**Corynebacterium phoceense** sp. nov., strain MC1<sup>T</sup> a new bacterial species isolated from human urine

M. Cresci<sup>1</sup>, C. Ibrahima Lo<sup>3</sup>, S. Khelafia<sup>1</sup>, D. Mouelhi<sup>1</sup>, J. Delerce<sup>1</sup>, F. Di Pinto<sup>1</sup>, C. Michelle<sup>1</sup>, P.-E. Fournier<sup>1</sup>, D. Raoult<sup>1</sup>, J.-C. Lagier<sup>1</sup> and V. Moal<sup>2</sup>

1) URMITE, UM63 CNRS 7278 IRD 198, Aix-Marseille Université, 2) Centre de Néphrologie et Transplantation Rénale, Assistance Publique, Hôpitaux de Marseille, Marseille and 3) Campus commun IRD-UCAD de Hann, France

Abstract

*Corynebacterium phoceense* strain MC1 (= CSUR P1905 = DSM 100570) is a novel *Corynebacterium* species isolated from the urine of a kidney transplant recipient as a part of a culturomics study. *Corynebacterium phoceense* is a Gram-positive, sporogenous, strictly aerobic, and nonmotile coccobacillus. Here we describe strain MC1 and provide its complete annotated genome sequence according to the taxonogenomics concept. Its genome is 2 793 568 bp long and contains 2575 protein-coding genes and 67 RNA genes, including eight rRNA genes.

© 2016 The Authors. Published by Elsevier Ltd on behalf of European Society of Clinical Microbiology and Infectious Diseases.

Keywords: *Corynebacterium phoceense*, culturomics, human urine, kidney transplant recipient, taxonogenomics

Original Submission: 26 July 2016; Accepted: 1 September 2016

Article published online: 13 September 2016

**Corresponding author:** V. Moal, Centre de Néphrologie et Transplantation Rénale, Assistance Publique, Hôpitaux de Marseille, Marseille, France

**E-mail:** valerie.moal@ap-hm.fr

The first two authors contributed equally to this article, and both should be considered first author.

Introduction

The genus *Corynebacterium* was described in 1896 by Lehmann and Neumann and belongs to the Actinobacteria class [1]. Currently it consists of a heterogeneous group of Gram-positive, non-spore-forming, rod-shaped bacteria with a high DNA G+C content [2]. In the genus *Corynebacterium* many species are involved in human and animal diseases, whereas many others are normal flora on skin and mucous membranes [3–5]. Corynebacteria are found in different environments such as water, soil, plants and human samples [6–10]. Among corynebacteria, the most significant human pathogen is *Corynebacterium diphtheriae*, which causes diphtheria worldwide [11]. However, most corynebacteria are opportunistic pathogens [6]. Bacteria found in urine are occasionally associated with urinary infection [12,13].

Currently bacterial classification is focused on a polyphasic approach with phenotypic and genotypic characteristics such as DNA-DNA hybridization, G+C content and 16S rRNA sequence similarity [14–16]. This classification system has its limitations, such as the high cost of the DNA-DNA hybridization technique and its low reproducibility [14,17]. A new bacterial description concept was developed in our laboratory [18–22] with the recent development of genome sequencing technology [23]. This concept, taxonogenomics [24], is a combination of proteomic description and matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS) profile [25] associated with a phenotypic description and the sequencing, annotation and comparison of the complete genome of the new bacteria species [26].

Here we describe *Corynebacterium phoceense* sp. nov., strain MC1 (= CSUR P1905 = DSM 100570), according the taxonogenomics concept.

Material and methods

Organism information

*Corynebacterium phoceense* was isolated from culture of a midstream urine specimen from a 25-year-old kidney transplant recipient.
recipient from Comoros. He underwent transplantation to treat faecal and segmental glomerulosclerosis in Marseille, France. A urine sample was collected 2 years after his kidney transplantation without clinical signs of urinary tract infection. The patient did not receive antibiotics at the time of urine collection. Informed consent was obtained from the patient, and the study was approved by the Institut Fédératif de Recherche 48, Faculty of Medicine, Marseille, France, under agreement 09-022.

