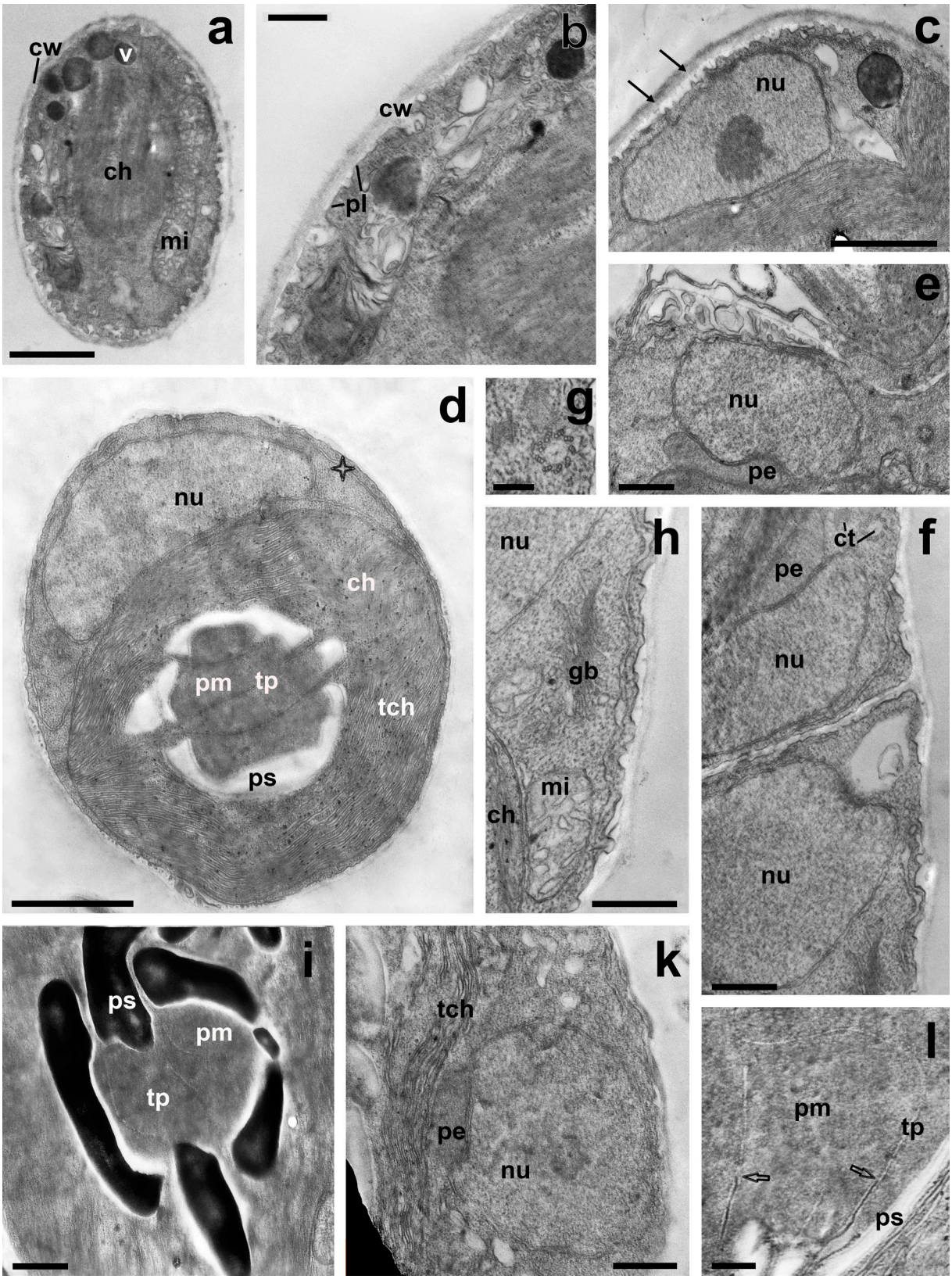

Fig. 6. TEM images of the cellular structure of the studied strains IRK–A: (a–c, i) IRK–A 417; (d–h, k, l) IRK–A 448. Designating: chloroplast (ch), centriole (ct), cell wall (cw), Golgi body (gb), mitochondrion (mi), nucleus (nu), peroxisome (pe), plasmalemma (pl), pyrenoid matrix (pm), pyrenoid starch sheath (ps), thylakoids in chloroplast (tch), thylakoid(s) in pyrenoid (tp), and v– vacuole. Simple arrows on c indicate the dark areas in the fibrillary wall structure; hollow arrows on l – two–thylakoid packs in pyrenoid; four–ray star on d – endoplasmic reticulum. Scale bars 1 μm (a, c, d), 0.5 μm (b, e, f, h, i and k) and 0.2 μm (g and l).

