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Form-Function Correlation Paradigm in Mammalogy. A Tribute to Leonard B. Radinsky (1937–1985)

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Abstract
This special issue of the Journal of Mammalian Evolution represents the proceedings from a symposium held in conjunction with the XXXI Jornadas Argentinas de Mastozoología (SAREM, La Rioja, Argentina, October 25, 2018), and entitled "El paradigma de correlación forma-función en mastozoología: un tributo a Leonard Radinsky (1937–1985)." In this introduction to the symposium proceedings, we provide a brief account of Radinsky's expertise and academic goals, and we remark on the textbook "The Evolution of Vertebrate Design" posthumously published, to introduce the contents of the present volume and highlight Len's academic (research and teaching) and social sensitivity from the perspective of current times.

Keywords Ecomorphology · Functional morphology · Biomechanics · Behavior · Adaptation

Introduction

Leonard Burton Radinsky (1937–1985) was an American paleontologist born in Staten Island, New York (Fig. 1). He is mostly known as a specialist in the study of primate, perissodactyl, and carnivoran ancestors with a clear focus on functional anatomy and brain structure. We also wish to highlight his evolutionist biology focus and his interest in the understanding of extinct mammal life habits. He did undergraduate studies at Cornell University and obtained his Master's and Ph.D. degrees at Yale University, taught at the University of Chicago from 1967 until his death, and was chairperson in the Department of Anatomy from 1978 to 1983.

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After his untimely death, his delightful textbook "The Evolution of Vertebrate Design" (Fig. 2) was published in 1987 thanks to the efforts of Sharon Emerson. The book was originally planned as a text for his vertebrate morphology, paleontology, and evolution course for biology non-majors at the University of Chicago. Radinsky wanted his students to appreciate how vertebrate body shape (or design) changed over the course of evolution. Not finding texts that combined information on functional morphology and paleontology, he decided to write his own book. Simple and clearly drawn diagrams illustrated biomechanical explanations for the evolution of the jaws, fins, joints, and body shape in general of vertebrates.

In the introduction, Radinsky laid the foundation for what we call the "form-function paradigm" by stating that "There are two main approaches to interpreting the functional significance of evolutionary changes and the ways of life of extinct species: form-function correlation and biomechanical design analysis" (Radinsky 1987: 8). From any biologist's perspective, in our case, it is relevant to highlight that, in Radinsky's own words, "Form-function correlation involves looking for the behaviors or functions that are correlated with a particular anatomical form in living species" (Radinsky 1987: 8), which constitutes a prerequisite step before extrapolating this correlation to extinct species to infer function based on their form. In this simple and direct statement (where echoes of Cuvier's Forms Correlation Principle resonate), the foundations and procedures followed in ecomorphological studies are

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Fig. 1 Leonard Burton Radinsky (1937–1985), an American paleontologist born in Staten Island, NewYork. Photo: courtesy of his son Adam Radinsky

recognized, which today converge on quantifying the variation in morphology of organisms and evaluating or explaining the proportion of such variation that can be attributed to the environment (adjustment to a functional task) and to history (ontogeny and phylogeny; see Vizcaíno et al. 2016). Later, Radinsky also suggested that "Ideally, form-function correlation and biomechanical design analysis approaches are used together to examine a given problem or question" (Radinsky 1987: 9), as appears to occur when the results of functional morphology and/or ecomorphology analyzes are elaborated or discussed.

From the reading of the chapter 17 "Diversity of Mammal Design" of "Evolution of Vertebrate Design," it follows that Radinsky was intrigued and interested in the convergences between distant lineages of herbivorous mammals, both in the masticatory and locomotor apparatus. We understand that the observation of this recurrence of forms associated with a given behavior must have promoted his interest in the form-function correlation paradigm.

The easy reading of "The Evolution of Vertebrate Design" led many teachers to incorporate it in their undergraduate biology courses (Bonnan 2016), particularly in South America (Vizcaíno et al. 2016). In addition, postgraduate courses on functional morphology include many of his key articles as well as those of his students Walter Greaves and Susan Herring (see Kay 2019). Therefore, it has successfully inspired young biology students to focus their doctoral studies on the form-function paradigm framework. Being entertaining but rigorous, concise, and clear, "The Evolution of Vertebrate Design" is the perfect, approachable textbook for introducing students to the evolution of form and function.

