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REVIEW

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An overview on biosystematics of actinomycetes

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ABSTRACT

Actinomycetes, are Gram-positive bacteria with high G+C content and diverse biosynthetic gene clusters. They synthesize various bioactive secondary metabolites, including antibiotics, antifungals, anticancer agents, and immunosuppressive compounds. Their genetic makeup supports regulatory mechanisms and horizontal gene transfer, enhancing their metabolic adaptability and ecological success. This review highlights methodologies such as genome sequencing and chemotaxonomic markers in identification of Actinomycetes, which have markedly enhanced researchers' capacity to explore these organisms for their full potential. Over 10,000 potential BGCs have been identified, but most are silent under standard laboratory conditions, highlighting a research deficiency in genotype-chemotype correlation. Genome sequencing has revolutionized genomics, but the structural prediction bottleneck makes it challenging for bioinformatics tools to accurately forecast new chemical scaffolds and biological functions. This review explores advanced strategies for activating silent BGCs, such as co-culture elicitation, synthetic biology, and integrative multi-omics techniques, in silico prediction. Actinomycetes play a crucial role in biomedical innovation, contributing to the discovery of novel pharmaceuticals and bioactive molecules for cancer and chronic diseases.

KEY WORDS

Actinomycetes; Streptomyces; Biosystematics; Biosynthetic pathways; Metabolites

ARTICLE HISTORY

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Introduction

Actinomycetes exhibit traits of both bacteria and fungi yet possess distinct characteristics that ensures their classification within the kingdom of bacteria. These are Gram-positive bacteria that produce branching hyphae capable of developing into mycelium, exhibit a complex life cycle and represent one of the largest taxonomic groupings among the 18 major lineages within the domain bacteria [1]. Actinobacteria represents one of the most significant taxonomic units within the bacterial domain. Currently, genomes of actinobacteria have been sequenced for species pertinent to human and veterinary medicine, biotechnology, and ecological studies. Genomic heterogeneity is believed to represent biodiversity. A significant number of actinobacteria exist as free-living organisms, inhabiting various terrestrial, aquatic, and marine ecosystems. Actinobacteria represent a group of Gram-positive filamentous bacteria characterized by their large G+C genomes. They expand through the branching of hyphae and the extension of tips. Their name is derived from the Greek words for ray (Aktas or Atkin) and for fungal and bacteria. A significant number of Actinobacteria produce a mycelium and engage in reproduction through sporulation, like filamentous fungi [2].

Actinomycetes, like all bacteria, possess thin cells characterized by a prokaryotic nucleoid and peptidoglycan cell walls, making them susceptible to antibacterial treatments. The majority of Actinobacteria thrive in aerobic conditions, although some do not require oxygen for their survival. The predominant organisms are chemoheterotrophic and can utilize a range of nutritional sources, such as complex polysaccharides. Actinobacteria can inhabit soil or aquatic environments such as *Streptomyces*, *Monospora*, *Rhodococcus*, and *Salinispora* species, function as plant symbionts like Frankia spp., act as plant or animal pathogens including *Corynebacterium*, *Mycobacterium*, or *Nocardia* species, or serve as gastrointestinal commensals such as *Bifidobacterium*. Streptomyces and other actinobacteria are saprophytic, soil-dwelling organisms that primarily exist as semidormant spores, particularly in environments where nutrients are scarce. Actinomycetes inhabit various environments, including soils, fresh and salt water, as well as the atmosphere [3].

Morphology

Actinobacteria, recognized for their remarkable morphological diversity among Gram-positive bacteria, maintain typical prokaryotic cell cultures that starkly contrast with fungal structures. Their hyphal cells exhibit a classic bacterial organization, featuring cytoplasmic regions containing genomic DNA, ribosomes, and storage inclusions such as polypeptides, lipids, or polysaccharides. Generally, actinomycetes develop a well-defined radial mycelium, while certain Actinobacteria can produce intricate structures, including spores, spore chains, and sporangia, and sporangiospores. Key morphological traits for classification encompass the growth and arrangements of substrate mycelium, the positioning and quantity of spores, the surface characteristics of spores, the morphology of sporangia, and perhaps the presence of flagella on the sporangiospores [4].

