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Mooreia alkaloidigena gen. nov., sp. nov. and *Catalinimonas alkaloidigena* gen. nov., sp. nov., alkaloid-producing marine bacteria in the proposed families *Mooreiaceae* fam. nov. and *Catalimonadaceae* fam. nov. in the phylum *Bacteroidetes*

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Bacterial strains CNX-216^T and CNU-914^T were isolated from marine sediment samples collected from Palmyra Atoll and off Catalina Island, respectively. Both strains were Gram-negative and aerobic and produce deep-orange to pink colonies and alkaloid secondary metabolites. Cells of strain CNX-216^T were short, non-motile rods, whereas cells of strain CNU-914^T were short, curved rods with gliding motility. The DNA G+C contents of CNX-216^T and CNU-914^T were respectively 57.7 and 44.4 mol%. Strains CNX-216^T and CNU-914^T contained MK-7 as the predominant menaquinone and iso-$C_{15:0}$ and $C_{16:1}\omega5c$ as the major fatty acids. Phylogenetic analyses revealed that both strains belong to the order *Cytophagales* in the phylum *Bacteroidetes*. Strain CNX-216^T exhibited low 16S rRNA gene sequence identity (87.1 %) to the nearest type strain, *Cesiribacter roseus* 311^T, and formed a well-supported lineage that is outside all currently described families in the order *Cytophagales*. Strain CNU-914^T shared 97.6 % 16S rRNA gene sequence identity with '*Porifericola rhodea*' N5EA6-3A2B and, together with '*Tunicatimonas pelagia*' N5DB8-4 and four uncharacterized marine bacteria isolated as part of this study, formed a lineage that is clearly distinguished from other families in the order *Cytophagales*. Based on our polyphasic taxonomic characterization, we propose that strains CNX-216^T and CNU-914^T represent novel genera and species, for which we propose the names *Mooreia alkaloidigena* gen. nov., sp. nov. (type strain CNX-216^T =DSM 25187^T =KCCM 90102^T) and *Catalinimonas alkaloidigena* gen. nov., sp. nov. (type strain CNU-914^T =DSM 25186^T =KCCM 90101^T) within the new families *Mooreiaceae* fam. nov. and *Catalimonadaceae* fam. nov.

Marine environments harbour remarkable levels of bacterial diversity (Giovannoni *et al.*, 1990), much of which appears to be uniquely marine. The vast majority of this diversity has yet to be cultured (Rappé & Giovannoni, 2003), creating a major void between that which is known to exist and that which has been subjected to systematic evaluation. Among the bacteria frequently observed in marine samples are members of the phylum *Bacteroidetes* (formerly the *Cytophaga–Flavobacteria–Bacteroidetes* group). Members of this phylum are known to colonize marine particles (Gómez-Pereira *et al.*, 2012) and have been reported to play a major role in the degradation of organic matter in marine ecosystems (Kirchman, 2002). While the phylum *Bacteroidetes* has been the subject of considerable taxonomic revision (Gupta, 2004), it is currently comprised of four large classes (*Bacteroidia*, *Cytophagia*, *Flavobacteria* and *Sphingobacteriia*) and corresponding orders (*Bacteroidales*, *Cytophagales*, *Flavobacteriales* and *Sphingobacteriales*) (Ludwig *et al.*, 2010).

Within the phylum *Bacteroidetes*, the order *Cytophagales* includes a morphologically diverse assemblage of unicellular Gram-negative bacteria, many of which display gliding motility (Reichenbach, 2006). Defining characteristics of the order *Cytophagales* include the production of

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains CNX-216^T and CNU-914^T are JN368460 and JN368461.

Two supplementary figures are available with the online version of this paper.

flexirubin-type pigments, starch hydrolysis and the possession of menaquinone 7 (MK-7) (Reichenbach, 2006). As with other members of the phylum *Bacteroidetes*, many of the species in the order *Cytophagales* occur in marine or saline environments. At the time of writing, there are four recognized families within this order (*Cyclobacteriaceae*, *Cytophagaceae*, *Flammeovirgaceae* and *Rhodothermaceae*) and 58 genera (http://www.bacterio.cict.fr/classifphyla.html).

We cultured two alkaloid-producing strains of Gram-negative bacteria from marine sediment samples collected from the remote Pacific island atoll of Palmyra (strain CNX-216^T) and off the Channel Islands, California (strain CNU-914^T). Based on a polyphasic taxonomic analysis, we propose that these two strains represent two novel genera and species within the proposed families *Mooreiaceae* fam. nov. and *Catalimonadaceae* fam. nov. within the order *Cytophagales*.

Marine sediment samples were collected in sterile Whirl-pac bags by divers and dried overnight in a laminar flow hood. Dried sediments were stamped onto P1 agar plates (18.0 g agar, 1 l filtered seawater) using sterile foam plugs as described previously (Jensen *et al.*, 2005) and incubated at room temperature (approx. 25 °C) for 2 months. The amount of sediment added to each plate varied depending on how well it adhered to the foam plug, but was estimated in most cases to be <100 mg. Both strains were subsequently obtained in pure culture by repeated streaking onto medium A1 (10.0 g starch, 4.0 g yeast extract, 2.0 g peptone, 18.0 g agar, 1 l filtered seawater). Each strain was then cultured in liquid A1 medium for 7 days while shaking at 230 r.p.m. (25 °C) and cryopreserved at −80 °C in 20 % (v/v) glycerol.

