The background of the cover is a dark blue, almost black, field filled with a complex, repeating pattern of molecular structures. These structures consist of spheres of varying sizes connected by thin, light-colored rods, creating a three-dimensional, crystalline appearance. The spheres and rods are arranged in a way that suggests a network or lattice of atoms and molecules, typical of a molecular model or a crystal structure.

The Handbook of Microbial Metabolism of Amino Acids

EDITED BY
J.P.F. D'MELLO



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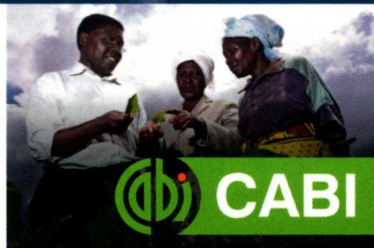
This book collates and reviews recent advances in the microbial metabolism of amino acids, emphasizing diversity – in terms of the range of organisms under investigation and their natural ecology – and the unique features of amino acid metabolism in bacteria, yeasts, fungi, protozoa and nematodes. As well as focusing on the individual amino acids, including arginine, sulfur amino acids, branched-chain amino acids and aromatic amino acids, a number of themes are explored throughout the work. These include:

- Comparative issues between the metabolism of microbes and that of higher organisms, including plants and mammals
- Potential for drug targets in pathways of both biosynthesis and degradation of amino acids
- Relationship between amino acids or associated enzymes and virulence in parasitic pathogens
- Practical implications for food microbiology and pathogen characterization
- Future priorities relating to fundamental biochemistry of microorganisms, food quality and safety, human and animal health, plant pathology, drug design and ecology

As the volume of research into the metabolism of amino acids grows, this comprehensive study of the subject is a vital tool for researchers in the fields of biological, medical and veterinary sciences, including microbiology, biochemistry, genetics and pathology. This book is also essential for corporate organizations with active research and development programmes, such as those in the pharmaceutical industry.

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D'MELLO



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Edited by

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The Handbook of Microbial Metabolism of Amino Acids

Edited by

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This volume is dedicated to my late daughter,
Deborah Claire D'Mello.

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Preface: Concluding the Series

This edition of *The Handbook of Microbial Metabolism of Amino Acids* completes my specialist CAB International monographs on the metabolism of amino acids in living organisms. The series commenced with the publication of *Amino Acids in Farm Animal Nutrition* (D'Mello, 1994), followed by an updated edition entitled *Amino Acids in Animal Nutrition* (D'Mello, 2003). *Amino Acids in Human Nutrition and Health* appeared 9 years later (D'Mello, 2012), while *Amino Acids in Higher Plants* represents my most recent addition in this sequence (D'Mello, 2015). I have always strived to reflect the rich diversity of unique and interspecies issues in pathways of amino acid utilization and this approach has been adopted again in the present handbook.

As with the preceding titles, *The Handbook of Microbial Metabolism of Amino Acids* has been designed specifically to promote research in the academic and corporate sectors in Europe, the USA, Canada, Japan, Australia and New Zealand, but generally in all countries where English is a primary medium of communication. The handbook should appeal to a wide readership, including advanced undergraduates and graduate students, as well as teaching and research staff in colleges, universities and state-funded institutes. It is anticipated that *The Handbook of Microbial Metabolism of Amino Acids* will be recommended reading for courses in the biological, medical and veterinary sciences, including microbiology, biochemistry, genetics and pathology. This volume should also be of interest to the commercial sector, particularly corporate organizations with active R&D programmes, as in the pharmaceutical industry.

The Handbook of Microbial Metabolism of Amino Acids: An Overview

The chapters in this volume are arranged in nine sections, each representing a particular theme and demonstrating the diversity of amino acid metabolism in disparate types of microorganisms. The nature of the subjects under review and the need for continuity necessarily involves a certain degree of overlap. This is not envisaged as a detraction, because as a consequence, individual chapters are self-contained, thereby reducing the need for cross-referencing to other parts of the book. More importantly, this approach has also allowed authors increased flexibility in terms of emphasis and interpretation. Indeed, the diversity of microorganisms under review means that the metabolism of key amino acids should be considered for bacteria, fungi and apicomplexan parasites in order to discern comparative issues.

