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EVOLUTIVE PATTERN OF *CALOMYS HUMMELICKI* (HUSSON 1960; RODENTIA, SIGMODONTINAE) INFERRED FROM CYTOGENETIC AND ALLOZYMIC DATA

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ABSTRACT. The main purpose of this research was to understand the evolutive history of the sigmodontine rodent *Calomys hummelincki* (Husson 1960), tribe Phyllotini from chromosomal and allozymic data, and evaluate the hypotheses that explains the colonization and evolution of sigmodontine rodents in South America. *C. hummelincki* is restricted to the Northern South American region, which comprises Venezuela, Aruba and Curaçao islands where specimen sampling was done. The cytogenetic analysis showed that all populations studied have the same diploid number (2n=60) and fundamental number (FN=64). Constitutive heterochromatin was observed on pericentromeric positions in almost all chromosomes. NOR regions were observed on four pairs of acrocentric chromosomes. G-banding allowed us to identify almost all pair positions in the *C. hummelincki* chromosome complement. The G-banding also permitted a comparison of the *C. hummelincki* pattern with those published for *C. callidus*, *C. venustus* and *C. laucha* species. G-banded information indicates that *hummelincki* is not directly derived from *laucha*. The results are constrained with published allozymic and molecular data obtained in previous studies. The overall analysis seems to support Reig´s hypothesis of a south to north colonization of genus *Calomys* in South America.

RESUMEN. Patrón evolutivo de *Calomys hummelicki* (Husson 1960; Rodentia, Sigmodontinae) inferido de información citogenética y aloenzimática. El principal objetivo de este estudio fue el de entender el patrón evolutivo del roedor sigmodontino *Calomys hummelincki* (Husson 1960), tribu Phyllotini, utilizando información cromosómica y aloenzimática, lo cual permitió evaluar las hipótesis que explican la colonización y evolución de este grupo de roedores sigmodontinos en Sur América. *C. hummelincki* está restringido a la región norte de Sur América, comprendiendo a Venezuela, Aruba y Curaçao, en donde fueron realizados los muestreos. El análisis citogenético demostró que todas las poblaciones estudiadas presentaron los mismos números diploides (2n=60) y fundamental (FN=64). La posición de la heterocromatina constitutiva fue pericentromérica en casi todos los cromosomas. Las regiones NOR se observaron en cuatro pares de cromosomas acrocéntricos. Las bandas G permitieron identificar la posición de casi todos los pares del complemento cromosómico de *C. hummelincki*, así como comparar el patrón obtenido con el publicado para las especies *C. callidus*, *C. venustus* y *C. laucha*. Los resultados obtenidos con las bandas G parecen indicar que *hummelincki* no es una especie directamente derivada de *laucha*. Estos resul-

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tados son confrontados con los datos provenientes de estudios aloenzimáticos y moleculares publicados. El análisis global de esta información apoya la hipótesis planteada por Reig sobre una ruta de dispersión y colonización sur-norte del género *Calomys* en Sud América.

Key words: C-bands, G-bands, NOR regions, Phyllotini, South America, cricetids, Netherland Antilles, Aruba.

Palabras clave: bandas C, bandas G, regiones NOR, Phyllotini, Sur América, cricetidae, Antillas Nerlandesas, Aruba.

INTRODUCTION

Among Sigmodontine rodents, the Tribe Phyllotini, with 13 recognized genera, is the third richest group in number of species (N=45) (Reig, 1984). In this tribe, the genus *Calomys* is considered the most primitive (Reig, 1984). Except for *Calomys hummelincki*, *Calomys* distribution includes mainly the southern part of South America (from Central Brazil to Perú, Bolivia, Argentina and Uruguay). *C. hummelincki* lives in northern South America (Aruba and Curaçao islands and Northern Venezuela adjacent to Colombia) disjoint from all the other species of this genus.

*C. hummelincki´*s presence was first noted in the 1940s in the Netherlands Antilles by W. Hummelinck, who tentatively identified it as *Hesperomys* sp. (Husson, 1960a). Husson (1960b) validated its status as a species, but assigned it to the genus *Baiomys*. Two years later, Hershkovitz (1962) claimed that it should be identified as *Calomys laucha*, based on a report by Butterworth (1960) on specimens captured in Venezuela. In his surveys in Venezuela, Handley (1976) found natural populations of *C. hummelincki* in at least four locations, and he established the use of this specific name. No further information was obtained for this species until the late 1980s. Basic karyological information from one specimen of *C. hummelincki* captured in the Venezuelan Llanos was provided by Pérez-Zapata et al. (1987), who established that it was karyologically different from *C. laucha*.

