**Paenibacillus arenilitoris** sp. nov., isolated from seashore sand and genome mining revealed the biosynthesis potential as antibiotic producer

Na Deng · Huiqin Huang · Yonghua Hu · Xu Wang · Kunlian Mo

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**Abstract** Strain IB182493\(^{T}\), a marine, aerobic, Gram-stain-negative and motile bacterium, was isolated from seashore sand of South China Sea. Cells grew optimally at 25–30 °C, pH 7.0–8.0 and with 2–4% NaCl (w/v). Phylogenetic analysis based on 16S rRNA gene sequence comparison revealed that the strain formed a distinct lineage within the genus *Paenibacillus*, and was most closely related to *Paenibacillus harenae* DSM 16969\(^{T}\) (similarity 96.6%) and *Paenibacillus alkaliterrae* DSM 17040\(^{T}\) (similarity 96.1%). The chemotaxonomic characteristics of strain IB182493\(^{T}\) included MK-7 as the predominant isoprenoid quinone, anteiso-C\(_{15:0}\) and iso-C\(_{16:0}\) as the major cellular fatty acids and *meso*-diaminopimelic acid as the diagnostic diaminoacid in cell wall peptidoglycan. The polar lipids consisted of phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and two unidentified phospholipids. The DNA G+C content of strain IB182493\(^{T}\) was 56.2 %. The values of whole genome average nucleotide identity (ANI) and digital DNA-DNA hybridization (dDDH) between the isolate and the closely related type strains were less than 84.7% and 23.6%, respectively. On the basis of phenotypic and chemotaxonomic properties, phylogenetic distinctiveness and genomic data, we named the strain as *Paenibacillus arenilitoris* sp. nov. and proposed that strain IB182493\(^{T}\) (=MCCC 1K04626\(^{T}\) = JCM 34215\(^{T}\)) in the genus *Paenibacillus* represents a novel species.

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H. Huang · Y. Hu · K. Mo
Hainan Provincial Key Laboratory for Functional Components Research and Utilization of Marine Bioresources, Haikou 571101, People’s Republic of China

Y. Hu
Laboratory for Marine Biology and Biotechnology, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao, People’s Republic of China

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Abbreviations

| Abbreviation | Description |
|--------------|-------------|
| MA           | Marine agar 2216 |
| MB           | Marine broth |
| NJ           | Neighbor-joining |
| MP           | Maximum-parsimony ML maximum-likelihood |
| ANI          | Average nucleotide identity |
| ANIb         | ANI calculated based on blast |
| ANIm         | ANI calculated based on MUMmer |
| orthoANIm    | ANI calculated based on usearch algorithm |
| dDDH         | Digital DNA–DNA hybridization |
| NA           | Nutrient agar |
| PDA          | Potato dextrose agar |
| MK-7         | Menaquione 7 |

Introduction

The genus *Paenibacillus*, a member of the family *Paenibacillaceae* (De Vos et al. 2009), was created for rRNA group 3 bacilli on the basis of 16S rRNA gene sequence analysis (Ash et al. 1993). Most members of the genus of *Paenibacillus* are non-pigmented, motile by means of peritrichous flagella, contain meso-diaminopimelic acid as the major diamino acid in the cell wall peptidoglycan and menaquinone 7 (MK-7) as the major menaquinone (Priest 2009). At the time of writing this manuscript, there were more than 270 species of this genus with validly published (https://lpsn.dsmz.de/ genus/ paenibacillus). Species of the genus *Paenibacillus* are widely distributed in various ecological niches, with many of the species being relevant to humans, animals, plants, and the environment (Grady et al. 2016). Recently, many new species of this genus have been isolated from various ecological habitats, including soil (Kim et al. 2021; Kämper et al. 2021; Klm et al. 2021; Yang et al. 2021a), *Arabidopsis thaliana* (Qi et al. 2021), nodules of soybean (Wang et al. 2021), seawater (Chen et al. 2021), corridor air (Liu et al. 2021) and salt lake (Yang et al. 2021, b). The *Paenibacillus* species have played an important role in industrial, agriculture and medical applications, such as degrading starch granules (Vander Maarel et al. 2000), enhancing plant growth through phosphate solubilization and nitrogen fixation (Lee et al. 2011; Jin et al. 2011) and producing antibiotics (Chung et al. 2000; Romanenko et al. 2013).