Both strains were inoculated onto A1 agar, marine agar 2216 (MA; Difco), nutrient agar (Difco), R2A agar (Difco), Czapek–Dox (CD) agar (Difco) and tryptic soy agar (TSA; Mediatech) and incubated at 25 °C for 7 days for morphological studies. The temperature range for growth of strains CNX-216^T and CNU-914^T was examined from 4 to 45 °C (in 5 °C intervals) on these same media. NaCl requirements were examined on A1 medium (using distilled water instead of filtered seawater) containing NaCl at concentrations from 0 to 15 % (w/v) (in 1 % intervals). Growth at pH 1–11 (in 1 pH unit intervals) was tested in marine broth. Gram staining was performed according to established protocols (Gerhardt, 1981). Anaerobic growth was tested for 7 days at 25 °C on A1 agar and MA in an anaerobic jar. Flexirubin-type pigment production and CM-cellulose hydrolysis were determined as described previously (Bernardet *et al.*, 2002). Casein, agar and starch hydrolysis was determined according to established methods (Smibert & Krieg, 1994), as was chitin hydrolysis (Høvik Hansen & Sørheim, 1991). Catalase activity was determined by assessing bubble production in 3 % (v/v) H_2O_2 and oxidase activity was determined using a 1 % (w/v) solution of tetramethyl-*p*-phenylenediamine (Kovács, 1956). Carbohydrate metabolism was investigated using API 50CH test strips (bioMérieux) according to the manufacturer's recommendations. In addition, API 20E, API 20NE and API ZYM kits (bioMérieux) were used to determine additional biochemical properties.

Fatty acid methyl esters were analysed according to the MIDI/Hewlett Packard Microbial Identification System protocols from biomass generated from strains CNX-216^T and CNU-914^T grown on MA plates for 72 h at 25 °C. DNA G+C content was determined by HPLC analysis as described previously (Martin *et al.*, 1997). Isoprenoid quinones were extracted and separated by HPLC as described previously (Bligh & Dyer, 1959; Collins & Jones, 1981). Cell motility and morphology were observed using phase-contrast microscopy and scanning electron microscopy. For electron microscopy, samples were prepared according to standard protocols (Collins *et al.*, 1993).

Chromosomal DNA from strains CNX-216^T and CNU-914^T was isolated using the QIAamp DNA Mini kit (Qiagen). 16S rRNA genes were amplified by PCR using the universal primers 27f and 1492r, purified using the MinElute PCR purification kit (Qiagen) according to the manufacturer's instructions and sequenced on a Perkin-Elmer capillary sequencer (model ABI 3730XL; Applied Biosystems) using the same primers. The sequences were analysed using the BLAST algorithm (Altschul *et al.*, 1990) and a multiple sequence alignment of representative sequences was created using CLUSTAL W version 1.8 (Thompson *et al.*, 1994). Neighbour-joining and maximum-likelihood trees were generated using MEGA5 (Tamura *et al.*, 2011).

Strain CNX-216^T was isolated from a marine sediment sample collected at a depth of 7 m from Penguin Spit, inside the fringing reef at Palmyra Atoll in the Northern Line Islands. This atoll is more than 1600 km from Hawaii and represents one of the most remote shallow-water marine ecosystems on Earth. CNX-216^T is a Gram-negative, aerobic, non-motile, rod-shaped bacterium. It forms dark-orange, rounded colonies on A1 agar and MA at 25 °C and produces umbonate colonies with lobate margins on nutrient agar and R2A agar. It grows well between 20 and 40 °C, with an optimal temperature of 30 °C. The strain did not grow at 4–15 or 45 °C on any media and only grew on nutrient agar and medium R2A at 20–30 °C. No growth was observed on CD agar or TSA at any temperature. Moreover, colonies were detected on medium prepared with 0–8 % NaCl but not at higher NaCl concentrations. Growth of strain CNX-216^T was observed at pH 5–8 but not at pH 1–4 or 9–11.

The 16S rRNA gene sequence of strain CNX-216^T (1424 bp) was analysed using the BLAST algorithm. CNX-216^T shares the closest sequence identity with *Cesiribacter roseus* 311^T (87.1 %) (Liu *et al.*, 2012), *C. andamanensis* AMV16^T (86.8 %) (Srinivas *et al.*, 2011), *Adhaeribacter aerolatus* 6515J-31^T (86.6 %), *A. aerophilus* 6424S-25^T (85.8 %) (Weon *et al.*, 2010) and *Litoribacter ruber* YIM CH208^T (85.7 %) (Tian *et al.*, 2010).

These type strains are members of the families *Flammeovirgaceae* and *Cytophagaceae* in the order *Cytophagales*.

A phylogenetic analysis was performed on the nearly complete 16S rRNA gene sequences of strains CNX-216^T and CNU-914^T. The 71 reference sequences used in the analysis include at least one type strain from each family in the order *Cytophagales*, representative top BLAST matches and four uncharacterized but morphologically similar bacterial strains (CNU-893, CNU-916, CNX-520 and CUA-287) that were isolated from marine sediments using the same methods that yielded strains CNX-216^T and CNU-914^T. Strain CNX-216^T forms a deeply branching sister lineage with CNU-914^T, '*Porifericola rhodea*' N5EA6-3A2B, '*Tunicatimonas pelagia*' N5DB8-4 and the four uncharacterized marine strains (Fig. 1). The most closely related type strains are in the family *Flammeovirgaceae* (*C. roseus* 311^T and *C. andamanensis* AMV16^T); however, the tree clearly places CNX-216^T in a distinct phylogenetic lineage.

Strain CNX-216^T exhibits many different characteristics in comparison with the most closely related type strains (Table 1). It is the only strain to have originated from a marine source, suggesting major habitat differences. Other differences include DNA G+C content and β-galactosidase and α-fucosidase activities. The whole-cell fatty acid composition of strain CNX-216^T was also very different from those of related strains and included at least one unknown (ECL 14.959) that was unique to this strain (Table 2). The major cellular fatty acids were $C_{16:1}\omega5c$ (32.4 %), iso-$C_{15:0}$ (20.0 %), summed feature 4 (anteiso-$C_{17:1}$ B and/or iso-$C_{17:1}$ I; 17.5 %) and iso-$C_{17:0}$ 3-OH (10.3 %). Based on its phylogenetic divergence and distinct characteristics, we propose that strain CNX-216^T belongs to a novel family-level taxonomic group within the phylum *Bacteroidetes*, *Mooreiaceae* fam. nov.

