Moorea producens gen. nov., sp. nov. and *Moorea bouillonii* comb. nov., tropical marine cyanobacteria rich in bioactive secondary metabolites

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The filamentous cyanobacterial genus *Moorea* gen. nov., described here under the provisions of the International Code of Botanical Nomenclature, is a cosmopolitan pan-tropical group abundant in the marine benthos. Members of the genus *Moorea* are photosynthetic (containing phycocyanin, phycoerythrin, allophycocyanin and chlorophyll *a*), but non-diazotrophic (lack heterocysts and nitrogenase reductase genes). The cells (discoid and 25–80 μm wide) are arranged in long filaments (<10 cm in length) and often form extensive mats or blooms in shallow water. The cells are surrounded by thick polysaccharide sheaths covered by a rich diversity of heterotrophic micro-organisms. A distinctive character of this genus is its extraordinarily rich production of bioactive secondary metabolites. This is matched by genomes rich in polyketide synthase and non-ribosomal peptide synthetase biosynthetic genes which are dedicated to secondary metabolism. The encoded natural products are sometimes responsible for harmful algae blooms and, due to morphological resemblance to the genus *Lyngbya*, this group has often been incorrectly cited in the literature. We here describe two species of the genus *Moorea*: *Moorea producens* sp. nov. (type species of the genus) with 3L^T as the nomenclature type, and *Moorea bouillonii* comb. nov. with PNG5-198^R as the nomenclature type.

Benthic filamentous marine cyanobacteria from the tropics have been of increasing biomedical interest due to their extraordinary richness in bioactive secondary metabolites (Tidgewell *et al.*, 2010). Many of these natural product molecules are potent toxins responsible for harmful algal blooms and thus are hazardous to humans as well as near-shore environments. At the same time, some of these cyanobacterial toxins and other natural products have properties of potential benefit to human health as pharmaceutical leads (Golubic *et al.*, 2010). Surprisingly, the majority of these unique natural products have been ascribed as being produced by members of a single genus, *Lyngbya*, and a preponderance of these come from a single species, *Lyngbya majuscula* (Liu & Rein, 2010). However, an unfortunate consequence of using traditional morphology-based taxonomic systems in these identifications has been that cyanobacteria of many recently explored biological frontiers (e.g. tropical marine environments) have been forced into existing morphological groupings and, thus, the true biodiversity of this group has been greatly underestimated (Casamatta *et al.*, 2005; Engene *et al.*, 2011).

The proposed cyanobacterial genus *Moorea* gen. nov. is a cosmopolitan, pan-tropical group abundant in the marine benthos. Strains of *Moorea* gen. nov. have often been incorrectly classified as the cyanobacterial genus *Lyngbya* due to morphological similarities between the two groups (Engene *et al.*, 2011). This misidentification of *Moorea* as *Lyngbya* has been a source of considerable taxonomic confusion as well as the major reason for the perceived chemical richness of the genus *Lyngbya* (Engene *et al.*,

Abbreviations: ITS, internal transcribed spacer; NRPS, non-ribosomal peptide synthetase; PKS, polyketide synthase.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain 3L^T is EU315909.

Three supplementary figures and a supplementary table are available with the online version of this paper.

2011). Herein, we firmly differentiate between these two phylogenetically distinct groups and describe *Moorea* as a novel generic entity (gen. nov.). This description and naming of *Moorea* gen. nov. was performed under the provisions of the International Code of Botanical Nomenclature.