Table 3. Genetic distances of *Streptosarcina* strains based on 18S rDNA–ITS.

Member (Region)	**Genetic distances**							
	collection number	**SAG 36.98**	**IRK–A 417**	**IRK–A 448**	**SAG 2653**	**SAG 2560**	**SAG 2562**	**WH 1312**
S. costaricana (Costa–Rica)*	SAG 36.98	ID						
***S. costaricana* var. *goloustica*, var. nov.**	IRK–A 417	0.0119	ID					
S. costaricana* var. *goloustica*, var. nov.	IRK–A 448	0.0119	0.0000	ID				
S. costaricana (USA)	SAG 2653	0.0313	0.0305	0.0305	ID			
S. arenaria (Slovakia)*	SAG 2560	0.0225	0.0229	0.0229	0.0300	ID		
S. arenaria (Ukraine)	SAG 2562	0.0229	0.0225	0.0225	0.0304	0.0027	ID	
S. sp. (China)	WH 1312	0.0304	0.0317	0.0317	0.0348	0.0225	0.0225	ID

Note. The strains marked with an asterisk are isolates from which the type material was derived for the description of the species/variety in the genus *Streptosarcina.* The algae studied in this work are marked in bold font.

from the chloroplast without changing their shape (Fig. 6l). The cytoplasm was highly granular, with numerous ribosomes (Fig. 6b–f, h, k). Each cell had only one nucleus (Fig. 6c–f, k). The nucleus was chromocentric (Fig. 6c, d, k). It was usually seen in peripheral position of the cytoplasm (Fig. 6c–f, k). Similar peripheral placement was also common for mitochondria (Fig. 6a, h), Golgi apparatus (Fig. 6h), vacuoles (Fig. 6a, b), as well as to the endoplasmic reticulum surrounding the nucleus (Fig. 6d, f, h). Single large peroxisome with a slightly curved shape was located between the nucleus and the chloroplast (Fig. 6e, f, k). A pair of centrioles was observed in just divided cells (Fig. 6f). One was in front position, the other was turned about 90 degrees to it (Fig. 6g).

Phylogeny of the studied strains

The phylogenetic reconstruction revealed that the strains IRK–A 417 and 448 belong to the *Streptosarcina* clade. This clade was related to the klebsormidiophyceans genera *Streptofilum*, *Interfilum*, *Klebsormidium*, *Hormidiella*, and *Entransia* (Fig. 7). The studied strains had identical 18S rDNA–ITS nucleotide sequences, which form a new sister branch to *S. costaricana* SAG 36.98 with high bootstrap support of 99.1/100 (Fig. 7). In turn, the *S. costaricana* SAG 36.98 and IRK–A strains clustered together as the sister clade to the type species of the genus *S. arenaria*. The strain SAG 2653, also registered as *S. costaricana* (by Bierenbrodspot et al. 2024), clustered as the sister lineage to the rest of the *Streptosarcina* clade. The undescribed strain WH 1312 (*S*. sp.) formed the distinct branch in this clade (Fig. 7). Genetic distances between the studied samples and *S. costaricana* SAG 36.98 (the reference strain of the species) were higher than the intraspecies distances between two known strains of *S. arenaria* but lower than those between the strains SAG 2653 and WH 1312, both of which formed well–distinguished phylogenetic lineages on the tree (Table 3, Fig. 7). The *rbc*L nucleotide sequences of both studied strains were identical and most related to the sequence of the *S. costaricana* strain SAG 36.98. This gene fragment had 99.6–100% nucleotide similarity among five GenBank sequences of *Streptosarcina* (*S. costaricana, S. arenaria*, and *S.* sp.) with four synonymous mutations, one of which was present in the strains IRK–A 417 and 448. With the weak phylogenetic signal, the rbcL gene was excluded from further analysis.