Natural products and their derivatives have occupied 50% of approved drugs in the world (Newman and Cragg 2020). For the discovery of pharmaceutical leads, tremendous studies have been found about the secondary metabolites from terrestrial plants and microorganisms. Therefore, the discovering number for novel natural products has reached a steady state, and the rate of finding compounds with unique novel skeletal structures has become extremely difficult over recent decades (Pye et al. 2017). Marine environments cover more than 70% of the surface of the earth, and are habitat of diverse microorganisms. Marine microorganisms are rich sources for a lot of bioactive natural products. Marine natural products are relatively efficient in the discovery of drug leads (Pereira 2019; Khalifa 2019), including the anti-cancer drugs trabectedin (discovered from a marine tunicate *Ecteinascidia turbinata*), eribulin mesylate (synthetic mimic to halichondrin B, which was isolated from a marine sponge *Halichondria okadai*) (Pereira 2019). It has become clear that the identification of new antimicrobial compounds is vigorously related with the discovery of novel species (Thumar et al. 2010). Thus, mining of microorganisms from various habitats is considered an advantageous approach to discover novel antibiotics (Baumann et al. 2014).

In this paper, we describe the strain IB182493T which has the potential to produce various biological activities such as receptor antagonist, enzyme inhibitor, anti-tumor metastases and antibacterial agents (Wilson et al. 2003; Knappe et al. 2010; Iwatsuki et al. 2006). The purpose of the present study was to establish the taxonomic position of a novel *Paenibacillus* like strain IB182493T based on polyphasic taxonomy.

Materials and methods

Collection and microbial isolation

A seashore sand sample was collected from Zhaoshu Island (16°58′53.3″ N, 112°16′33.6″ E), Hainan province, China, in March 2018. Sterilized PBS was used for suspending the sand sample and for serial dilutions. 100 μL suspension was spread plated on marine
agar 2216 (MA, Hopebio). After 5 days of culturing at 28 °C, colonies with different morphologies were picked up and purified. Among the bacteria, strain IB182493T was isolated and identified. The strains used in this study were sub-cultured on MA at 30 °C and stored at −80 °C in marine broth 2216 (MB, Hopebio) containing 20% glycerol (v/v).

Genome features and phylogenomic analysis

The draft genome sequencing of strain IB182493T and P. alkaliterrae DSM 17040 T were conducted using an Illumina HiSeq 2500 platform by Biomarker Technologies Co., Ltd. (Beijing, China). The de novo genome assembly was performed using SPAdes 3.5.0 (Bankevich et al. 2012). The G+C content was analyzed with the RAST server using the draft genome sequence (Brettin et al. 2015). The genome of P. harenae DSM 16969 T (NCBI accession number AULV01000000) was retrieved from the NCBI database.

The average nucleotide identity (ANI) values were calculated based on blast (ANIb), MUMmer (ANIm) and usearch algorithm (orthoANIu) as described previously (Chen et al. 2021). Digital DNA-DNA hybridization (dDDH) values were calculated using the genome-to-genome distance calculator with a website service (http://ggdc.dsmz.de/ggdc.php) (Meier-Kolthoff et al. 2013).

The phylogenomics tree of strain IB182493T and related species based on whole genome was constructed using a bioinformatics platform: Type (Strain) Genome Server (http://tygs.dsmz.de/) (Meier-Kolthoff et al. 2019). The obtained draft genome of IB182493T was annotated using the KEGG and COG analysis for gene function prediction (Kanehisa et al. 2016; Tatusov et al 2003). Both genomes of the strains IB182493T and P. alkaliterrae DSM 17040 T were deposited at GenBank /EMBL/ DDBJ with the accession numbers JACXIY0000000000 and JAKGAP000000000, respectively.

