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Chromosome Characterization of an Endemic South American Rodent, *Calomys hummelincki* (Husson, 1960) (Sigmodontinae, Phyllotini)

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Abstract - The main objective of this research was the chromosomal characterization of the sigmodontine rodent *Calomys hummelincki* (Husson, 1960), which belongs to the Tribe Phyllotini. The distribution of *C. hummelincki* is restricted to a region of northern South America, comprising Venezuela, Aruba, Curaçao and probably the Colombian llanos and Guajira Peninsula. For this study, we collected specimens in Venezuela, Aruba and Curaçao. The cytogenetic analysis showed that all six populations studied displayed the same diploid number ($2n$=60) and fundamental number (FN=64). Constitutive heterochromatin was observed in a pericentromeric position in almost all chromosomes. NOR regions were observed in four pairs of acrocentric chromosomes. Chromomycin/DAPI fluorescent staining revealed the presence of particular euchromatin fluorescent blocks in some chromosomes. G-banding allowed us to identify almost all pair positions of the *C. hummelincki* chromosome complement. G-banding also permitted a comparison of the *C. hummelincki* pattern with those published for *C. callidus, C. venustus* and *C. laucha*. The results indicate that *C. hummelincki* is not directly derived from *C. laucha*.

Key Words: Chromosomes, Karyotype Evolution, Rodents, South America.

INTRODUCTION

Calomys hummelincki is the only species of the genus *Calomys* living in a limited area of northern South America (Aruba, Curaçao and northern Venezuela); it has a disjunct distribution with respect to all the other species of this genus. Its presence was first noted in the 1940s in the Netherlands Antilles by W. Hummelinck, who tentatively identified this rodent 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 denomination. After that, 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 2N≥60. This hypothesis predicts that the *C. hummelincki* chromosome banding pattern should be similar to

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those of *C. sorellus* and/or *C. laucha* and share some chromosomes with the immediately derived species.

The present study had two objectives: first, to analyze the chromosomal composition of the various natural populations of this species within its distribution range; second, to describe the chromosome pattern, which would allow us to test the evolutionary relationship of *C. hummelincki* with other species of the *Calomys* group proposed by VITULLO *et al.* (1990).

MATERIAL AND METHODS

Animals 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 at Aruba Island (N=5)

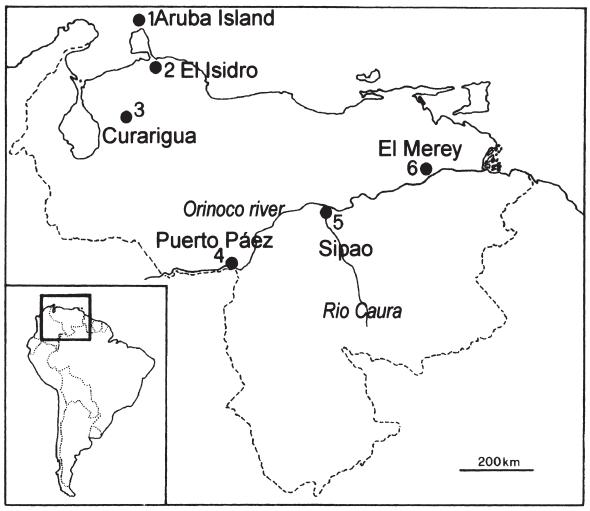

Fig. 1 – Location of the sampled populations of *C. hummelincki*. 1: Aruba Island (N=5); 2: El Isiro (N=14); 3: Curarigua (N=12); 4: Puerto Páez (N=12); 5: Sipao (N=3); 6: El Merey (N=3). All places are in Venezuela, except Aruba.