The ITS2 secondary structures of the strains IRK–A were similar to the previously published structures of *S. costaricana* and *S. arenaria* (Mikhailyuk et al. 2018). The nucleotide sequence of ITS2 of the IRK–A strains differed from the *S. costaricana* strain SAG 36.98 by 10 nucleotide substitutions and one deletion. There were three hemi–CBCs (helices I (site 39), II (73), III (178)) and seven substitutions of unpaired bases in the loop structures (the central loop (24, 103) and helices I (45), III (183), IV (222)), and the deletion at sites 236/237 (Fig. 8). No CBC was found between all known strains of *Streptosarcina*, except WH 1312, that differed from other strains, including IRK–A, by CBC in helix I (sites 40/48 (U/A)). In comparison with the other *Streptosarcina* strains, hemi–CBCs were found at sites 94 and 178 (IRK–A / *S. arenaria* AL–63 and *S.* sp. WH 1312), 119 (IRK–A/*S.* sp. WH 1312), and 177 (IRK–A/*S. arenaria* AL–63, *S*. sp. WH 1312), as well as indels and substitutions in the loop structures.

Taxonomic result

***Streptosarcina costaricana* Mikhailyuk et Lukešová var. *goloustica* I.N. Egorova, N.V. Kulakova et O.N. Boldina var. nov. (Figs 3–5)**

Description: Thalli consist of single cells and/or short, mainly uniseriate, non– or branching filaments, including two to four or more cells. The filaments are homo– or heteropolar. More rarely, thalli are complex systems of filaments branching in various directions. The branches

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are formed by bulging of the lateral cell wall. Thalli, or their parts resembling cell packages, are produced too. Vegetative cells are homo– and heteropolar. They have a mainly broadly ellipsoidal shape, cylindrical, elongated cylindrical, with or without swelling, often angular, curved, and/or asymmetrical, also hemi–globose, ovoid, pear–shaped, and globose. The width of the cells varied from 5.3–10(30) μm, and the length is (6.5)10–50(82.2) μm. The cell wall is smooth, without a gelatinous matrix. Sometimes the H–pieces are in the filament ends. The chloroplast is parietal, plate– or girdle–shaped, with an uneven or dissected margin. The pyrenoid with starch grains is single in young cells. With ages, several pyrenoids are placed along the long axis of the chloroplast. The starch grains surrounded the pyrenoid are often located in several rows. They are numerous, small or large, often irregular in shape. The starch can also be found in the chloroplast. The nucleus is one, located in a band of the cytoplasm, mainly nearby the pyrenoid. Usually, two large vacuoles are visible at the cell ends. The reproduction is vegetative, occurring by the fragmentation of the thalli, cell division, and by motile and non–motile reproductive cells. The motile cells, zoospores, are ovoidal to elongate, 7.3–14.2 μm in length and 6.0–9.2 μm in width. They have two equal flagella located subapically, two anterior contractile vacuoles, one chloroplast, and the pyrenoid with starch. The stigma is missing. One zoospore is formed by one cell. The release of the zoospore occurs through a small lateral hole. The zoospores are naked, become spherical at quiescence, 6.0–10.8(13.0) μm in diameter. The immotile reproductive cells, aplanospores, are produced one per mother cell. Their sizes depend on the sizes of the mature cell. The process of the immotile spore release is similar to that of zoospores. Occasionally, the break of the mature cell wall in the results of liberation occurs, and H–pieces at the filament ends are formed. Sexual reproduction is not observed. Old cultures are green or yellow. Numerous inclusions can be in large numbers in old cells. The content of the old cells often is granular. Akinetes are not registered.

Holotype: IRK 3118!, dried material prepared from the reference strain deposited in the Herbarium of the Siberian Institute of Plant Physiology and Biochemistry (SIPPB) of the Siberian Branch of the Russian Academy of Sciences (IRK), Irkutsk.
Isotypes: IRK 3118–1!, IRK 3118–2! IRK 3118–3!, LE A0007735!, LE A0007736!, LE A0007737!, dried material prepared from the reference strain.
Paratypes: IRK 3118–7!, IRK 3118–8!, IRK 3118–9!, IRK 3118–10! dried material derived from the strain IRK–A 417.
Type locality: The mountain steppe with *Stipa baicalensis*, the top layer of the chestnut soil, 52.05490°N, 105.40176°E, the Primorsky Range, the vicinity of the village Bolshoye Goloustnoye, the Irkutsk region, Russian Federation.
Habitat: Top layers of soils and soil biocrusts.
Etymology: The name *goloustica* refers to the type locality (from the village Bolshoye Goloustnoye).
Reference strain: IRK–A 448. Also, material of the reference strain is maintained at the All–Russian Collection of Microorganisms (VKM), G.K. Skryabin Institute of Biochemistry and Physiology of Microorganisms, Pushchino Scientific Center for Biological Research of the Russian Academy of Sciences, Pushchino, Russian Federation, under number VKM Al–499.
Materials analyzed: IRK–A 417, IRK–A 448.
GenBank accession numbers: 18S rDNA–ITS: PQ535701–PQ535702; rbcL: PQ553565–PQ553566.
Taxonomic notes: The described variety differs from *Streptosarcina arenaria* mainly by branching filamentous thalli and the shape of the cells. It is more similar to filamentous *S. costaricana*, but differs by the size and shape of cells, the production of motile and immotile spores, ecology, geography, and 18S rDNA–ITS genetic features.