A total of 51 geographically distributed populations of the genus *Moorea* were included in this taxonomic revision (geographical data for *Moorea* specimens are available in Table S1 in IJSEM Online). Field collections of cyanobacteria were carefully rinsed with autoclaved SWBG-11 medium (Castenholz, 1988) and visible macro-organisms were mechanically removed with sterile tweezers under an Olympus VMZ dissecting microscope. Clonal, non-axenic strains were derived from phototactically isolated single filaments on 0.5 % agar plates with SWBG-11 and cultured in SWBG-11 medium at 28 °C with 33 g Instant Ocean salt l^{-1} (Aquarium Systems). The cultures were kept at a light intensity of 7 μmol photons s^{-1} m^{-2} (16 h light/8 h dark). Two isolated strains, *Moorea producens* $3L^T$ and *Moorea bouillonii* PNG5-198^R, were deposited in the Canadian Phycological Culture Centre (CPCC) and the national marine phytoplankton collection (CCMP) as reference strains. Additionally, the *Lyngbya* reference strain PCC 7419^R was obtained from the Pasteur Culture Collection (PCC) for biological comparison. Light microscopy was performed using an Olympus IX51 epifluorescent microscope (1000×) equipped with an Olympus U-CMAD3 camera. Samples for scanning electron microscopy were placed on indium-tin-oxide glass slides that had been coated with 0.1 % polyethylenimine to facilitate adhesion. The samples were then fixed in 2.5 % glutaraldehyde buffered in 1× PBS for 30 min and a secondary fix of 2 % aqueous osmium tetroxide for 15 min. Dehydration was achieved with a graded ethanol series. The samples were then critical-point-dried and sputter-coated with gold palladium. A Hitachi SU6600 scanning electron microscope was used to view the samples. Samples for transmission electron microscopy were prepared using high pressure freezing and subsequent freeze substitution. The filaments were cut into pieces of <0.5 mm and placed into specimen holders with a drop of cryoprotectant hexadecane. The samples were frozen using a Bal-Tec HPM 010 high pressure freezing machine. Freeze substitution was done using a Leica EM AFS machine. Samples were transferred to pre-cooled 1 % glutaraldehyde with 0.2 % tannic acid in anhydrous acetone and left at −90 °C for 36 h, then washed with acetone three times for 15 min each and subsequently transferred to 1 % osmium tetroxide with 0.1 % uranyl acetate in acetone and held for 24 h. The temperature was raised to −60 °C, –30 °C and 0 °C, being held for 24 h between each step. At 0 °C, the samples were washed with acetone three times for 15 min each and transferred into 50 % Durcopan in acetone and held for 12 h. Once samples warmed to room temperature, they were embedded in Durcopan and left to polymerize for 48 h. Thin sections (70 nm) were obtained using a Reichart Ultracut E and then placed on Formvar-coated 75 and 200 mesh copper grids. The grids were subsequently stained with uranyl acetate and Sato lead. A JEOL 1200FX transmission electron microscope was used to view the samples. Photosynthetic pigments were characterized as described previously (Tandeau de Marsac & Houmard, 1988).

Genomic DNA was extracted using the Wizard Genomic DNA Purification kit (Promega) following the manufacturer's specifications. DNA concentration and purity were measured on a DU 800 spectrophotometer (Beckman Coulter). The PCR volumes were 25 μl, containing 0.5 μl (~50 ng) of DNA, 2.5 μl of 10× PfuUltra IV reaction buffer, 0.5 μl (25 mM) dNTP mix, 0.5 μl of each primer (10 μM), 0.5 μl PfuUltra IV fusion HS DNA polymerase and 20.5 μl distilled H_2O. PCRs were performed in an Eppendorf Mastercycler gradient as follows: initial denaturation for 2 min at 95 °C; 25 amplification cycles of 20 s at 95 °C, 20 s at 50 °C and 1.5 min at 72 °C; and final elongation for 3 min at 72 °C. PCR products were purified using a MinElute PCR Purification kit (Qiagen) before subcloning into the Zero Blunt TOPO PCR Cloning kit (Invitrogen). Plasmid DNA was isolated using the QIAprep Spin Miniprep kit (Qiagen) and sequenced bidirectionally with M13 vector-primers as well as internal primers. The gene sequences are available in DDBJ/EMBL/GenBank (see Table S1, available in IJSEM Online). The 16S (SSU) rRNA genes of all 51 *Moorea* specimens were included in the analysis. Representative reference strains were selected from *Bergey's Manual* (Castenholz, 2001). The unicellular *Gloeobacter violaceus* PCC 7421^T (GenBank accession no. NC_005125) was included as an evolutionarily distant outgroup. All gene sequences were aligned using the L-INS-I algorithm in MAFFT 6.717 (Katoh & Toh, 2008). The alignment was visually compared and refined using the SSU secondary structures model of *Escherichia coli* J01695 (Cannone *et al.*, 2002) without data exclusion. The multiple sequence alignments are available in the TreeBASE database (http://www.treebase.org) under the submission ID 11599. Pair-wise sequence divergences were calculated in PAUP* 4.0b10. Appropriate nucleotide substitution models were compared and selected using uncorrected/corrected Akaike Information Criterion (AIC/AICc), Bayesian Information Criterion (BIC) and the Decision-theoretic (DT) in jModeltest 0.1.1 (Posada, 2008). The maximum-likelihood inference was performed using GARLI 1.0 (Zwickl, 2006). The analysis was run using the GTR+I+G model assuming a heterogeneous substitution rate and gamma substitution of variable sites [proportion of invariable sites (pINV)=0.450, shape parameter (α)=0.449, number of rate categories=4]. Bootstrap resampling was performed on 1000 replicates. Bayesian analysis was conducted using MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 10 000 000 generations. MCMC convergence was determined using AWTY; the first 1 000 000 generations (10 %) were discarded as burn-in and

the following datasets were sampled with a frequency of every 1000 generations. The maximum-parsimony analysis was performed in PAUP* 4.0b10 using a heuristic search through the branch-swapping tree-bisection-reconnection algorithm with the addition of 10 000 random replicates to find the most parsimonious tree. Bootstrap support was obtained from 1000 replicates.