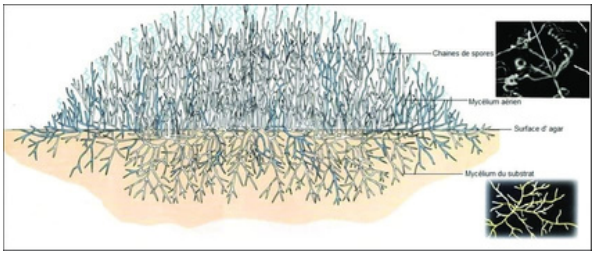

Figure 1. Morphology of Actinomycetes: Aerial and Substrate Mycelium with Spore Chains [4].

Substrate mycelium

Substrate mycelium, also known as vegetative or primary

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mycelium, is a crucial component of actinobacteria, primarily responsible for nutrient absorption and growth support. This mycelium grows either into or on the surface of culture media, characterized by slender, transparent hyphae that appear dark under phase-contrast microscopy. Typically, these hyphae range from 0.4 to 1.2 micrometers in thickness, lack diaphragms, and exhibit extensive branching, particularly in genera such as *Nocardia* [5].

The substrate mycelium serves as the fundamental vegetative phase for actinomycetes, forming a network of branched hyphae that facilitate environmental aggregation and nutrient uptake through the secretion of extracellular enzymes that decompose complex organic materials [6]. As growth progresses, especially in *Streptomyces* species, morphological differentiation occurs, leading to the formation of aerial mycelia and spores in response to nutrient depletion or environmental stress. This differentiation is not only structural but also metabolic, as the substrate mycelium plays a vital role in the biosynthesis of secondary metabolites, including antibiotics, during later vegetative stages or sporulation onset [7].

The taxonomic classification of organisms traditionally grouped with actinobacteria, such as *Calothrix*, *Nocardia*, and *Discomyces*, has been contentious, with varying classifications as bacteria or fungi [8]. Moreover, the relationship between actinomycosis in humans and cattle remains under scrutiny, necessitating a comprehensive understanding of the morphological variations of the causative microorganisms [9]. Recent studies have also focused on thermophilic actinomycetes, leading to the development of identification keys for various genera based on morphological and biochemical traits [10]. Therefore, substrate mycelium is integral to the ecological role of actinobacteria, influencing both their growth and their interactions within various environments, while also contributing to significant health implications in humans and animals.

Biochemistry

The biochemistry of actinomycetes, a diverse group of filamentous, Gram-positive microorganisms, is characterized by their complex secondary metabolic processes, which enable the production of a wide array of biologically active compounds, including antibiotics, antifungals, antivirals, and anticancer agents [11]. Central to these metabolic activities are sophisticated enzyme systems such as polyketide synthases (PKSs) and non-ribosomal peptide synthetases (NRPSs), which facilitate the biosynthesis of secondary metabolites. Actinomycetes also exhibit unique biochemical traits, including the synthesis of mycolic acids and the incorporation of unusual sugars in their cell walls, alongside pathways for nitrogen fixation and the degradation of complex substances like cellulose and chitin [11,12].

Historically, actinomycetes have been underexplored compared to other microorganisms, leading to ongoing debates regarding their classification whether they belong with bacteria, fungi, or in a distinct category [13]. Their ecological roles as saprophytes and parasites further complicate this classification. Recent studies have highlighted their metabolic versatility and adaptability, particularly in nutrient acquisition and growth, which are intricately linked to their secondary metabolism and developmental processes [14].

Molecular Systematics

Molecular systematics in actinomycetes utilizes DNA sequencing to elucidate their evolutionary relationships and refine taxonomy, addressing the limitations of traditional phenotypic methods such as morphological and biochemical profiling [15]. The 16S rRNA gene sequencing has emerged as the benchmark for identifying actinomycetes at both genus and species levels. Additionally, advanced techniques like multilocus sequence analysis (MLSA), DNA-DNA hybridization (DDH), whole genome sequencing, and phylogenomic approaches are increasingly adopted to resolve taxonomic ambiguities and improve classification accuracy within this diverse group of bacteria.

