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COMMENTARY

Paleobiogeography of South American cricetid rodents: a critique to Caviedes & Iriarte

Paleobiogeografía de los roedores cricétidos de Sudamérica: una crítica a Caviedes & Iriarte

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ABSTRACT

The scenario of rodent dispersal in South America proposed by Caviedes & Iriarte (1989) and the role of the geographic barrier that supposedly prevented their entry into Chile is assessed considering an alternative paleobiogeographic model as well as paleoclimatic evidence. It is shown that the Atacama desert probably did not represent a severe barrier to rodent dispersal from Pliocene to Pleistocene times, and that present patterns of distribution and low diversity of small mammals in the Atacama desert may be explained by a succession of colonization and extinction episodes.

Key words: Cricetids, Sigmodontinae, Paleobiogeography, Atacama Desert, South America.

RESUMEN

Se evalúa el escenario propuesto por Caviedes & Iriarte (1989) para la dispersión de roedores en América del Sur y el papel de las barreras geográficas que supuestamente impidieron su entrada a Chile, considerando un modelo paleobiogeográfico alternativo así como evidencia paleoclimática. Se muestra que el desierto de Atacama probablemente no representó una barrera severa a la dispersión de roedores durante el Plioceno y Pleistoceno, y que los patrones actuales de distribución y la baja diversidad de pequeños mamíferos en el desierto de Atacama pueden ser explicados por episodios sucesivos de colonización y extinción.

Palabras claves: Cricétidos, Sigmodontinae, Paleobiogeografía, desierto de Atacama, América del Sur.

Recently, Caviedes & Iriarte (1989) (C & I hereafter) reconstructed the migration routes of rodents in southern South America and explained their present distribution in central Chile considering the paleogeographic evidence. The scenario that they proposed suffers from serious deficiencies, primarily because they make uncritical use of current information and omit key evidence directly bearing on the topic addressed. My criticisms are concerned with the paleobiogeographic history of the South American cricetid rodents (subfamily Sigmodontinae) because it is misleading to test specific hypotheses about factors affecting the distribution of a closely related group of species (e.g., the cricetids) using evidence from a broader array of mammalian taxa (e.g., Caviomorpha, Edentata, Marsupialia) as did C & I. This is because the latter taxa exhibit constrasting food and habitat requirements as compared to cricetids, and more importantly, different histories of arrival and diversification (e.g., Webb & Marshall 1981). This criticism is valid at least within the spatial and temporal frame set up by C & I. In order to avoid future confusion I will point out those aspects of the paleobiogeography of South American cricetid rodents that C & I failed to address, and will outline some relevant questions for future research on this topic.

The scenario proposed by C & I

According to C & I, cricetid rodents spread along the Andean mountain range, from

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the northern to southern extremes of South America during Late Pliocene times. Specifically, they proposed that the southward cricetid expansion took place through two main dispersal routes, which avoided tropical lowland forests. These were: a) through a corridor located on the eastern slope of the Andes; and b) through a narrow belt in the western slope with an "abrupt halt at the Atacama desert" approximately south of latitude 22°S where "...coastal aridity increases and the interior vegetation of Puna and Paramo [sic] gives way to the halophytic Salar of the Puna de Atacama, presenting a formidable barrier for the southward penetration of Altiplano rodents species." (C & I: 184). Following their reasoning. C & I suggest that because no similar barrier existed along the eastern slope, these mice used the Altiplano as a southward migration corridor entering into the Monte of Argentina, while dispersing along the east slope of the Andes. Once in the Monte, westward migration to central Chile (30-33°S) was possible. This westward migration, C & I hypothesized, was favored by the decreased width of the Andes at this latitude, coupled with a northward shift of mesic vegetation during glacial periods (pluvials) which resulted in that "...the Andean valleys of east and west would have met at higher elevations thereby becoming practicable passes for trans-Andean migration." (C & I: 186).

First criticism: The entry of cricetids into South America and their southward migration

The time at which cricetid rodents entered South America and the schedule of their subsequent southward migration is a controversial issue that deserves further attention, especially if we are interested in the main barriers to their dispersal. This point is particularly apparent when we take into account the drastic landscape dynamics that South America underwent from Miocene to Pleistocene times (e.g., Cerqueira 1982, Simpson 1983). This dynamics made possible that a particular habitat once acting as a barrier, may have become a feasible corridor or a filter to dispersal at another time. The treatment that C & I make of this issue is weak. They incorrectly characterize the controversy about the cricetid entry into South America as if there were only two points of view (i.e., that proposing a Late Pliocene entry of these mice, and that proposing an Early Miocene arrival, see Webb 1985, Reig 1986). They overlooked a third proposition outlined by Marshall (1979).

