Carnivoran Evolution

Members of the mammalian clade Carnivora have invaded nearly every continent and ocean, evolving into bamboo-eating pandas, clam-eating walruses, and, of course, flesh-eating sabre-toothed cats. With this ecological, morphological, and taxonomic diversity and a fossil record spanning over sixty million years, Carnivora has proven to be a model clade for addressing questions of broad evolutionary significance. This volume brings together top international scientists with contributions that focus on current advances in our understanding of carnivoran relationships, ecomorphology, and macroevolutionary patterns. Topics range from the palaeoecology of the earliest fossil carnivorans to the influences of competition and constraint on diversity and biogeographic distributions. Several studies address ecomorphological convergences among carnivorans and other mammals with morphometric and Finite Element analyses, while others consider how new molecular and palaeontological data have changed our understanding of carnivoran phylogeny. Combined, these studies also illustrate the diverse suite of approaches and questions in evolutionary biology and palaeontology.

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Carnivoran Evolution: New Views on Phylogeny, Form, and Function
Edited by Anjali Goswami and Anthony Friscia

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Contents

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Preface

With its high taxonomic, morphological, and ecological diversity and excellent fossil record, the placental mammal order Carnivora has proven to be a model group for addressing questions of large evolutionary significance. Recent work has resulted in a well-resolved phylogeny of extant taxa, as well as for many extinct clades, allowing for rigorous analysis of a wide range of evolutionary questions. Although the order is named after its meat-eating members, the dietary breadth of living carnivorans (members of the order Carnivora) extends from frugivorous to insectivorous taxa, durophagous taxa, as well as the hypercarnivorous taxa that are usually associated with the group. Carnivoran locomotor diversity is also remarkable among mammals, with fully aquatic, semi-aquatic, arboreal, terrestrial, and fossorial taxa. Recent studies have shown that this diversity extends to their early fossil representatives. Multiple ecological and morphological convergences of carnivorans and distantly related clades, including the extinct creodonts and extant and extinct carnivorous marsupials, also strengthen the utility of carnivorans for comparative ecomorphological and biomechanical studies. This volume focuses not only on the current advances in our understanding of mammalian carnivoran evolution, but especially on how carnivorans are being used as a model clade for testing new methodologies and addressing fundamental issues in palaeontology, which can ultimately be applied to clades with poorer fossil records.

The subtitle of this volume – 'New Views on Phylogeny, Form, and Function' – while being pleasantly alliterative, highlights some of the most exciting fields of study in evolutionary biology and palaeontology to which carnivorans have lent themselves. In recent years, mammalian carnivorans have been the focus of extensive phylogenetic analyses, both molecular and morphological, and incorporating both extant and fossil taxa, which have resolved many long-standing issues in carnivoran relationships. Flynn *et al.* (Chapter 2) provide an overview of the state of overall carnivoran phylogeny, erect a new clade, and demonstrate some of the patterns that can be studied using a phylogenetic framework. Contributions by Veron (Chapter 3) and Morlo and Peigné (Chapter 4) look closely at some of the more interesting evolutionary problems within Carnivora. Veron tackles the viverrids, a diverse Old World group that has undergone extensive revision in recent years. Morlo and Peigné look closely at the evolution

of the red panda and its relatives in the Ailuridae. Although represented by only one taxon today, the fossil history of this family reveals more diversity in taxonomy and form.

All three of the phylogenetic studies use the latest in techniques, including combining molecular and morphological data, and especially data from fossil specimens, in their analyses. Goswami and Polly (Chapter 5) use carnivorans to investigate a potential issue in phylogenetic methodologies – the correlated evolution of characters. Using simulations and empirical data, they test whether character correlations influence discrete character states over evolutionary time scales, and assess methods to identify these correlations in existing analyses. Benoit (Chapter 6) addresses another issue in phylogeny and taxonomy – how to identify species. Using lions as an example, Benoit uses sophisticated analyses of allometric trajectories to assess the strength of characters used to justify the American lion as a separate species.

With this solid taxonomic and phylogenetic framework and their excellent fossil record, carnivorans easily lend themselves to interesting studies of macroevolutionary patterns and more fundamental issues of influences on diversity. Holliday (Chapter 7) uses a phylogenetic framework to assess biases in morphological evolution, testing whether hypercarnivory tends to limit further morphologic change and testing hypotheses of a macroevolutionary ratchet that leads hypercarnivores into an evolutionary 'dead end'. Both Werdelin and Wesley-Hunt (Chapter 8) and Wesley-Hunt *et al.* (Chapter 9) address the biogeographic distribution of carnivoran ecomorphologies. The broader study of Werdelin and Wesley-Hunt looks at morphological disparity across the entire order and compares disparity among families and among continents. Their companion piece, Wesley-Hunt *et al.*, focuses on just two of the more widely distributed families, civets and mongooses, to investigate how they divide up community ecospace in different regions.

Ecologies within communities can be traced across time as well as space, and both Morlo *et al.* (Chapter 10) and Friscia and Van Valkenburgh (Chapter 11) use this approach to look at the earliest carnivorans. In the Paleogene, carnivorans shared the meat-eating niche with the extinct creodonts, and how this temporal overlap affected their respective ecologies, as well as the history of their diversity, has long been a topic of research and debate. The broader, global study of Morlo *et al.* addresses how ecospace and guild structure vary temporally and spatially across the history of carnivorous mammals, as taxonomic membership varies. Friscia and Van Valkenburgh test the more specific question of whether creodonts were actively replaced by carnivorans, as the former decrease in diversity during the Eocene of North America.