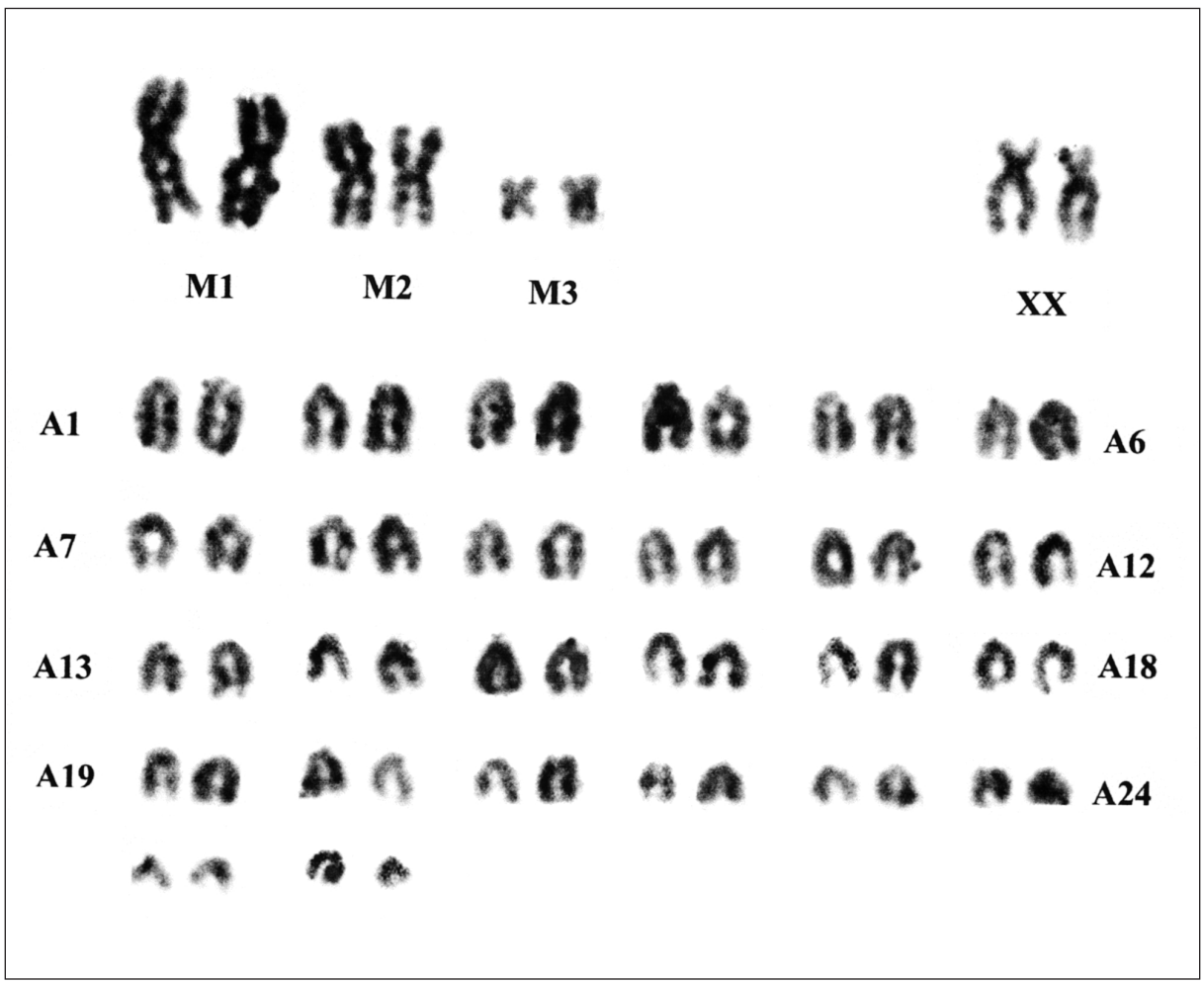

Fig. 2 – Giemsa stained karyotype of *C. hummelincki* (2*n*=60, FN=64).