Marshall's (1979) paleobiogeographic model suggests that sigmodontine rodents arrived at South America by waif dispersal across the Bolivar Trough marine barrier during the Messinian world-wide drop in sea level. After this waif dispersal event, in the Upper Miocene, these rodents underwent a major adaptive radiation in the savanna-grassland area of Venezuela, Colombia and the Guyanas (northern Andean area), where pastoral (grassland) forms evolved from ancestral sylvan (forest) forms. From this area, there was a southward migration of pastoral forms through a savanna-grassland corridor along the eastern foothills of the Andes connecting the northern and central Andean area with the Argentine pampas during the Late Pliocene.

In light of Marshall's (1979) model. C & I's model of cricetid migration along the eastern slope of the Andes into Argentina, appears an oversimplification with nothing new added (incidentally, C & I do not cite Marshall's 1979 paper). It may be argued, however, that the major contribution of C & I's model is to stress the role of the barriers to dispersal (in contrast to Marshall's model which emphasizes the routes available for dispersal), but as I point out below, the subject is more complex than C & I suppose.

Second criticism: The barriers to dispersal

C & I state that the Chilean territory harbors an impoverished mammalian fauna (particularly so of cricetid rodents) in comparison to Argentina, because their migration into Chile was prevented by biogeographic barriers. Among these, they single out the high elevation of the Andean range, the considerable width of the Andean area, and the dryness of the Atacama desert, all of them especially acute between latitudes 20 and 30°S. As evidence in support of their contention, C & I display the number of mammal species within the biogeographic regions of Chile (C & I: Fig. 1), where the high species richness found in the Chilean Altiplano region and in the mediterranean region is apparent. I raise serious doubts about the validity of the biogeographic scheme that C & I propose because it does not resemble any of the available biogeographic classifications now considered correct (see an informative review in Quintanilla 1983), and because there is no explicit mention about the criteria used in its construction.

The boundaries of the "Chilean Altiplano" region are particularly doubtful. Apparently, they were drawn based on the belief that "Between 17 and 27°S, the aridity of the coast and highlands is absolute..." (C & I: 183). Anyone well acquainted with the desert and highland landscapes of northern Chile would recognize a succession of vegetational belts along the Andean Pacific slope, from 2100 to 5000 m elevation (see Villagran *et al.*, 1981, 1982). Further, the Atacama desert never interrupts the vegetational belts along the western slope of the Andes between latitude 22 and 27°S, as C & I suggest. Instead, the progressive altitudinal penetration of the Atacama desert in a southeast direction from Arica to Antofagasta, results only in a reduction of the area that supports vegetation, at altitudinal ranges between 2800 and 4300 m (Villagrán *et al.* 1983). This vegetational zone corresponds to the "dry and arid puna" of Troll (1968), and to the "High Andean Vegetation without Major Classification" of Hueck & Seibert (1972). Incidentally, there is no Paramo vegetation at this latitude as erroneously stated by C & I. Farther south, this vegetational belt is gradually replaced by a sub-Andean desertic vegetation, and subsequently, by a sub-Andean mediterranean belt (Villagran *et al.* 1983).

That habitat continuity presently exists between northern Chile and north-central Chile along the western slope of the Andes is a matter of fact. Further, the demostration that gene flow occurs between *Phyllotis xanthopygus vaccarum*, a rodent currently found in the high mountains of central Chile, and *Phyllotis xanthopygus rupestris*, an Andean form living in northern Chile (Walker *et al.* 1984), supports the possibility of rodent movements along the western slope of the Andes, through the previously mentioned habitats, which currently may be considered a filter to dispersal.

Apparently, one of the main points of C & I is to stress the "barrier to migration" effect produced by the Atacama desert since late Pliocene times, coupled with the assumption that this effect was not ameliorated during the Pleistocene glacial (pluvials) events. In their analysis, however, C & I neglect a great amount of paleontological, paleobotanical and geological evidence that concurs in the suggestion that the extremely arid condition of the Atacama desert is of very recent origin, dating back only to Holocene times, with a Pliocene landscape dominated by a savanna-like vegetation at low elevations, and a Pleistocene characterized by markedly alternating wet and dry periods (for a review, see Arroyo *et al.* 1988). The key point, that invalidate the scenario proposed by C & I, is that during the Pleistocene pluvial periods, and surely during Pliocene times, the Atacama desert did not represent a severe barrier to dispersal (at least not so severe as it may currently be), thus rendering possible the colonization of marginal habitats, now discerned as geographic isolates within an hyperarid desert.