Strain CNU-914^T was isolated from a marine sediment sample collected at a depth of 8 m off Parson's Landing, Catalina Island, CA, USA. It is a Gram-negative, aerobic, motile bacterium that forms short, curved rods and rounded, pink colonies at 20–35 °C on A1 agar and MA. CNU-914^T failed to grow on nutrient agar, R2A agar, CD agar or TSA. The optimal growth temperature was 30 °C, while no growth was observed at 4–15 or 40–45 °C. Colony formation was observed on media prepared with 1–5 % NaCl but not in the absence of NaCl or in 6–15 % NaCl. Growth of strain CNU-914^T was observed at pH 6–8 but not at pH 1–5 or 9–11.

BLAST analysis of the 16S rRNA gene sequence of CNU-914^T (1425 bp) revealed that it was most similar to *Roseivirga spongicola* UST030701-084^T (88.2 % identity) (Lau *et al.*, 2006), *R. ehrenbergii* KMM 6017^T (87.6 %) (Nedashkovskaya *et al.*, 2005a), *R. echinicomitans* KMM 6058^T (87.0 %) (Nedashkovskaya *et al.*, 2005b) and *Fabibacter halotolerans* UST030701-097^T (87.0 %) (Lau *et al.*, 2006). All of these species belong to the family *Flammeovirgaceae* in the phylum *Bacteroidetes*. Closer sequence similarities were observed with strains for which the names '*P. rhodea*' N5EA6-3A2B (97.6 % similarity) and '*T. pelagia*' N5DB8-4 (88.8 %) have been proposed. Phylogenetic analysis placed CNU-914^T in a well-supported clade that includes '*P. rhodea*' N5EA6-3A2B, '*T. pelagia*' N5DB8-4 and the uncharacterized marine strains CNU-287, CNU-893, CNU-916 and CNX-520 (Fig. 1). This clade is sister to the deeply branching CNX-216^T sequence and is made up entirely of marine-derived strains.

Strain CNU-914^T displays a number of subtle differences from related type strains in the family *Flammeovirgaceae*, including a narrower temperature tolerance and slightly higher DNA G+C content (Table 3). With regard to cellular fatty acid composition, strain CNU-914^T possesses many differences, including five unique straight-chain fatty acids and four unique unsaturated fatty acids (Table 4). CNU-914^T also possesses four unknown fatty acids. Strain CNU-914^T, '*P. rhodea*' N5EA6-3A2B and '*T. pelagia*' N5DB8-4, which form a distinct clade in the phylogenetic tree, all contain iso-$C_{15:0}$, $C_{16:1}\omega5c$ and iso-$C_{17:0}$ 3-OH as major fatty acids. The type strains that fall outside of this lineage differ in that they contain iso-$C_{15:1}$ and not $C_{16:1}\omega5c$ as a major fatty acid. Based on its phylogenetic position and distinct characteristics, we propose that strain CNU-914^T belongs to a novel family-level taxonomic group, *Catalimonadaceae* fam. nov.

The proposed family *Catalimonadaceae* fam. nov. currently comprises the genus *Catalinimonas* only; however, the proposed taxa '*Porifericola*' (Yoon *et al.*, 2011b) and '*Tunicatimonas*' (Yoon *et al.*, 2012), as well as a number of uncharacterized strains, fall within this family (Fig. 1). Collectively, the families *Catalimonadaceae* fam. nov. and *Mooreiaceae* fam. nov. split the *Flammeovirgaceae* into two clades. One clade has strong bootstrap support and includes the type strain of the type species of the type genus of the family (*Flammeovirga aprica* NBRC 15941^T), suggesting that the family should be limited to this lineage. The second lineage is not well supported and includes *Roseivirga* and six other genera. This lineage may warrant taxonomic revision.

Despite the phylogenetic and phenotypic differences between strains CNX-216^T and CNU-914^T, they both produce related alkaloid secondary metabolites (results not shown). This is not a unique observation within the phylum *Bacteroidetes*, as the marine gliding bacterium *Rapidithrix thailandica* (Srisukchayakul *et al.*, 2007) and the non-motile species *Ohtaekwangia kribbensis* (Yoon *et al.*, 2011b) have both been reported to produce the alkaloid marinoquinoline A (Okanya *et al.*, 2011; Sangnoi *et al.*, 2008), which is structurally similar to compounds produced by strain CNX-216^T. Remarkably, these alkaloid-producing strains are all marine-derived and belong to as many as three different families within the phylum *Bacteroidetes*, suggesting that the production of these compounds is highly conserved and may represent an adaptation to survival in marine habitats.

