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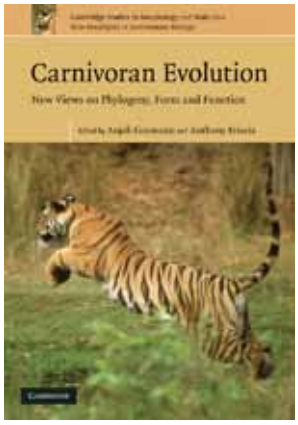

Carnivoran Evolution: New Views on Phylogeny, Form and Function, by Anjali Goswami and Anthony Friscia, editors, 2010, Cambridge University Press, Cambridge, UK, 506 p., ISBN 978-0-521-73586-5, USD59, paperback; ISBN 978-0-521-51529-0, USD135, hardback.

Carnivoran Evolution brings together an impressive collection of studies addressing the complicated lineage of Carnivora, arguably one of the most popular groups of mammals. This lineage is beginning to become clearer thanks to the presented works of over 20 international researchers, addressing a variety of topics from the evolution of carnivoran biogeography to cranial and postcranial mechanics of extant and fossil taxa.

The 2006 meeting of the American Society of Mammalogists in Amherst is the true origin of this collection, where the future editors and authors discussed the fact that there had never been a symposium on the evolution of carnivorans at a Society of Vertebrate Paleontology meeting. Such a symposium was also in need, as the previous comprehensive works on carnivoran evolution, behavior, and ecology (Gittleman 1989, 1996) were already more than a decade old and did not include updates on new techniques and phylogenies, nor the attention to ecomorphology included in this text. The following Society of Vertebrate Paleontology meeting held in Austin, Texas, in 2007, had such a symposium, where many of the presentations were later adapted to the chapters included in *Carnivoran Evolution.*

The first four chapters deal almost exclusively with carnivoran systematics, reviewing known carnivoran phylogeny and addressing some problematic issues, such as the phylogenetic placement of Viverridae (Chapter 3) and Ailuridae (Chapter 4). In Chapter 1, Goswami supplies an excellent introduction to the order Carnivora, and outlines their relationship to other placentals, going back to the early Cenozoic (Paleocene–Eocene). Included here is a discussion on how advances in molecular phylogenetics have significantly changed our understanding of carnivoran evolution, as it has for biology and paleontology in general. As Goswami walks us through the two major groups of carnivorans, Feliformia (e.g., felids, viverrids, hyaenids), and Caniformia (e.g., canids, mustelids, ursids), we see not only simple descriptions of extant groups, but also an overview of how such fossil taxa as nimravidae (such false saber-toothed cats as *Hoplophoneus*) and amphicyonidae (such bear-dogs as *Amphicyon*) fit into the lineage, along with the noncarnivoran carnivores, the creodonts (hyaenodtonids and oxyaenids). Chapter 1 concludes with a brief discussion on ecomorphology and macroevolutionary patterns, specifically on mammalian hypercarnivory and its unsustainability, a topic that is addressed further in Chapter 7. In Chapter 2, Flynn, Finarelli, and Spaulding provide a very detailed history of carnivoran systematics, and they discuss recent molecular, morphological, and total evidence character analyses. Results of these analyses suggest strong monophyly for nearly all members of carnivoramorpha, with the exceptions of viverrids (civets, binturongs, and genets) and mustelids (weasels), allowing for the diagnosis of a new clade, Carnivoraformes, which includes all carnivoramorphans except early Cenozoic viverravids and miacids. The inclusion of abundant fossil taxa in this study is discussed by Flynn et al., noting how crucial fossils are to interpreting evolutionary and temporal transformations, regardless of the lack of molecular data, which is a welcomed support for total evidence analyses.

