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REVIEW

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Ecological distribution and secondary metabolites of marine actinobacteria: a comprehensive review

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ABSTRACT

Actinobacteria are a diverse group of Gram-positive bacteria characterized by high guanine-cytosine (G+C) content and broad ecological distribution across terrestrial, marine, and extreme environments. Marine-derived and extremophilic actinobacteria have attracted significant scientific interest due to their ability to produce structurally diverse secondary metabolites and industrially important enzymes. This review highlights the ecology, taxonomy, morphology, and metabolic diversity of actinobacteria, with special emphasis on marine and extremophilic species. Their complex morphological structures, including filamentous mycelia and spore-forming capabilities, play an essential role in identification and adaptation to diverse habitats. The review further discusses the biosynthetic potential of actinobacteria, particularly the polyketide synthase (PKS) and non-ribosomal peptide synthetase (NRPS) pathways, which produce valuable bioactive compounds such as abyssomicin C and salinosporamide A, which exhibit antimicrobial, anticancer, and pharmaceutical significance. Additionally, extremophilic actinobacteria produce unique extremozymes that are remarkably stable under harsh environmental conditions, making them suitable for industrial and biotechnological applications. Despite their immense potential, challenges such as slow growth rates, low biomass yield, and difficulties in cultivation hinder large-scale production and enzyme recovery. Advanced approaches, including metagenomics, genome mining, and heterologous expression, have emerged as promising strategies for accessing uncultivable strains and cryptic biosynthetic gene clusters. Overall, marine and extremophilic actinobacteria represent an important resource for novel drug discovery, environmental sustainability, and future biotechnological innovation.

KEY WORDS

Actinobacteria; Streptomyces; Marine-bacteria; Secondary metabolites; Biosynthetic-gene-clusters

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Introduction

Actinobacteria are a well-known group of Gram-positive bacteria. They are known for having a lot of Guanine and Cytosine (G+C) in their DNA. They are very different in many environments, including the ocean, on land, and in harsh environments [1]. These bacteria can be found in many places, such as caves, deserts, and polar regions. They also coexist with other living organisms.

Actinobacteria show a wide range of shapes, from complex filamentous arrangements to single-celled forms [2]. Their primary mode of reproduction involves spores, necessitating fragmentation and the formation of conidia. The mycelium comes in different sizes, shapes, and colors, and can be divided into two types: substrate and aerial [3]. Most genera do well at mesophilic temperatures of around 28°C, but there are also psychrophilic and thermophilic types. Morphological characteristics, particularly those of mycelium and spore structures, are essential for the identification of actinobacterial isolates [4].

Some actinobacteria, which are extremophiles, have evolved unique metabolic pathways that generate compounds absent in terrestrial microorganisms, enabling them to flourish in extreme environments. These extremozymes, especially those from marine actinobacteria, are of great interest because they could be useful in industry and medicine. For instance, the marine actinomycete Saccharopolyspora sp. It produces the enzyme amylase. This is most efficient at pH 11.0 and remains stable over a wide pH range [5].

In microbiology, the cultivation of extremophiles poses considerable challenges necessitating innovative methodologies such as metagenomics to explore the genetic diversity of microbial communities without prior isolation [6].

Deep-sea extremophiles, predominantly located in the prokaryotic domains of Archaea and Bacteria, have evolved specialized physiological mechanisms for survival, enabling them to thrive in extreme physical and geochemical conditions [7].

Extremophiles exhibit reduced growth rates and lower biomass yields than non-extremophilic organisms, complicating enzyme production despite the promising potential of extremozymes [8]. In this case, larger culture volumes and longer fermentation times are needed, which makes the production process more difficult. Researchers often use heterologous expression systems to produce these enzymes, but this approach has its own drawbacks [9]. Actinobacteria are also important for breaking down organic matter and storing carbon.

Distribution of Actinobacteria

Actinobacteria exhibit a diverse distribution in terrestrial and aquatic ecosystems, significantly impacting antibiotic discovery and ecological functions. Their capacity to acclimatize to extreme conditions further suggests their potential as sources of novel bioactive compounds [10].