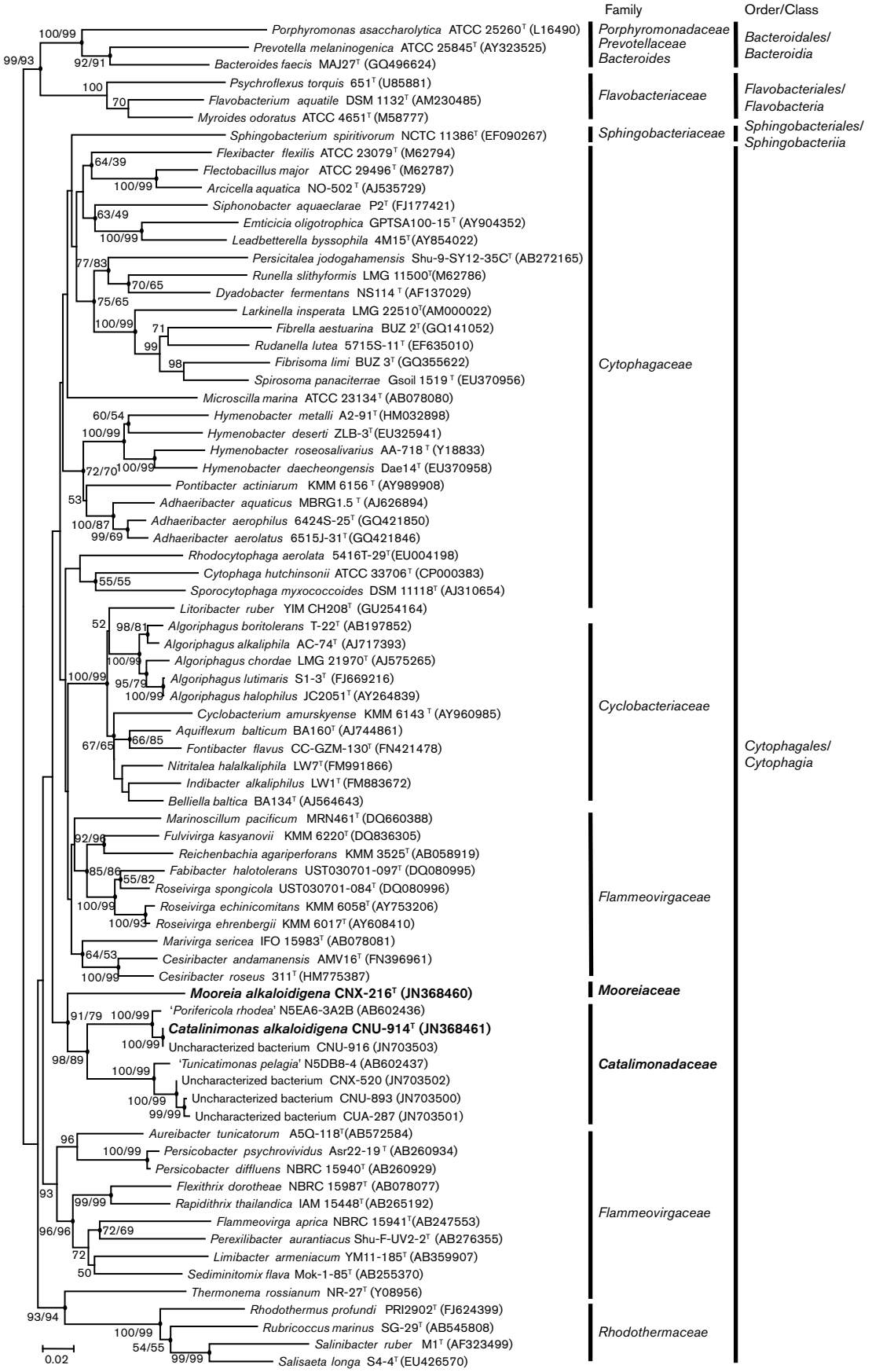
Family
Order/Class
Porphyromonas asaccharolytica ATCC 25260T (L16490)
Prevotella melaninogenica ATCC 25845T (AY323525)
Bacteroides faecis MAJ27T (GQ496624)
Porphyromonadaceae
Prevotellaceae
Bacteroides
Bacteroidales/
Bacteroidia
Psychroflexus torquis 651T (U85881)
Flavobacterium aquatile DSM 1132T (AM230485)
Myroides odoratus ATCC 4651T (M58777)
Flavobacteriaceae
Flavobacteriales/
Flavobacteria
Sphingobacterium spiritivorum NCTC 11386T (EF090267)
Sphingobacteriaceae
Sphingobacteriales/
Sphingobacteriia
Flexibacter flexilis ATCC 23079T (M62794)
Flectobacillus major ATCC 29496T (M62787)
Arcicella aquatica NO-502T (AJ535729)
Siphonobacter aquaeclarae P2T (FJ177421)
Emticicia oligotrophica GPTSA100-15T (AY904352)
Leadbetterella byssophila 4M15T (AY854022)
Persicitalea jodogahamensis Shu-9-SY12-35CT (AB272165)
Runella slithyformis LMG 11500T (M62786)
Dyadobacter fermentans NS114T (AF137029)
Larkinella insperata LMG 22510T (AM000022)
Fibrella aestuarina BUZ 2T (GQ141052)
Rudanella lutea 5715S-11T (EF635010)
Fibrisoma limi BUZ 3T (GQ355622)
Spirosoma panaciterrae Gsoil 1519T (EU370956)
Microscilla marina ATCC 23134T (AB078080)
Cytophagaceae
Hymenobacter metalli A2-91T (HM032898)
Hymenobacter deserti ZLB-3T (EU325941)
Hymenobacter roseosalivarius AA-718T (Y18833)
Hymenobacter daecheongensis Dae14T (EU370958)
Pontibacter actiniarum KMM 6156T (AY989908)
Adhaeribacter aquaticus MBRG1.5T (AJ626894)
Adhaeribacter aerophilus 6424S-25T (GQ421850)
Adhaeribacter aerolatus 6515J-31T (GQ421846)
Rhodocytophaga aerolata 5416T-29T (EU004198)
Cytophaga hutchinsonii ATCC 33706T (CP000383)
Sporocytophaga myxococcoides DSM 11118T (AJ310654)
Litoribacter ruber YIM CH208T (GU254164)
Algoriphagus boritolerans T-22T (AB197852)
Algoriphagus alkaliphila AC-74T (AJ717393)
Algoriphagus chordae LMG 21970T (AJ575265)
Algoriphagus lutimaris S1-3T (FJ669216)
Algoriphagus halophilus JC2051T (AY264839)
Cyclobacterium amurskyense KMM 6143T (AY960985)
Aquiflexum balticum BA160T (AJ744861)
Fontibacter flavus CC-GZM-130T (FN421478)
Nitritalea halalkaliphila LW7T (FM991866)
Indibacter alkaliphilus LW1T (FM883672)
Belliella baltica BA134T (AJ564643)
Cyclobacteriaceae
Cytophagales/
Cytophagia
Marinoscillum pacificum MRN461T (DQ660388)
Fulvivirga kasyanovii KMM 6220T (DQ836305)
Reichenbachia agariperforans KMM 3525T (AB058919)
Fabibacter halotolerans UST030701-097T (DQ080995)
Roseivirga spongicola UST030701-084T (DQ080996)
Roseivirga echinicomitans KMM 6058T (AY753206)
Roseivirga ehrenbergii KMM 6017T (AY608410)
Marivirga sericea IFO 15983T (AB078081)
Cesiribacter andamanensis AMV16T (FN396961)
Cesiribacter roseus 311T (HM775387)
Flammeovirgaceae
Mooreia alkaloidigena CNX-216T (JN368460)
Mooreiaceae
'Porifericola rhodea' N5EA6-3A2B (AB602436)
Catalinimonas alkaloidigena CNU-914T (JN368461)
Uncharacterized bacterium CNU-916 (JN703503)
'Tunicatimonas pelagia' N5DB8-4 (AB602437)
Uncharacterized bacterium CNX-520 (JN703502)
Uncharacterized bacterium CNU-893 (JN703500)
Uncharacterized bacterium CUA-287 (JN703501)
Catalimonadaceae
Aureibacter tunicatorum A5Q-118T (AB572584)
Persicobacter psychrovividus Asr22-19T (AB260934)
Persicobacter diffluens NBRC 15940T (AB260929)
Flexithrix dorotheae NBRC 15987T (AB078077)
Rapidithrix thailandica IAM 15448T (AB265192)
Flammeovirga aprica NBRC 15941T (AB247553)
Perexilibacter aurantiacus Shu-F-UV2-2T (AB276355)
Limibacter armeniacum YM11-185T (AB359907)
Sediminitomix flava Mok-1-85T (AB255370)
Flammeovirgaceae
Thermonema rossianum NR-27T (Y08956)
Rhodothermus profundi PRI2902T (FJ624399)
Rubricoccus marinus SG-29T (AB545808)
Salinibacter ruber M1T (AF323499)
Salisaeta longa S4-4T (EU426570)
Rhodothermaceae
0.02