As undergraduate students (i.e., GHC and NT) and teachers (i.e., SFV), we encountered Radinsky's book and agreed that Len's hope and purpose was accomplished, bringing us the excitement and appreciation of vertebrate life on Earth. Fortunately, we are not alone. In recent decades, functional morphology, biomechanics, and ecomorphology were the chosen methodological approaches for many doctoral theses on paleobiology and mammalogy in South America. For the two or three cohorts of students involved in those theses, it appears that the advice of Hopson and Radinsky (1980) – which encouraged paleontologist to improve the understanding of the relation of form with function in extant animals to aid in the functional interpretation of extinct ones – was understood as mandatory. Consequently, in South America it is not surprising to discover that the application of form-function correlation paradigm in mammalogy has been mostly achieved by young paleontologists. Year after year, and linked to advances in morphometry, morpho-functional studies have been gaining ground in the *Jornadas Argentinas de Mastozoología* (JAM) of the *Sociedad Argentina para el Estudio de los Mamíferos* (SAREM). It was not a coincidence that the organizers of the XXXI JAM shared with us the same fascination when we offered to organize the symposium: "El paradigma de correlación forma-función en mastozoología: un tributo a Leonard Radinsky (1937–1985)"; La Rioja, Argentina. 25 October, 2018.

We are convinced that the above-mentioned two or three cohorts of researchers devoted to the study of form and function constitute a true sign of Leonard Radinsky's influence on South American mammalogy. Today, and 33 years after the

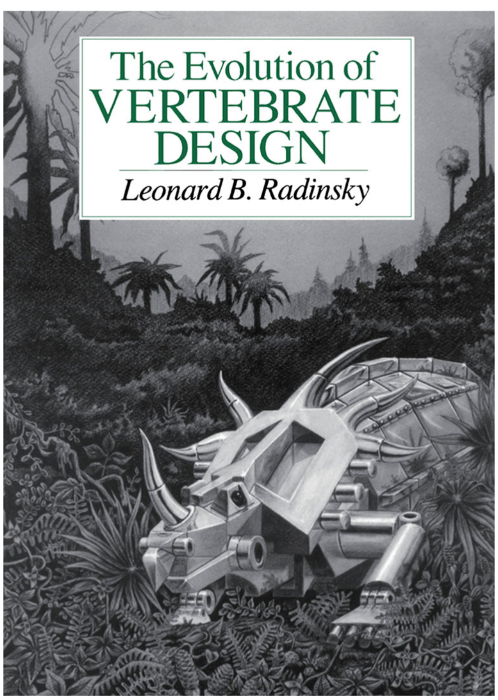

Fig. 2 Front cover of "The Evolution of Vertebrate Design" published by The University of Chicago Press. Cover art by Dennis Green

publication of his posthumous work, in this special issue different authors (both senior and young) have contributed their work as a tribute. In this sense, throughout the volume we have tried to delineate three main key issues: the temporal context in which Radinsky developed his ideas; the proposal and evolution of the form-function binomial; and how it was applied to the main groups of mammals from the Southern Cone.

The first contribution, by Kay (2019), reviews the academic and political aspects of Radinsky's career in the historical context of the nineteen-sixties to early nineteen-eighties, the different phases of his research, and his time at Yale University and the American Museum of Natural History, until his arrival at the University of Chicago. This enjoyable biographical note highlights little known aspects of Len's personality and radical views, as well as first-person anecdotes that grant a better understanding of the context of academic life in those tumultuous years.

This Special Issue goes on with the revision by Vizcaíno and Bargo (2019) of the evolution and dynamics of the views on the form-function binomial and biological design. These authors guide us through this fascinating theoretical framework from the early nineteenth century to our days. They revisit the change of paradigm from creationism to natural selection, how the basis of modern concepts in the form-function binomial was developed, the Radinsky legacy to the new biologist generations, and it finishes by presenting a southern perspective on the understanding of biological design.