Strain identification by MALDI-TOF MS and 16S rRNA sequencing

Among the 18 culture conditions previously selected by culturomics [27], strain MCI grew on sheep’s blood–enriched Colombia agar (bioMérieux, Marcy l’Etoile, France). The colonies were obtained by spreading samples on a solid medium. They were then purified by subculture and identified by MALDI-TOF MS [28,29]. Colonies were deposited in duplicate on a MTP 96 MALDI-TOF MS target plate (Bruker Daltonics, Leipzig, Germany), which was analysed with a Microflex spectrometer (Bruker). The 12 spectra obtained were matched against the references of the 7567 bacteria contained in the MALDI BioTyper database by standard pattern matching (with default parameter settings, with MALDI BioTyper database software 2.0 (Bruker). An identification score over 1.9 with a validated species allows identification at the species level, and a score under 1.7 does not enable any identification. When identification by MALDI-TOF MS failed, the 16S rRNA was sequenced [30]. Stackebrandt and Ebers [31] suggest similarity levels of 98.7% with the 16S rRNA sequence as a threshold to define a new species without performing DNA-DNA hybridization.

Growth conditions

To establish our strain’s optimal growth conditions, different temperatures (25, 28, 37, 45 and 56°C) and atmospheres (aerobic, microaerophilic and anaerobic) were tested. GENbag anaer and GENbag microaer systems (bioMérieux) were used respectively to test anaerobic and microaerophilic growth. Aerobic growth was carried out with and without 5% CO₂.

Morphologic, biochemical and antibiotic susceptibility testing

Gram staining, motility, catalase, oxidase and sporulation were tested as previously described [27]. To perform a biochemical description, according to the manufacturer’s instructions, we use API Coryne (bioMérieux) to identify coryneforms, API ZYM (bioMérieux) to search enzymatic activities and API 50CH (bioMérieux) to estimate capacity to ferment different carbohydrates. Cellular fatty acid methyl ester (FAME) analysis was performed by gas chromatography/mass spectrometry (GC/MS). Two samples were prepared with approximately 60 mg of bacterial biomass per tube collected from several culture plates. FAMEs were prepared as previously described (http://www.midi-inc.com/pdf/MIS_Technote_101.pdf), and GC/MS analyses were carried out as previously described [32]. Briefly, FAMEs were separated using an Elite 5-MS column and monitored by mass spectrometry (Clarus 500-SQ 8 S; Perkin Elmer, Courtaboeuf, France). A spectral database search was performed using MS Search 2.0 operated with the Standard Reference Database IA (NIST, Gaithersburg, MD, USA) and the FAMEs mass spectral database (Wiley, Chichester, UK).

Antibiotic susceptibility testing was performed using the disk diffusion method according to the European Committee on Antimicrobial Susceptibility Testing (EUCAST) 2015 recommendations (http://www.eucast.org/). Corynebacterium phoceense resistance and susceptibility are estimated with 22 antibiotic treatments (vancomycin 30 μg, rifampicin 30 μg, doxycycline 30 IU, erythromycin 15 IU, amoxicillin 25 μg, nitrofurantoin 300 μg, gentamicin 15 μg, ciprofloxacin 5 μg, ceftriaxone 30 μg, amoxicillin 20 μg + clavulanic acid 10 μg, penicillin G 10 μg, gentamicin 500 μg, trimethoprim 1.25 μg + sulfamethoxazole 23.75 μg, oxacillin 5 μg, imipenem 10 μg, tobramycin 10 g, metronidazole 4 μg, amikacin 30 μg, linezolid 30 μg, clindamycin 15 μg, daptomycin in stripe 0.016–256 μg (bioMérieux) and chloramphenicol 5 mg, (Sigma-Aldrich, St. Louis, MO, USA)). The bacterial suspension (0.5 McFarland standard) is made in 2 mL NaCl 0.85% medium. Petri dishes with Mueller-Hinton + 5% sheep’s blood (Becton Dickinson, San Diego, CA, USA) are seeded by swabbing with bacteria suspension. Different antibiotic dishes (SirScan) are dispensed on petri dishes. Electron microscopy figure was obtained by performing a negative staining of strain MCI. Detection Formvar-coated grids were deposited on a 40 μL bacterial suspension drop, then incubated at 37°C for 30 minutes and on ammonium molybdate 1% for 10 seconds. The dried grids on