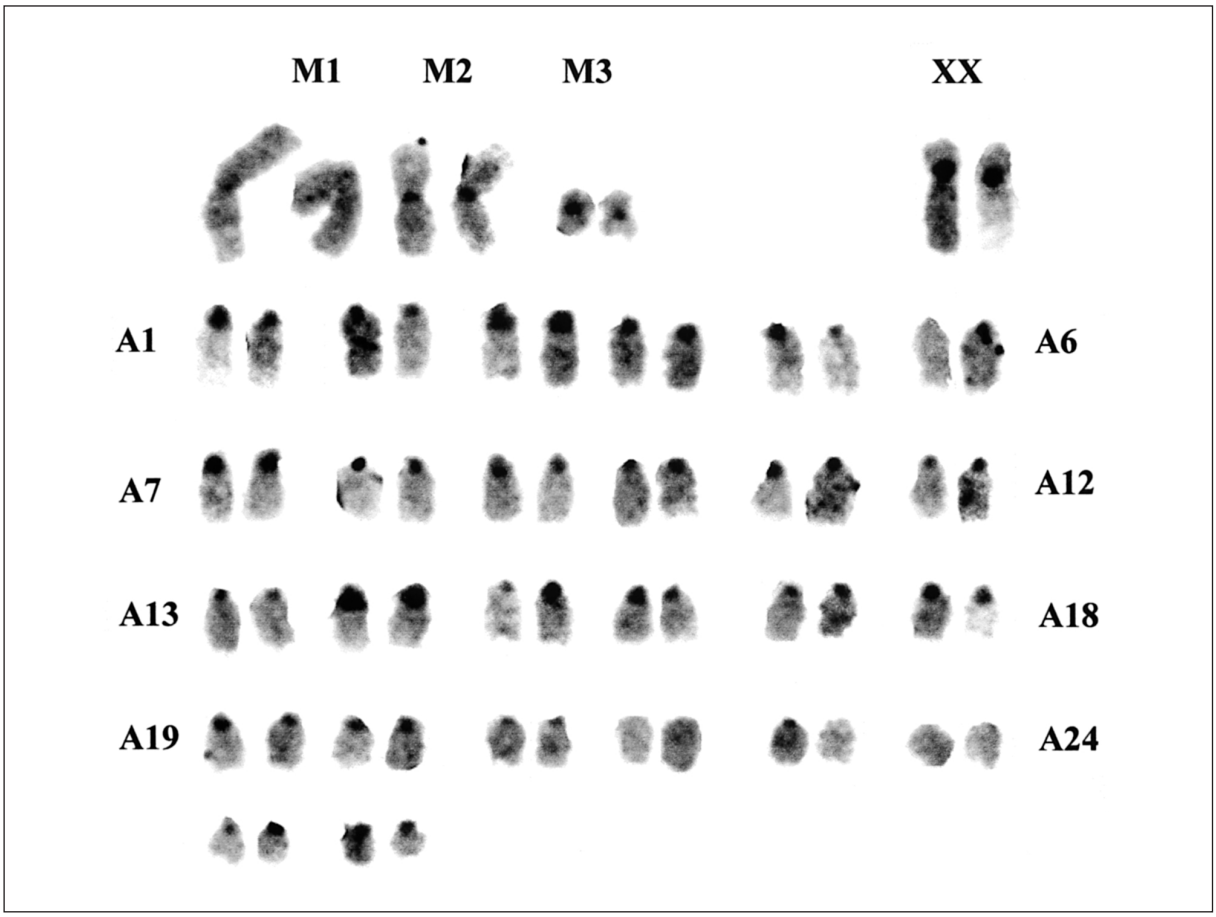

Fig. 3 – Representative C-banded karyotype of *C. hummelincki.*

(Fig. 1). After capture, all animals were identified and transported to the laboratory to obtain bone marrow preparations, following HSU and PATTON (1969). Voucher specimens were deposited at Museo de la Estación Biológica de Rancho Grande (MARNR, Maracay, Venezuela), Museo de Historia Natural La Salle (Caracas, Venezuela) and Museo de Biología de la Universidad Simón Bolívar (Caracas, Venezuela). C- and G-banding were performed following SUMNER (1972) and SEABRIGHT (1971) with slight modifications. NOR regions were revealed by Silver Nitrate reaction (HOWELL and BLACK 1980). Chromomycin A_3 (CMA) and 4,6-diamidino-2-phenyl-indol (DAPI) treatments were performed following SCHWEIZER (1976) with slight modifications.