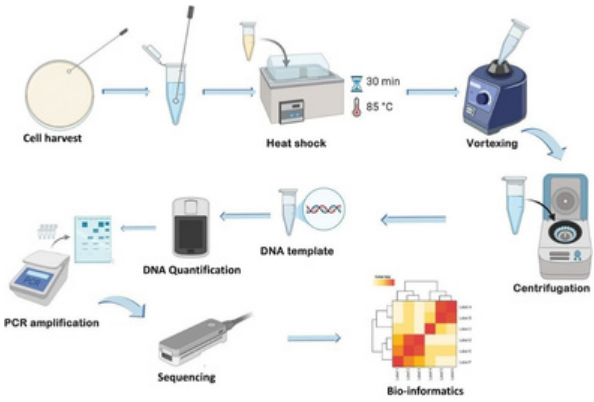

Figure 2. Schematic representation of Molecular identification of actinobacteria.

Isolation of DNA

The isolation of DNA from actinomycetes is a critical process for molecular research, enabling applications such as gene cloning, sequencing, and phylogenetic analysis. Actinomycetes, characterized by their thick peptidoglycan-rich cell walls and potential mycolic acid content, necessitate specialized lysis techniques for effective DNA extraction. The procedure typically initiates with cell harvesting, followed by either enzymatic (e.g., lysozyme) or mechanical disruption to breach the robust cell wall. Subsequent treatment with detergents, such as sodium dodecyl sulfate (SDS), and proteinase K facilitates the removal of proteins [16]. The DNA is then purified through organic solvents like phenol-chloroform and precipitated with alcohol, commonly ethanol or isopropanol. This meticulous process yields high-quality genomic DNA suitable for various downstream applications, including harvesting the cells, centrifugation and resuspended in TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 8.0) with lysozyme (2 mg/ml) for cellular lysis at 30°C for 30 minutes. Following this, 1.2 ml of 0.5 M EDTA and protease (0.2 mg/ml) are introduced, with an additional incubation period of 30 minutes to further degrade proteins. The subsequent addition of 0.7 ml of 10% sodium dodecyl sulfate (SDS), 1.8 ml of 5 M NaCl, and 1.5 ml of a 10% CTAB NaCl solution facilitates the extraction process, with incubation at 65°C for 20 minutes to enhance DNA solubilization [17].

Methods of DNA isolation

Classical chemical lysis method: The classical chemical lysis method is a well-established and commonly employed

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technique for extracting high-quality genomic DNA from actinomycetes, especially Streptomyces species. Because actinomycetes possess complex, rigid cell walls rich in peptidoglycan, this method combines enzymatic treatment with chemical agents such as detergents and organic solvents to effectively break down the cell structure and release the DNA [18].

CTAB (Cetyltrimethylammonium Bromide): It is a widely used protocol for the isolation of high-quality genomic DNA from actinomycetes, particularly from environmental or soil-derived strains that produce large amounts of extracellular polysaccharides and secondary metabolites. Actinomycetes, especially those belonging to the Streptomyces genus, often present difficulties in DNA extraction due to their tough, peptidoglycan-rich cell walls and the production of bioactive compounds that can interfere with DNA purity [19].

DNA extraction was performed utilizing a modified CTAB method, followed by the amplification of the 16S rDNA region through polymerase chain reaction (PCR) with universal primers 27F and 1525R (5'-AGAGTTTGATCMTGGCTCAG and 5'AAGGAGGTGWTCCARCC, respectively). The resulting PCR product was purified, sequenced, and analysed using BLAST against the NCBI database. The sequence showed high similarity with representative 16S rDNA sequences of *Streptomyces* species [20].

Mechanical disruption / Bead beating: Bead beating, a form of mechanical disruption, is a commonly employed technique for extracting genomic or metagenomic DNA from actinomycetes, especially those that are environmentally derived or resistant to standard enzymatic lysis. Due to their thick, multilayered cell walls, actinomycetes are often difficult to lyse using enzymes alone. In bead beating, microbial cells are combined with small glass or zirconia beads and subjected to vigorous agitation using a bead mill or vortex. This mechanical force physically shatters the robust cell walls, enabling the release of intracellular components, including DNA [21].

The efficient isolation of DNA from actinomycetes is essential for their molecular characterization and biotechnological applications, particularly in antibiotic production and environmental microbiology.