Draft genomes from *M. producens* strain 3L^T (GenBank accession no. AEPQ01000000) and *M. bouillonii* strain PNG5-198^R have been obtained recently and were used for phylogenomic and functional genomics comparison. Phylogenomic inference was performed bioinformatically on the basis of the *DNA-G*, *FRR*, *rpsB*, *NusA*, *PGK*, *PyrG*, *rpoB*, *rpsC*, *rpl2*, *rpl3*, *rpl4* and *TSF* genes. These gene sequences were downloaded from all 59 publicly available cyanobacterial genomes and concatenated for phylogenetic inference with the two *Moorea* genomes. Maximum-likelihood (RaxML) inference was performed on the WAG+I+G model assuming heterogeneous substitution rates and gamma substitution of variable sites [proportion of invariable sites (pINV)=0.265, shape parameter (α)=0868, number of rate categories=4] with a bootstrap resampling of 500 replicates.

Phylogenetic inference based on the 16S rRNA gene revealed that the *Moorea* lineage was evolutionarily distinct and distant from the *Lyngbya sensu stricto* (reference strain=PCC 7419^T; p-distance=9.2 %) (Fig. 1a). The *Moorea* lineage was nested between members of the closest related genera *Symploca* (reference strain=PCC 8002^R; p-distance=6.1 %) and *Coleofasciculus* (reference strain=PCC 7420^T; p-distance=6.9 %). The phylogenetic positions of *Moorea* and evolutionary distances from *Lyngbya* were corroborated by analysis of the RNA polymerase gamma subunit (*rpoC1*) gene (an evolutionary tree of the *rpoC1* gene is available as Fig. S1 in IJSEM Online). An additional 12 other protein-coding genes (*DNA-G*, *FRR*, *rpsB*, *NusA*, *PGK*, *PyrG*, *rpoB*, *rpsC*, *rpl2*, *rpl3*, *rpl4* and *TSF*) were selected from the *Moorea* genome drafts and the evolutionary histories of these genes were individually constructed and compared with all available sequenced genomes of cyanobacteria. As a result, each protein-coding gene showed an evolutionary history that was relatively congruent with that of the 16S rRNA gene phylogram. All 12 phylogenetically informative genes were concatenated for a more robust phylogenomic inference. The combined genes supported the phylogenetic distance between *Lyngbya* (i.e. PCC 8106) and *Moorea* (i.e. 3L^T and PNG5-198^R) as well as the overall evolutionary history of the phylum (a phylogenomic inference is available as Fig. S2 in IJSEM Online).

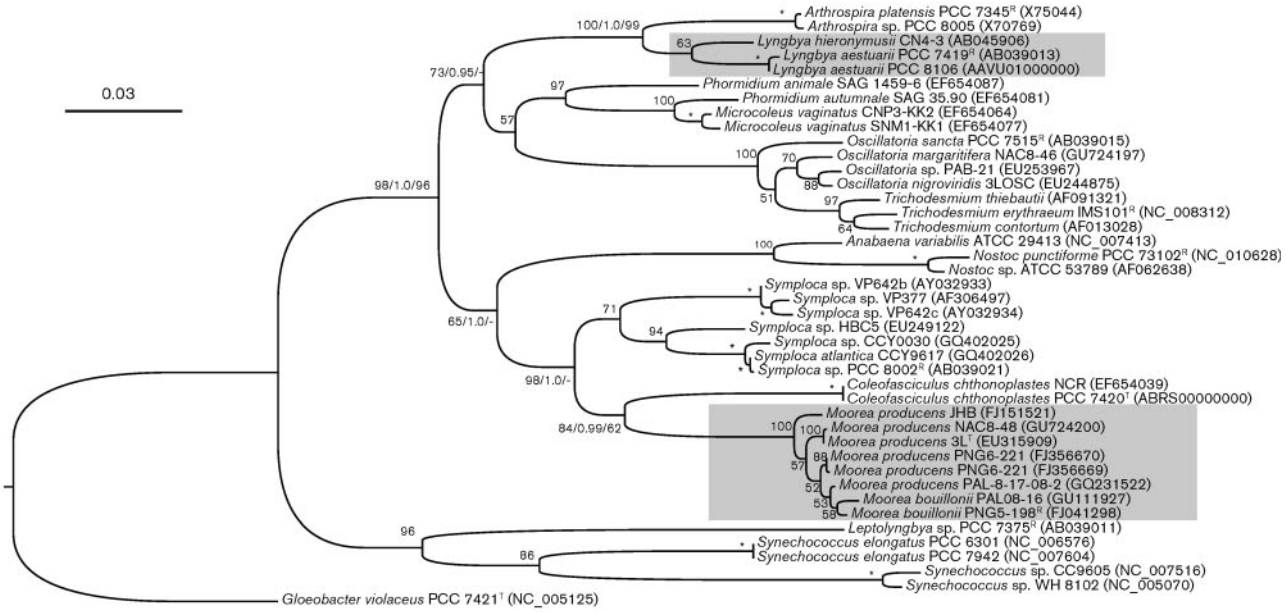
On a subgeneric level, the *Moorea* specimens formed a tight clade with low interior sequence divergence (p-distance: mean=0.5 %; max.=1.4 %) (Fig. 1b). This high DNA barcoding gap of the *Moorea* clade of more than 12 times further supports the exclusivity of this clade and the need to distinguish it from neighbouring genera (Fig. 1a). However, the genomes of *Moorea* specimens contain multiple and variable copies of their 16S rRNA genes (Engene *et al.*, 2010) and this relatively high level of intra-genomic gene heterogeneity in combination with the low subgeneric sequence divergence makes the 16S rRNA gene inadequate for speciation. The lack of phylogenetic resolution for species delineation was further indicated by low statistical node support at the terminal nodes and incongruence using different phylogenetic methods (Fig. 1b). The less conserved internal transcribed spacer (ITS) region linking the 16S and 23S ribosomal genes has been proposed to be taxonomically more informative on a subgeneric level and has often been used for species delineation in cyanobacteria (Otsuka *et al.*, 1999; Boyer *et al.*, 2001; Gugger *et al.*, 2005). Primer-sites on the adjacent 16S and 23S rRNA genes were used to PCR-amplify the 16S–23S ITS regions of 41 *Moorea* specimens. However, the 16S–23S ITS regions were, in accordance with the 16S rRNA genes, present in multiple and variable gene copies and, thus, this gene region was also not able to definitively distinguish between *Moorea* specimens (Fig. S3). In addition, the intra-genomic sequence heterogeneity of the 16S–23S ITS region was found to influence structurally informative domains, such as the D1-D1′ helix and the Box-B, secondary structures which are frequently used for taxonomic delineation (Boyer *et al.*, 2001). In the case of *Moorea*, we argue that the 16S–23S ITS regions are not able to further resolve species delineation.