RESULTS

All animals from all locations presented a stable diploid 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 in the large metacentrics and the acrocentric pairs A1, A21, A22, A23 and A24. Pairs A3, A7, A9, A11 A14, A18 and X exhibited conspicuous C bands (Fig. 3). The Y chromosome was fully heterochromatic. 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 (Fig. 4). Fluorescent banding revealed strong euchromatic blocks in several pairs: A1, A3, A5, A7, A8, A9, A12, A13,

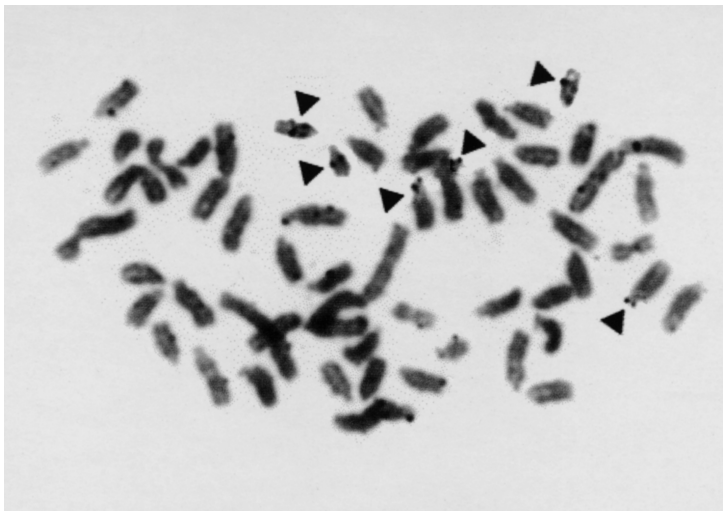

Fig. 4 – Metaphase cell of *C. hummelincki* showing the position (arrowheads) of Nucleolar Organizing Regions (NOR).

A17, A19 and A22. DAPI counterstaining showed a close complementary banding pattern with respect to CMA. Neither CMA nor DAPI revealed the pericentromeric heterochromatin (Fig. 5).

The G-banding allowed us to identify almost 90% of the chromosomal complement (Fig. 6), with only the very small chromosomes being difficult to discern. 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 of Universidad de Buenos Aires (Argentina). This comparison (Fig. 7) showed the correspondence of *C. hummelincki* and