Terrestrial actinobacteria

Actinomycetes, primarily saprophytic organisms, inhabit various terrestrial environments, including soils, lakes, and plants. These organisms thrive in soils where ecological factors, such as nutrient availability, pH, and moisture, are essential for their growth [11]. There are many actinomycetes, but only about 10% have been isolated. This shows that more research is needed to discover new antibiotic-producing

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species, especially those that are resistant to antibiotics. There are many species of the genus Streptomyces in soil ecosystems, and some of them have antibacterial properties [12].

Research has detected actinobacteria in diverse soil types, including sandy and alkaline soils, across various geographical areas [13]. Environmental factors, such as pH and organic matter content, greatly affect where actinomycetes live. Most of them do best in neutral to slightly alkaline conditions [14]. Actinobacteria originating from tropical and subtropical areas show promise for the synthesis of bioactive compounds that combat multidrug-resistant pathogens [11].

Aquatic actinobacteria

Freshwater ecosystems serve as significant reservoirs of actinobacteria, with Streptomyces predominant in river waters and Micromonospora frequently found in sediments [13]. These organisms are essential for their antifungal properties and potential as sources of novel antimycotic agents. Marine ecosystems, especially sponges, harbor substantial populations of actinobacteria that are essential for producing bioactive compounds [15].

Extremophilic actinobacteria

Extremophilic actinobacteria, capable of withstanding extreme conditions such as elevated salinity and temperature, have been identified in various habitats, including hypersaline soils and volcanic caves [16]. These organisms exhibit unique adaptations that allow them to thrive in extreme environments, often producing bioactive metabolites with antimicrobial properties [17]. Acidophilic actinobacteria reside in acidic soils, preferring a pH range of 4.5 to 6.5, and are categorized into specific taxonomic groups based on their chemotaxonomic characteristics [18].

Rhizosphere, Endophytic, and Symbiotic Niche

Actinobacteria live in the rhizosphere and plant tissues as endophytes. Rhizospheric Streptomyces protect plants by making antibiotics and lytic enzymes. Sponge-associated and other marine symbioses are significant; genera such as Salinispora, Micromonospora, Streptomyces, and Nocardiopsis often serve as sponge symbionts, contributing a substantial fraction of sponge-derived secondary metabolites [19].

Biosynthetic Gene Clusters and Metabolic Pathways

Polyketide synthases (PKSs) and non-ribosomal peptide synthetases (NRPSs) are the main things that make actinobacteria's secondary metabolism special. Polyketide synthases (PKSs) are divided into types I–III and make polyketide scaffolds by repeatedly condensing malonyl-CoA or other extender units. Non-ribosomal peptide synthetases (NRPSs) create peptides from certain amino acids by using condensation, adenylation, and thiolation domains [20]. Genome mining consistently reveals numerous 'silent' biosynthetic gene clusters (BGCs) within each strain, often exceeding 15, thereby propelling initiatives in elicitation and heterologous expression.

Polyketides and peptides are significant categories of natural products synthesized through complex enzymatic pathways, primarily involving polyketide synthases (PKSs) and non-ribosomal peptide synthetases (NRPSs). Polyketides are categorized into three classes, produced via the repetitive decarboxylative condensation of acyl-CoA-derived extender units [21]. Various biological activities have been demonstrated, with compounds such as epirubicin and doramectin used in therapeutic contexts [22].

Peptides are typically short chains of amino acids that often display cyclic structures and unique amino acid compositions. Mechercharmycins, derived from marine Thermoactinomyces sp., demonstrate significant antitumor activity [23]. Thiocoraline, a cyclic thiodepsipeptide obtained from Micromonospora sp., demonstrates considerable antitumor and antimicrobial efficacy against Gram-positive bacteria [22].

NRPSs and PKSs are large, multi-domain enzymes that synthesize secondary metabolites. Non-ribosomal peptide synthetases (NRPSs) create non-ribosomal peptides by joining amino acid monomers together in a chain. At the same time, polyketide synthases (PKSs) assemble polyketides from two-carbon ketide units derived from thioesters [23]. Each module in these synthases has core domains that are important for adding peptide or ketide units, as well as optional domains that can be used to change the structure. The biosynthetic process ends with the release of the final product by a thioesterase domain, and linkers allow functional domains to communicate [24].