Discussion

Based on the morphology of the studied strains, we previously assessed them as representatives of the Charophyta and the filamentous alga of the genus *Streptosarcina*. The combined data of the morphological and ultrastructural observations with the molecular genetic analysis unambiguously support that the studied plants belong to the genus *Streptosarcina* of the class Klebsormidiophyceae. This genus is the branch of a large clade, along with *Hormidiella* and *Entransia*, which is a sister to the other large clade formed by the genera *Klebsormidium*, *Interfilum*, and *Streptofilum* (Bierenbrodspot et al. 2024; this study). *Streptosarcina* and *Hormidiella* are members of the order Hormidiellales, according to recent studies (Bierenbrodspot et al. 2024).

The genus *Streptosarcina* shares the morphological traits with other charophyte algae and generally, klebsormidiophyceans: parietal plate– or disk–shaped chloroplast that covers a longitudinal cell wall; the chloroplast with the pyrenoid(s); the structure of the cell wall, the formation of cap/H–pieces at the ends of cells; the reproduction by naked zoospores with two subapical flagella and without stigma, and their release through the opening of the cell wall (e.g., Lokhorst 1996; Sánchez Puerta & Leonardi 2001; Cook 2004; Mikhailyuk et al. 2008, 2014; Rindi et al. 2008, 2011). Mikhailyuk et al. (2018) reported that *Streptosarcina* is most similar in morphology to such charophyte genera as sarcinoid *Chlorokybus* Geitler (Chlorokybophyceae), filamentous *Klebsormidium*, and *Interfilum*, combining two types of thalli (sarcinoid and filamentous). *Streptosarcina* differs from them by true branching and cell walls without mucilage. Data obtained in this study is correlated with previously published. *Hormidiella* and *Entransia* have more specific morphology and life cycles. The first has