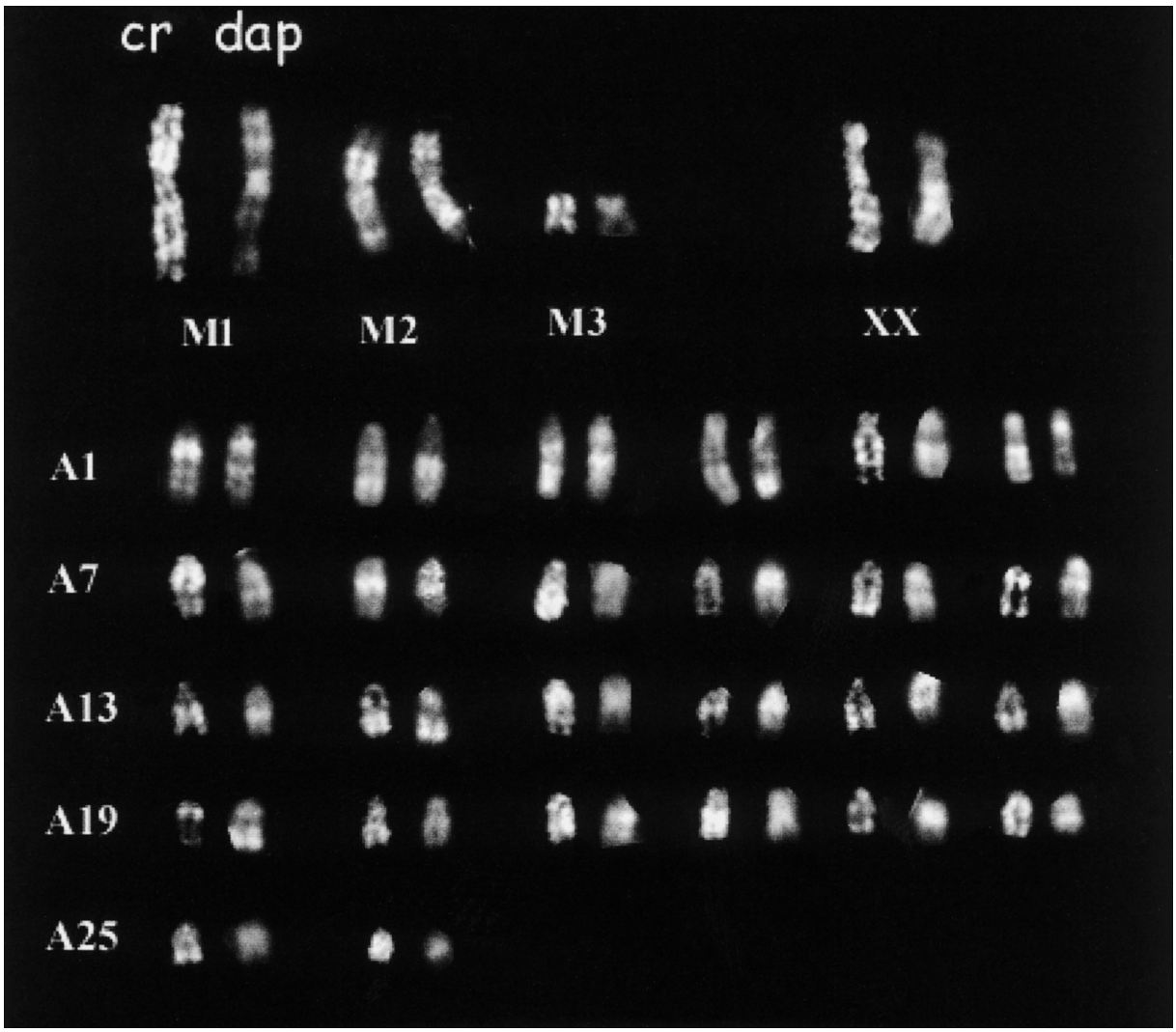

Fig. 5 – Karyotype of *C. hummelincki* metaphase stained sequentially with Chromomycin (A_3) (cr) and DAPI (dap).

C. laucha for almost all chromosomes. Some discrepancies are evident because it was not possible to obtain a better matching of some chromosomes pairs, e.g. pairs A6, A7 and A8 of *C. hummelincki* with pairs A7, A6 and A5 of *C. laucha*. However, the following points must be mentioned: M1 of *C. hummelincki* seems be the product of fusion of A2 and A3 of *C. laucha*; A1 of *C. hummelincki* seems be the result of fusion and posterior pericentric inversion of pairs A4 and A23 of *C. laucha*; the same seems be true for A2 of *C. hummelincki* and pairs A14 and A25 of *C. laucha*. The long arm of *C. laucha's* M2 is similar to *C. hummelincki's* A4, and the short arm of the same chromosome is similar to *C. hummelincki's* A24. In addition, there are probably two paracentric inversions on *C. laucha's* acrocentric pairs A1 and A12, which produce *C. hummelincki's* acrocentric pairs A5 and A14, respectively. Finally, it seems that *C. hummelincki's* acrocentric A3 is the result of duplication of a portion of *C. laucha's* acrocentric pair A8.