| Property                  | Term                          |
|---------------------------|-------------------------------|
| Domain                    | Bacteria                      |
| Phylum                    | Actinobacteria                |
| Class                     | Actinobacteria                |
| Order                     | Actinomycetales               |
| Family                    | Corynebacteriaceae            |
| Genus                     | Corynebacterium               |
| Species                   | Corynebacterium phoceense     |
| Type strain               | MCI                           |
| Gram stain                | Positive                      |
| Cell shape                | Rod                           |
| Motility                  | Nonmotile                     |
| Sporulation               | Non–spore forming             |
| Temperature range         | Mesophilic                    |
| Optimum temperature       | 37°C                          |
blotted paper were observed with a Tecnai G20 transmission electron microscope (FEI Company, Limel-Brevannes, France).

**Growth conditions and genomic DNA preparation**

*Corynebacterium phoceense* strain MC1 (= CSUR P1905 = DSM 100570) was grown on 5% sheep’s blood–enriched Columbia agar (bioMérieux) at 37°C in aerobic atmosphere. Bacteria grown on three petri dishes were collected and resuspended in 4 × 100 μL of Tris-EDTA (TE) buffer. Then 200 μL of this suspension was diluted in 1 mL TE buffer for lysis treatment that included a 30-minute incubation with 2.5 μg/μL lysozyme at 37°C, followed by an overnight incubation with 20 μg/μL

**FIG. 1.** Phylogenetic trees highlighting position of *Corynebacterium phoceense* strain MC1 (=CSUR P1905 = DSM 100570) relative to other strains within genus *Corynebacterium*. Sequences of 16S rRNA gene (A) and rpoB genes (B) were aligned by CLUSTALW. Scale bar represents 1 and 2% nucleotide sequence divergence for (A) and (B) respectively.

**FIG. 2.** Reference mass spectrum from *Corynebacterium phoceense* strain MC1. Spectra from 12 individual colonies were compared and reference spectrum was generated.
proteinase K at 37°C. Extracted DNA was then purified using three successive phenol–chloroform extractions and ethanol precipitations at −20°C overnight. After centrifugation, the DNA was resuspended in 160 μL TE buffer.

Genome sequencing and assembly
Genomic DNA (gDNA) of Corynebacterium phoceense was sequenced on the MiSeq Technology (Illumina, San Diego, CA, USA) with the mate pair strategy. The gDNA was barcoded in order to be mixed with nine other projects with the Nextera Mate Pair sample prep kit (Illumina).

gDNA was quantified by a Qubit assay with the high sensitivity kit (Life Technologies, Carlsbad, CA, USA) to 59.1 ng/μL.

The mate pair library was prepared with 1.5 μg of genomic DNA using the Nextera mate pair Illumina guide. The genomic DNA sample was simultaneously fragmented and tagged with a mate pair junction adapter. The fragmentation pattern was validated on an Agilent 2100 BioAnalyzer (Agilent Technologies, Santa Clara, CA, USA) with a DNA 7500 lab chip. The DNA fragments ranged in size from 1.5 to 11 kb, with an

FIG. 3. Gel view comparing Corynebacterium phoceense strain MC1 (= CSUR P1905 = DSM 100570) to other species within Corynebacteriaceae family. Gel view displays raw spectra of loaded spectrum files arranged in pseudo-gel-like look. x-axis records m/z value. Left y-axis displays running spectrum number originating from subsequent spectra loading. Peak intensity is expressed by greyscale scheme code. Colour bar and right y-axis indicate relation between peak colour displayed and peak intensity in arbitrary units. Displayed species are indicated at left.