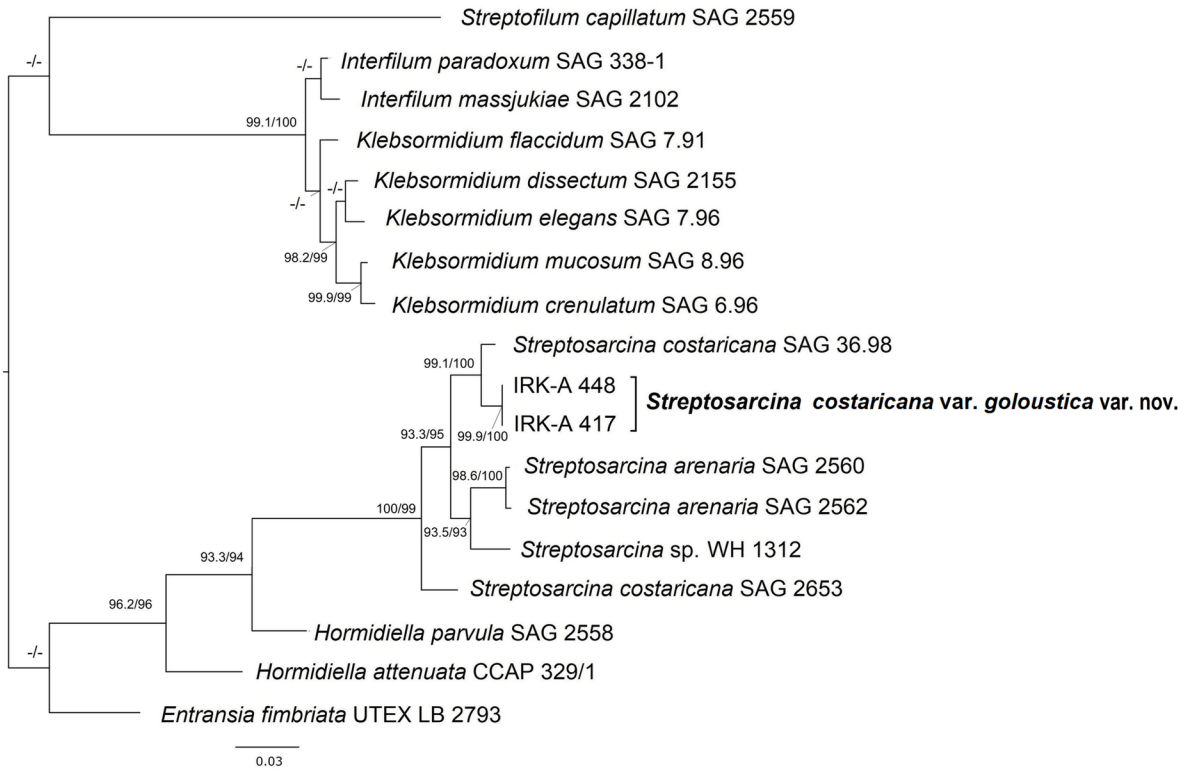

Fig. 7. The phylogenetic relationships of *Streptosarcina costaricana* var. *goloustica* var. nov. The maximum likelihood tree is based on 18S–ITS sequences. The SH–aLRT test and ultrafast bootstrap support values (SH–aLRT/UFBoot) are shown at the nodes (values below 80/90 are marked with –/–). The scale bar indicates the number of substitutions per site.

a filamentous thallus with a hyaline basal stalk at the germinating filaments (Iyengar & Kanthamma 1940; Subrahmanyan 1976; Mikhailyuk et al. 2018). For one of the representatives of *Hormidiella*, zoospores have the unequal flagella. Liberation of zoospores occurs by gelatinization of the parent cell wall. The sexual process (anisogamy) was reported (Subrahmanyan 1976). *Entransia* also has filamentous thallus with laminate or clearly lobed chloroplast and numerous pyrenoids, germinating filaments with condensed adhesive at the base, and tapering spine at the apical end (Cook 2004). *Streptofilum* is a more distant lineage, the cell cover of which is represented by the plasmalemma with the mucilage. The mucilage has specific piliform scales (Mikhailyuk et al. 2018; Glaser et al. 2025).

Despite the general morphological similarity of the genus *Streptosarcina* to *Klebsormidium* and *Interfilum*, some traits suggest its relationship with phylogenetically close–related genera *Hormidiella* and *Entransia*. It is the presence of numerous pyrenoids in the chloroplast (Mikhailyuk et al. 2018; this study); reproduction by zoospores and aplanospores (this study; Mikhailyuk et al. 2018); the ability to form *Hormidiella*–like homo– or heteropolar filaments, but without a hyaline stalk (this study). Aplanospores are also reported for the genus *Klebsormidium* but there is little information about them (Lokhorst 1996; Gaysina et al. 2009; Skaloud & Rindi 2013). In cells of the *Streptosarcina* strains, as well as in cells of *Hormidiella* and *Entransia,* centrioles are found (Cook 2004; Herburger et al. 2016; Mikhailyuk et al. 2018; this study). *Streptosarcina* has pyrenoid(s) that is traversed by thylakoids and surrounded by starch (Mikhailyuk et al. 2018; this study). A similar ultrastructure of the pyrenoid is observed in *Entransia* (Cook 2004; Herburger et al. 2016), *Klebsormidium*, and *Interfilum* (e.g., Floyd et al. 1972; Mikhailyuk et al. 2008, 2014), but not in *Hormidiella* and *Streptofilum,* which have a homogeneous pyrenoid stroma (Herburger et al. 2016; Mikhailyuk et al. 2018; Glaser et al 2025).

At present, *Streptosarcina* includes two species and three described strains (see Table 2, 3). The other two strains known from China (*Streptosarcina* sp. WH 1312) and the USA (*S. costaricana* SAG 2653) have published genetic data without morphological characteristics. The morphology of the examined plants is more similar to that of the reference strain of the species *S. costaricana*, SAG 36.98, and significantly differs from the type species of the genus, *S. arenaria*. The ultrastructure of IRK–A is also like that of *S. costaricana* SAG 36.98, except for the presence in their cells of the large starch plates of often irregular shape surrounding the pyrenoid and two–thylakoid packs traversing the matrix of the pyrenoid (Fig. 6). The comparison with the other strain, registered as *S. costaricana*, SAG 2653, is currently impossible.