16S rRNA phylogeny

The genomic DNA extraction and PCR amplification of the 16S rRNA gene sequence were performed as described previously (Chen et al. 2021). The determined 16S rRNA gene sequence was compared with those of other type strains using the EzBioCloud database (https://www.ezbiocloud.net/identify). For comparison, phylogenetic reconstructions based on 16S rRNA genes were performed by using MEGA 11 (Tamura et al. 2021). Neighbour-joining (NJ) (Saitou et al. 1987), maximum-parsimony (MP) (Fitch et al. 1971) and maximum-likelihood (ML) (Felsenstein et al. 1981) methods with 1000 bootstrap replicates were used to reconstruct phylogenetic trees. Distances were obtained using options according to the Kimura’s two-parameter model (Kimura et al. 1980). Bacillus subtilis NCIB 3610T was added to the phylogenetic trees to serve as an outgroup.

Phenotypic characterization

Gram-staining of strain IB182493T was performed using a Gram-staining kit (Solarbio), and the endospores were stained according to the Schaeffer-Fulton method (Smibert and Krieg 1994). The cell morphology was observed by light microscope (Leica DM6000B, ×1000 magnification). The images of cells grown on MA from the exponential phase were obtained by means of transmission electron microscope (HT7700, Hitachi, Japan) at an accelerating voltage of 100 kV. The motility of the strain was determined by observing the growth spread of cells in MB as described previously (Chen et al. 2021). Growth under anaerobic conditions was determined on MA for 7 days at 28 °C using the anaerobic jars containing AnaeroPack-CO2 bags (Mitsubishi). Cultural Characteristics of strain IB182493T were investigated on MA, yeast-malt extract agar (ISP2), oatmeal agar (ISP3), Reasoner’s 2A agar (R2A), nutrient agar (NA), tryptic soy agar (TSA), Gause’s agar and potato dextrose agar (PDA), all of the media were adjusted with NaCl to 2% (w/v).

The temperature range for growth was assessed at 4, 10, 15, 20, 25, 30, 35, 40, 45, 50 and 55 °C with MB for 7 days. Different initial pH values (4.0–10.0 at intervals of 0.5 pH units) of MB were adjusted by using the buffer systems according to Bhatt (2017). Growth at different salinities was tested in the presence of 0–20% (w/v) NaCl with modified nutrition broth (peptone 5 g L⁻¹, beef extract 3 g L⁻¹) at 28 °C for 7 days.

Catalase activity was evaluated with a 3% (v/v) hydrogen peroxide solution. The acid production from carbon sources, the enzyme activity and sole carbon source substrate utilization were determined...
using the API 50CH, API 20NE and API ZYM test strips (Bio–Mérieux, France) according to the manufacturer’s recommendations except that the AUX medium was adjusted to 2% (w/v) NaCl. All the strips were incubated at 30 °C and recorded after 24 and 48 h.

The antibiotics (HANGWEI) tested were performed with penicillin (10 U), oxacillin (1 μg), ampicillin (10 μg), carbenicillin (100 μg), piperacillin (100 μg), cephalxin (30 μg), cefazolin (30 μg), cefradine (30 μg), cefuroxime (30 μg), ceftazidime (30 μg), ceftriaxone (30 μg), cefoperazone (75 μg), amikacin (30 μg), gentamicin (10 μg), kanamycin (30 μg), neomycin (30 μg), tetracycline (30 μg), doxycycline (30 μg), minocycline (30 μg), erythromycin (15 μg), midecamycin (30 μg), norfloxacin (10 μg), ofloxacin (5 μg), ciprofloxacin (5 μg), vancomycin (30 μg), polymyxin B (300 IU), compound trimethoprim (23.75/1.25 μg), furazolidone (300 μg), flumycin (30 μg) and clindamycin (2 μg). Discs with no antibiotics were used as controls and the assays were replicated three times. The hydrolysis of starch (1.0%, w/v), CM-cellulose (0.5%, w/v) and Tweens 20, 40, 60 and 80 (1%, w/v) were tested using MA as the basal medium. The phenotypic characterization for the description of new aerobic, endospore-forming bacterial taxa is in agreement with the minimal standards proposed by Logan (2009).

