The natural history of cutaneous propionibacteria, and reclassification of selected species within the genus Propionibacterium to the proposed novel genera Acidipropionibacterium gen. nov., Cutibacterium gen. nov. and Pseudopropionibacterium gen. nov.

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The genus Propionibacterium in the family Propionibacteriaceae consists of species of various habitats, including mature cheese, cattle rumen and human skin. Traditionally, these species have been grouped as either classical or cutaneous propionibacteria based on characteristic phenotypes and source of isolation. To re-evaluate the taxonomy of the family and to elucidate the interspecies relatedness we compared 162 public whole-genome sequences of strains representing species of the family Propionibacteriaceae. We found substantial discrepancies between the phylogenetic signals of 16S rRNA gene sequence analysis and our high-resolution core-genome analysis. To accommodate these discrepancies, and to address the long-standing issue of the taxonomically problematic Propionibacterium propionicum, we propose three novel genera, Acidipropionibacterium gen. nov., Cutibacterium gen. nov. and Pseudopropionibacterium gen. nov., and an amended description of the genus Propionibacterium. Furthermore, our genome-based analyses support the amounting evidence that the subdivision of Propionibacterium freudenreichii into subspecies is not warranted. Our proposals are supported by phylogenetic analyses, DNA G+C content, peptidoglycan composition and patterns of the gene losses and acquisitions in the cutaneous propionibacteria during their adaptation to the human host.

Introduction

The genus Propionibacterium was described by Orla-Jensen in 1909 and constitutes species widely known for producing propionic acid as their end product of fermentation (Goodfellow et al., 2012). Most notable are the type species Propionibacterium freudenreichii for its valued contribution to Swiss cheese (Abeijón Mukdsi et al., 2014; Skerman et al., 1980; Thierry et al., 2011), Propionibacterium acidipropionici for its beneficial effects on the metabolism in the bovine rumen (Francisco et al., 2002) and Propionibacterium acnes for its implications in the common skin disorder acne vulgaris and its notorious habit of contaminating human samples (Lomholt & Kilian, 2010; Mollerup et al., 2016; Williams et al., 2012). Traditionally, species within the genus have been grouped as either classical or cutaneous propionibacteria (Stackebrandt et al., 2006). The informal term ‘classic propionibacteria’ has been ascribed to the species isolated from dairy products in contrast to the skin-associated, reclassified corynebacteria (Stackebrandt et al., 2006). The classic propionibacteria include the species Propionibacterium freudenreichii, Propionibacterium acidifaciens (Downes & Wade, 2009), Propionibacterium cyclohexanicum (Kusano et al., 1997), Propionibacterium australense (Bernard et al., 2002), Propionibacterium acidipropionici, Propionibacterium jenseni, Propionibacterium thoenii, Propionibacterium microaerophilum (Koussémon et al., 2001), Propionibacterium olivae (Lucena-Padrós et al., 2014), Propionibacterium damnosum (Lucena-Padrós et al., 2014) and Propionibacterium propionicum (Charfreitag et al., 1988). The cutaneous group comprises the species Propionibacterium acnes, Propionibacterium avidum and Propionibacterium granulosum. In addition to these, a novel cutaneous species, tentatively named ‘Propionibacterium humerusii’, was reported by Butler-Wu et al. (2011), but this name was neither effectively nor validly published. Subspecies

Abbreviations: GABA, gamma-aminobutyrate; LL-α-P, LL-2,6-diaminopimelic acid; meso-α-P, meso-2,6-diaminopimelic acid.

Six supplementary figures and one supplementary table are available with the online Supplementary Material.
classification has been used in two species. The Propionibacterium freudenreichii subspecies (Propionibacterium freudenreichii subsp. freudenreichii and Propionibacterium freudenreichii subsp. shermanii) are separated by two biochemical reactions important for cheese production (Stackebrandt et al., 2006). P. acnes has been divided into three phylogenetic types: I, II and III (Kilian et al., 2012; McDowell et al., 2005, 2008). Recently, it was proposed that P. acnes should be divided into two subspecies, Propionibacterium acnes subsp. acnes representing types I and II, and Propionibacterium acnes subsp. elongatum constituting type III (Dekio et al., 2015). A more comprehensive review of species, including historical changes in taxonomy has been presented by Stackebrandt et al. (2006).