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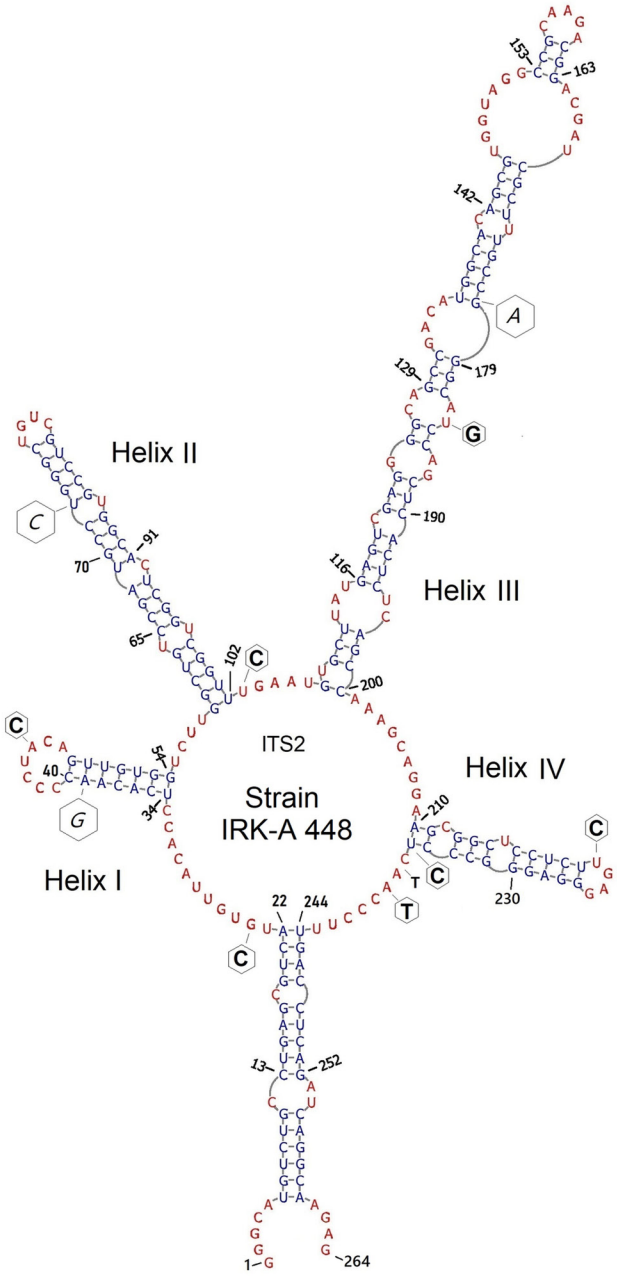

Fig. 8. The ITS2 secondary structure model of *Streptosarcina costaricana* var. *goloustica* var. nov. (strains IRK–A 417 and 448) in comparison with *S. costaricana* (SAG 36.98). Nucleotides in hexagons correspond to substitutions in *S. costaricana* (SAG 36.98). The hemi–CBCs are shown in italics, and the insertion is in smaller font.

Probably, this strain has a filamentous thallus, based on its name. The position of SAG 2653 on the phylogenetic tree (this study; Bierenbrodspot et al., 2024) and the higher value of the genetic distance between this strain and the type *S. costaricana* SAG 36.98 indicate its separate taxonomical status.

The examined plants have some differences from described *S. costaricana*: the larger sizes of cells, the shape of cells, the ability to form complex structures of branching filaments, and the presence of homo– and heteropolar filaments; reproduction by motile (zoo–) and immotile (aplanospores) reproductive cells. The data on the peculiarities of the reproduction of the IRK–A algae tell us more about how *Streptosarcina* reproduces. The reproduction by zoospores is established for *S. arenaria* but not *S. costaricana* SAG 36.98. The ability to produce aplanospores is reported for *Streptosarcina* representatives for the first time. Usually, the studied strains formed a low number of motile spores with a short motility period. We also observed a large number of rounded spores without flagella that were formed after the stopping. Probably, sometimes the reproduction by motile *Streptosarcina* cells can be plentiful, but drivers of this process are unknown. Aplanospores are formed more often.