Morphologically, the *Moorea* specimens were composed of long isopolar filaments enclosed in thick exopolysaccharide sheaths with discoid cells arranged in trichomes (Fig. 2). The exteriors of the sheaths were consistently covered by a rich fauna of heterotrophic bacteria and other microorganisms (Fig. 2). The two *Moorea* species *M. producens* and *M. bouillonii* had distinctively different colony morphologies. Environmental specimens of *M. bouillonii* always formed characteristic reddish cobweb-like mats firmly attached to surrounding substrate and each colony was also always found with an associated snapping shrimp (*Alpheus frontalis*) (Fig. 2).

M. producens has often been reported in the literature as either *Lyngbya majuscula* or *L. sordida*. The primary reason for combining tropical marine *L. majuscula* and *L. sordida* into a single species, *Moorea producens*, was variability in the morphological characters of these two former morphotypes. *M. bouillonii* was, in contrast to *L. majuscula* and *L. sordida*, initially described from tropical marine environments and will consequently keep its species nomenclature in order to preserve taxonomic stability (Hoffman & Demoulin, 1991).

The ultrastructure of *Moorea* cells contained a high degree of compartmentalization and cells were rich in intrathylakoidal spaces (widened thylakoids) (Fig. 3). The thylakoid membranes were arranged parallel to the cell walls. The filaments were surrounded by thick (2–3 μm) firm and laminated sheaths.