Vitullo et al. (1990) and Espinosa et al. (1997) proposed that, within the *Calomys* group, *C. hummelincki* belongs to the *Calomys* ancestral stock, together with *C. sorellus* and *C. laucha*, because all these species present 2N³60. This hypothesis predicts that the *C. hummelincki* chromosome banding pattern should be similar to those of *sorellus* and/or *laucha* patterns and share some chromosomes with the immediately derived species. More recently, García et al. (1999) showed by electrophoretic analysis, that *C. hummelincki* is more closely related to *C. venustus* than to *C. laucha*.

A satisfactory biogeographical explanation of the actual distribution of genus *Calomys* has been published only recently by Salazar-Bravo et al. (2001). The first hypothesis proposed to explain the origin of this genus was given by Baskin (1978, 1989) who postulated that a primitive *Calomys* arrived from North America, colonizing by steps the South American lowlands during the "Great Interamerican Interchange" at Quaternary time. On the contrary, according to Reig (1986) the tribe Phyllotine began its diversification in the South Central Andes region, before the Andes definitive uplift. This geological situation permitted the dispersal of the neo-*Calomys* species throughout the lowlands, maintaining a stock in the Protoandes Area, which differentiated definitively after the actual uplifting. Later, when the savanna habitats were reduced in area, the northern populations became isolated from the others, leading to an allopatric speciation. This last statement is supported by Marshall´s theory (1979), which describes the Miocene-Pleistocene climatic changes responsible for the expansion-contraction of savanna habitats, and their implication in the colonization and evolutive process of Sigmodontine rodents. Molecular systematic analysis performed by Engel et al. (1998) also support this hypothesis. Recently, Salazar-Bravo et al. (2001) concluded, after performing *cyt b* data analy-

sis, that the origin of the genus was in the Southern part of the actual Amazon basin where three events produced the main clades observed, one ending with only *C. hummelincki*, a second event led to the *C. lepidus*, *C. musculinus* and *C. sorellus* clade, and a third led to the clade which includes the other *Calomys* species.

In the present study we present cytogenetic data of six populations of *C. hummelincki* from Venezuela and Aruba island, and complement the analysis with allozymic data published by Martino et al. (2001), which would eventually allow us to test the evolutionary relationship of *C. hummelincki* with other species of *Calomys*, as proposed by Vitullo et al. (1990) and Espinosa et al.(1997), and to try to evaluate the possible pattern of colonization and subsequent isolation of this species in Northern South America.

MATERIAL AND METHODS

Specimens for the cytogenetic analysis were obtained by live trapping in five Venezuelan locations: Represa El Isiro (Falcón State, N=18), Curarigua (Lara State, N=13), Puerto Páez (Apure State, N=18), El Merey (Monagas State, N=5), Sipao (Bolívar State, N=3) and on Aruba Island (N=5) (**Fig. 1**).

For cytogenetic analysis all animals, after capture, were identified and transported to the laboratory to obtain bone marrow preparations, following Hsu and Patton´s (1969) procedure. C- and G-