FIG. 4. Gram staining of Corynebacterium phoceense strain MC1.

FIG. 5. Transmission electron microscopy of Corynebacterium phoceense strain MC1 with Morgani 268D (Philips, Amsterdam, the Netherlands) at operating voltage of 60 kV. Scale bar = 500 nm.
Differential characteristics of *Corynebacterium phoceense* strain CECT 4843T, *Corynebacterium freiburgense* strain 1045T, *Corynebacterium mastitidis* strain CECT 4843T, *Corynebacterium terpenotabidum* strain Y-1T, *Corynebacterium lactis* strain RW2-5T, *Corynebacterium aurimucosum* strain IMMIB D-1488T and *Corynebacterium mustelae* strain 3105T [41–46]
ORFome genome sequence were retrieved from the National Center for Biotechnology Information FTP site. All proteomes were analysed with proteinOrtho [38]. Then for each couple of genomes a similarity score was computed. This score is the mean value of nucleotide similarity between all orthologue couples between the two genomes studied (AGIOS) [26].

The entire proteome was annotated to define the distribution of functional classes of predicted genes according to the clusters of orthologous protein groups (using the same method as for the genome annotation). To evaluate the genomic similarity among the compared strains, we determined two parameters: digital DNA-DNA hybridization, which exhibits a high correlation with DNA-DNA hybridization (DDH) [39,40], and AGIOS [26], which was designed to be independent from DDH.

Results

Strain identification and phylogenetic analyses

Strain MC1 (Table 1) was first isolated in February 2015 by spreading a urine sample on 5% sheep’s blood–enriched Colombia agar (bioMérieux) in an aerobic atmosphere at 37°C after 48 hours of incubation.

Using MALDI-TOF MS for identification, no significant score was obtained for strain MC1, suggesting that this isolate’s spectrum did not match any spectra in our MALDI-TOF MS database. The nucleotide sequences of the 16S rRNA and the rpoB genes of strain MC1 (GenBank accession nos. LN849777 and LN849778 respectively) showed 96.3% similarity with Corynebacterium simulans, the phylogenetically closest species with a validly published name (Fig. 1), therefore defining it as a new species within the...
genus *Corynebacterium*. *C. phoceense* spectra (Fig. 2) were incremented in our database. The reference spectrum for *C. phoceense* was then compared to the spectra of phylogenetically close species within the genus *Corynebacterium*, and the differences were exhibited in a gel view photo (Fig. 3).

### Phenotypic description

Growth was observed from 25 to 56°C on 5% sheep's blood–enriched Columbia agar (bioMérieux), with optimal growth at 37°C in aerobic conditions after 48 hours of incubation.

Weak cell growth was observed under microaerophilic and anaerobic conditions. The motility test was negative, and after thermal shock, we observed bacterial growth, which means *Corynebacterium phoceense* is sporogenous. Cells were Gram-positive cocccobacillus (Fig. 4). On Columbia blood agar, colonies are circular with entire margin, up to 1.0 mm in diameter after 48 hours' growth at 37°C. Under electron microscopy, cells had a mean diameter of 0.5 μm and a length of 3 μm (Fig. 5).

The major fatty acids were 9-octadecenoic acid (51%) and hexadecanoic acid (46%). The other fatty acids described were below 3% (Table 2).