The unexplored transmission from food products or livestock rumen to the human host or vice versa is an exciting scientific case, which may provide new insights into conditions of life on the human skin. As of February 2016, NCBI hosts 162 genome sequences under the taxonomic id corresponding to Propionibacterium (txid1743), and representing 10 of the 16 species. It is now possible to re-evaluate the taxonomy of the propionibacteria and to take a first look at their evolutionary adaptation to different habitats. In this study, we explored the genomic foundation of the current taxonomic classification of the genus Propionibacterium, along with seeking insights into the adaptive processes affecting the cutaneous group of propionibacteria during their transition to human skin.

Methods

Analysis of 16S rRNA gene sequences. Nucleotide sequences of the gene encoding 16S rRNA were downloaded from NCBI for each type strain within Propionibacteriaceae as indicated by LPSN (www.bacterio.net), with the exception of Propionibacterium propionicum DSM 43307 (see Discussion) where the sequence of accession number NR_114803 was used. Phylogenetic analysis using minimum-evolution (Fig. 1) was conducted on sequences aligned with MUSCLE (Edgar, 2004) in MEGA V. 7 (Kumar et al., 2016). Additional trees using the algorithms maximum-likelihood, maximum-parsimony and neighbour-joining were reconstructed in MEGA V. 7. Detailed information on the phylogenetic analysis for each algorithm is provided in the supplementary information (available in the online Supplementary Material) for Fig. 2. The same settings were used for reconstructing Fig. 1.

Reconstruction of core-genome trees. Genomes of all strains belonging to the family Propionibacteriaceae (NCBI taxonomic id 31957), in addition to Corynebacterium diphtheriae DSM 43988, were downloaded from NCBI. The root, Corynebacterium diphtheriae, was chosen as a compromise between a taxon being distant enough to be a safe root irrespective of possible errors in the current classification and being as close as possible to give the largest common ancestor to analyze. Shared sequences were identified using tblastx (coverage <50%) (Camacho et al., 2009) on all coding sequences identified by annotation of the Propionibacterium acnes KPA171202 genome (Brüggemann et al., 2004). All homologous gene sequences were aligned using MUSCLE (Edgar, 2004) and concatenated using a Python script. This initial dataset was used to identify relevant unclassified strains, to correct wrong species assignments (Fig. S4) and to select genomes for inclusion in our analysis. The trees were built on the included genomes in MEGA 7 (Kumar et al., 2016) using 100 bootstrap replications and complete deletion.

Algorithms used were maximum-likelihood, maximum-parsimony, minimum-evolution and neighbour-joining (see figure legends). Detailed information on the phylogenetic analysis is provided in the supplementary information.

Comparative analysis of DNA G+C content and genome sizes. All genome sequences were downloaded from NCBI Genomes. Strain genomes were taken from all genome groups provided on the species page of NCBI Genomes to reduce the number of redundant strains. Wrongly identified genomes were identified and excluded by comparing core-genome sequences to those of related species. Genomic DNA G+C content and genome size were calculated on genome sequences using a Python script.

Software for drawing figures. Phylogenetic trees were made in MEGA 7 (Kumar et al., 2016). Illustration of comparative genome sizes and DNA G+C contents was drawn using matplotlib (Michael Droettboom et al., 2015). Circular genome maps were made in BRIG (Ali-khan et al., 2011).

Results

Topology determined by 16S rRNA gene sequences

In accordance with the current taxonomy, phylogenetic analysis of 16S rRNA gene sequences downloaded from NCBI for all type strains belonging to the family Propionibacteriaceae revealed a distinct and coherent Propionibacterium clade supported by the bootstrap analysis (bootstrap value 79) with the exception of Propionibacterium propionicum, which formed a distinct lineage (Fig. 1). The overall topology of the phylogenetic trees was confirmed in trees reconstructed by the algorithms maximum-likelihood, maximum-parsimony and neighbour-joining in MEGA V. 7 (see Figs S1–S3).