Fig. 1. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences (1335 bp), showing relationships between strains CNX-216^T and CNU-914^T and representatives from related families in the phylum *Bacteroidetes*. Bootstrap values $\geqslant$50 % (from 1000 replicates) from neighbour-joining/maximum-likelihood analyses are shown at nodes. Filled circles indicate nodes that were observed with both neighbour-joining and maximum-likelihood algorithms. Type strains outside of the *Cytophagales* were used as an outgroup. Bar, 0.02 substitutions per nucleotide position.

Description of *Mooreia* gen. nov.

Mooreia (Moore′i.a. N.L. fem. n. *Mooreia* named after the Gordon and Betty Moore Foundation).

Cells are Gram-negative, aerobic, non-motile and rod-shaped (Fig. S1, available in IJSEM Online). Oxidase and catalase are positive. Nitrate is not reduced. Acid is not produced from glucose fermentation. NaCl is not required for growth. Flexirubin-type pigments are absent. The predominant fatty acids are $C_{16:1}\omega5c$, iso-$C_{15:0}$, summed feature 4 (anteiso-$C_{17:1}$ B and/or iso-$C_{17:1}$ I) and iso-$C_{17:0}$ 3-OH. MK-7 is the predominant respiratory quinone. Phylogenetically, the genus belongs to the family *Mooreiaceae* fam. nov. in the order *Cytophagales*. The type species of the genus is *Mooreia alkaloidigena*.

Description of *Mooreia alkaloidigena* sp. nov.

Mooreia alkaloidigena [al.ka.loi.di′ge.na. N.L. n. *alkaloidum* alkaloid; L. fem. suff. *-gena* (from L. v. *gigno* to produce) producing; N.L. fem. adj. *alkaloidigena* producing alkaloids].

Main characteristics are as given for the genus. In addition, cells are 0.5–0.7 μm wide and 2–3 μm long. Colonies are circular, convex and deep orange on A1 medium, MA, nutrient agar and TSA. On nutrient agar and R2A agar at 20–30 °C, umbonate colonies with a lobate margin are observed. Grows at 20–40 °C with an optimum temperature of 30 °C. The DNA G+C content of the type strain is 57.7 mol%. Tolerates 0–8 % NaCl (w/v) and grows at pH 5–10. Tryptophan deaminase activity is not present. Indole and H_2S are not produced. The Voges–Proskauer reaction is negative. Starch, CM-cellulose, chitin, agar, chitosan, aesculin and gelatin are hydrolysed. Casein is hydrolysed weakly. Alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, α-galactosidase, β-galactosidase, α-glucosidase, *N*-acetyl-β-glucosaminidase and α-fucosidase activities are positive. No activities are detected for lipase (C14), β-glucuronidase, β-glucosidase, α-mannosidase, arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase or urease. Produces acid from D-xylose, D-galactose, D-glucose, D-fructose, D-mannose, methyl α-D-mannopyranoside, methyl α-D-glucopyranoside, *N*-acetylglucosamine, amygdalin, arbutin, aesculin, salicin, cellobiose, maltose, lactose, melibiose, sucrose, trehalose, inulin, melezitose, raffinose, turanose,

Table 1. Characteristics of strain CNX-216^T and related type strains

Strains: 1, CNX-216^T; 2, *C. roseus* 311^T (data from Liu *et al.*, 2012); 3, *C. andamanensis* AMV16^T (Srinivas *et al.*, 2011); 4, *A. aerolatus* 6515J-31^T (Weon *et al.*, 2010); 5, *A. aerophilus* 6424S-25^T (Weon *et al.*, 2010); 6, *L. ruber* YIM CH208^T (Tian *et al.*, 2010). NR, Not reported. Cells of all strains are rods.

Characteristic	1	2	3	4	5	6
Source	Sediment	Desert sand	Volcanic soil	Air	Air	Soda lake
Motility	−	+	−	−	−	−
Ranges for growth						
NaCl (%, w/v)	0–8	0–3	0–5	0–1.5	0–1	0–9
pH	5–8	7–10	6–8	6.5–9.0	6.5–8.5	7.5–10.5
Temperature for growth (°C)						
Range	20–40	4–37	18–37	10–35	10–37	20–37
Optimum	30	30	30–37	NR	NR	28
Nitrate reduction to nitrite	−	+	+	−	−	+
Hydrolysis of:						
Gelatin	+	+	−	+	+	−
Starch	+	+	−	+	+	+
DNA G+C content (mol%)	57.7	47.1	50.9	43.9	44.5	45.1
Major quinone	MK-7	MK-7	MK-4	MK-7	MK-7	MK-7
Enzyme activities						
β-Galactosidase	+	−	NR	−	−	−
α-Fucosidase	+	−	NR	−	−	−

Table 2. Cellular fatty acid profiles of strain CNX-216^T and related strains

Strains: 1, CNX-216^T; 2, *C. roseus* 311^T (data from Liu *et al.*, 2012); 3, *C. andamanensis* AMV16^T (Srinivas *et al.*, 2011); 4, *A. aerolatus* 6515J-31^T (Weon *et al.*, 2010); 5, *A. aerophilus* 6424S-25^T (Weon *et al.*, 2010); 6, *L. ruber* YIM CH208^T (Tian *et al.*, 2010). Values are percentages of the total fatty acids. −, Not detected/no data reported; tr, trace (<1 %).