While most studies of carnivorans focus exclusively on the terrestrial clades, the pinnipeds represent one of the most extraordinary transitions in mammal evolution. The study of Jones and Goswami (Chapter 12) bridges form and function, by using pinnipeds as a case study for investigating reproductive and ecological influences on cranial morphology, as well as identifying types of convergence across the three extant clades of pinnipeds.

Polly (Chapter 13) returns to the terrestrial realm, using sophisticated analyses of biomes and limb morphology to assess the relationship between locomotory styles and the environment in North American carnivorans and exploring its potential as a tool to reconstruct past environments. Lewis and Lague (Chapter 14) follow on the postcranial theme, comparing limb morphology in machairodontid sabretooth felids to modern felids to assess whether they employed similar locomotory and hunting styles, or were as distinct in the postcranium as they were in cranial and dental morphology.

Lastly, Wroe (Chapter 15) provides an overview of the latest in 3D imaging and finite-element techniques and presents several comparisons of skull mechanics in placental and mammalian carnivores. Finite element analysis has proven to be a unique and fascinating tool for reconstructing the mechanical capabilities of extinct morphologies, and Wroe's chapter details how these methods reveal surprising differences between superficially similar carnivores.

Few vertebrate groups can claim such a diversity of topics that can be rigorously tested with fossil and extant taxa as carnivorans can. Advances in development, genetics, phylogenetics, morphometrics, finite element analysis, and 3D imaging have all been extensively applied to carnivorans, keeping this clade at the forefront of research in evolutionary biology and palaeontology. We hope that this volume will serve not only as an overview of recent advances in carnivoran evolution, but also as a methodological guide for studying large-scale patterns in the fossil record and for addressing fundamental questions in evolutionary biology with morphological and palaeontological data.

Acknowledgements

As with most things in palaeontology, this book started with beer. At the American Society of Mammalogists' meeting in Amherst in June 2006, we were at the lobster bake, talking over our favourite beverage, and discussing how much we loved the taxa we studied – carnivorans. Through the course of our conversation we realised that there had never been a symposium on mammalian carnivores at the Society of Vertebrate Paleontology (SVP) meetings, and that the classic Gittleman volumes on carnivore behaviour, ecology, and evolution were already over 10 years old and quite out of date with respect to phylogeny and quantitative, macroevolutionary analyses (also with quite a different focus than a dedicated volume on evolution). Sure, the carnivore researchers tended to cluster together at the meetings, but we hadn't had a formal meeting of minds. A few emails, and a proposal to the SVP Program Committee a few months later, and our symposium (with the same name as this volume) was a reality at the 2007 SVP meeting in Austin, TX. So the first people we have to thank are Jason Head and the rest of the Program Committee of that meeting for allowing us to have that gathering which ultimately led to this volume. Many of the talks that were part of that symposium made it into this volume as chapters, and we thank all the participants of that day. It was especially gratifying for us all to gather over a meal afterwards and discuss what we had just shared with each other. Carnivorans are often called a 'charismatic' group, and the same can be said of the people who study them.

The creation of this volume took significantly longer than the year to get the symposium together, and we thank the contributors for their patience throughout this process, and for their continued faith that two, relatively young, researchers could pull this together. We believe that our contributors represent the full range of carnivoran workers, from the well-known heavyweights in the field to the recent graduates who are bringing new approaches, methods, and enthusiasm to the study of carnivoran evolution, making this quite a unique volume. Of course, all of the contributions were subject to rigorous scrutiny, and we have many people to thank for reviewing the contributed manuscripts. Jill Holliday, Stéphane Peigné, Geraldine Veron, Xiaoming Wang, Marcelo Sánchez-Villagra, John Finarelli, Alistair McGowan, Margaret Lewis, K. Elizabeth Townsend, Blaire Van Valkenburgh, Graham Slater, Lars Werdelin,

Annalisa Berta, Stephen Wroe, Olaf Bininda-Emonds, Rob Asher, Eleanor Weston, Norberto Giannini, Matt Benoit, P. David Polly, John Damuth, Vera Weisbecker, Laura Porro, and Alistair Crosby all provided an immense service in improving the quality of each chapter and the volume as a whole and we thank them all for the time and care they put into their reviews. John Finarelli in particular was an endlessly reliable reviewer and source for ideas, opinions on issues, and last-minute fact checking. We also of course have to thank our mentors, John Flynn and Blaire Van Valkenburgh, respectively, who have inspired us not only to pursue research in carnivorans, but to take a deeper view of evolution patterns and processes. A large part of the great advances in the study of carnivoran evolution discussed in this book are a reflection of their decades of work on this topic, and certainly we have them to thank directly for any of our own success.

Lastly, we would like to thank Rob Asher and Russell L. Ciochon for inviting us to submit our proposal for a volume in the series *Morphology and Molecules* at Cambridge University Press, to Dominic Lewis for guiding us through the proposal process and the early stages of preparation, and to Rachel Eley, our Assistant Editor, who answered all of our many questions as we came to the end of this project. It has been a long and occasionally trying experience, but we are very proud of this volume and grateful to all of the people who helped us get to this point.

Anjali Goswami and Tony Friscia