These paleobiogeographic phenomena may explain the disjunct distribution of several lowland cricetid rodents, as suggested by Meserve & Glanz (1978), and the assembly of Andean cricetid rodents such as *Eligmodontia typus puerulus*, *Akodon andinus*, and *Phyllotis xanthopygus rupestris* found at lowland localities in northern Chile (see collection records in Pine *et al.* 1979). The dispersal of these species probably was favored by the existence of deeply cut and vegetated valleys that traverse the currently arid depression in northern Chile (e.g., Lluta and Azapa valleys. Quebrada de Camarones), present since Miocene times (Mortimer 1980). Thus, the colonization of the Atacama desert by small mammals during Pliocene and Pleistocene times and the probable extinction of some forms during the increasingly arid Holocene are important processes likely to have shaped the biogeographic patterns of small mammals within the Atacama desert and the adjacent Andean area. At this point it is important to consider the possibility of rodent migration from northern to central Chile. Likely immigrants that used the Andean western slope were *Akodon andinus* and a form that gave rise to *Phyllotis xanthopygus vaccarum*, whereas *A. olivaceus* probably represents a lowland immigrant. This is because of the discontinuous distribution of said rodents from northernmost (Valle de Lluta, Pampa del Tamarugal) through central and to southern Chile, that suggests the fragmentation of a previously continuous distribution (but see Meserve & Glanz 1978).

This dynamics of colonization and extinction probably also applies to other groups. Fossil finds indicate that savanna-adapted vertebrates, both endemic and immigrants, inhabited the Pacific coastal desert during Pliocene and Pleistocene times (Webb 1978, Ochsenius 1985). Thus, the increased aridity that the Atacama desert underwent during Holocene times probably resulted in a drastic decrease in diversity, in a fashion similar to that reported for the Monte Desert (Mares 1985), but more acute, owing to the development of hyperarid conditions in the Pacific coast of Peru and northern Chile. This succession of colonization and extinction episodes coupled with simple area effect on species number (MacArthur & Wilson 1967) may account for the greater mammals species richness actually present in Argentina as compared to Chile, a pattern that C & I suggest to be the result of lack of colonization only. Future paleontological and zooarcheological work, coupled with extensive and exhaustive research on the extant mammalian fauna, should provide the key evidence needed to obtain a more accurate view of the dynamics of colonization and extinction in Chile.

Additionaly, and in order to correctly assess the contribution of C & I's paper, it must be said that the fundamental questions posed by them, that is, why so few cricetids reached Chile, and which were the possible dispersal routes available to them, were previosuly addressed by Meserve & Glanz (1978), who also emphasized the role of the Atacama desert and the Andean mountain range (see also Greer 1965). It is regrettable that C & I were not aware of this very important paper, published in the same journal as their's, but eleven years before.

CONCLUSION

Although there is still controversy about the paleobiogeography of cricetid (Sigmodontinae) rodents, it seems clear that their migration into South America was favored by the presence of a suitable habitat (savanna vegetation), same as for other vertebrate immigrant goups (Webb 1978, 1985, Marshall 1979). Some of these immigrants (cricetids included) together with endemics and early immigrant mammals (e.g., Caviomorphs) were inhabitants of the semidesertic vegetation that also ocurred in the Atacama desert during Pliocene and glacial (pluvial) Pleistocene times, as supported by paleontological, paleobotanical and geological evidence. During the Holocene, the development of hyperarid conditions that currently characterize the Pacific coastal desert, produced drastic habitat contractions that induced the local extinction of some species, and the current pattern of disjunct distribution of others. These extinctions were presumably the main factors responsible for the actual low faunal diversity in this region. Recognition that colonizations episodes were followed by a severe extinction episode account better for the pattern that C & I assume is the result of lack of colonization only.

Thus, contrary to the claims of C & I, there are different lines of evidence that concur in pointing out that the Atacama desert was not a severe barrier for mammalian dispersal. Further, current patterns of species distributions are in agreement with a southward migration of some species along the western slope of the Andes, and also with a probable lowland migration along the coastline.

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