Fatty acid	1	2	3	4	5	6
Straight						
$C_{12:0}$	−	−	7.0	−	−	−
$C_{14:0}$	0.5	−	−	−	−	−
$C_{16:0}$	0.5	3.7	2.6	1.8	1.7	1.8
$C_{18:0}$	0.2	3.7	−	−	−	−
Branched						
iso-$C_{13:0}$	−	tr	−	−	−	−
iso-$C_{15:0}$	20.0	21.9	14.4	15.0	19.1	−
iso-$C_{16:0}$	0.4	−	−	−	0.3	1.7
iso-$C_{17:0}$	2.0	3.2	−	1.6	1.8	2.5
iso-$C_{18:0}$	0.2	−	−	−	−	−
iso-$C_{19:0}$	−	−	9.7	−	−	−
iso-$C_{15:1}$	−	4.0	−	−	−	−
iso-$C_{15:1}$ G	−	−	15.9	−	−	3.0
iso-$C_{16:1}$ G	−	−	11.1	−	−	−
iso-$C_{16:1}$ H	−	−	−	0.4*	0.4*	1.7
iso-$C_{17:1}\omega9c$	−	−	−	0.6	−	19.9
anteiso-$C_{11:0}$	−	−	5.4	−	−	−
anteiso-$C_{12:0}$	−	−	4.1	−	−	−
anteiso-$C_{15:0}$	0.2	−	3.4	1.3	1.3	4.7
anteiso-$C_{16:0}$	−	−	3.0	−	−	−
anteiso-$C_{17:0}$	0.6	−	3.7	0.4	0.6	−
Unsaturated						
$C_{13:1}$	−	−	13.8	−	−	−
$C_{15:1}\omega6c$	−	−	−	−	0.7	3.1
$C_{16:1}\omega5c$	32.4	29.9	−	17.4	11.3	6.5
$C_{17:1}\omega6c$	1.6	−	−	1.3	3.6	8.7
$C_{17:1}\omega8c$	−	−	−	−	−	1.6
$C_{18:1}\omega7c$	−	1.2	−	−	−	−
$C_{18:1}\omega8c$	−	−	−	0.6	−	−
$C_{18:1}\omega9c$	−	1.3	−	−	−	−
Hydroxy						
$C_{15:0}$ 3-OH	−	−	−	−	−	12.1
$C_{16:0}$ 2-OH	−	−	−	0.4	−	−
$C_{16:0}$ 3-OH	0.4	−	−	0.3	−	0.8
$C_{17:0}$ 2-OH	−	−	−	−	−	0.4
$C_{17:0}$ 3-OH	0.4	−	−	−	−	−
iso-$C_{13:0}$ 3-OH	−	1.1	−	−	−	−
iso-$C_{15:0}$ 3-OH	1.7	3.1	−	2.9	2.9	4.1
iso-$C_{16:0}$ 3-OH	0.5	−	−	0.5	0.6	0.5
iso-$C_{17:0}$ 3-OH	10.3	13.3	−	6.2	8.7	11.3
Unknown						
ECL 11.543	0.2	−	−	0.8	0.6	−
ECL 13.565	2.4	−	−	3.6	3.3	−
ECL 14.959	3.0	−	−	−	−	−
ECL 16.582	1.4	−	−	0.7	0.8	−
ECL 18.814	−	−	−	−	0.3	−
Summed features†						
1	−	−	−	0.4	0.6	−
2	0.1	−	−	−	−	−
3	0.5	1.2	−	14.2	8.4	10.7
4	17.5	13.0	−	29.9	33.1	−
5	3.2	−	5.9	−	−	−

*Cited as 'iso-$C_{16:0}$ H' by Weon *et al.* (2010). This may be a typographical error.

†Summed features represent groups of two or three fatty acids that could not be separated by GLC with the MIDI system. Summed feature 1 contains $C_{13:0}$ 3-OH and/or iso-$C_{15:1}$ H; summed feature 2 contains $C_{14:0}$ 3-OH and/or iso-$C_{16:1}$ I; summed feature 3 contains $C_{16:1}\omega7c$ and/or iso-$C_{15:0}$ 2-OH; summed feature 4 contains anteiso-$C_{17:1}$ B and/or iso-$C_{17:1}$ I; summed feature 5 contains anteiso-$C_{18:0}$ and/or $C_{18:2}\omega6,9c$.

D-lyxose, D-tagatose and D- and L-fucose. A positive reaction is observed for β-galactosidase (substrate 4-nitrophenyl β-D-galactopyranoside) and negative reactions are observed for glucose fermentation, arginine dihydrolase and urease in API 20NE test strips. Does not assimilate D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetylglucosamine, maltose, potassium gluconate, capric acid, adipic acid, malic acid, trisodium citrate or phenylacetic acid. API 20E tests show positive reactions for β-galactosidase (substrate 2-nitrophenyl β-D-galactopyranoside) and negative reactions for arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, citrate utilization and oxidation of mannitol, inositol, sorbitol and rhamnose. Based on API 50CH and API 20NE tests, unable to utilize the following carbon sources for growth or acid production: glycerol, erythritol, D- and L-arabinose, D-ribose, L-xylose, D-adonitol, methyl β-D-xylopyranoside, D-glucose, L-sorbose, L-rhamnose, dulcitol, inositol, D-mannitol, D-sorbitol, starch, glycogen, xylitol, gentiobiose, D- and L-arabitol, potassium gluconate and potassium 2- and 5-ketogluconate.

The type strain, CNX-216^T (=DSM 25187^T =KCCM 90102^T), was isolated from a marine sediment sample collected at the Palmyra Atoll in the Northern Line Islands in the US Minor Outlying Islands.