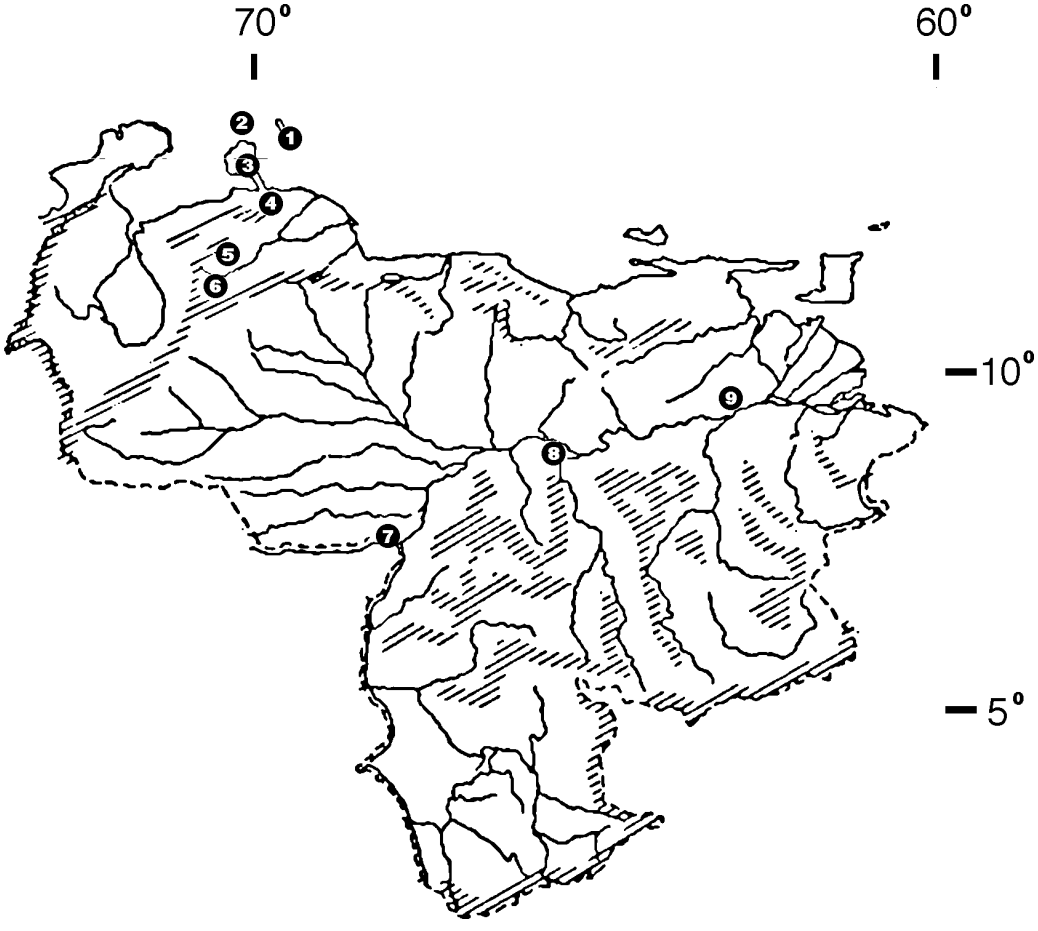

Fig. 1. Location of the sampled populations of *C. hummelincki*. All places are in Venezuela, except Aruba and Curaçao. 1. Curaçao (Nehterland Antilles); 2. Aruba; 3. Paraguaná; 4. El Isiro; 5. Baragua; 6. Curarigua; 7. Puerto Páez; 8. Sipao; 9. El Merey.

banding were obtained following the Sumner (1990) and Seabright (1971) protocols with slight modifications. NOR regions were evidenced by Silver Nitrate reaction (Howell and Black, 1980).

RESULTS

All animals from all locations presented a stable diploid number and fundamental number (2n=60, FN= 64); they also had the following karyological characteristics: two pairs of large metacentrics, a small metacentric, a submetacentric X, while the remaining chromosomes and chromosome Y were acrocentrics (**Fig 2**). We arranged the metacentrics in one group, calling them M1, M2 and M3, while the acrocentrics were numbered consecutively A1 to A26.

C-banding revealed the presence of pericentromeric heterochromatin in almost all homologous chromosomes, but it was very weak or almost nil on large metacentrics and in the acrocentric pairs A1, A21, A22, A23 and A24. Pairs A2, A7, A9, A11 A14, A18 and X exhibited conspicuous C bands. The Y chromosome was fully heterochromatic (**Fig. 3**). NOR regions were localized on the short arms of the telocentric pairs A8 and A21, and in interstitial positions on acrocentric pairs A11 and A22.

The G banding allowed us to identify almost 90% of the chromosomal complement (**Fig. 4**). We compared the G-banding pattern with those published for other *Calomys* species: *C. callidus*, *C. venustus* (Vitullo et al., 1990) and *C. laucha* (kindly facilitated by Dr. Maria Susana Merani from Universidad de Buenos Aires, Argentina). This comparison (**Fig. 5**) showed the correspondence of *C. hummelincki* and *C. laucha* for almost all chromosomes. Some discrepancies are evident because it was not possible