From there, the Issue continues with research articles on the application of the form-function paradigm to the main lineages of South American mammals, which with 1617 species harbors the greatest taxonomic richness among biogeographic regions (Burgin et al. 2018). Among the metatherians, one of the most ancient clades of Neotropical mammals, didelphimorphians represent one of the largest radiations of marsupials apart from those of Australia (Astúa 2015). Chemisquy et al. (2020) study the skulls of didelphids in relation with diet and vertical habitat use, considering the influence of size and phylogenetic legacy. The authors find that these two last factors are the most meaningful, which could be explained in terms of skull integration and lack of specialization.

Xenarthrans are one of the four major clades of placentals, and encompass some of the most conspicuous Neotropical mammals, including sloths, anteaters, and armadillos (Gardner 2007). Toledo et al. (2020) focus on their different morphologies of the ulna and life habits. The ratio between olecranon and ulnar shaft length emerges as the most relevant feature for quantifying the mechanical advantage of the triceps muscle; however, it is the allometry-free morphospace that allows the differentiation between substrate preferences. The authors point out that ulnar curvature has biomechanical implications in relation to the bone response to different loadings produced in the context of posture and locomotion in each substrate.

The Rodentia are without doubt the richest and most diverse order of mammals in the world (D'Elía et al. 2019) and in the Neotropics specifically (769 spp., see Burgin et al. 2018: supplementary data S1). The Issue includes four contributions offering different approaches to form-function in rodents. First, the high taxonomic and ecomorphological diversity of caviomorphs is covered by Álvarez et al. (2020), who combine functional and macroevolutionary analyses to study the direction and rates of shape diversification on the caviomorph mandible. They find that the main pulses of shape change were related to the differentiation of octodontoids and cavioids with subterranean and epigean habits, respectively. Vassallo et al. (2019) review the limb bones and claws, as well as skull and incisors of rodents, as digging tools. They evaluate different approaches (e.g., histochemistry, functional indices, finite element analysis, etc.) and provide examples of multiple morphological adaptations related to digging behavior in hystricomorph rodents. These findings strongly argue in favor of Radinsky's form-function paradigm. As was noted before, ontogeny is another source of morphological variation to be evaluated in ecomorphologic analyses. This kind of approach led Carrizo et al. (2020) to study how the specializations for different locomotor behavior in sigmodontine rats could affect limb bone morphology throughout ontogeny. In so doing, they use limb proportions, functional indices, and allometric equations together with multivariate analyses. An interesting pattern of an elongated, slender morphology that characterizes the epigean modes of locomotion from the robust morphology of semifossorial ones emerges, and surprisingly the morphology of young rats seems to be similar to that of adults, suggesting that locomotion is relatively constant throughout ontogeny. Finally, rodent limb morphology is compared to that of small carnivorans by Muñoz (2020) in an attempt to evaluate convergences in these two distinct and diverse clades with various specializations to different life habits. He discovers that, whereas forelimb morphological variation could be explained in terms of use of substrate, the hind limb reflects better the taxonomic affiliation. These findings lead Muñoz (2020) to conclude that the forelimb is more involved in activities other than walking (e.g., climbing and digging) than are the hind limbs.

Chiropterans constitute the second group of mammals in taxonomic richness and diversity after rodents (Simmons and Cirranello 2018), and are the only group of mammals capable of powered flight. This tribute has two valuable contributions that account for this unique faculty. The one of Amador et al. (2020), already published in volume 27 issue 3 of this journal, evaluates the macroevolutionary patterns of traditional aerodynamic variables (e.g., wing loading, aspect ratio, tip shape index, etc.) in a comprehensive phylogeny that includes almost four hundred species. These authors find that although the ancestral aerodynamic morphotype was maintained throughout most of the chiropteran diversification, specializations in some groups permitted divergence toward novel aerodynamic morphotypes in the latter half of chiropteran evolutionary history. These changes seem to be linked to an ecological release from echolocation constraints, dietary-foraging shifts, or even environmental opportunities. Sánchez and Carrizo (2020) focus their study on the relationship between forelimb bone anatomy and wing design. They find an important relationship between these features and ecological habits. In addition, some morphological patterns recovered are explained by evolutionary history, but phylogeny also presents a strong covariation with ecological habits.

