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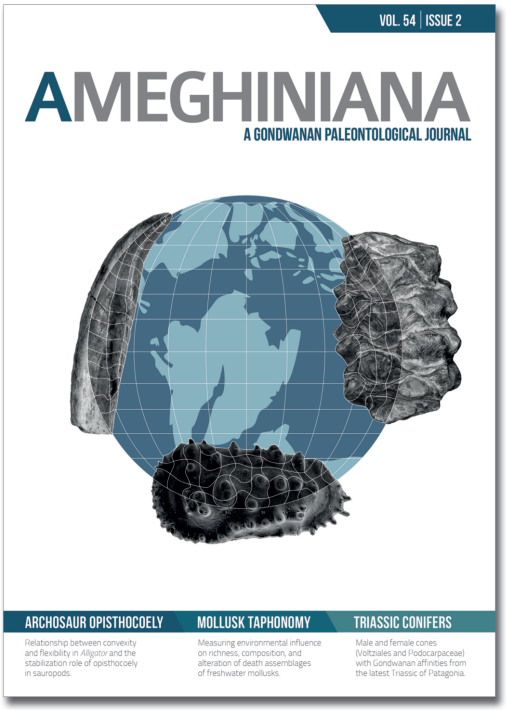

A BRIEF HISTORY OF SOUTH AMERICAN METATHERIANS: EVOLUTIONARY CONTEXTS AND INTERCONTINENTAL DISPERSAL

F.J. Goin, M.O. Woodburne, A.N. Zimicz, G.M. Martin & L. Chornogubsky, 2016. Springer Earth System Sciences, 237 pp. ISBN 978-94-017-7420-8

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A BRIEF HISTORY OF SOUTH AMERICAN METATHERIANS: EVOLUTIONARY CONTEXTS AND INTERCONTINENTAL DISPERSAL. F.J. Goin, M.O. Woodburne, A.N. Zimicz, G.M. Martin & L. Chornogubsky, 2016. Springer Earth System Sciences, 237 pp. ISBN 978-94-017-7420-8

"I give you this sword…", with this anecdote, 'A Brief History of South American Metatherians: Evolutionary Contexts and Intercontinental Dispersal' by Goin *et al.*, begins to inform the reader everything we currently know about the evolution of South American metatherians during Cenozoic times. In 7 comprehensive chapters the authors review a broad variety of topics (*e.g.*, paleobiology, natural history, geology and tectonics, biogeography, climate and biotas as well as taxonomy), providing a detailed summary of scientific facts and hypotheses about metatherian evolution and dispersal into South America, including the ideas that still engender controversy in science.

At least two qualities are essential for a well written scientifically important book: newly assembled and interesting facts related to an important subject, and inspiration. With regard to the first, the book by Goin *et al.*, is very good. Its scope is spectacular and the amount of material it synthesizes is staggering. To give you some idea for example, there have been about 158 phylogenetic studies involving metatheria published since 1980 (Cardillo *et al.*, 2004), ample testimony of the importance of metatheria to mammal evolutionary history. The book clearly conveys the excitement that abounds among those who study Cretaceous and later mammals of South America.

The book's central thesis is that the stability of mammal, and especially metatherian species richness and community structure has been affected by climatic and tectonic perturbations to the ecosystems within which they are woven. Despite their impressive capacity for adaptation, metatherian evolution demonstrates repeatedly their susceptibility to change, and so metatherians are especially useful in the study of the dynamics of change, to the extent that the fossil record permits.

The introduction gives a brief overview on the history of South American metatherian paleontology since 1878 and the people that shaped our current understanding of their morphology, taxonomy and radiation. All well illustrated with historical drawings and recent time tables. Fossil findings of the earliest ancestors of extant South American marsupials tell us that metatherians of the Cenozoic era of South America were small with a generalized morphology similar to extant *Monodelphis dimidiata*, and by comparison with Australasian metatheria, were not very diverse.

Whether nocturnal or crepuscular, arboreal or scansorial, or having broad, opportunistic and unspecialized diets, the remarkable flexibility of living metatheria enables them to range throughout the three-dimensional structure of their habitat. How caviomorph and later sigmodontine rodents successfully insinuated themselves into metatherian-dominated small-mammal ecospace is one of the greatest mysteries of the Cenozoic record and the Great American Biotic Interchange.

The authors voice a conviction that the land mammal age biochronologies of North America and South America, the NALMAs vs SALMAs, are comparable. While it is true that North and South American land-mammal ages should be compared, when they are, they turn out to be very different, dissimilar in composition, dissimilar in the precision of their boundaries, and dissimilar in their durations. On first principles, this should not be surprising, after all, the Northern Hemisphere is a terrestrial hemisphere where faunal exchange was frequent, whereas the Southern Hemisphere is an oceanic hemisphere, and South America was geographically isolated for much of the Cenozoic. If global events that influence mammalian faunal composition were instantaneous and had equal and identical impact on ecosystems throughout the world, we might expect North and South American land-mammal age boundaries to be of similar age. But even allowing for the imprecision of the

available geochronologies, these two geographically and latitudinally distinct continental land mammal histories do not show any trend toward convergence, even around supposed transcendental events.