The presence of catalase was tested using 3% (v/v) H2O2 and gave a positive result. The oxidase test was also negative for strain MC1. *Corynebacterium phoceense* strain MC1 was capable of fermenting glucose, ribose, maltose, saccharose, β-rubisco, D-galactose, D-glucose, D-fructose, D-mannose, arbutin, ferric citrate esculin, D-maltose and D-saccharose. Nitrates were reduced into nitrites. Alkaline phosphatase, esterase (C4), esterase lipase (CB), leucine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, β-glucosidase, pyrazinamidase, pyrrolidonyl arylamidase and naphthol-AS-BI-phosphohydrolase activities were highlighted.

*Corynebacterium phoceense* strain MC1 was susceptible to all antibiotic treatments tested except nitrofurantoin and metronidazole, to which it was resistant.

The biochemical and phenotypic features of strain MC1 were compared to the corresponding features of other close representatives of the genus *Corynebacterium* (Table 3). We particularly observed the absence of endospores forming in the closest *Corynebacterium* spp.

### Genome properties

The genome is 2,793,868 bp long with 63.23% GC content (Table 4, Fig. 6). It is composed of 14 scaffolds (composed of 71 contigs). Of the 2575 predicted genes, 2508 were protein-coding genes and 67 were RNAs (four genes are 5s rRNA, three genes are 16s rRNA, three genes are 23s rRNA and 57 genes are tRNA genes). A total of 1804 genes (71.93%) were assigned as putative function (by COGs or by NR BLAST). One hundred fifty-one genes were identified as ORFans (6.02%). The remaining 475 genes were annotated as hypothetical proteins (18.94%). The National Center for Biotechnology Information ID is PRJEB14666, and the genome is deposited under accession number FLT10100001. The distribution of genes into COGs functional categories is presented in Table 5.

### Genome comparison

Table 6 compares *Corynebacterium phoceense*’s genomic characteristics to other close species. The draft genome sequence of *C. phoceense* is smaller than those of *Corynebacterium* mustarde, *Corynebacterium freiburgense* and *Corynebacterium aurimu cusom* (2.794, 3.474, 2.91 and 2.905 Mb respectively), but larger than those of *Corynebacterium lactic*, *Corynebacterium ulcerans*, and...
Corynebacterium mastitidis and Corynebacterium terpenotabidum (2.77, 2.61, 2.37 and 2.75 Mb respectively).

The G+C content of Corynebacterium phoceense is smaller than those of Corynebacterium mastitidis and Corynebacterium terpenotabidum (63.23, 68.9 and 67.02% respectively), but larger than those of Corynebacterium lactis, Corynebacterium ulcerans, Corynebacterium mustelae, Corynebacterium freiburgense and Corynebacterium aurimucosum (60.53, 53.39, 52.57, 49.82 and 59.21% respectively).

The gene content of Corynebacterium phoceense is smaller than those of Corynebacterium mustelae, Corynebacterium freiburgense and Corynebacterium aurimucosum (2508, 3146, 2667 and 2769 respectively), but larger than those of Corynebacterium lactis, Corynebacterium ulcerans, Corynebacterium mastitidis and Corynebacterium terpenotabidum (2364, 2296, 2241 and 2369 respectively).

Finally, the distribution of genes into COGs categories was similar in all compared genomes except for those corresponding to the cell cycle control, mitosis and meiosis category, which were only present in C. mastitidis, C. mustelae and C. ulcerans (Fig. 7). C. phoceense strain MC1 shared 2667, 1358, 1332, 1248, 1128, 1211 and 1442 orthologous genes with C. freiburgense, C. aurimucosum, C. ulcerans, C. lactis, C. terpenotabidum, C. mastitidis and C. mustelae respectively (Table 7). Among species with standing in nomenclature, AGIOS values ranged from 54.12% between C. terpenotabidum and C. freiburgense to 74.86% between C. aurimucosum and C. phoceense. When C. phoceense was compared to the other

