**Gordonia: versatile actinobacteria for biotechnology**

A C Lienkamp, M Haarmann, D Tischler  
Research Group Microbial Biotechnology, Faculty of Biology and Biotechnology, Ruhr-Universität Bochum, Bochum, Germany  
E-mail: dirk.tischlder@rub.de

**Abstract.** The versatile genus *Gordonia* of the order *Actinomycetales* comprises numerous biotechnological interesting members. They often possess large genomes and plasmids which provide an arsenal of metabolic capabilities such as for the production of secondary metabolites, biosurfactants, bioactives, exopolysaccharides or carotenoids. Further, many can degrade a huge variety of complex organic molecules making them interesting for bioremediation. *Gordonia rubripertincta* CWB2 was found to harbour a novel styrene degradative pathway involving glutathione. This pathway is more similar to detoxification routes in higher organisms than to other bacterial routes for styrene metabolism. However, it seems to base on a mix of genes from styrene and isoprene pathways which created this novel pathway, likely by horizontal gene transfer. Now, we like to study this route in more detail and make use of it in order to produce phenylacetic acids such as ibuprofen.

1. **The Genus Gordonia**

*Gordonia* is either known as genus of the order of *Actinomycetales* or of flowering plants. However, herein we will focus on the bacteria only. The bacterial genus *Gordonia* was introduced according to descriptions by Tsukamura and Stackebrandt in 1997 [1–3]. *Gordonia* isolates were obtained from various sources such as soil, sludge, sand, rhizosphere among others. Typically, these were isolated by supplying non-natural carbon sources during enrichment cultures (e.g. aromatic carbons such as styrene; Figure 1) and thus were detected during bioremediation studies. Hence, an environmental or industrial biotechnology aspect was frequently posed towards these actinobacteria. In addition, some strains were found along medical studies and described as opportunistic pathogens. This bidirectional interest was described by Drzyzga as “the strengths” and “the weakness” of *Gordonia* [4].

![Figure 1. Gordonia-strains growing on minimal medium with aromatic substrates, in a shake flask (left) and on agar (right) while styrene was supplied over the gas atmosphere [5].](image-url)
As described above the genus belongs to the order of Actinomycetales (Table 1). In general, the representatives are described as Gram-positive with a high GC content (about 67%). They comprise mycolic acids in the cell wall as a characteristic feature. In related mycobacteria these cell wall components belong to the pathogenic signature and thus Gordonia can be employed as model organism to investigate related pathogens.

Table 1. Classification of the genus Gordonia.

| Kingdom | Bacteria |
|---------|----------|
| Phylum | Actinobacteria |
| Class | Actinobacteria |
| Order | Actinomycetales |
| Suborder | Corynebacteriales |
| Family | Gordoniaceae |
| Genus | Gordonia |

With the number of metagenomic studies and genome sequencing approaches of isolates or uncultured samples the number of available sequence information is steadily increasing. Thus, nowadays numerous genomes of Gordonia strains are available (Table 2).

Table 2. Genome sequenced Gordonia strains (selection taken from NCBI, Oct. 2020).