Chemotaxonomy

For fatty acid analysis, cell mass of strain IB182493<sup>T</sup>, <i>P. harenae</i> DSM 16969<sup>T</sup> and <i>P. alkaliterre</i>ae DSM 17040<sup>T</sup> were harvested from TSA (Hopebio, China) plates after incubation for 48 h at 28 °C. The whole-cell fatty acids were then extracted, methylated and analyzed using the standard protocol of the Microbial Identification System (Sherlock software version 6.3; MIDI library: RTSBA6) as described by Sasser et al. (2001). The respiratory quinones were extracted and analyzed using reversed-phase HPLC as described by Komagata and Suzuki (1988). Polar lipids were extracted and analyzed by two-dimensional TLC method according to the protocols of Minnikin et al. (1984). The amino acid composition in the peptidoglycan was determined by using the method described by Schumann (2011).

Analysis of bioactive compound biosynthetic gene clusters

Secondary metabolite biosynthetic gene clusters in the genome sequences of complete genome strain IB182493<sup>T</sup> (JACXIY000000000), <i>P. harenae</i> DSM 16969<sup>T</sup> (AULV000000000) and <i>P. alkaliterre</i>ae DSM 17040<sup>T</sup> (JAKGAP000000000) were identified with the bacterial version of antiSMASH 6.1.0 (https://antismash.secondarymetabolites.org/).

Results and discussion

The draft genome of strain IB182493<sup>T</sup> contained 86 contigs and with a size of 7.06 Mbp. 10 rRNAs (2, 5, 3 for 5S, 16S, 23S rRNA, respectively) and 70 tRNAs were detected. The general features of the genome of strain IB182493<sup>T</sup> were listed in table S1. The genomic DNA G+C content of the isolate was 56.2% and within the range of 40–59% reported for the genus <i>Paenibacillus</i> (Priest 2015) but higher than those of <i>P. harenae</i> DSM 16969<sup>T</sup> (49.9%) and <i>P. alkaliterre</i>ae DSM 17040<sup>T</sup> (49.4%). The distribution of the genes into clusters of orthologous groups (COGs) functional categories is presented in Fig. S1. In the phylogenomics tree (Fig. S2), strain IB182493<sup>T</sup> clustered with <i>P. harenae</i> DSM 16969<sup>T</sup>. The ANIb, ANIm and rthoANIu values of strain IB182493<sup>T</sup> and the closely related type strains ranged from 69.1–78.6%, 82.9–84.7% and 71.8–80.1%, respectively, while dDDH values ranged from 23.6–18.5% (Table S2). All of these values meet the criteria for bacterial species demarcation (Richter and Rosselló-Móra 2009; Chun et al. 2018) and support the hypothesis that IB182493<sup>T</sup> represents a novel species within the genus <i>Paenibacillus</i>. The obtained 16S rRNA gene sequence of strain IB182493<sup>T</sup> was 1470 bp long and the GenBank / EMBL / DDBJ accession number was MK249696. According to the EzBioCloud database, strain IB182493<sup>T</sup> represented a member of the genus <i>Paenibacillus</i> and showed the highest 16S rRNA gene sequence similarity to <i>P. harenae</i> DSM 16969<sup>T</sup> (96.6%), <i>P. alkaliterre</i>ae DSM 17040<sup>T</sup> (96.1%), <i>P. agaracedens</i> DSM 1327<sup>T</sup> (96.1%) and <i>P. agaridevorans</i> DSM 1355<sup>T</sup> (96.1%). Phylogenetic analyses showed that the isolate formed a discrete cluster with <i>P. harenae</i> DSM16969<sup>T</sup> and <i>P. alkaliterre</i>ae DSM.
17040T (Fig. 1). The ME and ML trees also showed the similar results (Figs. S3 and S4, available in the online version of this article). Based on 16S rRNA gene sequence similarities and phylogenetic analyses, the most closely related species, *P. harenae* DSM 16969T and *P. alkaliterrae* DSM 17040T were used as reference strains and examined for their genomic and phenotypic characteristics in comparison with those of the new isolate. Both of the two reference strains were obtained from the Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH (DSMZ).

