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C. Edward Stevens and Ian D. Hume
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COMPARATIVE PHYSIOLOGY OF THE
VERTEBRATE DIGESTIVE SYSTEM

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Comparative Physiology of the Vertebrate Digestive System is useful for anyone interested in the basic structural and functional characteristics of the digestive system and how these vary among vertebrate groups and species. It shows how fish, amphibians, reptiles, birds, and mammals have adopted various diets that range from other animals to plant fiber, and habitats that vary from fresh or salt water to extremely arid terrestrial environments.

This book is unique in several respects. It discusses all of the major aspects of nutrition, anatomy, and physiology in all of the major groups of vertebrates. It contains numerous figures and tables to aid in their comparison, including seventy-six illustrations of gastrointestinal tracts of amphibians, reptiles, birds, and mammals, prepared to allow for their direct comparison and labeled with animal silhouettes. The terminologies of scientific specialties and subspecialties are defined, and animals are referred to by both their common and scientific names. Relationships between digestive strategies and the diet and environment are discussed throughout the text and brought together in Chapter 11 on the evolution of the digestive system. Chapter 12 offers a brief summary of the major concepts covered in this book and suggests future directions for research.

The first edition of this book, published in 1988, was prepared as a response to the needs of veterinary, physiology, zoology, and nutrition graduate students enrolled in an NIH-sponsored program on comparative gastroenterology. This second edition takes advantage of the considerable research conducted in the intervening years. It contains three additional chapters, on nutrition, digesta transit, and evolution. Each of the other chapters has been updated and expanded. These changes provide a more complete discussion of the subjects and a broader interpretation of the information.

The authors have collectively studied the nutrition and digestive physiology of a wide range of vertebrates in North and South America, Australia, Europe, Africa, Indonesia, and Israel, and they have taught these subjects to undergraduate, graduate, and veterinary students for over two decades.

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Second Edition

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FOR ALVIN SELLERS and REG MOIR,
who introduced us to the wonders of the
digestive system and the value of the comparative approach

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Preface

Studies of comparative physiology provide us with the information needed for the understanding of physiological mechanisms, the management of domesticated animals, and the preservation of wild species. This edition of *Comparative Physiology of the Vertebrate Digestive System*, like the previous edition, is designed for use by nutritionists, physiologists, zoologists, veterinarians, and others interested in the vertebrate digestive system and its many variations. Its objectives are to describe the anatomical and physiological characteristics of this system in relation to nutritional niches and other characteristics of the environment.

Most concepts and theories of functional mechanisms are predicted from the study of animals that perform these functions in a different or simpler manner. Many vertebrates are propagated for the production of food or fiber, raised as pets or companion animals, or maintained as captive (zoo) animals. The numbers of many wild species and even classes of vertebrates, such as the amphibians, are decreasing at rates that have been compared with those seen during the demise of the dinosaurs. Therefore, studies of the vertebrate digestive system provide information needed for the understanding of basic physiological mechanisms, the proper maintenance of domesticated and captive animals, and the preservation of endangered species.

In this edition chapters that deal with the general characteristics of the vertebrate digestive system and its enormous range of structural and functional variations were updated and expanded to include new material and recent interpretations. A chapter on energy and nutrient requirements was added to provide information about metabolic and nutrient requirements and how these vary across vertebrate groups and accommodate to physiological states and changing needs. The related topics of motor activity and digesta transit have been separated into two chapters, reflecting significant advances in the past seven years. Chapter 11, on evolution of the digestive system, summarizes current thoughts and several themes that run through earlier chapters. The final chapter has been expanded to include both general conclusions and suggestions for future studies.

Research on the digestive system has resulted in a veritable explosion of new information and concepts. New techniques for the examination of mechanisms at the cellular and molecular levels have expanded knowledge on both the basic mechanisms and their adaptations to the diet and environment. The expansion in scientific specialties and techniques makes it impossible to discuss the significance of all of this new information. This book does not attempt to provide an encyclopedic coverage or exhaustive review of the available literature. However, earlier classical studies of comparative anatomy and physiology are discussed for their contributions, and reference is made to the authors of important discover-

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ies or ideas as often as possible. Readers are directed to recent reviews and other sources that give more detailed or extensive coverage of many of these subjects.

We are grateful to the many people who helped in the preparation of this book. Many colleagues have provided specimens or photographs for the series of line drawings comparing the gastrointestinal tracts of amphibians, reptiles, birds, and mammals. Erica Melack again deserves special recognition for the preparation of most of the earlier drawings. We are grateful to Frank Knight for his preparation of the animal silhouettes that grace these figures and the book cover and to Brenda Bunch for the preparation or modification of many of the new illustrations. We greatly appreciate the help of Robert Argenzio in reviewing portions of the manuscript, Kendall Clements for information and insights on herbivory in fish and, Judith Caton for information and insights on folivorous primates. We appreciate the contributions of Sylvia Bennett for her assistance in editing the manuscript and Rebecca Bladon for her aid in its preparation. Completion of this project would have been difficult without the encouragement of our respective wives, Barbara and Desley – to them our heartfelt thanks.

C. Edward Stevens
Ian D. Hume