Topology of the family Propionibacteriaceae based on genome analysis

To better resolve the interspecies relatedness we extracted shared nucleotide sequences from all whole-genome-sequenced species, together with one out-group species, Corynebacterium diphtheriae (from the family Corynebacteriaceae). The concatenated sequences amounted to 50.9 kb and were used to reconstruct phylogenetic trees using four different algorithms (Fig. 2). Based on these phylogenetic analyses, the genus Propionibacterium does not form a monophyletic cluster. All four algorithms revealed two major branches of species of the genus Propionibacterium, one of which is connected to a branch representing a cluster composed of the genera Granulicoccus, Microbacterium, Propionicellula, Aestuariimicrobium and Tessaracoccus, in addition to one strain of Propionibacterium propionicum and an unidentified member of the family Propionibacteriaceae (strain P6A17). One of the Propionibacterium clades consists of the representatives of ‘classic species of the genus Propionibacterium’, the type species Propionibacterium freudenreichii and Propionibacterium acidifaciens. The other Propionibacterium clade consists of two sub-clades, one including the skin-associated species of the genus Propionibacterium, Propionibacterium acnes,
Fig. 1. Minimum-evolution tree of 16S rRNA gene sequences from all type strains within the family Propionibacteriaceae. Numbers at nodes indicate results of 100 bootstrap replications. See Figs S1, S2 and S3 for replicate trees using different algorithms. Bar, 0.02 base substitutions per site.
Propionibacterium avidum, Propionibacterium granulosum and ‘Propionibacterium humerus’, and the other including other ‘classic species of the genus Propionibacterium’, Propionibacterium acidipropionici, Propionibacterium jensenii and Propionibacterium thoenii, Propionimicrobium lymphophilum (Stackebrandt et al., 2002) and an unclassified strain, Propionibacterium sp. oral taxon 192 str. F0372 and the root, Corynebacterium diphtheriae, all form distinct lineages. The two clades of species of the genus Propionibacterium with Propionibacterium propionicum as an outlier are also supported by the 16S rRNA gene sequence tree.

Phylogenetic analysis with improved resolution

In the next step to improve the resolution, the outgroup Corynebacterium diphtheriae was eliminated from the process of extracting core genome sequences. A new tree reconstructed on an almost three times larger dataset of shared sequences (135 kb) supports the findings represented in Fig. 2 and clearly highlights the non-monophyletic nature of the genus Propionibacterium (Fig. 3). It becomes apparent that the cutaneous propionibacteria form a distinct and coherent clade and that the ‘classic propionibacteria’ constitute two separate clusters. Furthermore, it is evident from Fig. 3 that the current classification does not reflect the relative phylogenetic distances to the type species Propionibacterium freudenreichii.

DNA G+C content and genome size

To further elucidate the intra-genus diversity we mapped the DNA G+C-content and size of genomes of species in the family Propionibacteriaceae and Corynebacterium diphtheriae (Fig. 4). The lowest DNA G+C content was found in

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Corynebacterium diphtheriae (53.5 mol%) followed by Propionibacterium acnes (56.0 mol%), supporting their separate position in the trees shown in Figs 1, 2 and 3. Interestingly, Fig. 4 displays a movement towards lower DNA G+C contents in the cutaneous species (Propionibacterium acnes, ‘Propionibacterium humerusii’, Propionibacterium avidum and Propionibacterium granulosum). These four species have lower DNA G+C contents (59.9–64.2 mol%) than the remaining propionibacteria (66.1–70.6 mol%), with an evident decrease in the species Propionibacterium acnes and ‘Propionibacterium humerusii’ that, according to the parsimonious analysis, are end-branches (Fig. 2b). Furthermore, the cutaneous species have smaller genomes than the other propionibacteria, with the only exception being Propionibacterium freudenreichii.