The facts that the composition of South American mammal faunas is unique, and the mammals look very different morphologically from mammals on other continents, suggests their evolutionary history probably occurred at different rates and in different directions. Comparing SALMAs with those of Africa, or Antarctica, or Australia would be of more fundamental interest, but such schemes don't yet exist for these other southern continents. Similarly, it might make more sense to compare separate mammal biochronologies for austral vs neotropical South America, or from tropical vs temperate latitudes across the arid diagonal within South America.

Goin *et al.*, depict the relationships between metatherian evolution and the events of earth climate history as a series of more-or-less stable "phases" punctuated by sharp climate-induced faunal turnovers. Taking the four most obvious of these events: (1) the Late Gondwanan to Early South American transition that includes the K-Pg boundary sometime before the Tiupampan SALMA, (2) the Early to Late South American transition that includes the Eocene-Oligocene boundary sometime in the Tinguiririan SALMA, (3) the Late South American to Interamerican phases marked by the first appearance of North American heralds sometime within the Chasicoan SALMA, and (4) the Interamerican to Hypoamerican transition sometime during the Lujanian SALMA, the global events implicated in these turnovers actually occur within conventional SALMAs, not at the boundaries between them.

Chapter 2 lacks information about many living metatherian species, in terms of diet, reproduction (reproductive strategy, gestation length, litter size, litters/year), developmental timing, etc. This is not a fault of the authors, and is not peculiar to metatheria, but rather reflects the deplorable state of knowledge of the ecology of most of South American mammalian diversity. The remedy for this would be a continent-wide initiative that would enable zoologists, biology teachers and all their students to conduct the difficult and time-consuming fieldwork that is required.

Chapter 3 deals with the record of mammalian faunal interchange between South America and its continental neighbors, interpreted on the basis of very sporadic occurrences and rather meagre fossil remains (limited primarily to teeth). From such evidence, a southern history of faunal exchange is attempted.

Some of the highlights of this southern history include the following. Alamitan SALMA (Maestrichtian) mammal faunal composition in Patagonia is entirely non-tribosphenic and comprises ecologically diverse but "endemic" dryolestoids and gondwanatheres (plus some dinosaurs, *e.g.* hadrosaurs). Then, with the Tiupampan (early Paleocene) of Bolivia, we see that everything changed. Metatherians flourished, and in walked condylarths and pantodonts, an odd assortment (lots of other groups were present in North America but did not transit) from the north. The North American marsupial and multituberculates dominating faunas of the latest Cretaceous were largely but not entirely replaced by diverse eutherians in the Paleocene. In South America, the turnover was much less pronounced, as many primitive groups dryolestoids (*Necrolestes*), monotremes, gondwanatheres (*Groeberia*, *Patagonia*), and diverse primitive metatheria survived into the Miocene. So different was the K-Pg event and its consequences on the two continents, that it is no wonder the international community of stratigraphers does not include mammal first appearance datums as part of the definition for the K-Pg boundary.

Chapter 4 discusses the restricted area of southern South America where all three orders of metatherians (Didelphimorphia = "ameridelphia", Microbiotheria = Australidelphia, and Paucituberculata = Australodelphia or Didelphimorphia) can be found today and the details of this geographic "overlap" are interesting. This area of "overlap" lays south of the arid diagonal, the great biogeographic boundary that separates neotropical from austral South America. The zone of overlap extends across the Andes from the semi-arid shrub grasslands of Argentina to the wet temperate forests of Chile west of the meteorological divide of the Andes. Despite the heterogeneity of habitat in this transition, all the metatherian taxa in the "overlap", *Rhyncholestes* (Paucituberculata), *Dromiciops* (Australodelphia), *Thylamys* and *Lestodelphys* ("ameridelphia") are insectivores. Are bugs that abundant and tasty?

In Chapter 4 the authors claim "[g]rasslands seem to have been established, at least in southern South America,

by the late Oligocene" and attribute this to Barreda & Palazzesi (2007). Although the book was published in 2016, the reader gets the impression that parts of the text were written before 2013. More recent work on a much more continuous record by Carlini and colleagues [including Strömberg *et al.* (2013), Dunn et al. (2013, 2015), Selkin *et al.* (2015) and Kohn *et al.* (2015)], establishes pretty convincingly that although grasses occurred in the Paleogene of Patagonia, open grasslands did not become established there until the middle Miocene. The timing of the first appearance of open vegetation in Patagonia, and its consequence for metatherians, is bound up with the history of ocean and atmospheric conditions through Drake Passage and over Patagonia, and then intimately related to mountain-building that extended the arid belt and Andean subdivision northward. This is reflected among Patagonian metatheria by the progressive decline in tropical types and the emerging geographic coincidence of the arid "monte" belt with the biogeographic boundary between Neotropical and Andean-Patagonia.

