Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay

Eric J. Sargis and Marian Dagosto (eds.)
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Mammalian Evolutionary Morphology is the most recent publication in Springer's Vertebrate Paleobiology and Paleoanthropology Series edited by Eric Delson and Ross MacPhee. This volume, like others in the series, is an extremely professional and well-produced book presenting up-to-date and cutting-edge research. However, in one respect this book stands out from the others; it is a tribute to the long and ongoing career of one scientist—Frederick S. Szalay, evolutionary morphologist *par excellence*.

To say that Szalay has had a successful career and significant influence on many areas of evolutionary morphology is something of an understatement. Eric Sargis and Marion Dagosto, who edited the book, know firsthand of his influence, having completed their Ph.D.s under his tutelage. They carefully document Szalay's impact on the field in their own editorial comments and in the organization of the volume, which includes thoughtful and thought-provoking contributions from many who have been taught or inspired by him during his more than forty-year career. Sargis and Dagosto first provide a sometimes poignant account of Szalay's entry into American academics after growing up in his native Hungary and the intellectual path he followed as a young researcher. They point out that his influence is evidenced by the ten mammalian species that have been named after him before detailing the research areas in which he has made major contributions, including primate evolutionary morphology, mammalian evolutionary morphology, and theory and practice of phylogeny reconstruction and adaptive scenarios. A seven page bibliography of his publications spanning from his first in 1965 to one article in press at the time of the book's printing, bears further testament to the breadth and depth of his knowledge.

The book is divided into two sections. While the audience of this journal may be most familiar with Szalay's work on primates, to which the second half is dedicated, his vast compendium of research also includes major contributions to our understanding of other mammal groups including marsupials and Archonta. Naturally, the two halves of this book will interest a different subset of evolutionary morphologists. Those interested in the evolution of primates may not find the first half of the book as relevant or engaging, and vice versa for those involved in mammalian evolutionary research of other families. For this reason my only criticism of the book as a whole is that readers might have found the chapters easier to navigate had they provided abstracts at the outset; certainly those with summaries or short concluding sections demystified some of the material during my own reading of chapters regarding taxa with which I was not very familiar. Regardless of this minor point, all readers will recognise the merit of both sections for the methodological and analytical issues under consideration and the thought provoking discussions of how skeletal and dental characters can be appropriately used in the reconstruction of phylogenetic relationships and evolutionary trends. Szalay was once unique amongst his peers for pioneering phylogenetic analyses based on postcranial material—tarsals, in particular—when the majority of workers believed wholeheartedly that dental characters more accurately reflected relatedness. Many of the papers in this book reflect his interest in tarsal functional morphology, as well as his insistence upon the inseparability of phylogeny and function in any analysis and a historical approach to understanding adaptation. These contributions also make it clear that recent fossil discoveries, additional morphological analyses and genetics have often borne out Szalay's sometimes controversial conclusions regarding systematics.

Section I (Non-primate Mammals) begins with Davis et al.'s detailed dental descriptions of two species representing the earliest known North American deltatheroidans, considered to be a stem group of Metatheria, including a new species herein named *Oklatheridum szalayi* in honour of Szalay's contributions to our understanding of metatherian radiations. Their reassessment of deltatheroidan material indicates a previously unacknowledged level of morphological diversity during the Early Cretaceous and, as these species predate Asian taxa, suggests that a North American origin for the group might have been possible. Kear et al. follow with a short paper detailing a functional analysis of the hindlimb of extant and fossil macropodoids, investigating the relationship between limb bone length, locomotor habits, and phylogeny. By viewing morphological trends over time and comparing analyses that excluded and included fossil species, they demonstrate that a range of metapodial proportions was established early in kangaroo evolution and an increase in metatarsal length is not correlated to an increase in aridity during the late Tertiary. The third contribution, from Argot, stands out for providing an account of the changing interpretations of the giant ground sloth, *Megatherium americanum*. Beginning with Cuvier's interpretations of the species' behavior based on its skeletal anatomy and tracing historical shifts in the portrayal of this animal over the years, Argot ties these various in-

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terpretations to our limited modern understanding of the species' behavior. She points out that this famous large-bodied mammal has never been subjected to a systematic functional analysis and, although one might wish that the chapter provided something more along these lines, it is nonetheless an interesting story. The fourth chapter, by Salton and Sargis, outlines a comprehensive functional analysis of the tenrecoid forelimb skeleton. Summaries of the morphologies of the species typifying different locomotor patterns are provided and it is one of many chapters where extremely useful, clear black and white photos are in abundance. A lengthy fifth chapter from Penkot et al. is the first of two focussing on condylarths. It provides detailed descriptions of postcranial remains definitively assigned to *Apheliscus* and *Haplomylus*, two North American species of apheliscid which were previously best known from dental material. Their analysis links them to early macroscelideans, the first non-African taxa which affiliate in this way. The sixth chapter, by Bergqvist, presents a reassessment of condylarth postcrania from the Itaboraí Basin, Brazil. The morphologies of each element are described and assigned to a species already known from the locale (and Bergqvist here supports the somewhat contentious position of *Victorlemoinea prototypica* within Condylarthra). A brief functional interpretation of the material infers that all of the species were generalised terrestrial mammals, although there is some suggestion in the astragalus and forelimb long bones that cursorial locomotion may have been possible. Shockey and Anaya follow with a contribution containing another honorific species announcement. *Fredszalaya hunteri* is named as a new species of carnivorous marsupial in a chapter that presents a straightforward description of the fauna from Salla, Bolivia, during the late Oligocene when species richness and diversity was particularly high. The authors emphasize anatomical descriptions of hindlimb morphology, tarsals in particular, and suggest phylogenetic histories for the families represented in the fauna. The penultimate chapter of Section I is a very short piece investigating the use of third proximal phalanx indices in resolving equid systematics in the Oligocene and Miocene of Florida. The introduction is an excellent summary of the topic but the relevant text and figures of the chapter comprise approximately five pages and the introduction accounts for half of this. Although the results are communicated succinctly—phalangeal data improves phylogenetic analyses compared to analyses based entirely on dental characters—realistically the analysis and discussion require further explanation. The section concludes with an engaging and thorough chapter by Polly on the evolution of the pinniped calcaneum and astragalus, addressing issues of both locomotor function and phylogeny. He clearly situates his work within a wider body of research, including Szalay's interests, assessing the relationship between tarsal morphology, behavior and relatedness.