Chapter 3, by Veron, examines the phylogeny of viverrids (not to be confused with viverravids) and viverrid-like feliformes, the latter of which includes taxa such as the African Palm Civet and the Malagasy carnivores. Here, Veron reevaluates the clade of Viverridae, and based on molecular analyses, Veron excludes African Palm Civets, Malagasy viverrids, and Asian linsangs from Viverridae. This leads to a new description of Viverridae, which consists of four subfamilies: Asian (Hemigalinae, Paradonxurinae), African (Genettinae), and Afro-Asian (Viverrinae). These results also highlight challenges of traditional morphological features used to classify feliform carnivores, such as apparent convergent or primitive characters of dental and basicranial features. Similarly, Chapter 4 (Morlo and Peigne) reviews the family Ailuridae and investigates its phylogenetic placement, which has previously been problematic. Ailuridae is currently represented by only one living genus, *Ailurus fulgens* (Red Panda). While currently exclusive to Asia, ailurids have strong fossil roots in Europe, where they held their highest diversity in the Oligocene through Miocene. Morlo and Peigne conduct phylogenetic analyses, including both molecular

and morphological data of extant and fossil taxa, yielding results that suggest a placement for Ailuridae within Musteloidea in Arctoidea in Caniformia. The chapter concludes with an historical overview of *Ailurus* studies and comparisons to giant panda, and a highly detailed review of ailurid evolution.

The remainder of the book takes a considerable shift in attention from phylogenetic analyses to comparative methods and novel techniques toward an understanding of carnivoran ecomorphology. Chapter 5 addresses character dependence, a major assumption in many morphology-based phylogenetic analyses, although most studies of modularity and morphologic integration find significant correlations among phenotypic traits. Here, authors Goswami and Polly call the validity of this assumption into question, and they use empirically derived data in cranial modularity and morphological integration in the carnivoran skull to assess the impact of trait correlations on phylogeneic analyses of Carnivora. By testing whether individual modules differ in their relationships between shape and phylogenetic relatedness or whether correlated characters significantly misled previous phylogenetic analyses of Carnivora based on morphology, this chapter takes a very novel approach to the problem of potential biases in analyses. The utilization of 3D morphometrics and Monte Carlo simulations to investigate the correlations of characters also has potential for other avenues in vertebrate paleontology, where it has not been broadly used or investigated to date.

In Chapter 6, Benoit discusses the challenges of assigning fossil specimens to extant taxa. Notable size differences of the modern and American lion (*Pantera leo* and *Pantera leo atrox*, respectively) have led to several misidentifications of distinguishing features, because the differences between the taxa were not considered allometrically. This study examines features that revealed some of these characteristics are not allometrically distinct in the two taxa, while some are. While the results do not disprove the hypothesis that American Lion and modern lions are separate species, the argument is weakened by these results.

Chapters 7 through 13 focus more on carnivoran morphospace and disparity, the latter of which is used here to address ecomorphology (evolutionary diversification of form). In Chapter 7, Holliday analyzes directionality of the character evolution of hypercarnivorous specializations in carnivoran dentition, suggesting that the repeated and unsustainable reemergence of hypercarnivory in Mammalia may be influenced by increasingly specialized morphospaces, leading to decreases in the long-term success of hypercarnivores, such as nimravids or hyaenids. Chapters 8 and 9 discuss ecomorphology and biogeography of Carnivora, and focus specifically on herpestids and viverrids (mongooses and civets). Chapter 8 investigates ecomorphological disparity and distribution among extant members of Carnivora. Authors Werdenlin and Wesley-Hunt report that the different families of Carnivora significantly differ in mean ecomorphological disparity, the lowest being hypercarnivorans (e.g., felidae), compared to high disparity in hyaenids and ursids, despite no detectable difference in mean disparity of continental differences. Chapter 9 expands upon this analytical method and focuses on herpestids and viverrids, small tropical-subtropical feliformes from Africa and Southeast Asia. Compared to the results in Chapter 8, Wesley-Hunt, Dehghani, and Werdenlin report that even though potential for morphospace overlap exists, there is little or no overlap in morphospace occupation when members of either clade have interaction potential; this suggests that the ecological roles of taxa in the two families differs between Africa and Asia. Despite this result, understanding the processes underlying the pattern is still problematic.