Adaptation of cutaneous propionibacteria to their human host

To examine potential adaptive changes in cutaneous propionibacteria we searched the dataset of homologous genes (tblastx hits covering >50% of query) for genes uniquely present in strains of the four species of cutaneous propionibacteria. A total of 108 genes were found (Fig. S5). Most notable, many of these genes clustered in pairs of two or more on the spatial representation in Fig. S5. Many of these clusters encode sugar transporters in forms of ABC transporters, symporters and phosphotransferase systems (PTS). Another interesting theme is iron-acquisition, of which we identified three clusters of genes in addition to a small siderophore-related gene. We identified an island of seven genes encoding several aminomutases related to ornithine metabolism. Another smaller island was found encoding three
The initial enzyme for shunting (GABA).

L-

of a glutamate decarboxylase catalysing the conversion of chain amino acids. Another noteworthy absence is the lack of branched-chain amino acids. Propionibacteria lack the genes for transporting branched-chain amino acids. The search for homologous sequences present in at least one strain of each of the species Propionibacterium jensenii, Propionibacterium thoenii and Propionibacterium acidipropionici and none of the cutaneous species resulted in 26 annotated genes (Fig. S6). Interestingly, levanase was found among the absent genes. Levanase catalyses the degradation of fructose polymers of the levan type (or phlein) found excessively in grasses (Martin et al., 1987; Suzuki & Chatterton, 1993). Furthermore, cutaneous propionibacteria lack the genes for transporting branched-chain amino acids. Another noteworthy absence is the lack of a glutamate decarboxylase catalysing the conversion of L-glutamate to the neurotransmitter gamma-aminobutyrate (GABA).

The initial enzyme for shunting L-rhamnose into the glycolysis pathway is absent, and the KEGG database confirms that all three enzymes of the rhamnose pathway are missing in Propionibacterium acnes and Propionibacterium avidum (Kanehisa et al., 2014).

The gene encoding ‘glutamate-cysteine ligase’ is the first step in de novo synthesis of glutathione and its analogue ophthalic acid; this rate-limiting enzyme is not present in the cutaneous species.

The end product of the mevalonate pathway is isopentenyl diphosphate, and the final step is catalysed by diphosphomevalonate decarboxylase. This end product is essential for the biosynthesis of polyisoprenoids and peptidoglycan (Barta et al., 2012). The diphosphomevalonate decarboxylase is absent in the cutaneous species; however, in contrast to Propionibacterium acidipropionici, Propionibacterium acnes has an intact MEP/DOXP pathway, providing an effective alternative production of isopentenyl diphosphate.

\[\text{Propionibacterium acnes} \quad \text{Propionibacterium humerusii} \quad \text{Propionibacterium avidum} \quad \text{Propionibacterium acidipropionici} \quad \text{Propionibacterium granulosum} \]

- Propionibacterium jensenii
- Aestuariimicrobium kwangyangense
- Granulicoccus phenolivorans
- Microlunatus phosphorus
- Propionibacterium propionicum
- Propionibacterium acidipropionici
- Propionibacterium thoenii
- Corynebacterium diphtheriae

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<th>DNA G+C content (mol%)</th>
<th>Genome size (Mb)</th>
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**Fig. 4.** Plot of genomic DNA G+C content calculated for each strain in each species. Species are listed in accordance with the topology of Fig. 3.