Table 1. Comparison of different approaches of DNA isolation of Actinobacteria

Method	Principle / Mechanism	Key Reagents	Advantages	Limitations	DNA Yield & Purity
Classical ChemicalLysis Method	Combines enzymatic digestion (e.g., lysozyme) and chemical lysis (detergents, organic solvents) to disrupt thick peptidoglycan cell walls and release DNA.	Lysozyme, SDS, phenol: chloroform, ethanol or isopropanol for precipitation.	Produces high-molecular-weight DNA suitable for downstream applications like PCR and sequencing.	Labor-intensive, uses toxic chemicals (phenol/chloroform); time-consuming.	High yield and good purity; A260/280 ~1.8.
CTAB (Cetyltrimethyl ammonium Bromide) Method	Cationic detergent (CTAB) lyses cells and binds polysaccharides and secondary metabolites, allowing purification of nucleic acids from complex actinomycetes.	CTAB buffer (CTAB, NaCl, EDTA, Tris), chloroform: isoamyl alcohol, ethanol.	Efficiently removes polysaccharides and pigments; yields high-purity DNA suitable for PCR and sequencing.	May require optimization for each strain; residual CTAB may inhibit enzymes if not fully removed.	High yield and purity; good for GC-rich genomes; suitable for PCR amplification of 16S rDNA.
Mechanical Disruption (Bead Beating)	Physical disruption of tough actinomycete cell walls using high-speed agitation with small beads to mechanically shear cell envelopes and release DNA.	Bead mill or vortex, zirconia/silica or glass beads, lysis buffer.	Rapid and efficient lysis, effective for strains resistant to enzymatic/chemical methods; suitable for metagenomic studies.	Risk of DNA shearing; heat generation can degrade DNA; may need cooling cycles.	Moderate to high yield, but DNA may be fragmented; suitable for PCR or metagenomic sequencing.

G+C of actinomycetes

Actinomycetes, a group of filamentous, Gram-positive bacteria within the phylum Actinobacteria, are distinguished by their high guanine-cytosine (G+C) content in DNA, typically ranging from 63% to 78%. This elevated G+C content is crucial for DNA stability and supports complex metabolic processes, enhancing their adaptability to various environments [22]. It serves as a key evolutionary and taxonomic marker, particularly within the genus Streptomyces, renowned for its antibiotic production , which often exhibits G+C values exceeding 70%. The richness in G+C content not only aids in microbial classification but also underpins the expression of extensive biosynthetic gene clusters responsible for synthesizing secondary metabolites, highlighting the ecological significance and metabolic diversity of actinomycetes [23].

The genus Actinomyces, classified within the phylum Actinobacteria, is a group of Gram-positive bacteria characterized by a notable guanine-cytosine (G+C) content in their DNA, typically ranging from 59% to 61%. This G+C content, which is moderate compared to the broader ctinomycete range of 55% to 75%, contributes to the thermal stability of their DNA, influences codon usage, and regulates gene expression, thereby playing a crucial role in genomic architecture. Furthermore, variations in G+C levels among different Actinomyces strains provide insights into their ecological adaptations and genetic diversity, making it a significant molecular marker for taxonomy and phylogenetics [24].

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Chemosystematics

Chemosystematics plays a pivotal role in the taxonomy and identification of actinomycetes, a morphologically similar yet chemically diverse group of bacteria. Traditional reliance on phenotypic characteristics can lead to misclassification due to overlapping traits among species. Instead, chemical markers such as the composition of cell wall amino acids (e.g., LL-diaminopimelic acid), specific sugar residues, menaquinone types, phospholipid profiles, and fatty acid methyl ester (FAME) patterns provide a more reliable means of distinguishing between genera and species [25]. For example, variations in cell wall chemotypes are crucial for differentiating genera like *Streptomyces*, *Nocardia*, and Actinomyces, each characterized by unique peptidoglycan types and sugar compositions.

Cell-wall fatty acids: Cell wall fatty acids are increasingly recognized as critical chemotaxonomic tools for the classification and identification of actinomycetes, a diverse group of Gram-positive filamentous bacteria. These microorganisms are characterized by complex cell envelopes that contain unique fatty acids, which vary in chain length, saturation, and branching, particularly in the form of iso branched chains [26]. The analysis of these fatty acids is typically conducted through gas chromatography of their fatty acid methyl ester (FAME) derivatives, producing consistent chemical profiles that facilitate differentiation at both the genus and species levels [27].