In order to maximize benefits, readers are recommended to consult *Amino Acids in Higher Plants* as a companion text to *The Handbook of Microbial Metabolism of Amino Acids*. There are numerous instances of comparisons, particularly in biosynthetic pathways. Equally, there are examples of contrasting issues now emerging across several chapters which demonstrate the unique biochemical diversity of microorganisms.

Rationale

The conceptual basis of each section and its constituent chapters is presented below. Although this volume is structured along conventional lines with chapters on the metabolism of individual amino acids, it was considered important that recent developments should be viewed in terms of the practical implications for food microbiology and pathogen characterization. An understanding of the metabolic pathways underlying the design of novel drugs has been a recurring theme in the scientific literature. Furthermore, the ecological and environmental interactions influencing the microbial metabolism of amino acids deserve detailed attention. Here, the emphasis is currently directed at aspects relating to microniches, the mammalian/avian microbiome and the impact on amino acid metabolism in host–microbe relationships.

Part I Glutamate

Glutamate occupies a key position in the biochemistry of all living organisms, to the extent that Young and Ajami (2000) identified it as an amino acid of 'particular distinction', albeit in the context of mammalian metabolism. As in other living things, the fate of glutamate in microorganisms is defined by specific enzymes with dehydrogenase, transaminase and decarboxylase activities. It is appropriate, therefore, that chapters on glutamate dehydrogenase and glutamate decarboxylase should form the basis of this section. In conjunction with similar chapters in *Amino Acids in Higher Plants* (D'Mello, 2015) and *Amino Acids in Human Nutrition and Health* (D'Mello, 2012), readers will be provided with the opportunity to become familiar with important issues in the comparative biochemistry of the glutamate family.

Part II Lysine, arginine and hydroxyproline

Physical characteristics, including structural configuration and chromatographic elution sequence, unite the basic amino acids, but there is ample evidence of shared biochemistry in the metabolic fate of lysine, arginine and ornithine in microorganisms. Thus, all three amino acids undergo decarboxylation reactions, although catalysis is effected by enzymes with differing specificities. Ornithine is derived from arginine through the action of arginase. In comparison with arginine, however, lysine is still regarded as an inert amino acid. Arginine metabolism ultimately leads to the synthesis of polyamines via ornithine and is also the precursor of the signalling molecule, nitric oxide, through the action of nitric oxide synthase. The universal synthesis of nitric oxide in living organisms is now emerging as significant function of arginine. The clinical implications of arginine metabolism are currently under active consideration regarding microbial pathogenicity and the identification of potential therapeutic targets. Comparative issues are highlighted in the metabolism of several amino acids in this section, including hydroxyproline, with differences and similarities between microorganisms and higher animals noted. There are opportunities in this section to evaluate differences between yeast, bacteria and trypanosomatids in the metabolism of basic amino acids.

Part III Serine and threonine

Although serine and threonine follow distinct pathways in the metabolism of living organisms, there are common features which are at an appropriate stage for review. Hence, there is continuing interest in the classical serine–glycine interconversion and the mediation of the enzyme serine hydroxymethyltransferase in this reaction. The degradation of threonine is also under regular review as part of an effort to compare pathways in hyperthermophilic and other microorganisms. It is known that organisms that thrive in harsh environments display unusual biological features, and amino acid metabolism under these conditions is perceived as an attractive research topic. At the post-translational level, several recent studies demonstrate the role of serine/threonine kinases in bacterial signalling and regulation. Other investigations highlight the modulation of host–pathogen interactions by bacterial serine/threonine protein kinases. The role of these protein kinases in the physiology and pathogenicity of important disease organisms is becoming ever more apparent.