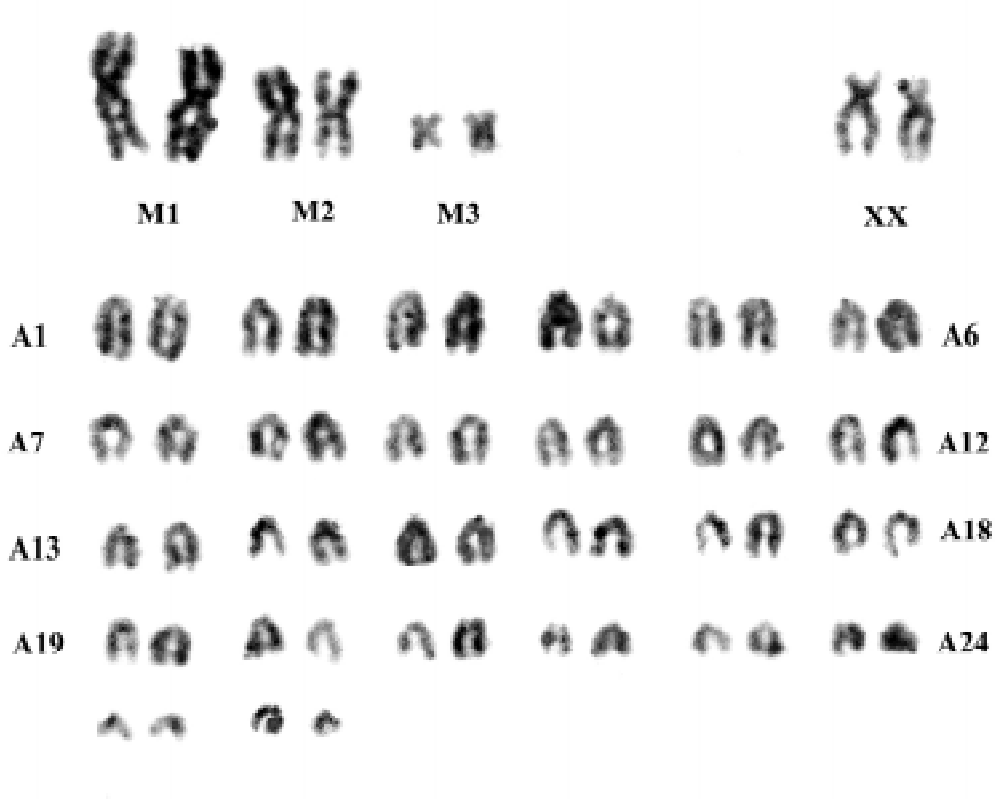

Fig. 2. Giemsa stained karyotype of *C. hummelincki* (2n= 60, FN= 64).