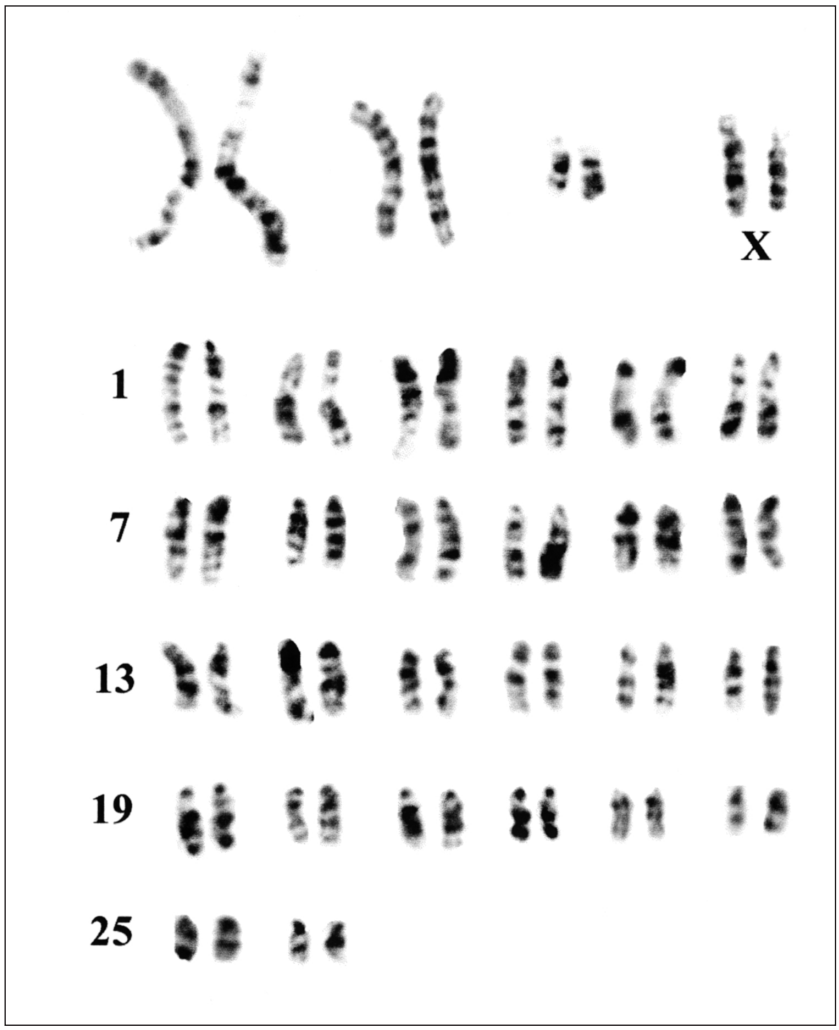

Fig. 6 – Representative G-banded karyotype of *C. hummelincki.*

A similar comparison of G-band karyotypes showed good correspondence between *C. hummelincki* and *C. venustus* (VITULLO *et al.* 1990), 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 *C. hummelincki* match the two biggest metacentrics of *C. venustus*, and the small metacentric 19 of *C. venustus* matches M3 of *C. hummelincki*. In addition, pair 4 of *C. venustus* seems be the result of a pericentric inversion of *C. hummelincki's* A1. The possible fusion of *hummelincki's* A3 with A5 should result in metacentric 3 of *C. venustus*, and fusion of *C. hummelincki's* A10 with A15 will form metacentric 5 of *C. venustus*.

We do not present the comparison with *C. callidus*, since the comparison of it with *C. venustus* is given in VITULLO *et al.* (1990); thus with this work it is easy to establish its correspondence with *C. hummelincki.*

DISCUSSION

The diploid and fundamental number and the beta karyological characteristics described for *C. hummelincki* are 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 likely the situation for the other populations spread throughout the distribution range.

The position of constitutive heterochromatin on the autosomal and X chromosomes in *C. hummelincki* is similar to what has been found in other species of *Calomys*. The karyologically close *C. laucha* shows conspicuous pericentromeric