(a)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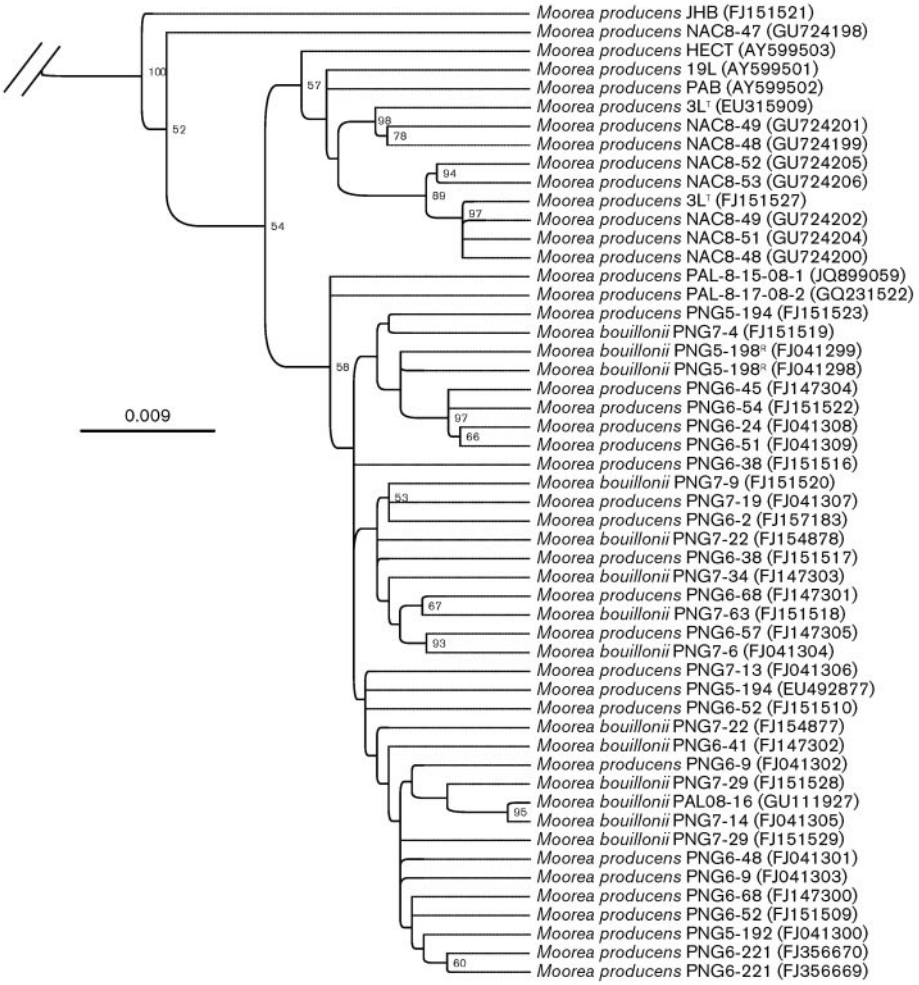
Lyngbya hieronymusii CN4-3 (AB045906)
Lyngbya aestuarii PCC 7419T (AB039013)
Lyngbya aestuarii PCC 8106 (AAVU01000000)
Phormidium animale SAG 1459-6 (EF654087)
Phormidium autumnale SAG 35.90 (EF654081)
Microcoleus vaginatus CNP3-KK2 (EF654064)
Microcoleus vaginatus SNM1-KK1 (EF654077)
Oscillatoria sancta PCC 7515R (AB039015)
Oscillatoria margaritifera NAC8-46 (GU724197)
Oscillatoria sp. PAB-21 (EU253967)
Oscillatoria nigroviridis 3LOSC (EU244875)
Trichodesmium thiebautii (AF091321)
Trichodesmium erythraeum IMS101R (NC_008312)
Trichodesmium contortum (AF013028)
Anabaena variabilis ATCC 29413 (NC_007413)
Nostoc punctiforme PCC 73102R (NC_010628)
Nostoc sp. ATCC 53789 (AF062638)
Symploca sp. VP642b (AY032933)
Symploca sp. VP377 (AF306497)
Symploca sp. VP642c (AY032934)
Symploca sp. HBC5 (EU249122)
Symploca sp. CCY0030 (GQ402025)
Symploca atlantica CCY9617 (GQ402026)
Symploca sp. PCC 8002R (AB039021)
Coleofasciculus chthonoplastes NCR (EF654039)
Coleofasciculus chthonoplastes PCC 7420T (ABRS00000000)
Moorea producens JHB (FJ151521)
Moorea producens NAC8-48 (GU724200)
Moorea producens 3LT (EU315909)
Moorea producens PNG6-221 (FJ356670)
Moorea producens PNG6-221 (FJ356669)
Moorea producens PAL-8-17-08-2 (GQ231522)
Moorea bouillonii PAL08-16 (GU111927)
Moorea bouillonii PNG5-198R (FJ041298)
Leptolyngbya sp. PCC 7375R (AB039011)
Synechococcus elongatus PCC 6301 (NC_006576)
Synechococcus elongatus PCC 7942 (NC_007604)
Synechococcus sp. CC9605 (NC_007516)
Synechococcus sp. WH 8102 (NC_005070)
Gloeobacter violaceus PCC 7421T (NC_005125)
100/1.0/99
73/0.95/-
98/1.0/96
65/1.0/-
98/1.0/-
84/0.99/62

(b)


0.009
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Moorea producens NAC8-47 (GU724198)
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Moorea producens PAB (AY599502)
Moorea producens 3LT (EU315909)
Moorea producens NAC8-49 (GU724201)
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Moorea bouillonii PNG7-4 (FJ151519)
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Moorea bouillonii PNG7-9 (FJ151520)
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Moorea producens PNG6-2 (FJ157183)
Moorea bouillonii PNG7-22 (FJ154878)
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Moorea producens PNG6-9 (FJ041302)
Moorea bouillonii PNG7-29 (FJ151528)
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Moorea producens PNG6-48 (FJ041301)
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Moorea producens PNG6-68 (FJ147300)
Moorea producens PNG6-52 (FJ151509)
Moorea producens PNG5-192 (FJ041300)
Moorea producens PNG6-221 (FJ356670)
Moorea producens PNG6-221 (FJ356669)

Fig. 1. (a) Phylogenetic inferences (GARLI) of *Lyngbya* and *Moorea* diversification based on SSU (16S) rRNA nucleotide sequences (these two genera are highlighted with shaded boxes). Species and strain numbers of the specimens are given with accession numbers in parentheses. Reference strain (^{R}) and type strain (^{T}) numbers were obtained from *Bergey's Manual* (Castenholz, 2001). Support values are indicated as bootstrap and posterior probability for the maximum-likelihood/Bayesian inference/maximum-parsimony methods (*= bootstrap of 100% and a posterior probability of 1.0). Bar, 0.03 estimated nucleotide substitutions per site using the GTR+I+G substitution model. (b) A close-up of the *Moorea* lineage. Bar, 0.009 expected substitutions per site.