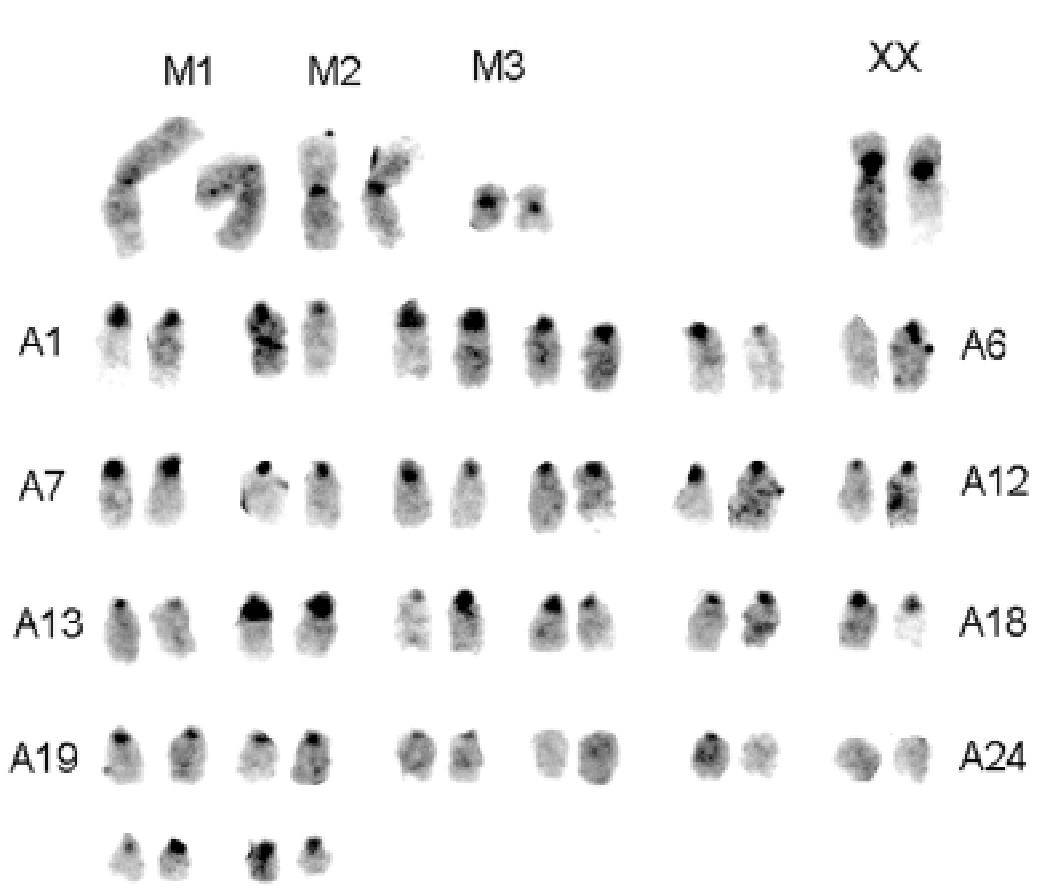

Fig. 3. Representative C-banded karyotype of *C. hummelincki.*

obtain a good matching of some chromosomes pairs, e.g. pairs A6, A7, and A8 of *hummelincki* with pairs A7, A6 and A5 of *laucha*. However, the following points must be mentioned: M1 of *hummelincki* seems be the product of the fusion A2 and A3 of *laucha*; A1 of *hummelincki* seems to be the result of fusion and posterior pericentric inversion of pairs A4 and A23 of *laucha*; the same seems true for A2 of *hummelincki* and pairs A14 with A25 of *laucha.* The long arm of *laucha´*s M2 is similar to *hummelincki´*s A4, and the short arm of the same chromosome is similar to *hummelincki´*s A24. In addition, there are probably two paracentric inversions on *laucha´*s acrocentric pairs A1 and A12, which produce *hummelincki´*s acrocentric pairs A5 and A14. Finally, it seems that *hummelincki´*s acrocentric A3 is the result of a duplication of a portion of *laucha´*s acrocentric pair A8.

A similar comparison of G-band karyotypes showed a good correspondence between *C. hummelincki* and *C. venustus* (Vitullo et al., 1990) G-banded, with the sole exception of a few discrepancies in the matching of some chromosome pairs. It should be noted that the two large metacentrics of *hummelincki* match the two largest metacentrics of *venustus*, and the small metacentric 19 of *venustus* matches M3 of *hummelincki*. In addition, pair 4 of *venustus* seems to be the result of a pericentric inversion of *hummelincki´*s A1. The possible fusion of *hummelincki´*s A3 with A5 would result in the metacentric 3 of *venustus*, and fusion of *hummelincki´*s A10 with A15 forms the metacentric 5 of *venustus*.

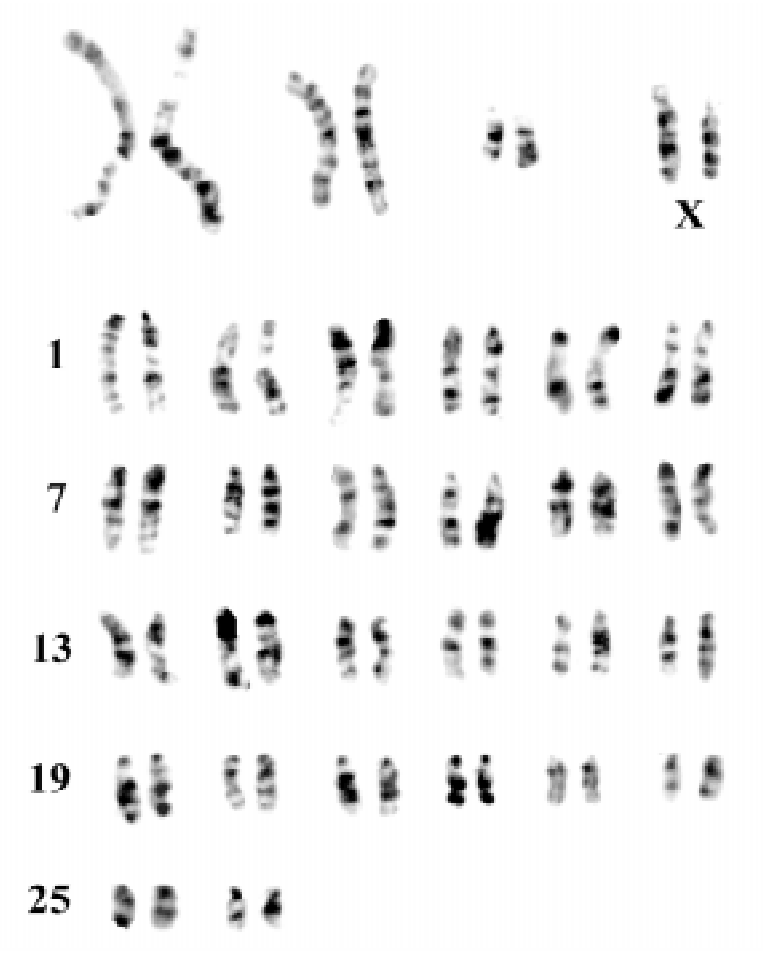

Fig. 4. Representative G-banded karyotype of *C. hummelincki*

DISCUSSION

The diploid and fundamental numbers and the beta karyological characteristics described for *C. hummelincki,* were the same as those reported by Pérez-Zapata et al. (1987). Our results also indicate the lack of chromosomal polymorphism in the populations examined, which is probably true for the other populations spread throughout the distribution range.