Chapter 5 gives an overview of the numerous phylogenetic analyses carried out in recent years and presents different views on the relationships among South American metatherians. In addition, the six main groups or clades (*e.g.*, "Ameridelphia" incertae sedis, Sparassodonta, Didelphimorphia, Paucituberculata, Microbiotheria, Polydolopimorphia) and their different morphological characteristics are presented. The authors present impressive images of the variety of known fossil remains, exclusively of skull fragments, jaw parts and isolated teeth, although some of the earlier cited analyses are based also on postcranial characters.

Chapter 6 presents a view of the paleobiology and adaptations of Paleogene metatherian molar morphology. It presents a capsule history of the major changes in trophic specialization and richness, and attributes these to rainfall and temperature trends and events. For example, the extinction of "ameridelphians", decline of Polidolopiformes, and the appearance of Argyrolagoidea, occurred with the advent of arid conditions. More specifically, the Eocene-Oligocene boundary saw the extinction of larger frugivore-folivores (Polydolopiformes) and small granivores (Bonapartheriiformes) and their replacement by specialized seed eaters (Paucituberculata), insectivores (Microbiotheria), and herbivores (Argyrolagoidea). This change in trophic diversity is attributed to a "sharp drop in the rainfall regime" and the change in taxonomic diversity is attributed to a "sharp drop in ambient temperatures". There is actually little evidence for any "sharp drop" in the record of terrestrial temperature in Patagonia (notwithstanding the pronounced change in ice volume at Oi-1), and the rainfall record is also relatively constant, unless the changes that are documented are associated with environmental thresholds, either in depositional regime (from water to wind-dominated routing systems) or the density of foliage and its control over erosion, or simplification of habitat structure documented by decreasing leaf area index, or unless the temporal gaps in the Patagonian record are assumed to imply unchanging conditions.

Chapter 7 precisely summarizes the milestones in the evolution of South American methatherians that have been elaborately discussed in the chapters before. By putting the pieces together, the story of the South American metatheria is demonstrated in the context of their paleogeography, their origin and evolutionary radiation, all is placed in the context of plate tectonics. By defining three phases (*i.e.*, Late South American Phase, Interamerican Phase, Hypoamerican Phase) the authors are able to describe a comprehensive picture about the evolution and dispersal of South American metatherians.

Overall, we recognize the significance of the scope and contents of this book and the provocative thinking it has inspired in us, and we hope it proves equally stimulating to readers with a broad interest of natural history as well as scientists focused on mammal evolution. It is our conviction that anyone who ignores the lessons from the most extraordinary natural experiment that South American metatheria and all the other examples in the mammal and plant records there, does so at the cost of limiting our collective understanding of causation in evolutionary morphology.

REFERENCES

Barreda, V., and Palazzesi, I. 2007. Patagonian vegetation turnovers during the Paleogene-early Neogene: origin of arid-adapted floras. Botanical Review 73: 31–50.

Cardillo, M., Bininda-Emonds, O.R.P., Boakes, E., and Purvis, A. 2014. A species-level phylogenetic supertree of marsupials. Journal of Zoology 264: 11–31.

Dunn, R.E., Madden, R.H., Kohn, M.J., Schmitz, M.D., Strömberg,

C.A.E., Carlini, A.A., Ré, G.H., and Crowley, J. 2013. A new chronology for middle Eocene-early Miocene South American Land Mammal Ages. GSA Bulletin 125(3/4): 539–555.

Dunn, R.E., Strömberg, C.A.E., Madden, R.H., Kohn, M.J., and Carlini, A.A. 2015. Linked canopy, climate and faunal change in the Cenozoic of Patagonia. Science 247(6219): 258–261.

Kohn, M.J., Strömberg, C.A.E., Madden, R.H., Dunn, R.E., Evans, S., Palacios, A., and Carlini, A.A. 2015. Quasi-static Eocene-Oligocene climate in Patagonia promotes slow faunal evolution and mid-Cenozoic global cooling. Palaeogeography, Palaeoclimatology, and Palaeoecology, 435: 24–37.

Selkin, P.A., Strömberg, C.A.E., Dunn, R., Kohn, M.J., Carlini, A.A., Davies-Vollum, K.S., and Madden, R.H. 2015. Climate, dust, and fire across the Eocene-Oligocene transition, Patagonia. Geology 43(7): 567–570.

Strömberg, C.A.E., Dunn, R.E., Madden, R.H., Kohn, M.J., and Carlini, A.A. 2013. Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. Nature Communications, DOI: 10.1038/ncomms2508, 8 pages.

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