Geographically, *Moorea* is a widely distributed group that is abundant in tropical marine regions (see Table S1, available in IJSEM Online). The latitudinal distribution of this group, according to current sampling and records, ranges approximately between the Tropic of Cancer and the Tropic of Capricorn. The most northern reported collection of *Moorea* is Florida (26° 04′ N) just north of the Tropic of Cancer (Sharp *et al.*, 2009). The habitats of *Moorea* include diverse shallow-water marine environments such as coral reefs, sandy beaches and mangroves. While *M. producens* is a cosmopolitan species and has been found pantropically in shallow marine waters, *M. bouillonii* has only been reported from tropical Pacific locations (see Table S1, available in IJSEM Online).

Biochemically, extracts from the three *Moorea* strains 3L^T, PNG5-198^R, and JHB showed UV absorption at 565, 620, 650 and 665 nm, corresponding to the photosynthetic pigments phycocyanin, phycoerythrin, allophycocyanin and chlorophyll *a*, respectively (Table 1). In addition to these basic cyanobacterial photosynthetic pigments, all three *Moorea* strains contained at least two structurally unique bioactive secondary metabolites, as characterized by LC-MS and NMR (Table 1).

The DNA G+C contents of *M. producens* 3L^T and *M. bouillonii* PNG5-198^R were 41.0 mol% and 42.3 mol%, respectively (Table 1), which were comparable to other filamentous cyanobacteria (mean DNA G+C content=41.2 mol%). The genome size of *M. producens* 3L^T (8.5 Mbp) was larger than the mean genome of filamentous cyanobacteria (6.1 Mbp) and the second largest after the evolutionarily related *Coleofasciculus* PCC 7420^T (genome size=8.7 Mbp). The relatively large genome of *M. producens* 3L^T was reflected in a high abundance of protein-coding genes (7415 compared with the mean copy number of protein-coding genes in filamentous cyanobacteria of 5468 copies). A potential reason for the large