The position of constitutive heterochromatin on the autosomal and X chromosomes in *C. hummelinki* is similar to what has been found in other species of *Calomys*. The karyologically related *C. laucha* shows conspicuous pericentromeric bands in almost all chromosomes (Brum-Zorrilla et al., 1990; Svartman and Almeida, 1992). Nevertheless, the C-band pattern of *C. hummelincki* is similar to that of *C. lepidus* (Espinosa et al., 1997). In this species, the large metacentrics do not present pericentromeric heterochromatin as do some acrocentrics. Other species of *Calomys*, e.g. *C. musculinus* and *C. lepidus*, show weak pericentromeric heterochromatic bands on the large metacentrics, which may indicate their Robertsonian origin (Lisanti et al., 1976; Forcone et al., 1980, Ciccioli, 1991), while the other chromosomes present more or less conspicuous pericentromeric bands. This observa-

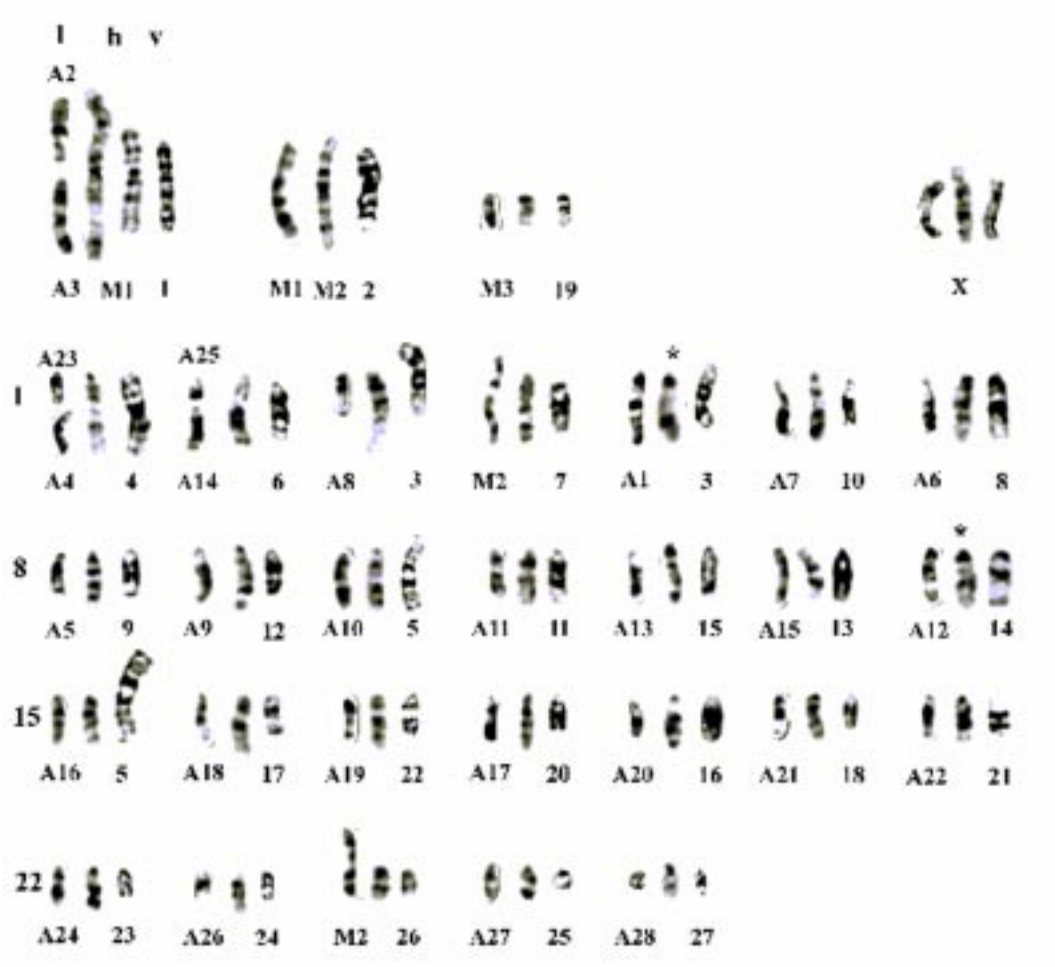

Fig. 5. Comparison of G-banded karyotypes of *C. laucha* (l), *C. hummelincki* (h) and *C. venustus* (v). Asterics indicates the presence of paracentric inversions.