Part IV Sulfur amino acids

Research on the sulfur amino acids inevitably gravitates towards methionine, not least due to its multiple roles in diverse pathways of amino acid metabolism of microorganisms and its vital role in the initiation of protein synthesis. Its functions as a source of sulfur and methyl groups confer additional significance, resulting in the synthesis of critical molecules, not just in microorganisms. In addition, methionine is widely associated with metabolic interactions, providing links with disparate amino acid families. Methionine is an essential amino acid for animals, serving as a precursor of cysteine via an irreversible pathway. Results at the gene level reveals novel aspects of methionine biosynthesis in bacteria and pathogenic fungi. RNA-based regulatory mechanisms in methionine biosynthesis may present opportunities for the development of novel antibacterial drugs. The characterization of key enzymes and the potential biopharmaceutical implications of recent results point to a favourable research scenario for sulfur amino acids. The catabolism of methionine proceeds along established pathways, but of particular relevance is its degradation to those volatile sulfur compounds associated with the development of flavour in cheese and the microbial interactions occurring within this process. The scope for extracting practical value should be a powerful driving force in such investigations.

Part V Branched-chain amino acids

The branched-chain amino acids have long been associated with profound metabolic and regulatory roles in living organisms, characterized by complex structurally related interactions not only within the group but also with other amino acids, particularly methionine. The association between the branched amino acids and methionine occurs in plants as well as microorganisms, while the mechanisms underlying this interaction appear to be linked with the activity of a branched-chain amino acid aminotransferase. The expression in certain bacteria of functional genes linked to amino acid breakdown and cheese flavour appears to be determined by branched-chain amino acids. The role of transamination reactions as an initial step in the pathway to *S*-methyl thioesters has been proposed. In addition, there is an emerging consensus that branched-chain amino acid biosynthesis is essential for effective symbiosis in rhizobia–legume relationships. Furthermore, transport and availability may be important for pathogenicity and virulence in disease-causing microorganisms. There is also interest in the putative role of branched-chain amino acid aminotransferase in conferring acid tolerance to bacteria involved in the development of carious lesions. As the biosynthesis of the branched-chain amino acids is absent in humans, it has been suggested that key enzymes involved in *de novo* synthesis of these amino acids in bacterial pathogens may offer potential for the development of new drugs.

Part VI Aromatic amino acids and histidine

In this section, the microbial metabolism of the aromatic amino acids justifies enhanced significance due to its impacts on food quality and safety, human pathology and the synthesis of bioactive compounds. In general, the degradation of certain aromatic amino acids is associated with the synthesis of undesirable floral aromas in cheese. Aromatic amino acids also directly or indirectly contribute to the structures or provide precursors or act as donors of active groups in the biosynthesis of mycotoxins, the secondary compounds produced by a wide range of plant pathogenic or storage fungi. The aromatic amino acids are well recognized as sources of important secondary metabolites with marked bioactive properties. In at least one case, signalling compounds may be generated to affect pathogenic virulence and biofilm formation. Increasingly, the experimental evidence points to these metabolites serving as scaffolds for drug design and development. Specific chapters address biosynthesis as well as degradation, but aspects of host–pathogen interactions are also considered in the context of drug targets and immunology. The molecular characterization of specific pathogens in relation to the metabolism and post-translational modifications of amino acids is an important development worth exploring in this section.

Part VII D-Amino acids

The occurrence of D-amino acids in the structure of peptidoglycan has long been recognized as a characteristic feature of bacteria. However, there is a need to update traditional concepts of the functions of particular D-amino acids and the characterization of specific and broad-spectrum racemases as well as of those enzymes with different cofactor requirements. Fermentation reactions in the rumen mean that substantial quantities of bacterial protein become available to the ruminant animal. The fate and dynamics of the D-amino acids derived from the peptidoglycan components will be considered in this section. In addition, it is important to recall that D-serine serves as a central nervous system co-agonist in higher animals, including humans. It has been suggested that in plants, D-amino acids taken up from the soil may be utilized via central metabolic hubs.

