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Introduction

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1.1 Introduction

The last 25 years witnessed substantial advances in the knowledge of the evolutionary history of snakes. Detailed (re)investigations of key fossils, such as the legged snakes from the Upper Cretaceous, have helped to reinvigorate debates about snake origins. Along with palaeontological evidence, new genomic and evolutionary developmental ('evo-devo') studies have provided novel insights into the interrelationships of squamates and mechanisms underlying the serpentiform body. New methods and technologies have been applied to a wealth of new and existing data, with analyses addressing evolutionary issues related to topics such as body elongation, limblessness, fossoriality, and envenomation. However, large knowledge gaps remain for some key morphological complexes and taxa.

This book was prompted by our joint organization of a conference held at the Linnean Society of London in June 2019. Without the pretence of being comprehensive in terms of coverage of topics and of range of opinions (see § 1.3), this volume's aims are to help fill some of the main knowledge gaps, to review, summarize, and synthesize recent advances and remaining debates, and to highlight fruitful avenues for future research. This is undertaken via contributions from a range of experts in squamate (especially snake) systematics, palaeontology, phylogeny, physiology, and comparative and functional anatomy and genomics.

1.2 Scope and Coverage

Other than this introduction, the volume comprises 18 chapters, written by 34 authors based in 13 countries, and covers a wide range of subjects, including temporal and spatial aspects of the fossil record, palaeobiology, phylogenetics, anatomy, sensory biology, ancestral-state estimation, the history of science, inference of function from form,

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genomics, venomics, feeding systems and diet, and reproductive biology. However, some important topics are not covered by this volume. For example, it includes almost no evolutionary developmental biology ('evo-devo') even though this is clearly of interest in terms of, for example, axial regionalization and loss of limbs (e.g., [1]). And there is very little coverage of recent applications (e.g., [2]) of 3D geometric morphometrics to cranial or vertebral evolution across the lizard-snake transition.

The volume is subdivided into five main parts. Part I comprises four contributions on the fossil record of snakes and their closest relatives among squamates. The first chapter of this section covers the possible origin of squamates in the Early Triassic (ca 250 million years ago (Ma)) to the earliest known unequivocal squamate fossils (Middle Jurassic: *c.* 174–163 Ma) and the further diversification of Squamata into the Cretaceous. The other three chapters in this section focus on diversity and diversification early in snake history as inferred from the Cretaceous to Miocene fossil record. Part II addresses the controversial Marine-Origin Hypothesis of snakes from a palaeontological perspective. The first chapter provides an epistemological approach to the idea of a marine origin of snakes. The three other chapters reassess morphological evidence for the Marine Hypothesis. Part III examines the rapidly growing set of molecular genetic data available for understanding aspects of the origin and early history of snakes, applied to a diversity of questions about phylogenetic relationships, inferences of diet across the lizard–snake transition, and the origin and diversification of snake venoms. Part IV assesses what some sensory systems (ears, brains, eyes) can tell us about early snake history. The ear and brain chapters focus on comparative morphology and on drawing inferences about early events in snake evolutionary history by identifying correlates of soft tissue and ecology and behaviour from more readily fossilized hard tissues. The eye chapter provides an overview of the visual system of the ancestral snake that can be inferred from anatomy, physiology, and molecular genetic data for extant snakes. Part V comprises four contributions on comparative and functional morphology of primarily soft-tissue systems of mostly extant snakes. In addition to a new perspective on feeding systems and early snake history, three of the chapters (hemipenes, sperm storage, oral glands) offer reviews of topics that have been largely overlooked in terms of what they can tell us about the ancestral snake, and snake origins and early evolutionary history.