Description of *Mooreiaceae* fam. nov.

Mooreiaceae (Moore.i.a.ce′a.e. N.L. fem. n. *Mooreia* type genus of the family; suff. *-aceae* ending to denote a family; N.L. fem. pl. n. *Mooreiaceae* the family of the genus *Mooreia*).

Falls is within the order *Cytophagales* and encompasses Gram-negative bacteria retrieved from marine samples.

Table 3. Characteristics of strain CNU-914^T and related strains

Strains: 1, CNU-914^T; 2, '*P. rhodea*' N5EA6-3A2B (data from Yoon *et al.*, 2011a); 3, '*T. pelagia*' N5DB8-4 (Yoon *et al.*, 2012); 4, *R. spongicola* UST030701-084^T (Lau *et al.*, 2006); 5, *R. ehrenbergii* KMM 6017^T (Nedashkovskaya *et al.*, 2005a); 6, *R. echinicomitans* KMM 6058^T (Nedashkovskaya *et al.*, 2005b); 7, *F. halotolerans* UST030701-097^T (Lau *et al.*, 2006). (+), Weakly positive; NR, not reported. All strains contain MK-7 as the major quinone, are positive for catalase and are negative for hydrolysis of agar.

Characteristic	1	2	3	4	5	6	7
Source	Sediment	Sponge	Sea anemone	Sponge	Sea water	Sea urchin	Sponge
Pigmentation	Pink	Red/pink	Red/pink	Pink	Orange	Pink	Pink
Cell morphology	Short curved rods	Straight rods	Straight rods	Straight rods	Rods	Rods	Short curved rods
Gliding motility	+	−	−	+	+	−	+
Ranges for growth							
Temperature (°C)	20–35	15–37	20–37	12–44	4–40	4–31	12–36
NaCl (%, w/v)	1–5	1–10	1–8	0–16	5.5–8	4–8	0–12
pH	6–8	6–9	6–10	5–10	5.5–8	NR	5–10
Flexirubin	−	−	−	−	+	−	−
Nitrate reduction	−	−	−	−	−	+	−
Oxidase	+	−	−	+	+	+	+
Hydrolysis of:							
Gelatin	−	+	−	+	−	+	−
Starch	−	−	−	−	−	−	(+)
DNA G+C content (mol%)	44.4	43.0	52.6	43.7	40.3	41.3	42.5

Currently, the family comprises only the genus *Mooreia*. The delineation of the family is determined primarily from the phylogenetic position of the 16S rRNA gene sequence. The detailed description is the same as that given for the genus *Mooreia*. The type genus of the family is *Mooreia*.

Description of *Catalinimonas* gen. nov.

Catalinimonas (Ca.ta.li.ni.mo′nas. N.L. n. *Catalina* Catalina Island in the Channel Islands, CA, USA; L. fem. n. *monas* a unit, monad; *Catalinimonas* a monad from Catalina Island, referring to the isolation of the type strain of the type species).

Cells are Gram-negative, aerobic, motile, short, curved rods (Fig. S2). Oxidase and catalase are positive. NaCl is required for growth. Nitrate is not reduced. Acid is produced (weakly) from glucose fermentation. Flexirubin-type pigments are absent. The major respiratory quinone is MK-7. The predominant fatty acids are iso-$C_{15:0}$, $C_{16:1}\omega5c$ and iso-$C_{17:0}$ 3-OH. The type species is *Catalinimonas alkaloidigena*.

Description of *Catalinimonas alkaloidigena* sp. nov.

Catalinimonas alkaloidigena [al.ka.loi.di.ge′na. N.L. n. *alkaloidum* alkaloid; L. fem. suff. *-gena* (from L. v. *gigno* to produce) producing; N.L. fem. adj. *alkaloidigena* producing alkaloids].

Main characteristics are as given for the genus. The DNA G+C content of the type strain is 44.4 mol%. Pink-pigmented colonies are formed on A1 medium and MA. Growth is observed at 15–30 °C and is optimal at 25 °C. Growth is not observed at 4–15, 40 or 45 °C. No growth is detected at NaCl concentrations higher than 9 % (w/v). Grows at pH 5–10 but not at pH 4. Arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase and tryptophan deaminase activities are not present. H_2S, urease, indole and acetone are not produced. Aesculin is hydrolysed but starch, casein, agar, chitin, chitosan, CM-cellulose and gelatin are not hydrolysed. API ZYM assays reveal activities of alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase and *N*-acetyl-β-glucosaminidase. Lipase (C14), trypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, α-mannosidase and α-fucosidase activities are not detected in API ZYM tests. In API 50CH test strips, acid is produced from D-mannose, inositol, aesculin and D-glucose (weakly). In API 20NE test strips, positive reactions are observed for β-glucosidase hydrolysis and β-galactosidase (substrate 4-nitrophenyl β-D-galactopyranoside). Assimilates L-arabinose, D-mannose, *N*-acetylglucosamine, maltose, potassium gluconate, trisodium citrate and phenylacetic acid but not D-glucose, D-mannitol, capric acid, adipic acid or malic acid. In API 20E tests, a positive reaction is detected for gelatinase and negative reactions are detected for β-galactosidase, citrate utilization and oxidation of mannitol, inositol, sorbitol, rhamnose and arabinose. Based on API 50CH and API

Table 4. Cellular fatty acid profiles for strain CNU-914^T and related strains

Strains: 1, CNU-914^T; 2, '*P. rhodea*' N5EA6-3A2B (data from Yoon *et al.*, 2011a); 3, '*T. pelagia*' N5DB8-4 (Yoon *et al.*, 2012); 4, *R. spongicola* UST030701-084^T (Lau *et al.*, 2006); 5, *R. ehrenbergii* KMM 6017^T (Nedashkovskaya *et al.*, 2005a); 6, *R. echinicomitans* KMM 6058^T (Nedashkovskaya *et al.*, 2005b); 7, *F. halotolerans* UST030701-097^T (Lau *et al.*, 2006). Values are percentages of total fatty acids. NR, Not recorded; −, not detected; tr, trace (<1 %).