| Species       | Strain                  | Chromosome / Plasmid | Median total length (Mb) | Median GC% |
|---------------|-------------------------|----------------------|--------------------------|------------|
| G. aichinensis | NBRC 108223 (-)         | GCA_900105725 / NZ_BANR000000000 / - | 5.09                     | 65.3       |
| G. ajoococcus | A2 (-)                  | GCA_012974285 / -    | 5.09                     | 67.3       |
| G. alkanivorans| YC-RL2 (plus 3 other)   | NZ_CP027114 / NZ_CP027115 | 5.05                     | 67.4       |
| G. amarae     | NBRC 15530 (-)          | NZ_BAED000000000 / - | 5.31                     | 67.4       |
| G. amicalis   | CCMA-559 (plus 4 other) | GCA_000472025 / -    | 4.93                     | 67.4       |
| G. araii      | NBRC 100433 (plus 1 other) | GCA_000241265.2 / - | 3.91                     | 68.0       |
| G. bronchialis* | DSM 43247 (plus 2 other) | NC_013441 / NC_013442 | 5.3                      | 67.1       |
| G. croceae    | NBRC 107697 (-)         | NZ_BJOU000000000 / - | 3.78                     | 69.0       |
| G. desulfuricans| NBRC 100010 (plus 1 other) | GCA_001485495 / - | 5.49                     | 68.1       |
| G. effuse     | NBRC 100432 (-)         | NZ_BAEO000000000 / - | 4.7                      | 62.5       |
| G. hankookensis| ON-33 (-)              | JACWMS000000000 / -  | 5.22                     | 66.8       |
| G. hirsuta    | DSM 44140 = NBRC 16056  | GCA_000333015 / -    | 3.49                     | 68.4       |
| G. hydrophobica| NBRC 16057 (-)         | NZ_BCVU000000000 / - | 4.58                     | 67.5       |
| G. insulae   | NP8-5 (-)              | GCA_000380485 / -    | 4.23                     | 67.1       |
| G. iterans   | Co17 (-)               | GCA_002993285 / -    | 4.0                      | 69.0       |
| G. jacobaeae | mv1(-)                 | NZ_LDTZ000000000 / - | 4.93                     | 65.3       |
| G. lacucae   | BS2 (-)                | GCA_002149015 / -    | 5.76                     | 68.1       |
| G. malaicae  | NBRC 108250 (plus 1 other) | GCA_000344135 / - | 4.59                     | 66.3       |
| G. namibiensis| NBRC 108229 (-)        | NZ_BAHE000000000 / - | 4.94                     | 67.6       |
| G. neofelliciis| NRRL B-59395 (-)      | NZ_AEUU000000000 / - | 4.26                     | 68.2       |
| G. ottidis   | NBRC 100426 (-)        | NZ_BAFB000000000 / - | 5.3                      | 65.4       |
| G. paraffinivorans | NBRC 108238 (plus 11 other) | GCA_000344155 / - | 4.35                     | 69.2       |
| G. phthalatica| OH-11 (-)              | GCA_001305675 / -    | 4.43                     | 68.0       |
| G. polyisopenivorans| VH2 (plus 6 other)   | NC_016906 / NC_016907 | 6.18                     | 66.9       |
| G. rhizosphere| NBRC 16068 (-)         | NZ_BAHCO000000000 / - | 6.43                     | 67.0       |
| G. rubripertincta| CWB2 (plus 4 other) | NZ_CP022580 / NZ_CP022581 | 5.26                     | 67.4       |
| G. sedimidis | AMA120 (-)             | GCA_004193205 / -    | 7.83                     | 66.6       |
| G. shandongensis | DSM 45094 (-)     | NZ_AUHE000000000 / - | 3.33                     | 69.3       |
| G. siwensis | NBRC 108236 (plus 1 other) | GCA_000333035 / - | 4.15                     | 68.1       |
| G. soli | NBRC 108243 (-)       | NZ_BANX000000000 / - | 5.38                     | 67.7       |
| G. species (n.a.) | 42 samples         | various              | 5.19                     | 67.4       |
| G. spumicola | NBRC 107696 (-)       | NZ_BJOU000000000 / - | 4.89                     | 68.1       |
| G. spuit | NBRC 100414 (plus 1 other) | GCA_000248055.2 / - | 4.95                     | 65.3       |
| G. terrae | 3612 (plus 8 other)   | NZ_CP016594 / -      | 5.67                     | 67.8       |
| G. westfalica | DSM 44215 (plus 1 other) | GCA_900105725 / - | 5.42                     | 66.7       |

* potential (opportunistic) pathogens; “-” no other strain, plasmid or assembly data available.
In the recent years, several those strains were investigated for their properties and application in various direction [4, 6]. Also, with respect to phylogeny, several studies were conducted and we are looking forward to obtain descriptions of these species in more detail [2, 4]. Nowadays, this can be linked to the genomic context and provide a solid base for classification as well as for uncovering novel functions. While genome mining these interesting strains, we find many hidden activities to be explored in future.

2. Biotechnological Relevance of Gordonia species
Some earlier reviews on the genus Gordonia introduced the biological as well as biotechnological repertoire and possibilities [4, 6]. Most studies are related to the identification of these actinobacteria during bioremediation studies in contaminated soil or water layers. Hence, it is not surprising that these bacteria are often used to treat contaminated samples and to study the removal of toxic compounds such as diesel or aromatic compounds [6, 7]. Further, many Gordonia develop pigments during the growth and late growth or in stationary phases and thus the carotenoid production became obvious and a target for biotechnology as well [4]. The progress in genomics and other omics made it easy to screen for other properties among organisms and also Gordonia strains were investigated. Hence, the production of secondary metabolites in comparison to related actinobacteria became interesting. Some of those features are listed below.