**Discussion**

The group of cutaneous propionibacteria constitutes species of a distinct phylogenetic clade in the genus Propionibacterium as indicated by Figs 2 and 3, which is also largely supported by the 16S rRNA gene sequence tree displayed in Fig. 1. The maximum-parsimony tree displayed in Fig. 2b illustrates the evolutionary history of these cutaneous species. Evidently, Propionibacterium granulosum is the oldest, followed by Propionibacterium avidum, then ‘Propionibacterium humerusii’ and the intermediate strain SK187B-JCVI and, finally, Propionibacterium acnes of which phylotype I is suggested as the most recent lineage. We envisage an evolutionary model where the initial transmission into the new niche, human skin, was followed by an iterative process of better and better adapted clones expanding at the expense of the founders. It was previously reported that clonal complex 18 (MLST8) in type IAi, includes clones that have been able to spread worldwide (Kilian et al., 2012; Lomholt & Kilian, 2010). Conceivably, this process was driven by the large potential benefit of even the smallest adaptive changes that follow a ‘recent’ transmission to a new habitat. This hypothesised model fits the staircase-like tree structure of the maximum-parsimony tree and the scarcity of isolated ‘older’ species compared with the wide-spread lineages of the more recent Propionibacterium acnes.

The adaptation of propionibacteria to a human host involves new challenges, but also new benefits (Figs S5 and S6). Iron is essential for many processes in bacteria, while...
the human proteins transferrin and ferritin reduce the accessibility of free iron. It is therefore not surprising to find genes related to iron absorption among the acquisitions. Similarly, the change in environment-provided carbon sources is expectedly reflected in the acquisition of several sugar-uptake-related genes and lipases. The change in carbon sources is also reflected in the adaptive deletions. The two lipases acquired by species associated with human skin, triacylglycerol lipase and lysophospholipase, conceivably facilitate their survival in the hostile environment of sebaceous follicles.

Strikingly, levanase (or phleinase), an enzyme catalysing the degradation of levans-type fructans, unlikely to be encountered on human skin, was lost. To our knowledge, levanase activity has not been described for propionibacteria, but may be an uncounted benefit, in addition to the propionate activity. The two lipases acquired by species associated with human skin, triacylglycerol lipase and lysophospholipase, conceivably facilitate their survival in the hostile environment of sebaceous follicles.

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Reclassification of the genus Propionibacterium

During the last century, the genus Propionibacterium has been populated with species based on phenotypic traits and 16S rRNA gene sequence similarity. With the advent of whole-genome sequencing, the possibility of high-resolution phylogenetic analysis merits a revision of the taxonomy. From our genome analysis of species in the family Propionibacteriaceae, it is evident that 16S rRNA gene sequences largely reflect the true topology of subclades within the genus Propionibacterium, but are insufficient to describe the genetic distance from species of other genera. This discrepancy in resolution has resulted in some related species being assigned to the genus Propionibacterium and others not, while showing the same level of sequence similarity to Propionibacterium freudenreichii. Our results show that the taxonomy of propionibacteria does not reflect the genetic constitution of its species.

Recognizing the uncertainties involved in defining the level of differentiation of taxa in the taxonomic hierarchy, there are two ways the taxonomy of propionibacteria could be changed to reflect the genetic constitution of the species. One option is to include the members of the genera Granulicoccus, Microlunatus, Propionicicella, Aestuariumicrobium and Tessaracoccus in the genus Propionibacterium. That would render the genus Propionibacterium monophyletic,
and even allow Propionibacterium propionicum to remain unchanged. The drawback is that the genus Propionibacterium would then encompass species of such diverse habitats as activated sludge, flat-water sediment, matured cheeses and human skin/oral cavity. In addition to being inconsistent with the biology, 16S rRNA gene sequence based analysis will no longer display a distinct and coherent Propionibacterium clade, rendering classification of novel species by this method prone to error. The other option is a more practical approach that retains the functionality of sequencing 16S rRNA genes and provides a more coherent genus with regard to DNA G+C content, genome size, phenotypic traits and habitat. This option consists of reducing the genus Propionibacterium to accommodate one branch of the classic propionibacteria and creating a new genus for the other branch. In this way, the cutaneous group will be collected under a separate genus. Finally, the outlier Propionibacterium propionicum will be accommodated in a third genus. We propose that the genus Propionibacterium contains Propionibacterium freudenreichii (type species), Propionibacterium cyclohexanicum, Propionibacterium acidifaciens and Propionibacterium australiense. The novel genus Acidipropionibacterium gen. nov. will encompass the former species Propionibacterium jensenii (type species), Propionibacterium thoenii, Propionibacterium acidipropionici, Propionibacterium microaerophilum, Propionibacterium damnosum and Propionibacterium olivae. The novel genus Cutibacterium gen. nov. will contain the cutaneous species formerly known as Propionibacterium acnes (type species), Propionibacterium avidum, Propionibacterium granulosum and ‘Propionibacterium humerusii’. Finally, the novel genus Pseudopropionibacterium gen. nov. will accommodate the former species Propionibacterium propionicum (type species). Table S1 summarizes all novel and former species names.