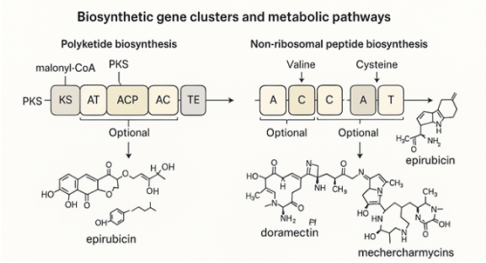

Figure 1. The intricate enzymatic pathways involved in the biosynthesis of polyketides and peptides and their importance in pharmacology and biotechnology highlight the potential for novel therapeutic agents derived from these natural products.

Secondary Metabolites and Bioactivities

Secondary metabolites are non-essential compounds produced by organisms, especially actinobacteria, that facilitate environmental interactions and provide defense against biotic and abiotic stresses. The metabolites comprise diverse chemical families, exhibit significant inducibility in response to environmental stressors, and possess considerable economic significance due to their utilization in pharmaceuticals, flavorings, fragrances, insecticides, and dyes [25]. Secondary metabolites have several medical uses, including fighting infections, inhibiting tumor growth, and suppressing the immune system.

Marine actinobacteria produce numerous bioactive compounds, including polyketides, non-ribosomal peptides, alkaloids, terpenes, and halogenated compounds. Medically significant molecules encompass erythromycin (a polyketide macrolide), avermectin, salinosporamide A (a proteasome inhibitor), abyssomicin C (an antibacterial folate pathway inhibitor), the thiocoraline (an antitumor agent), among others [26]. Amphotericin B and polyketides, such as erythromycin and rapamycin, are utilized in the treatment of infections and cancer [11].

Agents with antibacterial and antifungal properties

Actinomycetes, which belong to the order Actinomycetales, are important sources of secondary metabolites. They produce more than 10,000 known antimicrobial agents that are used in

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medicine. These microorganisms can make vitamin B12, which is important for many biological processes. When cobalt is added to fermentation media, it can also help produce antibiotics such as streptomycin and erythromycin [27].

Antibiotics, primarily produced by actinomycetes, are low-molecular-weight organic compounds that inhibit microbial proliferation. About 75% of antibiotics come from these organisms, with Streptomyces being the main one. It makes up about 45% of all known bioactive metabolites [28]. Recent discoveries of new antibiotics, such as mediomycins A and B, underscore the importance of actinomycetes in drug discovery.

Marine actinobacteria, particularly those in the genus Streptomyces, are recognized for their considerable biosynthetic capacity, enabling the production of various secondary metabolites, including antibiotics [29]. About 10,000 of the 23,000 known antibiotics are derived from actinobacteria, underscoring their importance in developing new medicines [30]. Marine species of Streptomyces and Actinomadura produce chitinases and antifungal metabolites that are useful in medicine and farming [22].

Marine actinomycetes in aquaculture are recognized for their capacity to enhance growth in juvenile fish and shrimp by producing bioactive compounds, such as boromycin and azalomycin, which also exhibit antimicrobial properties. Abyssomicin C and related polyketides are effective against Gram-positive pathogens resistant to multiple drugs, such as vancomycin-resistant Enterococcus (VRE) [22].

Compounds with anticancer and antitumor properties

Salinosporamide A, obtained from Salinispora tropica, is a notable marine-derived proteasome inhibitor that has advanced to clinical trials for multiple myeloma [31]. Streptomyces-derived compounds demonstrate antitumor activity, with Mitomycin C serving as a prominent example employed in cancer treatment due to its ability to disrupt DNA replication [32].

Biosurfactant compounds

Actinomycetes are significant sources of biosurfactants, surface-active agents that reduce surface tension and function effectively in extreme environmental conditions. This characteristic makes them useful in a variety of fields, including aquaculture [33].

Biopesticide compounds

Actinomycetes have been utilized as biopesticide agents, proving effective in managing insect populations, such as house flies and mosquitoes [34].

Compounds that promote plant growth

They also produce plant growth hormones, such as indole-3-acetic acid (IAA), which is very important for controlling plant growth and development [35].

Secondary metabolites from actinomycetes and other microorganisms are essential in various fields, including medicine, agriculture, and biotechnology, highlighting their potential as sustainable sources of valuable compounds.

Collection, Pretreatment, and Isolation

To harness marine actinobacteria's biosynthetic potential and discover new bioactive compounds, it is important to collect and process samples systematically. This will help with pharmaceutical applications.