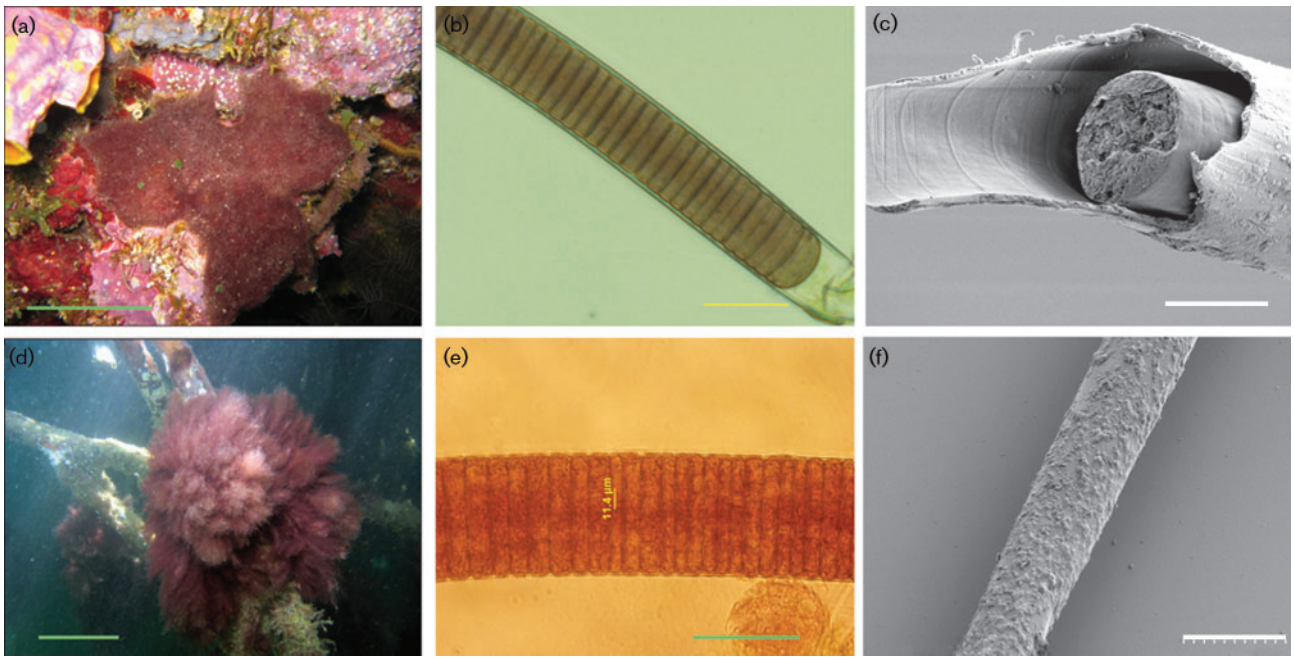

Fig. 2. Morphological characterization of *Moorea* gen. nov. (a–c) *M. bouillonii* PNG5-198^R and (d–e) *M. producens* 3L^T. (a) Underwater pictures of *M. bouillonii* at 10 m depth forming a characteristic cobweb mat firmly attached to the surrounding corals. (d) Tuft colony morphology of *M. producens* growing on shallow-water mangrove roots. Microphotographs of cyanobacterial filaments of (b) *M. bouillonii* and (e) *M. producens* and scanning electron micrographs of (c) *M. bouillonii* and (f) *M. producens*. Bars: a, 10 cm; b, 29.5 µm; c, *ca.* 20 µm; d, 10 cm; e, 50 µm; f, 50 µm.

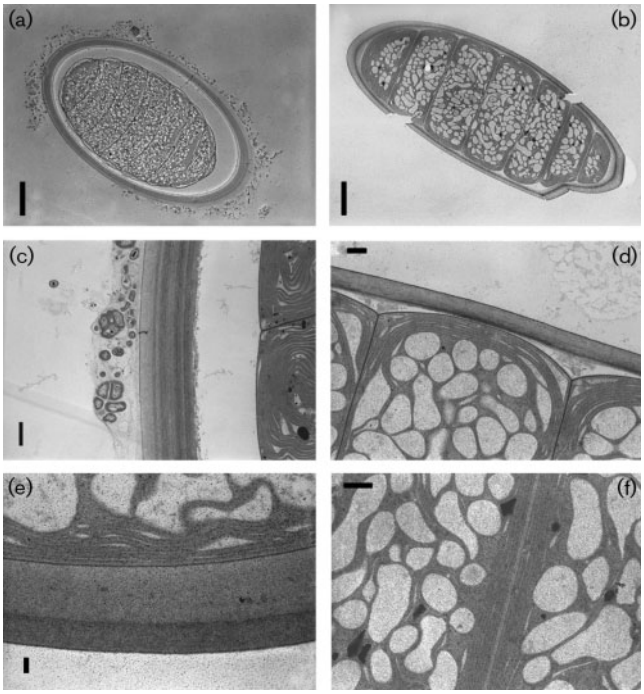

Fig. 3. Microphotographs of cyanobacterial filaments obtained by transmission electron microscopy. Filament transections of *Moorea producens* 3L^T (a) and *M. producens* JHB (b); polysaccharide sheaths and thylakoid arrangements in *M. producens* 3L^T with heterotrophic bacteria on the exterior (c), *M. producens* JHB (d), polysaccharide sheath of *M. producens* 3L^T (e) and thylakoid arrangements in adjacent cells in *M. producens* JHB (f). Bars: a, 10 μm; b, 10μm; c, 1 μm; d, 2 μm; e, 0.5 μm; f, 2 μm.

genome is the relatively large number of genes involved in the biosynthesis of bioactive secondary metabolites. For example, genome analysis of strain 3L^T has revealed that approximately 3 % of its genome contains polyketide synthase (PKS), non-ribosomal protein synthetase (NRPS), or other biosynthetic genes dedicated to secondary metabolism (Jones & Monroe *et al.*, 2011). The partial genome of *M. bouillonii* PNG05-198^T also contained multiple copies of PKS and NRPS genes with high identity to biosynthetic genes involved in secondary metabolite production. The genome of *M. producens* 3L^T has been shown to lack genes involved in nitrogen fixation (Jones & Monroe *et al.*, 2011). This was further supported by a BLAST search (E-value= 1e-5) of the *M. bouillonii* PNG5-198^R genome, which also lacked the *nifHDK* genes necessary for nitrogen fixation. The presence of *nif* genes in the closely related genera *Coleofasciculus* and *Symploca* suggests a loss of these vertically inherited genes in *Moorea* as a relatively recent evolutionary event, which further supports the delineation of *Moorea* as an exclusive genus.

Table 1. Genomic and biochemical characteristics of *Moorea*

Strains: 1, *Moorea producens* 3L^T; 2, *Moorea bouillonii* PNG5-198^R. Both strains had PKS/NRPS secondary metabolite genes, possessed chlorophyll *a*, and had the phycobiliproteins phycocyanin, phycoerythrin and allophycocyanin. Neither strain had nitrogen-fixing genes. ND, Not determined.

Characteristic	1	2
Genome size	8.5 Mbp	ND
DNA G+C content (mol%)	41	42
Protein-coding genes	7415	ND
Secondary metabolites*	cur/car/bar	apr/lbn

*cur, Curacins; car, carmabins; bar, barbamide; apr, apratoxins; lbn, lyngbyabellins.

Latin diagnosis of *Moorea* gen. nov.