Section II (Primates) begins with Silcox's excellent review of evidence in support of the suggestion that the order Primates has an Asian origin. Based on an increasing awareness of a more diverse fossil record of plesiadapiforms and primitive primate and euprimate taxa in Asia than previously acknowledged, she concludes that the scenario is possible but certainly not proven. The chapter outlines this mounting evidence and presents a cladistic analysis of relevant taxa, as well as two lengthy but useful appendices of data and character definitions. Boyer and Bloch follow with a discussion of the mitten-gliding hypothesis for paromomyid and micromomyid plesiadapiforms, focussing on functional interpretations of the postcrania, the phalanges in particular. Their analysis, which includes new material, suggests that these taxa do not share the suite of adaptive mitten-gliding characteristics proposed in an earlier study and are thus more likely to be allied with primates than with dermopterans, a belief also championed by Szalay. The third chapter, by Godinot and Couette, comments on the morphology and phylogeny of large adapines. They identify and compare the cranial material of two genera, *Leptadapis* and their newly named *Magnadapis*, which comprise a total of seven species including *Magnadapis fredi*, in honour of Szalay. Dagosto et al. provide the fourth contribution in a brief and straightforward description of tibiae from Middle Eocene sediments at Shanghuang, China. This builds on previous work in which analyses of the tarsal and dental remains suggested the presence of five different small-bodied primate groups. The tibiae, however, appear to belong entirely to two haplorhine groups, one with fused tibiafibulae and one displaying the unfused condition, but both bearing functional hallmarks of a leaping primate. Rosenberger et al. follow with an investigation of the "incipient" form of postorbital closure found in the late Eocene *Rooneyia viejaensis* noted by Szalay in the mid-1970's. This feature is a major hallmark of Anthropoidea, but researchers argue as to whether or not it links anthropoids and tarsiers or if it is a convergent feature of the two groups. This study is a detailed look at the craniofacial architecture associated with primate orbital morphology using 3D laser scans. The complexities of placing *Rooneyia* in the context of the major primate clades create difficulties in interpreting the meaning of this feature, but ultimately the authors conclude that the genus is more closely related to anthropoids and that the postorbital closure observed in both tarsiers and anthropoids arose independently. The sixth contribution is Maier's study of the inner ear anatomy of primates, situated in the broader context of comparative mammalian anatomy. Histological serial sections allow for an investigation of the chorda tympani nerve; the position of the nerve above the tensor tympani muscle is shown to be a synapomorphy defining Anthropoidea. Sargis et al. then examine guenon postcrania and locomotor strategies, which range from arboreal to semi-terrestrial to completely terrestrial. Full terrestriality is unique to only three guenon groups, but this analysis suggests that it evolved only once. However, these three groups of species have diversified substantially in terms of their substrate use and postcranial morphology, inferring that further research in this area may provide a new avenue for distinguishing between more subtle differences in locomotor behavior in extant and fossil primates. Harcourt-Smith et al. provide the eighth chapter in this sec-

tion, wherein the authors report briefly on the initial results from a 3D morphometric analysis of hominoid tibiae and talus joint surface congruence. This will ultimately aid in the matching of unarticulated fossil elements from single localities and in the identification of fossil genera and species. The book concludes with a lengthy contribution from Warshaw in which she discusses the variation in mid-shaft bone tissue microstructure in extant primates. This novel approach can be used to tackle various questions about function and phylogeny in living primates and, possibly in the future, similar kinds of questions about fossil taxa. This detailed report notes a dominance of slow growing tissues in all primates, but also identifies variation between taxa as well as between hind and forelimb bones, highlighting the need for further research in this unique area.

Mammalian Evolutionary Morphology is a highly recommended advanced volume that will prove to be a relevant resource for professionals and postgraduate students in many evolutionary and palaeontological disciplines. Anyone with an interest in mammalian evolution, primate or otherwise, should be familiar with the name Fred Szalay and certainly will recognise that this volume is more than a handy academic textbook. It is a meaningful tribute to the breadth and depth of Szalay's long career; the work of his students and colleagues herein provide a sincere and grateful testament to the influence of one person on the development of a unique branch of science. It is the sort of tribute that all academics should aspire towards, but which only a handful of the most worthy will achieve.