In Chapter 10, Morlo, Gunnell, and Nagel provide an extremely comprehensive ecomorphological analysis of Laurentian carnivoran guilds from the Eocene through Miocene to investigate the usefulness of carnivoran guild analyses for paleoclimate and paleoenvironment estimates. Comparisons of carnivore guild structures are made based on parameters such as body mass, diet class, and locomotor class, and they yield suggestions on the role climate, environment, and time depth across faunal turnover have on guild structures throughout the Cenozoic. Furthermore, throughout the Cenozoic, guilds differ significantly in terms of taxonomic composition and diversity, although structurally they remain quite similar.

Chapter 11, by Friscia and Valkenburgh, takes a slight shift in direction and investigates evidence for direct competition between carnivorans and creodonts in the Eocene. This study investigates craniodental features, diet, and body size diversity in Eocene carnivores over time to explore the potential for ecological overlap, and hence competition between creodonts and carnivorans. The case for competition is strengthened by this study, also suggesting that competition may have been influential in the extinction of the creodonts, due to the lack of specialization in carnivoran dental plasticity.

Chapter 12, by Jones and Goswami, utilizes 3D morphometric data to quantitatively assess pinneped cranial morphology to address whether differences in cranial shape correlate with phylogenetic relationships among pinnepeds or their ecological attributes. The authors also investigate how differences in cranial ontogeny reflect different reproductive strategies among pinnepeds. The results show a surprising pattern in the repeated evolution of mating and feeding specializations toward walrus-like morphology.

Chapters 13 and 14 both discuss postcranial analyses of carnivorans. In Chapter 13, Polly addresses faunal ecomorphology and living carnivoran locomotor systems in the context of modern climate, and relying on the calcaneal gear ratio, in which high ratios are associated with digigrady in canids and felids of arid regions, and low ratios associated with plantigrady among ursids and mustelids of temperate forests. Chapter 14 examines the postcrania of machairodontine felids, specifically addressing scaling patterns in extant felids. The results of this study suggest that contrary to popular belief, saber-toothed cats are not scaled-up versions of extant felids. Furthermore, multivariate comparisons performed in this study imply different forelimb and hindlimb locomotor function than extant felids.

In the last chapter, Wroe investigates carnivoran cranial mechanics with a novel approach. Chapter 15 utilizes finite element modeling analysis to reconstruct cranial mechanics and predatory behavior in *Smilodon fatalis*. Finite element modeling (FEM) is a relatively new technique, but has previously been applied to (and embraced by) vertebrate paleontology (Snively and Cox, 2008; Snively and Theodor, 2011). The results of this comparison concur with previous studies, which suggest a head-depressing bite. An interesting comparison is also made

between morphometric bite force and canine shape analysis of hypercarnivorous marsupials and placentals, the marsupial wolf (*Thylacinus cynocephalus*) and the dingo (*Canis lupus dingo*) respectively. The results of this analysis suggest a significant niche overlap, implying considerable competition as a contributing factor to the ultimate extinction of the Thylacine.

This volume is very well organized and written. The diversity of the topics covered by the contributors relieved the potential for significant overlap in chapters and content, which is somewhat common with compiled volumes such as this, especially when they arise out of conference symposia. Many of the novel and unique approaches to carnivoran evolutionary study, such as FEM, character modules, or integration analysis, have not been as heavily utilized in other fields of vertebrate paleontology, although the potential for such study certainly exists.

The figures and tables produced for this book are nicely placed, although the color appendix in middle of book is somewhat distracting. I highly recommend this text; the organization and content make it an ideal piece for any paleontology or biology professional or graduate student's library, though it is not off-putting to upper-level undergraduates who may pursue mammalian paleontology or biology. *Carnivoran Evolution* is, at the very least, an excellent reference for not only mammalian researchers, but vertebrate paleontologists and zoologists in general.

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