2.1. Bioremediation and environmental biotechnology
An earlier review by the Steinbüchel group summarized nicely some capabilities of Gordonia in biodegradation such as phthalic acid esters, S-triazine, alkylpyridines, aromatic and heteroaromatic compounds, polyaromatics and ether like structures among others [6]. Some species are able to degrade natural as well as synthetic rubber (e.g. cis-1,4-polyisoprene). Those strains do utilize the polymer as carbon and energy source [8–11]. Oil and diesel can be degraded by many bacteria and among those, Gordonia species were frequently described [6, 7]. In addition, they can desulfurize fuels which can lead to a reduced emission of SOx-species [12]. Recently, a number Gordonia strains were isolated with styrene as sole source of carbon and energy [5, 13]. Styrene is one of the high-amount produced aromatics by man and used in polymer industry. It is quite toxic due to its metabolism via the reactive styrene epoxide. Interestingly, strain CWB2 utilises a pathway for styrene, which is either similar to human styrene detoxification as well as to bacterial isoprene metabolism [13, 14]. The latter might be linked to the polyisoprene degradation to be discussed [6]. See also section 4 for the detailed description of this styrene specific pathway, which can actually be used to synthesize phenylacetic acid and derivatives such as ibuprofen [5, 14].

2.2. Whole-cell biosynthesis or biotransformation
The metabolic diversity of Gordonia can be used either to produce desired compounds by means of biotransformation employing enzymes/pathways in no-natural fashion or to utilize anabolic capabilities to create target molecules [4, 6]. The latter was described for some compounds such as biosurfactants and pigments (see below in section 2.4). In addition, the co-metabolic production of compounds can be an effective method to use the metabolic repertoire of a strain to overproduce a target compound. This was described for various bacteria, which degrade styrene [5]. The styrene-induced pathway was used to metabolize substituted styrene analogous compounds, which yielded respective phenylacetic acids [5, 14]. However, to use these strains in a fermenter can be problematic. Gordonia is known to have a hydrophobic cell-surface [1–6] and thus sticks often to the wall of the fermentation or reaction vessel. This can even be seen in the flask experiment shown in Figure 1 in which the strain seems to escape from broth and moves on the glass surface to the top. This hampers productivity in a significant manner.

2.3. Enzymes from Gordonia
A number of interesting genes have been identified in genomes of Gordonia (Table 2) and subsequently be cloned for recombinant protein production. Just to mention some interesting enzymes: latex clearing
protein, acetone monooxygenase, nitrile hydratases, styrene monooxygenase, phenylacetaldehyde dehydrogenase, glutathione S-transferase, \(N\)-hydroxylating monooxygenase, lysine decarboxylase among others [4, 6, 15–20]. Details on those biocatalysts can be found in those original publications.

2.4. Secondary metabolites
A number of molecules are produced under certain growth conditions but not necessarily linked to survival of a strain [4, 6]. Often limitations of nutrients or changing habitats effect strains to start the production of such metabolites. Here we like to describe some secondary metabolites produced by Gordonia species to adapt to their environment and which could be used for biotechnological purposes.

2.4.1. Gordonan
Gordonan is an extracellular acidic polysaccharide produced by Gordonia [6, 21]. This biopolymer is composed of repeating trisaccharide units and has an effect on cell aggregation of insect cell lines. It does actually foster them to form aggregates [21]. Thus, it is described as a potential bioactive compound, which might be part of the opportunistic pathogens mechanism to infect or fix the cells to a potential host [4]. It seems to be participating as a component or trigger in biofilm formation and thus can be of relevance for biotechnological processes. However, it need to be studied how distributed the production of these bioactive molecules is among the actinobacteria and especially the genus Gordonia.

2.4.2. Biosurfactants
Biosurfactants are produced by many actinobacteria [6, 22] and therefore it is not surprising that members of the genus Gordonia produce these compounds for various reasons [23–29]. These compounds can be extracellular or bound to the cell wall. They were identified as trehalose lipids, lipopeptides and other glycolipids [4, 6]. Often the biosurfactant production by Gordonia can be triggered by either nutrient limitation and/or feeding oil or lipids and in this area they are actually also applied to degrade contaminations [7]. Hence, biosurfactant producing Gordonia are employed in environmental biotechnology or bioremediation [6]. The degradation of contamination after an oil spill comprises various carbons such as alkanes (short to long chains), aromatics and polyaromatic compounds. All those can be degraded by Gordonia making them interesting for those applications in soil or water environments [4, 6].