1.3 Debate, Disagreement, and Consensus

Some of the debates over the origin of snakes, at least in the past 25 years, have been somewhat fractious. Even where the debate has been less antagonistic, there remain some sharply divided opinions. Importantly, the reader should be aware that the combined authorship (and reviewership) of this book does not represent the full span of expert opinions currently in circulation (for example, for an overview of some opposing views concerning extant and fossil anatomical evidence for snake origins, see [3], and review of that work by [4]). Disagreements about the biology of snake origins have generally been more prominent and noisy for palaeontology than neontology, perhaps because the former typically involves greater overlap between more observers of the same, imperfectly

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preserved specimens that are being interpreted within a less-constrained phylogenetic framework, but it is likely not difficult to find people who disagree with aspects of this volume's neontological chapters also. This volume is a good place to find a way into the palaeontological and neontological debates. Careful readers will also note some disagreements among the contributions in this volume. For example, the chapters by Head et al. (Chapter 3) and by Smith and Georgalis (Chapter 4) present different opinions on the extent to which vertebral morphology is useful for palaeobiological interpretations of snake evolution. And Yi (Chapter 13) and Scanferla (Chapter 14) disagree about the inferences on ecology that can be made from the inner ear morphology of the extinct stem snake *Dinilysia patagonica*.

The two of us also have some differing opinions and perspectives, explainable to some degree by our different trajectories. Although both were undergraduates in zoology, one of us (DJG) went on to do a PhD in archosaur palaeontology before choosing to largely move back into neontological herpetology, while the other (HZ) did a PhD in neontology and established a career in that field but became very interested in palaeontology and has worked substantially in that field. Despite our different experiences and perspectives, through co-editing this book we found ourselves sharing some views. For example, we agree that palaeontology will likely lead the way in further clarifying the closest relatives of crown snakes (and perhaps also of some of the major lineages therein), but we also believe that neontology, including molecular genetics, has a major role to play in advancing inferences of the natural history of the earliest snakes, and in clarifying some interrelationships of the major extant lineages at the base of the snake crown. We both learned much about the origin and early evolutionary history of snakes from organizing the 2019 meeting and editing this volume. We have been reminded how unusual snakes are among squamates. Although obviously partly an artefact of the idiosyncrasies of extinction and survival, in so many ways snakes are an exceptionally disparate lineage of elongate, limbless squamates.

We both owe a debt of gratitude to many colleagues over many years, as well as to previous biologists neither of us met. Two particularly important, relevant and missed colleagues deserve special mention here. The title of the 2019 meeting associated with this book, *A Contribution to the Origin and Early Evolution of Snakes,* was devised in reference to the late Garth L. Underwood's highly influential 1967 book *A Contribution to the Classification of Snakes.* This was chosen because we have long been fans of Garth's inspiring science and writing, and both benefited from his insight, generosity, and wealth of knowledge during discussions with him about snakes. One of us (HZ) also benefited greatly from many discussions about snake evolution with the late Jean-Claude Rage, who made substantial contributions to snake palaeontology.

1.4 Concluding Remarks

Although snake origins encompasses several topics that have been much-debated over many years, we are struck by how much vitality remains in this area of science. This is partly

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because of technological advances, especially in the generation and analysis of genetic data, and in imaging. However, it is also because of a large and diverse array of researchers recently approaching the subject, because of new fossil discoveries, and because there remains so much to be discovered about extant snakes – their anatomy, development, phylogenetic relationships, ways of life, and the genetics underpinning this diversity – information that can feed into inferences about extinct geno- and phenotypes and testing of hypotheses of events that occurred tens of millions of years ago.

This volume is replete with instances where making inferences about the most-recent common ancestor of major lineages of crown snakes is difficult because of the patchiness of comparative data for extant (especially non-caenophidian) snakes. We anticipate exciting years ahead, with rapid and substantial progress in more compellingly resolved phylogenetic relationships, discovery and documentation of fossils of stem and early crown snakes, analyses of greatly expanded genomic data, refined correlations between ossified structures and soft tissues and habits, and more complete and detailed surveys of extant snake anatomy and ecology. This joint volume will fulfil its objective if it helps to stimulate and contribute to future breakthroughs in this exciting chapter of vertebrate evolutionary history.

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