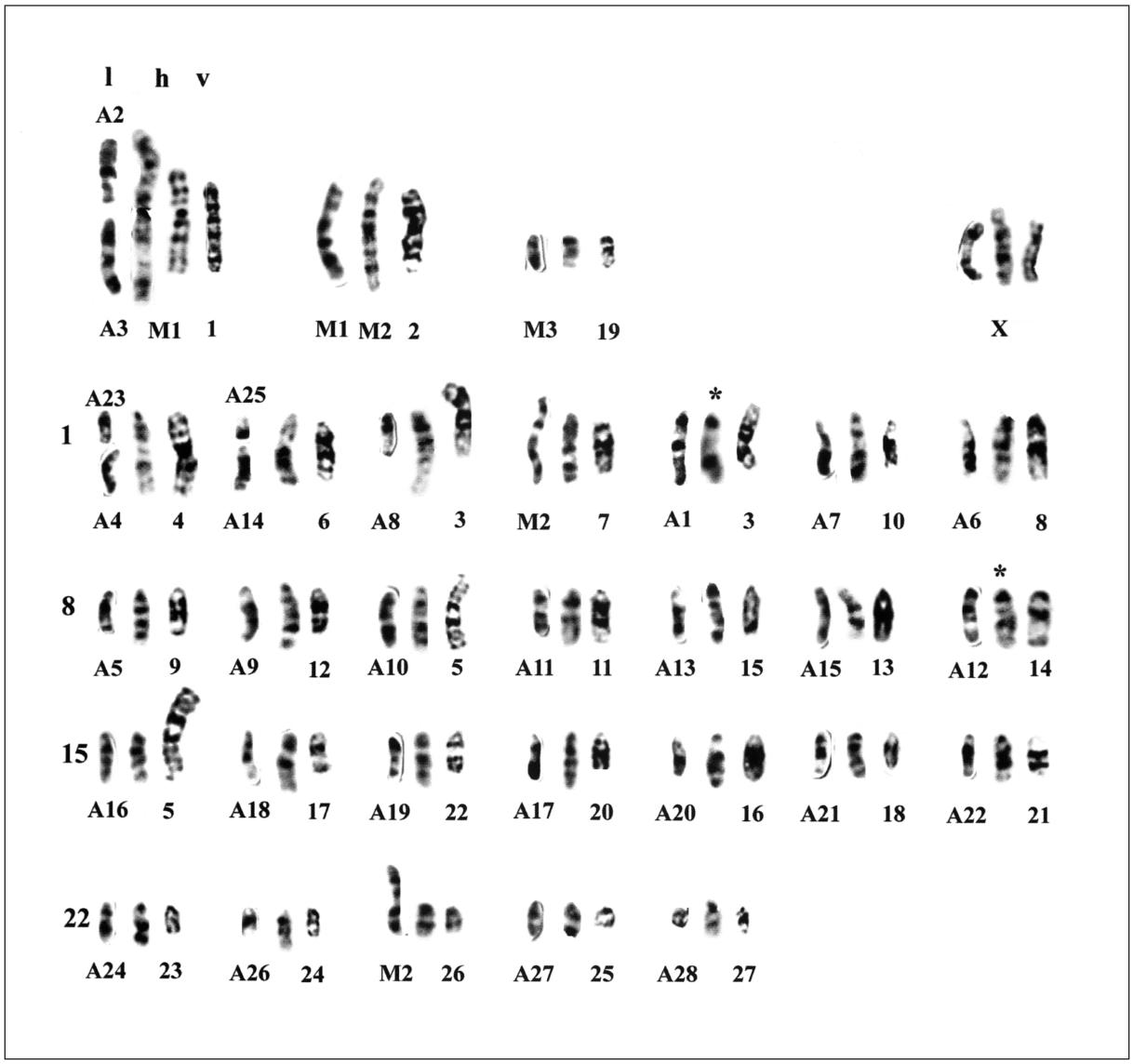

Fig. 7 – Comparison of G-banded karyotypes of *C. laucha* (l), *C. hummelincki* (h) and *C. venustus* (v). Asterisks indicate the presence of paracentric inversions.

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 like 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. 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* (FORCONE *et al.* 1980; LISANTI *et al.* 1996).

The position of NOR in *C. hummelincki* is different from those 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 CARDOSO 1992).

In *C. musculinus*, they are on the long arms of four metacentrics and the first submetacentric chromosome (CICCIOLI 1991).

Chromomycin/DAPI fluorescent staining showed that *C. hummelincki* presents heavy fluorescent euchromatic regions with a weak R-banding pattern, which indicates a very rich concentration of C-G or A-T bases in some places depending on the fluorochrome used. The lack of evidence of pericentromeric heterochromatin with these dyes seems to indicate that the composition of constitutive heterochromatin is not the same in all chromosomes and it is included in the fluorescent block revealed by the fluorochrome used. In this case, it is necessary to carry out a more detailed analysis with DNA probes, which will permit a better characterization of this constitutive heterochromatin. A similar result was obtained in human chromosomes by SCHWEIZER (1976), who found that the CMA procedure gave a weak R-banding pattern, while AMD/DAPI staining showed strong fluorescence blocks, complementary to the CMA pattern. Among *Calomys* species, this kind of banding has been performed only in *C. musculinus*: DAPI fluorescence revealed only pericentromeric heterochromatic regions, while Chromomycin showed an R-like banding pattern. In other rodents, e.g. *Thomomys bottae*, the pericentromeric C-bands were not revealed by CMA/DAPI fluorochromes, which only showed a weak R-like banding (BARROS and PATTON 1985). Meanwhile, in the chromosomes presenting heterochromatic regions, CMA and DAPI fluorochromes show different fluorescent patterns. In four species of *Microtus*, BURGOS *et al.* (1990) found a differential response of heterochromatic fluorescent blocks, concluding that it could be due to modifications of the nucleotide composition or cluster organization, or to changes in the DNA-protein content which may alter the access of the fluorescent dyes to the DNA. A similar explanation of the results for the *Calomys* species is possible.