2.4.3. Siderophores
Siderophores are low molecular weight iron chelating compounds produced by many organisms and besides iron some can complex other metals and metalloids [30]. Gordonia species also produce siderophores such as desferrioxamines and citrate [31]. Recently, it was demonstrated that strain CWB2 does produce various desferrioxamine-like compounds, mostly desferrioxamine E, in dependency of the medium and growth condition [31–34]. Some of those compounds were assigned by LC-MS and others are predicted and await their molecular characterization [34]. It seems that the complex mixture of siderophores from Gordonia can be employed to selectively enrich metal ions and metalloids [34]. However, with respect to those secondary metabolites only little is known for the genus Gordonia yet.

3. Molecular biological tools for Gordonia
As alluded before, the genus Gordonia belongs to Gram-positive actinobacteria with a high GC content. Because of its complex cell wall (hydrophobic, mycolic-acid-containing cell envelope structures [6]) and low transformation efficiency, this genus shows problems within molecular biological work. There are limited molecular tools available for Gordonia, so far (see Table 3).

Because no suitable genetic transfer system has been described before, Arenskötter et al. identified plasmids, which were transferred to Gordonia polyisoprenivorans and related species by electroporation or conjugation [35]. They introduced an Escherichia coli/Rhodococcus shuttle vector (pNC9503 and derivative pNC9501) in G. polyisoprenivorans by electroporation [35]. These plasmids base on an origin of replication (oriV) of a native Rhodococcus plasmid (pNC903, isolated from Rhodococcus rhodochrous). Besides the optimization of the electroporation protocol Arenskötter et al. optimized the transformation efficiencies, which depend on different factors like cultivation conditions, media and
additives like cell wall-weakening supplements [35]. Furthermore, they investigated the conjugational transfer of vectors because the electroporation efficiency decreased with increasing plasmid sizes [36, 37]. Therefore, two mobilizable vectors (pBBRKnNC903 and cosmID pOpACOS) with E. coli S17-1 as donor were constructed. Further, Arenskötter et al. created recombinant G. polyisoprenivorans strains to analyze the suitability of these plasmids for transfer and heterologous expression of foreign genes [35].

### Table 3. Overview of molecular biological tools for Gordonia.

| Example | Methods | Aims of study | Ref. |
|---------|---------|---------------|------|
| G. polyisoprenivorans strain VH2, Y2K | Electroporation, conjugation | Establishment and Optimization of gene transfer systems for G. polyisoprenivorans strains and other members of genus Gordonia | [6, 35] |
| G. westfalica strain Kb1 | Shuttle vector construction | Characterization and Transfer of Megaplasmid pKB1 from G. westfalica Kb1 | [6, 38, 39] |
| G. polyisoprenivorans strain VH2 | Transposon mutagenesis | Identification of transposon for generation of insertional mutant libraries of G. polyisoprenivorans | [6, 40, 41] |
| G. jacobaeas strain MV-1, MV-26 | Electroporation | Electroporation method to transfer plasmid to G. jacobaea | [42] |
| G. alkanivorans strain | Shuttle vector construction | Establishment of a gene transfer system for G. alkanivorans RIP90A | [43, 44] |
| G. choledosterivorans strain Chol-3 | Mutagenesis by targeted gene disruption | Expression of dszABC genes of dibenzothiophene desulfurization pathway | [45] |
| Shortly afterwards the first extrachromosomal DNA of a Gordonia genus, G. westfalica Kb1, a circular megaplasmid called pKB1, was described [38]. The oriV of this 101-kbp megaplasmid was used for the construction of mobilizable E. coli-Gordonia shuttle vectors, which are also appropriate for other Gordonia species and related genera [38, 39]. For this, broad-host-range cloning vectors pBBR1MCS-2 and pBBR1MCS-5 were elected and an oriV-containing fragment of pKB1 were ligated, leading to pDBMCS-2 and pDBMMCS-5 as shuttle vectors. Both possess a multiple cloning site (MCS) and allow blue-white selection in E. coli via alpha complementation. Furthermore, these plasmids are compatible with different plasmid groups and are mobilizable. Testing the host range of oriV from plasmid pKB1
in different species of genera *Gordonia*, *Rhodococcus* and *Mycobacterium* by electroporation showed a narrow range, limited to *Gordonia* strains and closely related bacteria [38, 39]. These two plasmids represent a second functional replication system and are suitable for gene cloning and expression [6]. Since molecular tools like transposon mutagenesis or the generation of *Gordonia* knockout mutants were still rare, Banh et al. established the Tn5096-based transposon mutagenesis for *G. polyisoprenivorans* in 2005 [41]. As Arenskötter et al. described before, suicide transposon vectors haboring Tn5096 seemed to be applicable for transposon-induced mutagenesis [6]. These vectors were used to generate auxotrophic mutants with defects in amino acid-synthesizing pathways and carotenoid biosynthesis. Those were identified and characterized at the molecular level subsequently [6]. Therefore, Tn5096 was cloned into non-replicative pBluescript SK+. The resulting pMA5096 plasmid was transferred by electrotransformation and tested for its appropriateness for insertional mutagenesis in *G. polyisoprenivorans*, accordingly [41]. In conclusion, pMA5096 seemed to be suitable for mapping genes in *G. polyisoprenivorans* VH2 by integrational mutagenesis and stable mutants were obtained by this transposon mutagenesis [41].