Strain IB182493T was strictly aerobic and motile by means of peritrichous flagella. Rod-shaped cells are Gram-stain-negative and subterminal ellipsoidal endospores were observed (Fig. S6). Under the electron microscope, cells were approximately 0.5–0.9 μm in diameter and 2.8–3.3 μm in length (Fig. 2). Cells grow well on R2A agar, LB, TSA, MA and NA, while poor on ISP 3, but could not grow on ISP 2 and PDA. Growth occurred at temperatures ranging from 20–40 °C (optimum 25–30 °C), pH 5.0–10.0 (optimum pH 7.0–8.0) and 0–9% (w/v) NaCl (optimum 2–4%). The strain was positive for catalase. Starch, CM-cellulose, Tweens 20, 40, 60 and 80 were not hydrolysed. In antibiotic tests, strain IB182493T was found to be sensitive to cefamezin, cefradine, cefuroxime, ceftazidime, ceftriaxone, cefoperazone, norfloxacain and polymyxin B; but resistant to all of the other antibiotics tested. In the API 20NE kit tests, strain IB182493T was found to be unable to reduce nitrate to nitrite, showed positivity for β-glucosidase and β-galactosidase; assimilated glucose, mannitol and maltose. With API ZYM kit, strain IB182493T was found to be positive for the activities of esterase (C4), acid phosphatase, naphthol-AS-BI-phosphohydrolase, β-galactosidase and β-glucosidase. In the API 50CH B kit, cells produce acid from arbutin, salicin, D-cellulbiose, maltose, D-lactose, D-melibiose, D-saccharose sucrose, D-trehalose, inulin, D-melezitose, D-raffinose, starch amylase, D-gentiobiose, D-turanose; weakly produce acid from methyl-β-D-xylopyranoside, D-galactose methyl, D-glucose, D-fructose, D-mannose, L-rhamnose, D-mannitol, esculin ferric citrate, glycogen and potassium 5-ketogluconate. The phenotypic characteristics of strain IB182493T which were used for comparison

![Fig. 1 Reconstruction of the phylogenetic position of strain IB182493T based on almost full length 16S rRNA gene sequences. Shown is a neighbour-joining tree. Bootstrap values greater than 70% are shown at branch points. The scale bar represents 0.01 nucleotide substitutions per position. *Bacillus subtilis* NCIB 3610T was used as an outgroup](image-url)
with the reference species were summarized in Table 1.

The predominant respiratory quinone of strain IB182493^T^ was MK-7, which is also the major menaquinone in other species of the genus *Paenibacillus* (Priest 2009). The diagnostic diamino acid in the cell-wall peptidoglycan was meso-diaminopimelic acid. The polar lipids included phosphatidylethanolamine (PE), phosphatidylglycerol (PG), diphosphatidylglycerol (DPG) and two unidentified phospholipids (PL1–PL2) (Fig. S5). The major cellular fatty acids (> 5%) were anteiso-C\textsubscript{15:0} (47.1%), iso-C\textsubscript{16:0} (23.4%), C\textsubscript{16:0} (8.9%) and iso-C\textsubscript{15:0} (6.1%).

The novel isolate had similar proportions of the fatty acids to the reference strains (Table S3).

Based on the result of the gene cluster prediction, strain IB182493^T^ contained 9 secondary metabolite gene clusters in the genome (Table S4), while 8 clusters in *P. harenae* DSM16969^T^ and *P. alkaliterra* DSM 17040^T^. The genome mining revealed that the novel strain has the potential to produce many secondary metabolites including lasso peptide paeninodin, ectoine, basiliskamide A/B and staphylobactin, etc (Table S4). The lasso peptide belongs to a new class of natural product with highly compact and stable structure, which has various biological activities such as anti-tumor metastases, receptor antagonist, enzyme