tion lasts doubts on a Robertsonian origin of the karyotypes, which was published by Vitullo et al. (1990), from species with a high chromosome number, like *C. laucha*. The sex chromosomes show more variability: for example, the X chromosome of *C. lepidus* has a terminal heterochromatic band (Espinosa et al., 1997). Chromosome Y in *C. hummelincki* is fully heterochromatic, as in *C. lepidus* (Espinosa et al., 1997) and *C. callosus*, while this chromosome is not heterochromatic in *C. musculinus* (Lisanti et al., 1996).

The position of NOR in *C. hummelincki* is different from that observed in other *Calomys* species. In *C. laucha* NOR are present in a centromeric position (Brum-Zorrilla et al., 1990), while in *C. callosus expulsus* they are present on the short arms of the acrocentric chromosomes (Svartman and Almeida, 1992). In *C. musculinus* they are on the long arms of four metacentrics and the first submetacentric chromosome (Ciccioli, 1991).

It was not possible to perform G-banding directly in the other species, so we found some discrepancies in the comparison of the chromosome pairs. However, it was possible to establish the correspondence of almost all chromosome pairs of *C. hummelincki* with those of *C. venustus* and *C. laucha*. Indeed, 22 pairs of chromosomes are similar among the three spe-

cies (**Fig. 5**), suggesting a close relationship among them. With *hummelincki´*s chromosome positions as reference, these chromosomes are two metacentric pairs (one large and one small), the acrocentric pairs A6 to A9, A11, A13 to A23, A25, A26 and X. It is interesting that the small metacentric pair in the *C. hummelincki* karyotype (equivalent in size to the medium to small acrocentric pairs) is observed in almost all species of *Calomys* with known karyotype (Hurtado de Catalfo and Wainberg, 1974; Lisanti et al., 1976; Gardenal et al., 1977; Brum-Zorrilla et al., 1990; Ciccioli, 1991). The presence of this particular chromosome, which has pericentric heterochromatin in all species studied, suggests that the ancestral diploid number of *Calomys* was 68 [not 70 as was originally proposed by Pearson and Patton (1976)].

In spite of the chromosome uniformity observed in the sampled populations, Martino et al. (2001) showed that almost all populations presented a well genetic divergence pattern as indicated by the Nm values estimated, suggesting demes or inbreed group structure. The known distribution of *C. hummelincki* (**Fig. 1**) is represented by a few sites spread throughout Aruba and Curaçao islands, some lowlands of Venezuela and the border between northwestern Venezuela and Colombia (Eisenberg, 1989; Linares, 1998) at elevations from sea level to 600 m. The geographic disposition of the sampled sites and the presence of significant geographical barriers (sea between Aruba and the mainland, mountains passes that reach 800 m covered by woodlands, between Isiro and Llanos populations, the Orinoco river separating Sipao from northern populations) that separate them, contributed to cause the relatively high and similar values of F_{ST} (0.241) and F_{IT} (0.251) observed by Martino et al. (2001) for these populations. These data allow Martino et al. (2001) to distinguish three main clades of differentiated populations, of which the most similar were the Llanos populations and the most differentiated was the southern population of Sipao. The electrophoretic data suggest that the current distribution of *C. hummelincki* could be the consequence of successive south to north invasions related to expansions and contractions of suitable grasslands areas during Pleistocene climatic changes (Vuilleumier, 1973; Webb, 1978; Marshall, 1979; Engel et al., 1998; Salazar-Bravo et al., 2001).