These differences in the IRK–A strains phenotype

and reproduction from other *Streptosarcina* are appreciable, but their relevance to date is not entirely clear. These features may indicate insufficient knowledge of the genus members and a manifestation of both inter– and intraspecies variability. The original descriptions of the two known species in the genus are quite brief. For other klebsormidiophyceans, there are large overlaps in morphology and size, in particular for the genus *Klebsormidium,* which has a large number of studied strains (e.g., Škaloud 2006; Škaloud & Rindi 2013; Mikhailyuk et al. 2015; Rindi et al. 2017; Samolov et al. 2019). Different strains of the same species in the genera *Entransia* and *Klebsormidium* can form spores or not in culture conditions (Cook 2004; Rindi et al. 2008). The production of motile reproductive cells for some klebsormidiophyceans members in culture seems to be a significantly rarer process than reproduction by vegetative cell division or fragmentation of thalli (e.g., Škaloud & Rindi 2013; Samolov et al. 2019). Motile cells are often formed in few numbers. They lose their motility quickly, which makes additional trouble during observations.

The present study shows that all strains of *Streptosarcina* (7), including IRK–A, belong to five separate genetic lineages (Fig. 6; Table 3). The statistical support of these lineages is significant based on the 18S–ITS phylogeny. The analysis of nucleotide sequences of the gene rbcL of the strains of *Streptosarcina* infers their low resolution that also has been shown previously (Mikhailyuk et al. 2018). A similar situation is noted in the superclade G of the genus *Klebsormidium* (Samolov et al. 2019). In the 18S–ITS phylogenetic tree, the filamentous *Streptosarcina* strains, SAG 36.98, IRK–A 448, and IRK–A 417, are placed in a sister clade to the type species of the genus, *S. arenaria* (with sarcinoid packages), along with the sequence of the undescribed strain WH 1312. The distinctive phylogenetic position of the strain SAG 2653 does not support its close relationship with the species *S. costaricana* and taxonomy of this strain should be clarified further. Similar placement of SAG 2653 can also be seen on the phylogenetic tree that includes three strains of *Streptosarcina* analyzed in the study of Bierenbrodspot et al. (2024). The phylogenetic tree shows IRK–A strains as distinct evolutionary lineage in the clade of *S. costaricana* (SAG 36.98). The limited number of strains and only two known species does not allow to establish clear genetic borders within the genus *Streptosarcina*. The calculated in this study values of the genetic distances between *S. costaricana* SAG 36.98 and IRK–A strains are intermediate (between intra– and interspecific). Based on the 18S–ITS phylogenetic tree and analysis of the genetic distances, IRK–A strains can be attributed to the new genetic variant closely related to *S. costaricana* SAG 36.98.

The comparison of ITS2 secondary structure of a few *Streptosarcina* strains reveals their similarity (this study; Mikhailyuk et al. 2018). Three hemi–CBCs differ ITS2 of the IRK–A algae from close–related *S. costaricana* SAG 36.98. Earlier studies show that the number of CBCs in the secondary structures of ITS2 of different lineages of the Klebsormidiophyceae can be low, or no CBCs can be present (Rindi et al. 2011; Škaloud & Rindi 2013; Škaloud et al. 2014; Glaser et al. 2017; Mikhailyuk et al. 2018; Samolov et al. 2019). The applicability of this criterion for delimitations of klebsormidiophyceans is debatable. Among studied strains of *Streptosarcina*, CBC is found only for the undescribed strain WH 1312. Hemi–CBCs are present more often. For example, six hemi–CBCs are found in the secondary structure of ITS2 of two described species, *S. arenaria* and *S. costaricana* SAG 36.98. The authors of these species took this data into account when erecting the taxa (Mikhailyuk et al. 2018).

Currently, the available morphological and molecular data on *Streptosarcina* members do not allow us to conclude that the IRK–A strains are an independent species taxon within the genus. In this work, we erected the studied algae as variety of *S. costaricana* although eco–geography of the IRK–A strains supported the uniqueness of this lineage. A habitat of the type strain of *S. costaricana*, SAG 36.98, is soil of Costa Rica. The IRK–A strains were found in soils of Asian Russia which are located at a distance of several thousand kilometers from Costa Rica and in other climatic conditions. A number of studies have shown that when defining the boundaries of algae species, it is essential to consider their eco–geographical characteristics (e.g., Škaloud & Rindi 2013; Mikhailyuk et al. 2015; Malavasi et al. 2016; Jusko & Johansen 2023). However, choosing criteria for distinguishing of protist species remains a significant challenge and cases where new intraspecies taxa have been established from eco–geographically distant areas are also known. For example, new varieties of some species of *Klebsormidium* (Samolov et al. 2019), chlorophycean genera *Pleurastrosarcina* Sluiman & Blommers and *Coelastrella* Chodat from geographically remote territories were established (Darienko et al. 2019; Wang et al. 2019). The results of this study also highlight the problem of selecting criteria for differentiating between microalgae species. Perhaps future research will change the understanding of the taxonomical status of IRK–A strains.