![Fig. 2](https://example.com/fig2.png) Transmission electron micrograph of cells of strain IB182493^T^. Cells were from a 36-h-old culture grown on marine agar 2216. Bar, 2.0 μm
Table 1  Characteristics that distinguish strain IB182493\textsuperscript{T} from the type strains of the most closely related *Paenibacillus* species

| Characteristic                                      | 1                          | 2                          | 3                          |
|-----------------------------------------------------|----------------------------|-----------------------------|-----------------------------|
| Isolation source                                   | Seashore sand              | Desert sand                 | Alkaline soil               |
| Temperature range (°C)                              | 20–40                      | 15–45                       | 15–35                       |
| Optimum                                            | 25–30                      | 20–35                       | 25–30                       |
| pH Range                                           | 5.0–10.0                   | 6.0–10.0                    | 6.0–9.5                     |
| Optimum                                            | 7.0–8.0                    | 7.0–7.5                     | 7.5–8.0                     |
| NaCl range (%), w/v                                | 0–9                        | 0–3                         | 0–2                         |
| Optimum                                            | 2–4                        | 0–2                         | 0–1                         |
| Assimilation of (API 20NE)                          |                            |                             |                             |
| D–Glucose                                          | +                          | −                           | +                           |
| L–Arabinose                                        | −                          | +                           | −                           |
| Mannitol                                            | +                          | −                           | +                           |
| N–Acetyl-glucosamine                               | −                          | −                           | +                           |
| Gluconate                                          | W                          | −                           | +                           |
| Malic acid                                         | −                          | W                           | +                           |
| Citric acid                                        | −                          | W                           | +                           |
| Enzyme activity (API ZYM)                           |                            |                             |                             |
| Alkaline phosphatase                               | −                          | +                           | +                           |
| Esterase lipase                                    | −                          | +                           | W                           |
| Esterase                                           | W                          | +                           | W                           |
| Leucine arylamidase                                | −                          | +                           | W                           |
| α-Galactosidase                                    | −                          | +                           | W                           |
| β-Glucosidase                                      | W                          | −                           | +                           |
| Acid production from                                |                            |                             |                             |
| Glycerol                                           | −                          | −                           | +                           |
| Arabinose                                           | −                          | −                           | +                           |
| D–Ribose                                           | −                          | −                           | +                           |
| D–Xylose                                           | −                          | −                           | +                           |
| L–Xylose                                           | −                          | −                           | +                           |
| D–Galactose                                        | W                          | −                           | +                           |
| D–Mannose                                          | W                          | −                           | +                           |
| L–Rhamnose                                         | W                          | +                           | −                           |
| Inositol                                           | −                          | +                           | W                           |
| Methyl α-d-glucopyranoside                         | −                          | −                           | +                           |
| N-Acetyl-glucosamine                               | −                          | −                           | +                           |
| Amygdalin                                          | −                          | −                           | +                           |
| D–Cellobiose                                       | +                          | −                           | +                           |
| Maltose                                             | +                          | −                           | +                           |
| D–Lactose                                          | +                          | −                           | +                           |
| D–Sucrose saccharose                               | +                          | −                           | +                           |
| Trehalose                                          | +                          | −                           | +                           |
| Inulin                                              | +                          | −                           | −                           |
| D–Melezitose                                       | +                          | −                           | +                           |
| Glycogen                                           | W                          | −                           | +                           |
| D–Gentiobiose                                      | +                          | −                           | +                           |
| D–Turanose                                         | +                          | −                           | +                           |
| L–arabitol                                         | −                          | +                           | −                           |
inhibitor and antibacterial agents (Wilson et al. 2003; Knappe et al. 2010; Iwatsuki et al. 2006). As known that lasso peptides are non-pathogenic, and have great resistibility to high temperature, acidic condition and most proteases, therefore lasso peptides may be used as multifunctional backbones for further medical use (Knappe et al. 2011; Hegemann et al. 2014; Meyer et al. 2006). In the genome of strain IB182493T, lasso peptide paeninodin biosynthetic gene clusters with 100% similarity to that of strain P. dendritiformis C454 (Sirota-Madi et al. 2012) were found. The lasso peptide paeninodin cluster has a gene encoding a kinase, which was represented as member of a new class of lasso peptide tailoring kinases. By employing a wide variety of peptide substrates, it was shown that the novel type of kinase specifically phosphorylates the C-terminal serine residue while ignoring those located elsewhere (Zhu et al. 2016). In genomic data analysis, 75% similarity of ectoine gene cluster was found in the genome of strain IB182493T compared to Streptomyces anulatus (Beijerinck 1912). The isolate and the closely related species (P. harenae DSM16969T and P. alkaliterrae DSM 17040T) contain ectoine gene cluster and were isolated from the similar extreme habitat such as sand and soil which were dry, salinity or alkaline-like extreme. This evidence suggests that the ectoine is primarily associated with extreme environments, as has been reported by Brown (1976) that ectoine is essential for extremophiles to survive in extreme environments. In addition, basiliskamide A/B biosynthetic gene cluster with 9% similarity to that of strain Brevibacillus laterosporus PE36 (Theodore et al. 2014) were found in the genome of strain IB182493T. Despite the relatively closeness, no basiliskamide A/B biosynthetic gene clusters were detected in the genome sequence of strain P. harenae DSM16969T and P. alkaliterrae DSM 17040T. In conclusion, the complete genome of strain IB182493T will help further studies regarding the biosynthesis of diverse secondary metabolites and their regulatory mechanisms.