Summarizing all above, although different tools like transformation, shuttle vectors or mutagenesis via transposons were established for several years and many *Gordonia*-specific genes were analyzed so far, molecular tools like vectors for transposon mutagenesis are still limited for the genus *Gordonia*. In future, we plan to apply related systems (Table 3) to *G. rubripertincta*, in order to uncover the regulation and functionality of novel pathways as for example glutathione dependent styrene degradation [14].

4. A styrene specific pathway for the production of ibuprofen

As the use of glutathione (GSH) is already a rare coincidence in actinobacteria, *Gordonia rubripertincta* CWB2 is even more interesting by featuring a pathway which not only utilizes GSH but can also lead to the formation of ibuprofen making it pharmacologically relevant. This was first discovered by Oelschlägel et al. wherein the feeding of CWB2 cultures with 4-isobutyl-α-methyl styrene yielded 3.45 μmol g cdw⁻¹ 4-isobutyl-α-methylphenylacetic acid (ibuprofen) within 12 h of biotransformation [5]. Styrene specific and isoprene specific degradation seem to be homologous pathways in actinobacteria [13, 14], still CWB2 is so far the only known candidate to convert lager substituted styrenes. Heine et al. investigated this interesting pathway of CWB2s metabolism which revealed the involvement of a glutathione S-transferase to conduct conversions where usually, in homologous pathways, isomerases act [5, 13, 46]. The pathway starts with a monooxygenase (StyA/StyB) which forms styrene oxide from styrene. The epoxide is then further metabolized by the addition and removal of glutathione through the glutathione S-transferase (StyI). This allows the formation of phenylacetic acid (PAA) after a series of multiple enzymatic steps, which have not been experimentally proven so far (Figure 2). This exchange of an isomerase to a glutathione S-transferase allows for a broader substrate range and thus the generation of ibuprofen *via* this natural pathway.

In *vivo* the conversion of styrene and its derivatives to the corresponding phenylacetic acids (PAAs) enables the organism not only a route for detoxification of this toxic compounds but also a utilization as carbon source when it can be funneled *via* multiple conversions steps to finally enter the central metabolism. From a biotechnological point, this detoxification route might enable the easy and cost efficient production of versatile valuable compounds, as PAA derivatives serve as precursors for several pharmaceutics, flavors and fragrances [5, 46–49]. Thus, an application of the pathway either in biotransformation or as enzyme cascade is desirable.
Figure 2. Production of ibuprofen in *Gordonia rubripertincta* CWB2. The styrene derivative 4-isobutyl-α-methylstyrene is converted in the styrene specific degradation pathway by action of a monooxygenase (StyA/StyB) and a glutathione S-transferase (Styl) followed by subsequent enzymatic conversions to finally form ibuprofen (4-isobutyl-α-methylphenylacetic acid).

5. Conclusion
Most *Gordonia* species are related to either the degradation of toxic and/or man-made compounds in bioremediation studies or applied in biotransformation studies to produce valuable compounds. The latter are for example biosurfactants or biopolymers which is currently a growing market. In this context, we could demonstrate earlier that styrene degradation enables *Gordonia rubripertincta* CWB2 to consume toxic styrenes while leading to valuable phenylacetic acids [5]. A number of molecular biological tools have been developed for actinobacteria and can be used to manipulate *Gordonia* as well. This we will now employ to evaluate the individual parts of the above described novel styrene degradative pathway in order to uncover its detailed functionality and regulatory machinery [13, 14]. Further, we will try to improve the use of this pathway to overproduce valuable compounds such as ibuprofen [5]. This strain might become a model organism in order to study degradation of aromatic compounds or to produce secondary metabolites.

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