Only a few records of *Streptosarcina* are known in the world, mainly in northern hemisphere. These algae are found in soils of Europe (Slovakia and Ukraine), Asia (China), Central (Costa Rica), and North America (USA) (Mikhailyuk et al. 2018; Bierenbrodspot et al. 2024). The alga named *S. costaricana* was observed in a biocrust from the Murmansk Region of Russia (Davydov & Redkina 2021). Published information about this plant is quite formal and concise, based on some morphological traits. According to the photo, the alga looks more like a branched representative of the genus *Interfilum*. In 1936, one of the first papers on soil algae was published in Russia (Gollerbakh 1936). The research was conducted in the Leningrad Region. In this

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work, a description and drawings of the algae designated as *Stichococcus variabilis* W. et G.S.West were given (Gollerbakh 1936: 256–257). The author noted that this alga has differences from *Stichococcus* Nägeli. It is also similar to *Hormidium* Kütz. (=*Klebsormidium*) members, although it differs from them as well. Considering the information available at that time about algae, the author decided to classify it as known *Stichococcus* species. In our opinion, the characteristics and drawings of this alga may indicate that it belongs to *Streptosarcina*. It requires additional studies in the mentioned northwestern regions of Russia to confirm findings of *Streptosarcina*.

The records of representatives of the genus are known from regions with tropical and temperate (?) climates (Mikhailyuk et al. 2018; Bierenbrodspot et al. 2024). The *Streptosarcina* strains we studied are found in plant communities in the temperate continental climate. Explored plant communities are mountain steppe and forest–steppe phytocenoses (Fig. 2). They are developed on chestnut soils formed on carbonate rock formation. In the upper horizons of soils, there is a large amount of calcium and magnesium compounds. These are dry and skeletal soils with slightly acidic and neutral to alkaline reactions of the soil solution (Egorova et al. 2024). In our study, *Streptosarcina* was additionally observed in other pine and larch forest communities developing on mountain slopes and adjacent steppe cenoses. Only two strains are isolated by us. *Streptosarcina* may not be very rare organisms, but they require specific living conditions. Observations in culture show that soil amoebae actively ate the studied IRK–A strains cells. These amoebae were present in soil samples from which *Streptosarcina* was isolated. According to ITS nucleotide sequence (authors unpublished data), the mentioned protozoa belong to genera *Vahlkampfia* Chatton et Lalung–Bonnaire and *Vermamoeba* Cavalier–Smith et Smirnov. Along with other free–living amoebae, they live in different terrestrial and aquatic biotopes. They act as predators, controlling populations of microorganisms. These amoebae feed on bacteria, fungi, yeast, algae, and other protozoa (cit. by Horn et al. 2000; Dumack et al. 2016). So, *Streptosarcina* can be considered participants of food chains.

Conclusion

Among klebsormidiophycean algae, the genus *Streptosarcina* is one of the least studied, with few known members to date. The phylogenetic studies show that the clade *Streptosarcina* includes two taxa of the species rank, *S. costaricana* and *S. arenaria*, and sequenced but undescribed strains SAG 2653 and WH 1312, which presumably are new species. The two phylogenetic subclades of *S. costaricana* and *S. arenaria* correlate with the two types of thalli, filamentous or sarcinoid, respectively. The two terrestrial strains collected in Siberia near Lake Baikal are the first justified finding of *Streptosarcina* in Russia. The detailed analysis of morphology (LM, TEM), nuclear and plastid DNA, and the ITS2 secondary structure showed specific features of the studied strains. They represent a new phylogenetic lineage that is assigned as the new variety *S. costaricana* var. *goloustica.* The results obtained provide new data on cell morphology, thallus types, and reproduction of *Streptosarcina* and reveal its greater diversity and distribution than currently known.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Strains used in the phylogenetic analysis.

S2-S4. The nucleotide alignments used in the study.

This material is available as part of the online article (http://fottea.czechphycology.cz/contents)

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