![FIG. 7. Distribution of functional classes of predicted genes according to COGs of proteins.](image)

|                  | C. freiburgense | C. aurimucosum | C. ulcerans | C. lactis | C. phoceense | C. terpenotabidum | C. mastitidis | C. mustelae |
|------------------|-----------------|----------------|-------------|-----------|--------------|-------------------|---------------|-------------|
| Corynebacterium freiburgense strain 1046 | 2667            | 1358           | 1332        | 1248      | 1232         | 1128              | 1211          | 1442        |
| Corynebacterium aurimucosum strain IMMIB | 63.97           | 2769           | 1336        | 1252      | 1407         | 1189              | 1315          | 1392        |
| Corynebacterium ulcerans strain NCTC 7910 | 57.66           | 58.26          | 2296        | 1197      | 1221         | 1091              | 1213          | 1354        |
| Corynebacterium lactis strain RV2-5      | 57.63           | 60.50          | 58.47       | 2364      | 1116         | 1105              | 1149          | 1249        |
| Corynebacterium phoceense strain MC1     | 63.56           | 74.86          | 58.13       | 61.48     | 2508         | 1079              | 1194          | 1264        |
| Corynebacterium terpenotabidum strain Y-11 IFO 14764 | 54.12           | 58.32          | 54.92       | 56.16     | 59.86        | 2369              | 1123          | 1146        |
| Corynebacterium mastitidis strain 58-CEPT 4843 | 63.90           | 69.01          | 57.33       | 61.39     | 70.81        | 60.55             | 2241          | 1252        |
| Corynebacterium mustelae strain 3105     | 65.46           | 64.85          | 58.55       | 58.25     | 64.48        | 55.39             | 64.16         | 3146        |

*Average percentage similarity of nucleotides corresponding to orthologous protein shared between genomes (lower left) and numbers of proteins per genome (bold)."
species, AGIOS values ranged from 58.13% with C. ulcers to 74.86% with C. aurimucosum.

**Conclusion**

On the basis of phenotypic, phylogenetic and genomic analyses, we formally propose the creation of *Corynebacterium phoceense* which contains the type strain MC1T. This bacterial strain has been isolated from the urine of a kidney transplant recipient.

**Description of Corynebacterium phoceense type strain MC1T sp. nov.**

*Corynebacterium phoceense* (pho.ce.ense, L. gen. masc., phoce-ense, “of Phocée,” the old Latin name of the city of Marseille, where strain MC1T was isolated). Cells have mean diameter of 0.5 μm and a mean length of 3 μm. Colonies are round and 1.0 mm in diameter on 5% sheep’s blood–enriched Columbia agar (bioMérieux). Positive reactions are observed for glucose, ribose, maltose, saccharose, alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, β-glucosidase, pyrazinamidase, pyrrolidonyl arylamidase and naphthol-AS-BI-phosphohydrolase. D-Ribose, D-galactose, D-glucose, D-fructose, D-mannose, arbutin, D-maltose and D-saccharose were metabolized. Cells were susceptible to vancomycin, rifampicin, doxycycline, erythromycin, amoxicillin, nitrofurantoin, gentamicin, ciprofloxacin, ceftriaxone, amoxicillin + clavulanic acid, penicillin G, gentamicin, trimethoprim + sulmefamoxazole, oxacillin, imipenem, tobramycin, metronidazole, amikacin, linezolid, clindamycin, daptomycin and chloramphenicol.

The G+C content of the genome is 63.23%. The 16S rRNA gene sequence and whole-genome shotgun sequence of *C. phoceense* strain MC1T are deposited in GenBank under accession numbers LN849777 and FLTI01000001, respectively. The type strain MC1T (= CSUR P1905 = DSM 100570) was isolated from the urine of a kidney transplant recipient.

**Acknowledgements**

The authors thank the Xegen Company (www.xegen.fr) for automating the genomic annotation process. This study was funded by the Fondation Méditerranée Infection.

**Conflict of Interest**

None declared.