Fatty acid	1	2	3	4	5	6	7
Straight							
$C_{12:0}$	0.03	NR	NR	−	NR	NR	−
$C_{14:0}$	0.5	NR	NR	−	NR	NR	−
$C_{15:0}$	1.2	NR	NR	−	1.1	NR	−
$C_{16:0}$	1.0	NR	NR	−	NR	NR	−
$C_{17:0}$	0.6	NR	NR	−	NR	NR	−
$C_{18:0}$	0.3	NR	NR	−	NR	NR	−
Branched							
iso-$C_{13:0}$	0.1	NR	9.8	0.7	5.2	2.9	1.6
iso-$C_{14:0}$	−	1.0	tr	−	NR	1.9	4.7
iso-$C_{15:0}$	26.8	34.4	24.5	18.6	33.5	20.2	18.3
iso-$C_{16:0}$	0.4	1.2	−	2.0	1.2	1.8	1.2
iso-$C_{17:0}$	0.6	NR	NR	−	NR	1.0	0.5
iso-$C_{15:1}$	−	NR	NR	12.5	20.5	20.2	14.2
iso-$C_{16:1}$	−	NR	NR	−	NR	2.0	1.2
iso-$C_{15:1}$ G	5.8	4.9	11.3	−	NR	NR	−
iso-$C_{16:1}$ G	0.1	NR	NR	−	NR	NR	−
iso-$C_{17:1}\omega 9c$	−	NR	NR	10.8	NR	1.1	−
anteiso-$C_{15:0}$	5.2	7.4	−	12.5	2.4	13.1	2.5
anteiso-$C_{15:1}$	−	NR	NR	−	NR	2.4	0.8
anteiso-$C_{17:0}$	0.2	NR	NR	−	NR	NR	−
Unsaturated							
$C_{13:1}$ at 12–13	0.2	NR	NR	−	NR	NR	−
$C_{14:1}\omega 5c$	0.1	NR	NR	−	NR	NR	−
$C_{15:1}\omega 8c$	0.2	NR	NR	−	NR	NR	−
$C_{16:1}\omega 5c$	22.6	17.5	21.3	−	NR	NR	−
$C_{17:1}\omega 6c$	1.2	NR	NR	−	NR	NR	−
Hydroxy							
$C_{12:0}$ 2-OH	0.1	NR	NR	−	NR	NR	−
$C_{15:0}$ 2-OH	0.7	NR	NR	3.2	NR	NR	1.9
$C_{15:0}$ 3-OH	−	NR	NR	−	NR	NR	1.3
$C_{16:0}$ 3-OH	1.8	1.9	3.2	−	1.8	1.4	1.2
$C_{17:0}$ 2-OH	0.5	NR	NR	10.1	NR	2.0	1.3
$C_{17:0}$ 3-OH	0.4	NR	NR	−	NR	NR	−
iso-$C_{14:0}$ 3-OH	0.2	NR	NR	−	NR	NR	1.1
iso-$C_{15:0}$ 3-OH	4.4	3.4	5.1	4.9	5.6	4.1	12.5
iso-$C_{16:0}$ 3-OH	0.4	1.0	−	1.2	7.2	4.2	12.7
iso-$C_{17:0}$ 3-OH	12.0	12.4	9.8	18.3	11.2	12.1	9.3
Unknown							
ECL 11.543	0.3	NR	NR	−	NR	NR	−
ECL 13.565	1.4	NR	NR	−	NR	NR	−
ECL 14.959	5.6	NR	NR	−	NR	NR	−
ECL 16.582	1.2	NR	NR	−	NR	NR	−
Unidentified						5.3	
Summed features*							
2	0.4	NR	NR	−	NR	NR	−
3	2.4	2.7	5.3	5.5	4.8	1.0	13.7
4	1.2	1.2	−	−	NR	NR	−
5	0.1	NR	NR	−	NR	NR	−

*Summed features represent groups of two or three fatty acids that could not be separated by GLC with the MIDI system. Summed feature 2 contains $C_{14:0}$ 3-OH and/or iso-$C_{16:1}$ I; summed feature 3 contains $C_{16:1}\omega 7c$ and/or iso-$C_{15:0}$ 2-OH; summed feature 4 contains anteiso-$C_{17:1}$ B and/or iso-$C_{17:1}$ I; summed feature 5 contains anteiso-$C_{18:0}$ and/or $C_{18:2}\omega 6,9c$.

20NE test results, unable to utilize the following carbon sources for growth or acid production: glycerol, erythritol, D- and L-arabinose, D-ribose, D- and L-xylose, D-adonitol, methyl β-D-xylopyranoside, D-galactose, D-fructose, L-sorbose, L-rhamnose, dulcitol, D-mannitol, D-sorbitol, methyl α-D-mannopyranoside, methyl α-D-glucopyranoside, *N*-acetylglucosamine, amygdalin, arbutin, salicin, cellobiose, maltose, lactose, melibiose, sucrose, trehalose, inulin, melezitose, raffinose, starch, glycogen, xylitol, gentiobiose, turanose, D-lyxose, D-tagatose, D- and L-fucose, D- and L-arabitol, potassium gluconate and potassium 2- and 5-ketogluconate.

The type strain is CNU-914^T (=DSM 25186^T =KCCM 90101^T), isolated from a marine sediment sample collected off Catalina Island in the Channel Islands, CA, USA.

Description of *Catalimonadaceae* fam. nov.

Catalimonadaceae (Ca.ta.li.mo.na.da.ce′a.e. N.L. fem. n. *Catalinimonas* type genus of the family; suff. *-aceae* ending to denote a family; N.L. fem. pl. n. *Catalimonadaceae* the family of the genus *Catalinimonas*.

Falls within the order *Cytophagales* and encompasses a group of Gram-negative marine bacteria that until quite recently had only been observed in culture-independent studies. The delineation of the family is primarily recognized by 16S rRNA gene sequence phylogeny, which reveals a deeply branching and well-supported clade that is sister to the proposed family *Mooreiaceae*. The detailed description of the family *Catalimonadaceae* is the same as that given for the genus *Catalinimonas*. The type genus of the family is *Catalinimonas*.

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