Cell wall sugars: Cell wall sugars serve as crucial chemotaxonomic indicators in the classification and differentiation of actinomycetes, providing significant insights into their taxonomic categorization. These sugars, integral to the peptidoglycan matrix and teichoic acid components of the cell wall, exhibit variability across different taxa, thereby offering distinctive features for identification. Commonly identified sugars in whole-cell hydrolysates include arabinose, galactose, glucose, rhamnose, ribose, mannose, and maduros. The presence or absence of these sugars can effectively differentiate various genera and species within the actinomycetes. For instance, members of the genus Streptomyces are typically characterized by a lack of distinctive diagnostic sugars, whereas genera such as Nocardia and Actinophages are noted for their content of arabinose and galactose, categorizing them into defined sugar types of Type IV and Type V respectively [28].

Menaquinones: Menaquinones, commonly referred to as vitamin K_2 derivatives, play an essential role in the electron transport chain of various Gram-positive bacteria, notably within the actinomycetes group. Their significance extends beyond metabolic functions, as they exhibit considerable structural diversity, particularly in the number of isoprene units, denoted as MK-n, and the extent of hydrogenation. This variability renders menaquinones reliable chemical markers in the field of chemosystematics [29].

Polar lipids: In a recent study, polar lipids were categorized based on their pigment production on oatmeal and peptone-yeast extract-iron agars. A total of 44 representative strains from various pigment groups were meticulously identified through complete 16S rRNA gene sequencing. These strains were subsequently classified into the genera *Dactyl sporangium*, *Micromonospora*, and *Streptomyces* [30].

Neutral fatty acids: Neutral fatty acids play a crucial role as chemotaxonomic indicators in the classification of actinomycetes, significantly contributing to the analysis of cellular lipids. These fatty acids, predominantly found within the cell membrane and cytoplasmic compartments, exhibit considerable variation in terms of chain length, saturation, and branching patterns. Such diversity provides distinct chemical profiles that facilitate the differentiation of various species and genera within this group [31].

In the context of actinomycetes, the most prevalent neutral fatty acids include straight-chain, iso-branched, and ante-iso-branched saturated types. Notably, species within the genus *Streptomyces* are characterized by elevated levels of ante iso C15:0 and iso C16:0 [32].

Chemosystematics, the classification of organisms based on their chemical composition, significantly enhances the genetics and taxonomy of actinomycetes. One of its primary advantages is the provision of stable biochemical markers, such as cell wall amino acids, fatty acids, sugars, and isoprenoid quinones, which complement genetic data and facilitate the accurate differentiation of morphologically similar or genetically close strains. For example, specific cell wall diamino acids like LL-diaminopimelic acid and diagnostic sugars such as arabinose and galactose are instrumental in distinguishing genera like *Streptomyces*, *Nocardia*, and *Micromonospora* [33].

Moreover, chemosystematics proves invaluable in discovering and characterizing novel taxa, particularly from unexplored ecological niches. Many newly isolated actinomycetes from marine and extreme environments exhibit unique chemical profiles that can lead to the identification of new species or genera, especially when genetic similarities are ambiguous. Additionally, variations in chemical profiles often reflect niche-specific metabolic capabilities encoded by biosynthetic gene clusters (BGCs), thereby illuminating evolutionary relationships and ecological adaptations [34].

Chemosystematics has made significant contributions to the taxonomy of actinomycetes; however, it faces notable limitations in genetic studies. A primary concern is the variability of chemical profiles influenced by environmental factors such as growth medium and temperature, which can lead to inconsistencies in species identification [35]. This variability hampers reproducibility and complicates cross-laboratory comparisons. Furthermore, chemosystematic traits often lack resolution at the strain or subspecies level, as closely related strains may exhibit conserved chemical characteristics, making differentiation challenging. In contrast, genomic methods like average nucleotide identity and digital DNA-DNA hybridization provide superior discriminatory power. Additionally, the labor-intensive nature of chemosystematics, which requires specialized techniques such as gas chromatography and mass spectrometry, may limit its accessibility in many microbiology laboratories [36].

Disclosure Statement

The author does not have conflict of interest in this research.

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