Scuba, grab samplers, or cores are used to take samples in the field in marine environments. The samples are kept cold and processed quickly. Dry heat and phenol exposure, as well as selective media such as starch-casein, Kuster's, ISP2, and Bennett's, work together with antibiotics and antifungals to help actinobacteria grow while preventing fast-growing contaminants from growing. It is often necessary to incubate for 2 to 6 weeks at 28°C [34-36].

There are many ways to collect marine samples to isolate actinobacteria. Montalvo et al. recorded the acquisition of sponge samples via scuba diving at Conch Reef, Florida, and in Manado, Indonesia, with the condition that samples be processed within two hours of collection [37]. Meena et al. collected marine sediment samples from Minnie Bay and selected 26 unique colonies for characterization based on morphology [38].

Maldonado et al. delineated selective isolation methodologies for sediment samples retrieved from depths of 300 meters in the Gulf of California and the Gulf of Mexico [36]. A total of 126 marine sediment samples were taken from the Japan Trench and the Canary Basin during two expeditions [26]. The samples were meticulously handled, preserved in sterile conditions, and conveyed to laboratories for further analysis, as evidenced by the methodologies utilized by Dhanasekaran and Jiang in their study of the Gulf of California [39].

To isolate actinomycetes, you can use methods like dry heat treatment followed by plating on starch-casein agar, or exposure to 1% phenol followed by subculturing on glucose-asparagine agar. Additionally, specific sediments were directly inoculated onto chitin agar or filtered through cellulose ester membrane filters, resulting in isolation on modified Bennett agar. Cycloheximide (100 µg/ml) was added to the modified Bennett agar to prevent contamination [12].

Morphology and Spore Morphology

The morphological characterization of Actinobacteria, particularly within the genus Streptomyces, employs both macroscopic and microscopic methodologies to distinguish species and clarify their taxonomy. Microscopic examination delineates critical characteristics, including substrate and aerial mycelium, spore arrangement, and pigmentation, vital for precise identification [15]. The cover slip culture method permits meticulous examination of mycelial structures and spore types via oil immersion microscopy, facilitating comparison with recognized taxonomic references, including Bergey's Manual of Determinative Bacteriology [29].

Morphological classification is based on microscopic morphology and chemotaxonomy, which examine features such as cell wall composition and sugar distribution. Actinobacteria exhibit various morphologies, including coccoid forms and highly branched mycelia, as well as variations in spore production and pigmentation.

Their branched mycelium and spore chains characterize Streptomyces species, and they display pigmentation ranging from gray to yellow, with some strains containing melanin [37]. The mycelial structure of Actinobacteria typically involves the development of substrate mycelium, whereas some species form aerial hyphae for spore production [9]. The morphology of spore chains is crucial for taxonomy, as different genera exhibit variations in spore arrangement and length. Micromonospora makes single spores, while Streptomyces can make long chains of up to 100 spores. Melanoid pigments

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generated by various strains are crucial for taxonomic classification and enhance the survival of these organisms in varied environments [40].

Morphological characteristics of classical importance, including substrate and aerial mycelia, spore-chain morphology, pigment production (e.g., melanoid pigments), and cell-wall chemotype (e.g., LL-diaminopimelic acid in Streptomyces), are essential for preliminary identification and enhance the application of molecular techniques [40].

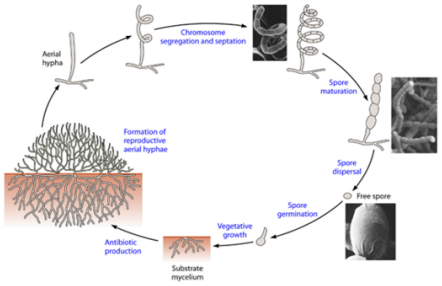

Figure 2. Sporulation and life cycle of Actinobacteria [40].

Chemotaxonomy

Chemotaxonomy is the study of the chemical differences in microbial cells. These differences are used to classify and identify bacteria, such as actinobacteria. This technique has demonstrated efficacy in clarifying phylogenetic relationships, as analyses of chemotaxonomic markers meet the standards for accurate classification. This is especially important in modern bacterial taxonomy and is recommended as part of a polyphasic approach that works at different taxonomic levels, such as species, genus, and higher taxa.