Unfortunately, we did not directly perform G-banding in the other species, resulting in a different elongation and resolution of the karyotypes of the various species compared. Thus we found some discrepancies in the comparison of the chromosome pairs. However, despite this limitation, 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 species (Fig. 7), suggesting a close relationship among them. With *C. hummelincki's* chromosome position 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 (CICCIOLI 1991; GARDENAL *et al.* 1977; BRUM-ZORRILLA *et al.* 1990; HURTADO DE CATALFO and WAINBERG 1974; LISANTI *et al.* 1976). The presence of this particular chromosome, which presents pericentric heterochromatin in all species studied, suggests that the ancestral diploid number of the *Calomys* group was 68 instead of 70 as originally proposed by PEARSON and PATTON (1976).

REIG (1986) postulated that the phyllotine rodents, the tribe to which *Calomys* belongs, differentiated in the south-central Andes area and from there colonized the highlands and low open lands. The *Calomys* group has species present in puna areas (*C. lepidus*, ESPINOSA *et al.* 1997) and in low-altitude areas (*C. hummelincki*, HANDLEY 1976; MARTINO 1997). 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 (1976) 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 do not suggest a direct derivation of *C. hummelincki* from *C. laucha*, as suggested by VITULLO *et al.* (1990). Indeed, to obtain a *C. hummelincki* karyotype from that of *C. laucha* would require three fusions, one fission, two pericentric inversions plus another two paracentric inversions. Considering the law of parsimony, it seems that all these events would have had a low probability of occurring at one time. On the other hand, it is probable that a *C. hummelincki* ancestor gave rise to the *C. venustus*-*C. lepidus* group, since it was possible to identify the two fusions and inversions necessary to convert a *C. hummelincki* karyotype into a *C. venustus* form. These results indicate that the chromosomal characteristics of *C. hum-*

melincki are closer to those shown by the *C. venustus-C. lepidus* group. The heterochromatic evidence induces some doubt about a Robertsonian origin, postulated by VITULLO *et al.* (1990), of the karyotypes with a smaller number of chromosomes from species with a higher chromosome number, like *C. laucha.* This evidence indicates no close or direct relationship between *C. hummelincki* and *C. musculinus*, which is also supported by the poor matching of the G-band karyotypes in a preliminary comparison of the two species.

It would be interesting to study the chromosomal characteristics of *C. sorellus*, a key species in this evolutionary pattern, which would permit us to establish if it was the antecedent of *C. laucha* or *C. hummelincki*. Nevertheless, studies on morphology and cytochrome b DNA indicate that the *Calomys* group could have a polyphyletic origin (STEPPAN 1995, 1998), in which case *C. sorellus* should be assigned to a new genus within the phyllotine group. CORACH *et al.* (1988) analyzed the DNA characteristics of three species of *Calomys* and found that *C. callosus* has a different DNA composition from that of *C. laucha* and *C. musculinus*. These authors proposed that the three species derived from different evolutionary lines. Recently, from sequences of cytochrome b DNA, SALAZAR-BRAVO *et al.* (in prep.) concluded that *Calomys* species are organized into two clusters, one including *C. venustus*, *C. lepidus* and *C. sorellus*, and the other *C. fecundus*, *C. venustus*, *C. callidus*, *C. callosus*, *C. laucha* and *C. hummelincki*. The last species seems to be the oldest, splitting in an independent branch from the other species. The chromosomal characteristics described for *C. hummelincki* indicate that it did not derive from *C. laucha* directly and that *C. musculinus* did not derive, at least directly, from *C. hummelincki* or *C. laucha.* However, it is necessary to conduct similar chromosome characterization studies on other species of *Calomys* for a clearer understanding of the evolutionary patterns of this interesting phyllotine group.

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