Part VIII Ecology

The ubiquitous distribution of microorganisms in diverse ecosystems justifies an entire section of chapters to address the adaptive complexities in amino acid metabolism and the implications for plant growth and human health. The bacteroids residing in the root nodules of leguminous plants utilize host dicarboxylic acids as sources of energy to reduce atmospheric nitrogen to ammonia which is exported to the plant for the synthesis of amino acids. Another example of considerable interest in microecology is amino acid biosynthesis in endosymbiont-harbouring parasites of vertebrates and plants. Nevertheless, the overriding issue in parasitism is the acquisition of nutrients, especially amino acids, at the expense of host metabolism and survival. Intracellular pathogens consistently rely on their respective hosts to provide essential nutrients, particularly amino acids, to satisfy their requirements for protein biosynthesis, energy, one-carbon units and sulfur, usually under limiting physical conditions such as local hypoxia, salinity and adverse pH. The concept of 'nutritional virulence' has recently been advanced to exemplify the changing emphasis in studies on host–pathogen interactions. Thus, it is essential to identify the amino acid requirements of parasites and other pathogens as a prerequisite for the characterization of immune responses and potential treatments to mitigate adverse effects. While the issues of host–microbe relationships form an underlying theme throughout *The Handbook of Microbial Metabolism of Amino Acids*, this section of the volume provides the opportunity to explore further the molecular dynamics of such interactions. Anoxic microniches occur widely in soils, sewage and sediments, and the microbial degradation of

amino acids under anaerobic conditions is highly relevant in this section. Other environmental bacteria utilize the derivatives of several amino acids as sources of nutrients and for osmoprotection. Hence, the role of amino acids in microbial stress responses is an emerging issue, which in the long term, may have implications for biotechnology and environmental remediation. Future advances in biofilm and gut microbiome research should highlight the impact of interspecific and intraspecific interactions in microbial amino acid metabolism.

Part IX Conclusions

The underlying aim in this section is to unlock the practical implications of recent and ongoing research on the amino acid metabolism of diverse types of microorganisms. Even in a volume as comprehensive as this handbook, there is scope to integrate developments from a wide and fast-moving field of research. Emerging advances centre on food quality and safety, the biochemical characterization of pathogenicity and virulence in disease-causing microorganisms as exemplified in pathways of amino acid biosynthesis and degradation, and the application of the results to identify potential targets for the design of more effective drugs against a wide range of pathogens. The transport and metabolism of amino acids in microorganisms, particularly involving pathways absent in the mammalian host, provide multiple sites for testing a wide range of inhibitory compounds. However, further developments will depend on an improved understanding of amino acid metabolism in host–pathogen interactions. In addition, the safety of any new drugs will have to be established in rigorous clinical trials.

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As in the preceding volumes of this series, I have assembled an international team of authors with an established reputation in publishing original papers in peer-reviewed research journals. I am indebted to them for devoting valuable time to preparing authoritative and comprehensive chapters. I am convinced that their efforts will serve our readers well for many years to come.

In planning this volume, I decided that authors should be given freedom of expression in their unique specialisms, while recognizing that the terminology and technology becomes increasingly more complex with successive advances in the amino acid metabolism of living organisms.

Disclaimer

The Handbook of Microbial Metabolism of Amino Acids inevitably contains references to and descriptors of experimental and commercial products. Authors were asked to refrain from excessive usage of trade names unless there were compelling reasons for doing so. It is emphasized that no endorsement of these products is implied or should be attributed to the Editor or to CAB International, the publisher of this volume. We confirm our absolute impartiality in the selection of chapter titles and in the appointment of authors and that there has been no conflict of interests during this process.

The information set out in this volume is presented in good faith and in accordance with the principles of 'best practice' and 'due diligence'. Although every effort has been made to verify the facts and figures, neither the Editor nor CAB International can accept responsibility for the data presented in individual chapters or for any consequences of their use.

The popular press and particularly Internet sites contain numerous articles extolling the virtues of a variety of amino acids. A number of amino acids are also available in health food stores in the high street. However, publication of this volume should not be interpreted as a recommendation for readers to use these or any other amino acid or any microbial or antimicrobial preparation for whatever purpose. This handbook is intended exclusively for use as a text in education and research.

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