**References**

[1] Approved lists of bacterial names. Skerman VBD, McGowan V, Sneath PHA, editors. Int J Syst Bacterial 1980;30:225–420.
[2] Collins MD, Smida J, Stackebrandt E. Phylogenetic evidence for the transfer of *Corynebacterium polymorphus* (Crombach) to the genus *Corynebacterium*. Int J Syst Evol Microbiol 1989;39:7–9.
[3] Coyle MB, Lipsky BA. Coryneform bacteria in infectious diseases: clinical and laboratory aspects. Clin Microbiol Rev 1990;3:327–46.
[4] Colt HG, Morris JF, Marston BJ, Sewell DL. Necrotizing tracheitis caused by *Corynebacterium pseudodiphtheriticum*: unique case and review. J Infect Dis 1991;13:73–6.
[5] Soriano F, Fernandez-Roblas R. Infections caused by antibiotic-resistant *Corynebacterium* group D2. Eur J Clin Microbiol Infect Dis 1988;7:337–41.
[6] Aravena-Román M, Spröer C, Siering C, Inglis T, Schumann P, Yassin AF. *Corynebacterium aquatimens* sp. nov., a lipophilic *Corynebacterium* isolated from blood cultures of a patient with bacteremia. Syst Appl Microbiol 2012;35:380–4.
[7] Collins MD, Hoyles L, Lawson PA, Felsen E, Robson RL, Foster G. Phenotypic and phylogentic characterization of a new *Corynebacterium* species from dogs: description of *Corynebacterium auricuculatens* sp. nov. J Clin Microbiol 1999;37:3443–7.
[8] Chen HH, Li WL, Tang SK, Krooppenstedt RM, Stackebrandt E, Xu LH, et al. *Corynebacterium halotolerans* sp. nov., isolated from saline soil in the west of China. Int J Syst Evol Microbiol 2004;54:779–82.
[9] Edouard S, Babi F, Dhamodharan R, Lagier JC, Azhar EI, Robert C, et al. Non-contiguous finished genome sequence and description of *Corynebacterium jeddahense* sp. nov. Stand Genomic Sci 2014;9:987–1002.
[10] Du ZJ, Jordan EM, Rooney AP, Chen GJ, Austin B. *Corynebacterium marinum* sp. nov. isolated from coastal sediment. Int J Syst Evol Microbiol 2010;60:1944–7.
[11] Sangal V, Haskisson PA. Evolution, epidemiology and diversity of *Corynebacterium* diphtheriae: new perspectives on an old foe. Infect Genet Evol 2016;43:364–70.
[12] Funke G, von Graevenitz A, Clarridge JE, Bernard KA. Clinical microbiology of *corynebacterium* bacteria. Clin Microbiol Rev 1997;10:125–9.
[13] Johnson WD, Kaye D. Serious infections caused by diphtheroids. Ann N Y Acad Sci 1970;174:568–76.
[14] Rosselló-Móra R. DNA-DNA reassociation methods applied to microorganisms: proposals for the domains Archaea, Bacteria, and Eucarya. Proc Natl Acad Sci U S A 1990;87:4576–9.
[15] Wayne LG, Brenner DJ, Colwell RR, Grimont PAD, Kandler O, Krichevsky MI, et al. Report of the ad hoc committee on reconciliation of non-contiguous *Corynebacterium* jeddahense sequences comparison. Int J Syst Bacteriol 2014;64:273–6.
[16] Woese R, Kandler O, Wheelis ML. Towards a natural system of organisms: proposals for the domains Archaea, Bacteria, and Eucarya. Proc Natl Acad Sci U S A 1990;87:4576–9.
[17] Viale AM, Arakaki AK, Soncini FC, Ferreyra RG. Evolutionary relationships among eubacterial groups as inferred from GroEL sequences comparison. Int J Syst Bacteriol 1990;40:73–82.
[18] Krichevsky MI, et al. Report of the ad hoc committee on reconciliation of non-contiguous *Corynebacterium* sp. nov. 81.
[19] Haddad A, Faye N, et al. High-quality genome sequence and description of