Filamenta solitaria vel in fasciculis irregularis, ad macroscopica, ad <10 cm *longa*, 25–65 (82) μm *lata, non divaricata nec ramosa. Trichoma cylindrical, ad dissepimenta non vel paucim constrincta, aeruginosa, olivacea vel rubentes. Vaginae firmae, plus minusve tenues vel paucim dilatatae, externe saepe mucosae, sine colore, paucim lamellosae. Cellulae semper distincte brevior quam latae* [20–55 (70) × (2) 3–10 μm], *discoidae; cellula apicalis late rotundata. Reproductio hormogoniis necridiis separatur. Heterocytae akinetaeque carentes.*

Typus generis: *Moorea producens spec. nova.*

Etymologia: *ad honorem in memoriam* Professor Richard E. Moore *nominate.*

Description of *Moorea* gen. nov.

Moorea gen. nov. (Mo.o.re′a. N.L. fem. n. *Moorea* in memory of Professor Richard E. Moore).

Large filamentous cyanobacteria common in tropical marine oceans, abundant on coral reefs, rocks or mangroves at depths ranging between 0.3–30 m. Filaments are unbranched, <10 cm in length, with wide diameters [25–65 (82) μm]. Trichomes are cylindrical, not attenuated towards ends, constricted or not constricted on crosswalls, surrounded by thick (3–5 μm) and distinct polysaccharide sheaths. The sheaths are typically covered by a rich diversity of mucus (often containing heterotrophic bacteria and other micro-organisms). The cells are discoid, always shorter than they are wide [20–55 (70) μm wide and (2) 3–10 μm long]. The trichomes contain necridic cells separating the trichomes into hormogonia. The terminal cells of the filaments and those of the hormogonia are rounded. Non-diazotrophic and the filaments lack heterocysts or other specialized cells. Members of the genus are photosynthetic and contain phycobiliproteins (phycocyanin, phycoerythrin, and allophycocyanin) and chlorophyll *a*. Strains are often rich in bioactive secondary metabolites typically biosynthesized by PKS, NRPS or mixed PKS/NRPS pathways.

Type species: *Moorea producens* sp. nov.

Latin diagnosis of *Moorea producens* sp. nov.

Thalus caespitosus vel prostratus, coloratus, rubescens ad viride-fuscus. Filamenta 30–67 (82) μm *crassa. Vaginae sine colore, plus minusve tenues,* 1–2 (12) μm *latae, paucim lamellosae. Trichomata rubra vel praecipue olivaceae, cylindrica, apicem non attenuata, ad dissepimenta constricta* (25) 30–65 (70) μm *lata. Cellulae* 3–7 μm *longae, cellula apicalis rotundata, calyptra nulla.*

DNA G+C *contentus*=41.2 mol%.

Holotypus: *cultura* 3L, *in* CPCC *et* CCMP *deposita*; *exemplum conservatum in herbario Musei Moravici Brno* (BRNM/HY 2364) *depositum*; *icona typical* Fig. 2.

Habitatio: *ad radices arborum mangrovis, ad oras Antillarum Hollandicum, in profunditate* 2–3 m.

Etymologia: *contentuu multis producti chemicis.*

Description of *Moorea producens* sp. nov.

Moorea producens (pro.du′cens. L. part. adj. *producens* making, producing, referring to the fact that the species is rich in metabolic products).

The thallus morphology ranges from tuft to extensive mats. The coloration is highly varied, ranging from dark red to greenish-brown. Filaments 30–67 (82) μm width. Sheaths are colourless, thin (1–2 μm, but can be 12 μm wide in extreme situations), slightly lamellose. Trichomes are cylindrical, attenuated on the end, constricted on the cell walls, cells (25) 30–65 (70) μm wide and 3–7 μm long. Apical cells are rounded, without calyptra.

The type strain, 3L^T, was isolated from coral rubble and rocks at 2–3 m depth in Curaçao, Netherlands Antilles. The genomic DNA G+C content of the type strain is 41.2 mol%.

Holotype: strain 3L, deposited in the CPCC and CCMP collections; dried material deposited at the herbarium of the Moravian Museum Brno (BRNM/HY 2364); typical morphology is shown in Fig. 2.

This species has often been incorrectly cited in the literature as *L. majuscula* or *L. sordida*.

Description of *Moorea bouillonii* comb. nov.

Basionym: *Lyngbya bouillonii* (Hoffmann et Demoulin *Belg J Bot* 124: 85, 1991).

For a basic description see Hoffmann & Demoulin (1991).

The colony morphology is mat-like and tenaciously attached to surrounding substrate. The colonies are found in association with the snapping shrimp (*Alpheus frontalis*). Coloration fluctuates between brownish-red and dark red depending on depth.

The reference strain, PNG5-198^R, was isolated from coral reefs at a depth of 10 m in New Ireland, Papua New Guinea. The DNA G+C content of the reference strain is 42.3 mol%.

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