All species of the proposed reduced genus Propionibacterium are characterized by meso-2,6-diaminopimelic acid (meso-A3PM) as the diagnostic amino acid in the peptidoglycan, which separates them from species of the proposed novel genus Acidipropionibacterium gen. nov. characterized by LII-2,6-diaminopimelic acid (LII-A3PM) (Goodfellow et al., 2012). The proposed new genus Cutibacterium gen. nov. is mainly characterized by LII-A3PM in the peptidoglycan, with few strains using meso-A3PM, but the genus is readily separated from the proposed genera Propionibacterium and Acidipropionibacterium gen. nov. by 5–10 mol% lower genomic DNA G+C content (Fig. 4).

Abandoning subspecies of Propionibacterium freudenreichii

According to the descriptions, Propionibacterium freudenreichii subsp. freudenreichii is able to reduce nitrate but does not ferment lactose, and vice versa for Propionibacterium freudenreichii subsp. shermanii. These are the only two distinguishing characteristics of these subspecies (Goodfellow et al., 2012). However, fermentation of lactose is not genetically coupled with the inability to reduce nitrate and, accordingly, four phenotypes have been observed, two of which fit neither of the two subspecies (de Freitas et al., 2015). Comparing phenotypic traits to multilocus sequence typing (MLST) data, Dalmasso et al. (2011) conclude that characteristics of the subspecies are prone to recurrent changes and that these do not reflect the ancestral relationship. Furthermore, de Freitas et al. (2015) have shown that the subspecies do not correlate with aroma compounds important for cheese production. By whole-genome sequencing and comparison of genomes, Loux et al. (2015) found that the lactose fermentation is encoded by an island flanked by highly repeated transposase sequences. Furthermore, Loux et al. (2015) using core-genome analysis demonstrated that the phenotypes do not follow the phylogenetic history (in accordance with Fig. S4), definitively proving that the subdivision is not warranted. It is evident that the current definition of the two subspecies of Propionibacterium freudenreichii does not allow the classification of all strains belonging to the species. Therefore, and in accordance with our perceived impression of a consensus within the field, we propose that the subspecies are later synonyms of the species Propionibacterium freudenreichii.

Conclusion

In conclusion, we propose a reclassification of the genus Propionibacterium, on the basis of genomic evidence. The proposal is consistent with the 16S rRNA gene sequence tree and allows novel species to be assigned by 16S rRNA gene sequence homology. The proposed changes are consistent with species habitats, genomic topology, DNA G+C content and peptidoglycan composition.

Emended description of the genus Propionibacterium (Approved Lists 1980)

The description is as given for the genus Propionibacterium in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012) with the following amendments. DNA G+C content ranges from 67 to 71 mol%. Diagnostic amino acid in peptidoglycan is meso-A3PM.

Description of Acidipropionibacterium gen. nov.

Acidipropionibacterium (A.ci.di.pro.pi.o.ni.bac.te’ri.um. N. L. n. acidum propionicum propionic acid; N.L. neut. bacterium, a rod; N.L. neut. n. Acidipropionibacterium a propionic acid bacterium).

The description is as given for the genus Propionibacterium in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012) with the following amendments. DNA G+C content is 68 mol%. Diagnostic amino acid in peptidoglycan is LII-A3PM. Some strains are haemolytic. The type species is Acidipropionibacterium jensenii.
Description of *Cutibacterium* gen. nov.