Deer are the most abundant and diverse group of ungulates in the Neotropics. Cassini and Toledo (2020) apply a novel approach to understand the relationship between craniomandibular integration and feeding behavior in this group. The covariation between skull features with diets high in monocot, fruit, or dicot plant material underscored the importance of relative toughness of food items as an important ecological factor shaping skull variation. These associations reveal convergences within small and large Neotropical deer that are explained by a complex interplay of size and biomechanically significant features.

Marchesi et al. (2020) study the vertebral column of cetaceans with a morphogeometric approach and analyze the complex relationship of shape and size with foraging strategies, prey, and habitat preferences. They study the magnitude of the different levels of allometry (static, ontogenetic, and evolutionary) in four dolphins from the southern hemisphere, partially sympatric and sharing a recent evolutionary history. The authors discover that while the species that feed cooperatively on pelagic prey retain the morphology from the proposed pelagic ancestor, those preferring coastal habitats could have promoted a design for better maneuverability.

Platyrrhine primates constitute a monophyletic clade that diversified in Central and South America and are considered a major primate adaptive radiation that unfolded along body size and locomotion axes, among others (Aristide et al. 2015). The contribution of del Rio et al. (2020) deals with the relationship between inner ear morphological variation and body size, vocalization frequencies and repertories, and locomotor behavior. The authors find that inner ear shape diversification occurs early in the platyrrhine radiation, and would not be associated with changes in vocalization features or locomotion behaviors, but is subject to a strong body size allometric effect.

The last two contributions deal with carnivorans, the fifth major clade of Neotropical mammals (Burgin et al. 2018: supplementary data S1). Segura et al. (2020) study integration in the canid mandible, as these animals have great diversity in feeding behavior and hunting strategy. These authors discover that canids evolved mostly within a restricted spectrum of morphologies, a sort of generalized shape that can be used in different diets, but some lineages of highly specialized taxa (hypercarnivores and insectivores) diverged toward robust or slender mandibles, respectively. Segura et al. (2020) conclude that surprising morphological conservatism and adaptive change can be at play at the same time in the canid mandible. Finally, Tarquini (2019) studies the hind limb of procyonids and its relationship with locomotor modes and substrate preferences. She finds that most morphological variation among procyonids can be explained based on ecological characteristics of their locomotion or substrate preference (particularly semi-aquatic and terrestrial-cursorial) but also body size (particularly caudo-proximal shape).

One reflection arises from the contributions united in this Issue. The advent of the age of computers allowed for access to powerful devices to quantify morphology (e.g., digital calipers, coordinate measurement machines –Microscribe–, 3D surface scanners, X-Ray tomography, etc). In addition, the development and availability of useful free statistic and morphometric software (e.g., MorphoJ, the TPS family, and the R suite among others; Klingenberg 2011; Rohlf 2015; R Core Team 2020) granted the possibility of applying a great diversity of state-of-the-art analyses in reasonable computing times and very affordably, especially important for researchers in developing countries. These factors positively enriched the ecomorphology, functional morphology, and biomechanic analyses throughout this volume.

We hope that this collection of works constitutes a rich contribution to Radinsky's legacy to South American mammalogy and, more specifically, to the study of the form-function relationship of mammals in Argentina.

Finally we want to highlight aspects of Radinsky's personality, in addition to his being an outstanding researcher renowned for his numerous publications, and passionate about teaching. Radinsky was undoubtedly a staunch defender of minority rights. His life and career reminds everyone that being a brilliant, dedicated scientist and teacher is not at odds with being a political person sensitive to major social issues. In present times, in which the equality of rights and the need for a sustainable approach to the natural world are recognized as urgent needs, the memory of his person should also function as a symbol of the importance of academic life as well as the role played by scientists and their advances in science and technology in our modern societies.

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