Chemotaxonomy in actinobacteria investigates the localization of specific chemical components within the cell envelope, encompassing amino acids, sugars, polar lipids, menaquinones, mycolic acids, and fatty acids. Techniques such as extraction, fractionation, and purification are used to elucidate the roles of these compounds in classification.

Streptomyces is a big group of bacteria in the phylum Actinobacteria [41]. It is known for living in many different places, including soil, the ocean, and with plants. The strains have a velvety or powdery appearance, with very branched mycelia that grow on various ISP media. When fully grown, the aerial mycelium produces 14 to 20 spores arranged in straight to recti flexible chains, with a prevalence of 56.7%.

Secondary Metabolites

Marine actinobacteria are an important source of secondary metabolites with a wide range of biological effects, especially in antibiotic resistance, a major global health problem. This literature review summarizes the antibacterial, antifungal, anticancer, antitumor, and antiviral properties of compounds derived from marine actinobacteria.

Antibacterial agents are essential for combating infections caused by resistant microorganisms. Abyssomicin C is a polycyclic polyketide antibiotic produced by a marine Verrucosispora strain. This shows that marine actinobacteria can make antibiotics. This compound prevents the body from making para-aminobenzoic acid, which in turn prevents it from making folic acid. It is antagonistic against resistant strains of Staphylococcus aureus [22]. The urgent need for new antibacterial agents underscores the importance of exploring marine actinobacteria as a potential source of novel compounds.

Marine actinobacteria show promise for use as antifungals. A Streptomyces species obtained from the sponge Craniella australiensis synthesized chitinase exhibiting antifungal efficacy against Aspergillus niger and Candida albicans (Chandrananimycin A). Chitinase is biocompatible and possesses antifungal properties, making it suitable for biomedical applications such as drug delivery and wound healing [22]. Chandrananimycin A has a wide range of antifungal and antibacterial effects, demonstrating the potential of marine-derived compounds in medicine.

The study of marine actinobacteria has emerged as a promising avenue for the discovery of effective anticancer agents. Salinosporamide A, derived from Salinispora tropica, is a notable proteasome inhibitor that induces apoptosis in multiple myeloma cells and is currently undergoing clinical trials [17]. Its unique mode of action sets it apart from other treatments, and its potential as an antimalarial drug demonstrates its flexibility. Other compounds, such as Chinikomycin A and marinomycins, have shown strong anti-timor effects against a range of cancer cell lines. This shows how marine actinobacteria can help find new drugs [36].

The development of multidrug resistance in tumor cells underscores the need to discover new antitumor agents. Marine actinobacteria are a major source of biologically active metabolites with diverse structures. Aureoverticillactam, derived from Streptomyces aureoverticillatus, exhibits inhibitory effects on the proliferation of colorectal and leukemia cell lines. The isolation of mechercharmycin A from Thermoactinomyces sp. demonstrates the potential of marine-derived compounds in cancer therapy [22].

Recent studies have highlighted the antiviral properties of marine actinobacteria. Marine actinomycin is effective against coxsackievirus by preventing viral attachment to cells and altering ICAM-1 expression in cells already infected [41]. Compounds derived from Nocardia alba exhibit antiviral activity against both Newcastle disease virus and infectious bursal disease virus, highlighting the significant antiviral potential of marine actinobacteria.

Marine actinobacteria are a rich source of secondary metabolites with strong antibacterial, antifungal, anticancer, antitumor, and antiviral activities. Continued research in this field is essential for the therapeutic application of these natural products, particularly given the rise in antibiotic resistance and the need for novel treatment options.

Applications

Actinobacterial natural products form the basis for antibiotics, enzyme inhibitors, biosurfactants, vitamins (such as B12), single-cell protein for aquaculture, biopesticides, and industrial enzymes, including amylases, cellulases, lipases, and L-asparaginase.Extremozymes from halophiles and thermophiles are especially useful for industrial use in very hot or very cold places [14].

The assessment of antibacterial secondary metabolites from actinomycetes, particularly those extracted from soil samples in the mountainous regions of eastern Nepal, has garnered significant attention due to their potential as bioactive compounds. Actinomycetes, a group of Gram-positive bacteria that grow slowly, are a major source of metabolites. This study employed 16S rRNA sequencing for molecular identification of actinomycetes isolated on starch-casein agar medium and confirmed through primary and secondary screenings.