*Cutibacterium* (Cu.ti.bac.te’ri.um. L. n. cutis skin; N.L. neut. n. *bacterium* a rod; N.L. neut. n. *Cutibacterium* a skin bacterium).

The description is as given for the genus *Propionibacterium* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012) with the following amendments. Members of the genus are predominately isolated from human skin. DNA G+C content is 59–64 mol%. Diagnostic amino acid in peptidoglycan is I1-A,PM, but may be meso-A,PM in occasional strains. Strains are non-haemolytic. The type species is *Cutibacterium acnes*.

Description of *Pseudopropionibacterium* gen. nov.


The description is as given for *Propionibacterium propionici* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012). The type species is *Pseudopropionibacterium propionici*.

Description of *Cutibacterium acnes* comb. nov.


The description is as given for *Propionibacterium acnes* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).

The type strain is deposited in repositories under the following strain identification numbers: ATCC 6919T=CCUG 1794T=CIP 53.117T=DSM 1897T=JCM 6425T=LMG 16711T=NCTC 737T=NRRL B-4224T=VKM Ac-1450T.

Description of *Cutibacterium avidum* comb. nov.


The description is as given for *Propionibacterium avidum* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).

The type strain is deposited in repositories under the following strain identification numbers: ATCC 25577T=CCUG 36754T=CIP 103261T=DSM 4901T=IFO (now NBRC) 15671T=NCTC 11864T.

Description of *Cutibacterium granulosum* comb. nov.


The description is as given for *Propionibacterium granulosum* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).

The type strain is deposited in repositories under the following strain identification numbers: ATCC 25564T=CCUG 32987T=CIP 103262T=DSM 20700T=JCM 6498T=LMG 16726T=NCTC 11865T.

Description of *Acidipropionibacterium jensenii* comb. nov.


The description is as given for *Propionibacterium jensenii* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).

The type strain is deposited in repositories under the following strain identification numbers: ATCC 4868T=CCUG 48883T=CIP 103028T=DSM 20535T.

Description of *Acidipropionibacterium thoenii* comb. nov.


The description is as given for *Propionibacterium thoenii* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).

The type strain is deposited in repositories under the following strain identification numbers: ATCC 4874T=CCUG 28149T=CIP 103029T=DSM 20276T=HMBI 247T=JCM 6437T=LMG 16455T.

Description of *Acidipropionibacterium acidipropionici* comb. nov.


The description is as given for *Propionibacterium acidipropionici* in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).

The type strain is deposited in repositories under the following strain identification numbers: ATCC 25562T=CCUG 28149T=CIP 103029T=DSM 4900T.
The type strain is deposited in repositories under the following strain identification numbers: M5T=NCIM 1-2360T=DSM 13435T.

**Description of Acidipropionibacterium olivae**

Basonym: Propionibacterium olivae Lucena-Padró et al. 2014.
The description is as given for Propionibacterium olivae in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).
The type strain is deposited in repositories under the following strain identification numbers: IGBL1T=CECT 8061T=DSM 25436T.

**Description of Acidipropionibacterium damnosum**

Basonym: Propionibacterium damnosum Lucena-Padró et al. 2014.
The description is as given for Propionibacterium damnosum in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012).
The type strain is deposited in repositories under the following strain identification numbers: IGBL13T=CECT 8062T=DSM 25450T.

**Description of Pseudopropionibacterium propionicum**

The description is as given for Propionibacterium propionicum in Bergey’s Manual of Systematic Bacteriology (Goodfellow et al., 2012) with the following amendment. The accession number for the 16S rRNA gene sequence of type strain DSM 43307 is NR_114803.
The type strain is deposited in repositories under the following strain identification numbers: ATCC 14157T=CCUG 4939T=NCIM 1-201941T=DSM 43307T=IFO (now NBRC) 14587T=JCM 5830T=NCTC 12967T=VKM Ac-1449T.

**References**