Based on phenotypic, phylogenetic and genomic analyses, strain IB182493T is considered as a type strain of a novel species with the proposed name, Paenibacillus arenilitoris.

**Description of Paenibacillus arenilitoris sp. nov.**

Paenibacillus arenilitoris sp. nov. (a.re.ni.li.to’ris. L. n. arena sand; L. n. litus-oris the seashore, coast; N.L. gen. n. arenilitoris of sand of the seashore, from which the type strain was isolated).

Cells are Gram-stain-negative, strictly aerobic and motile with peritrichous flagella. Cells are rod-shaped with 0.5–0.9 × 2.8–3.3 μm in size. Subterminal ellipsoidal endospores are observed in swollen sporangia. Colonies are non-pigmented, white-cream, punctiform circular and smooth, with 0.5–1.5 mm in diameter on MA after 48 h. Growth occurs at 20–40 °C (optimum 25–30 °C), pH 5.0–10.0 (optimum pH 7.0–8.0) and 0–9% (w/v) NaCl (optimum 2–4%). Cells are catalase-positive, but nitrate, urease and oxidase were negative. Starch, CM-cellulose, Tweens 20, 40, 60 and 80 are not hydrolysed.

The predominant isoprenoid quinone is MK-7 and the cell-wall peptidoglycan contains meso-diaminopimelic acid. The major cellular fatty acids are anteiso-C15:0 and iso-C16:0. The polar lipids comprised phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and two unidentified phospholipids. The G+C content of the DNA is 56.2%. The genome analyses predicted 9 secondary metabolite gene clusters and revealed that this strain

| Characteristic | 1 θ | 2 | 3 |
|---------------|-----|---|---|
| DNA G+C content (mol %) | 56.2 | 49.9<sup>a</sup> | 49.4<sup>b</sup> |

| Strains: 1, IB182493T; 2, P. harenae DSM16969T; 3, P. alkaliterrae DSM 17040T. Symbols: +, positive; −, negative; w, weakly positive. Data were obtained in this study unless indicated (All of strains were positive for esculin, β-galactosidase, maltose; negative for tryptophane indole, glucose, arginine dihydrolase, urease, gelatin, mannoside, glyoxylic acid, adipic acid, phenyl acetic acid; Acids were not produced from Erythritol, L-xyllose, D-adonitol, L-sorbose, Dulcitol, Sorbitol, D-lyxose, D-tagatose, D-fucose, L-arabitol, kalium Gluconate and potassium 2-ketogluconate.)<sup>a</sup>| Data form Jeon et al. 2009; <sup>b</sup>Data form Yoon et al. 2005 |

<sup>a</sup>Data form Jeon et al. 2009; <sup>b</sup>Data form Yoon et al. 2005
has the potential to produce many multifunctional active ingredients including lasso peptide paeninodin, ectoine, basiliskamide A/B and staphylobactin, etc.

The type strain IB182493T (=MCCC 1K04626T =JCM 34215 T), was isolated from seashore sand of South China Sea. The GenBank/ ENBL/DDBJ accession numbers of 16S rRNA gene and the draft genome sequences are MK249696 and JACXIY000000000, respectively.

Authors’ contributions YH and XW conceived and designed research. ND conducted experiments. HI analyzed data. KM wrote the manuscript and edited the manuscript. All authors read and approved the manuscript.

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Declarations Conflict of interest The authors declare that there are no conflicts of interest.

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