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The primary screening phase involved assessing the inhibitory effects of isolated actinomycetes on diverse microbial species through a duplicate perpendicular streak method on Muller-Hinton agar plates. Pathogenic organisms, including Staphylococcus aureus, Bacillus subtilis, and Escherichia coli, were streaked adjacent to actinomycetes colonies and incubated at 37°C [42]. Moreover, antifungal activity was initially evaluated against phytopathogens, such as Aspergillus niger and Fusarium sp., using the agar plug technique, with inhibition zones quantified to assess the strains' antagonistic capacity.

The agar well diffusion method was employed in the secondary screening to evaluate the antibacterial effectiveness of the isolates. Actinomycete strains were grown in Mueller-Hinton broth, and the turbidity was adjusted to the McFarland standard before testing against different pathogens. Antibiotic fractions obtained by organic solvent extraction were introduced into wells formed in the agar, and the plates were incubated to evaluate the inhibition zones [41].

Primary and secondary screening techniques are vital for identifying actinomycetes with significant antibacterial properties. The perpendicular streak method and agar well diffusion are useful methods for testing their effectiveness against various harmful microorganisms [40]. Actinomycetes are a unique group of prokaryotic organisms that can break down a wide range of hydrocarbons, pesticides, and both aliphatic and aromatic compounds. They have their own unique morphological, cultural, biochemical, and physiological characteristics. The ability to perform microbial transformations of organic compounds offers significant commercial opportunities.

Actinomycetes are a major source of antibiotics. Until 1974, Streptomyces was the main genus from which antibiotics from Actinomycetes were obtained. Recent studies have expanded the search for new antibiotics to include rare Actinomycetes, such as Actinomadura, Actinoplanes, Ampullariella, Actinosynnema, and Dactylosporangium. As a result, important antibiotics such as anthracyclines, aminoglycosides, beta-lactams, chloramphenicol, macrolides, tetracyclines, nucleosides, peptides, and polyethers have been identified [43].

Actinomycetes, in addition to producing antibiotics, also produce low-molecular-weight enzyme inhibitors. More than 60 inhibitors have been identified, including leupeptins and antipain, which target specific proteases. Researchers are investigating enzyme inhibitors as potential cancer treatments. For example, revistin and streptonigrin are two compounds that stop reverse transcriptase.

Actinomycetes produce enzymes useful in industry. They produce amylases, cellulases, and lipases, which are very important in many areas of biotechnology, such as food production, fermentation, and the paper and textile industries. L-asparaginase, produced by diverse Actinobacteria species, has garnered attention for its therapeutic applications [14].

Actinobacteria produce Vitamin B12 via fermentation processes that employ cobalt salts as precursors. This synthesis is important for the production of antibiotics because the same fermentation processes can produce both antibiotics and Vitamin B12 [44].

Actinomycetes are a very important resource in biotechnology. They are used to make antibiotics, enzymes, and vitamins, and to treat cancer, which shows how important they are in both medical and industrial settings.

Conclusion

Actinobacteria, particularly Streptomyces and its associated genera, are highly efficient providers of bioactive secondary metabolites. Marine and extreme-environment actinobacteria represent largely unexplored reservoirs of novel chemical compounds. Advanced cultivation strategies, genome mining, and synthetic biology are crucial for converting biodiversity into innovative therapeutics and industrial products.

Actinobacteria, particularly the genus Streptomyces, are recognized as significant producers of secondary metabolites, constituting approximately 50% of known microbial natural products and over 75% of clinically utilized antibiotics. The metabolites encompass diverse chemical classes, including polyketides (e.g., oxytetracycline, streptomycin, erythromycin), non-ribosomal peptides (e.g., actinomycin), siderophores, alkaloids, and additional compounds such as prodiginines and anthracyclines. These compounds have a wide range of bioactivities, including antibacterial, antitumor, antiparasitic, anti-inflammatory, and plant growth-promoting effects. They can be used in medicine, agriculture, and biotechnology.

Genomic studies indicate that individual Actinobacteria strains typically possess 15–25 biosynthetic gene clusters, many of which remain uncharacterized until activated by modern genome mining techniques or elicitation strategies. The rising threat of antimicrobial resistance requires examining inadequately characterized strains, particularly those from rare or extreme environments, to identify novel metabolites that could accelerate drug development.

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Disclosure statement

The Authors declare that there is no conflict of interest.

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