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TESTING PATTERNS AND PROCESSES OF DIVERSIFICATION OF A SOUTH AMERICAN GROUP OF LAND MAMMALS (RODENTIA, CRICETIDAE, SIGMODONTINAE)

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The subfamily Sigmodontinae is a highly diverse group that has attracted the attention of biologists interested in a broad range of disciplines. In addition to neontologists and paleontologists interested in systematics, paleoenvironmentalists, ecologists, physiologists, ethologists, epidemiologists, parasitologists, quantitative geneticists, and molecular biologists have also studied sigmodontines. As a result, a sound understanding of sigmodontine systematics directly impacts research in several other areas, some of which are of direct interest to human health and economy. In spite of sigmodontines having been studied intensively for a century and a half, our understanding of their systematics is far from complete. Obscure areas range from very basic issues, such as the extent of current and past diversity, to more complex aspects of their evolutionary history such as the elucidation of their temporal and spatial diversification patterns or the processes that underlie their tremendous diversity.

In this dissertation I tackle some of these issues. Each one of the three analytical parts of the study deals with a different level of organization and provides different insights into sigmodontine systematics. Chapter one sheds new light on the major patterns of the radiation of the group. Chapter two clarifies the species boundaries within one genus. Chapter three approaches the question of how sigmodontine diversity arises, by testing the predictions of one diversification model.

The phylogenetic analysis of chapter one, apart from corroborating many previous hypotheses, just as it rejects others and suggests new ones, shows two other things. First, sigmodontine morphologic, chromosomal and ecological evolution has followed an intricate set of pathways. The independent appearance of similar morphologies has been a recurrent theme in sigmodontine evolutionary history (this does not mean that morphological characters are not appropriate for studying sigmodontine phylogenetics, but only that they have to be used within an explicit cladistic framework). For example, which was previously thought to be a single group (e.g., the phyllotines) in fact represents more than one evolutionary line (e.g., true phyllotines on one hand and *Euneomys* or *Reithrodon* on the other). In view of these results, some researchers may feel that this study has increased the taxonomic chaos of the group instead of shedding light onto sigmodontine taxonomy. But, if one believes, as I do, that classifications must reflect the hierarchy of nature (i.e., the evolutionary history of organisms), this should not be seen as a problem; in fact, it tells us that sigmodontine diversity is even greater than previously acknowledged.

Second, the phylogenetic results also show that sigmodontine biogeography is by far more complex than previously envisioned. It is a history with repeated colonizations of temperate and tropical lowlands and highlands. The important role of the Atlantic forest and associated open biomes as main diversification areas is only now starting to being acknowledged. Here, the discoveries of new fossils that constitute conclusive evidence of the presence of one taxon in a specific geologic time and place would be extremely useful. In addition, it would be desirable to incorporate extinct taxa into phylogenetic analyses together with extant taxa to pose more rigorous test of hypotheses. This is critical because of the importance of sigmodontines to overall South American mammalian biodiversity; a sound hypothesis of sigmodontine origins would account for the origin of about 20% of the South American mammalian fauna.

The second chapter constitutes a study of alpha taxonomy. It uses, as several studies do today, a phylogeographic approach to assess species boundaries, in this case limits within the genus *Scapteromys*. However, the present study differs from others in its use of molecular information. The most common approach used by molecular taxonomists consists of identifying phylogeographic breaks and then exploring whether there is any agreement with the patterns of variation at other levels, mostly morphology and karyotypes. In these cases the molecular information is not used beyond the identification of the different species. In particular, it is not used to diagnose the species, what seems to me inconsistent because in these studies the species were first identified on the basis of molecular information. In the case of *Scapteromys*, I provide molecular synapomorphies that unambiguously determine if *Scapteromys* specimens belong to *S. aquaticus* or *S. tumidus*. Future sequencing of additional specimens may prove that some character states now thought to be derived are in fact primitive. Also, it may be shown that some character states now thought to be good indicators of historical relationships in fact appeared more than once during the history of the group. In those cases, amendments to the diagnoses would need to be made.

The third chapter is a study that belongs to a short series of studies aimed at assessing the role of different diversification models in the differentiation of the South American fauna. It focuses on testing the Riverine Barrier Hypothesis in the northern part of the Río de la Plata basin. The high levels of diversity in this region have received little attention, and we do not know if the processes credited with giving rise to lowland and Andean Amazonia diversity also account for the diversification of taxa from this and other more temperate South American regions. The results of chapter three indicate, as is the case in the Amazonian region that riverine distribution does not seem to affect the diversification of sigmodontine rodents, neither as a vicariating agent nor as secondary barrier. While it would be of interest to further test the RBH along rivers outside humid tropical areas, it also seems necessary to assess the role that other geographic barriers may have played in sigmodontine diversification. In addition, other possibilities that do not rely on isolation as a prerequisite to differentiation (i.e., divergence with gene flow) should also be considered.

As a whole, this research contributes to filling in a gap between theory and evidence with regards to the diversification of the South American fauna by integrating cladistics, phylogeography, evolutionary genetics and traditional systematics. Together with other accounts it will be the basis for the understanding of microevolutionary processes and macroevolutionary patterns behind the diversification of South American land mammals. Finally, from a personal perspective, this project constitutes a fundamental step in my long-term objective of studying the sigmodontine evolutionary history as well as the biogeography of the Río de la Plata basin.