EVOLUTIONARY CONSIDERATIONS

Reig (1986) postulated that phyllotine rodents, the tribe to which *Calomys* belongs, differentiated in the south-central Andes area, and from there, colonized highland and low open lands. In particular, *Calomys* has species in puna (highland) areas (*C. lepidus*, Espinosa et al., 1997), and in low-altitude areas (*C. hummelincki*, Handley, 1976; Martino, 1995). Pearson and Patton (1976) postulated that *C. sorellus* should have the most primitive karyotype of the *Calomys* group, and they proposed an evolutionary derivation of the other species from *C. sorellus*. Vitullo et al. (1990), with new karyological evidence, modified the Pearson and Patton hypothesis, suggesting a more or less direct derivation of *C. musculinus* from the ancestral stock. In this hypothesis *C. hummelincki* is intermediate between the *C. laucha/C. sorellus* (2n=64) stock and the *C. venustus* (2n=56) stock. However, our results did not suggest a direct derivation of *C. hummelincki* from *C. laucha*, such as was suggested by Vitullo et al. (1990). Indeed, to obtain a *C. hummelincki* karyotype from that of *C. laucha* would require three fusions, one fission and two pericentric inversions plus another two paracentric inversions. Considering a parsimony criterium, it seems that all these events would have a low probability of occurring at one time. On the other hand, it is probable that a *hummelincki* ancestor gave rise to the *C. venustus*-*C. lepidus* group, since it was possible to identify two fusions and inversions necessary to convert a *hummelincki* karyotype into a *venustus* form. These results indicate that the chromosomal characteristics of *C. hummelincki*, are closer to those shown by the *C. venustus*-*C. lepidus* group. The heterochromatic evidence lasts doubts on a Robertsonian origin, such as was postulated by Vitullo et al. (1990), of the karyotypes with a smaller number of chromosomes from species with a higher chromosome num-

ber, like *C. laucha*. Additionally, the poor matching of the G-band karyotypes observed, in a preliminary comparison, between *C. hummelincki* and *C. musculinus* indicates no close or direct relationship between them. This evidence indicates that *C. hummelincki* does not derive from *C. laucha* directly, and that *C. musculinus* did not derive, at least directly, from *hummelincki* or *laucha*. Karyological data contrast with the limited comparison on genetic divergence calculated among *hummelincki*, *laucha* and *venustus* by García et al. (1999) and Martino et al. (2001), who found that *hummelincki* is either closer to *laucha* or to *musculinus*, respectively.

Further data, such as the earlier study of Corach et al. (1988), related with analysis of DNA characteristics of three species of *Calomys*, found that *C. callosus* has a different DNA composition from that of *C. laucha* and *C. musculinus*, leading to the conclusion that the three species derived from different evolutionary lines. Subsequent studies on morphology (Steppan, 1995) and on molecular characterization (Steppan, 1995; Engel et al., 1998) indicate that *Calomys* group could have a polyphyletic origin. Salazar-Bravo et al. (2001) using *cyt b* analysis, did not find this polyphyletic origin, but their finding supports Corach data related with different *Calomys* evolutionary lines. The phylogenetic tree proposed by them for *Calomys* species, gives strong support to our chromosomal considerations, showing that from a basal group, this taxon split in three different evolutive events, one of which ended in differentiation of *C. hummelincki* in an independent branch from the *laucha* and *venustus* groups, not as a basal species as Vitullo et al. (1990) postulated from cytogenetic data.

From an historical point of view, the values of genetic variation and genetic distances known for the populations of *C. hummelincki* seem to support Reig's hypothesis of invasion of ancient *Calomys* populations from South to North. Considering that the Guayana Shield is one of the most ancient formations of South America, and has not suffered much from changes in sea level, it is possible that the primitive *Calomys* species reached this area during the late Miocene savanna-like environment present before the uplifting of Andean cordillera. After the uplifting, coupled with expansion and contraction of savannas, variations of the water transgressions and changes of the coastline, the ancient *Calomys* populations probably colonized the most suitable areas by steps, and became isolated from other populations. This isolation would be partially responsible for the speciation process in this genus, by chromosomal arrangements which originated different species. In *C. hummelincki*, the colonization and differentiation process seems to reflect a south to north direction. It is probable that oldest populations first established themselves in the savannas on the right side of Orinoco (or paleo-Orinoco) river. After that, Pleistocene climatic changes allowed the Llanos region to reach its actual configuration and allowed sedimentation between late Miocene and the Pleistocene (see Horn et al., 1995), so the populations present in this area, due to a later colonization, are less differentiated than those from Sipao. The populations from Aruba and Isiro probably were separated by changes of sea level during the Pleistocene and then reached their present slight level of differentiation. This scenario is supported by Salazar-Bravo et al. (2001), who concluded that in the southern part of the actual Amazon Basin, a proto-*Calomys* population began to disperse and diversify over all suitable habitats in South America, leading to the present known differentiation. In this hypothesis, the ancestors of *C. hummelincki* migrated from south to north, reaching an independent karyological differentiation from the southern populations of *Calomys*.

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