**Rev. Brasil. Genet. 13, 1,** 33-46 (1990)
**(Brazil. J. Genetics)**

# CYTOGENETIC ANALYSIS OF THRUSH (*Turdus*, MUSCICAPIDAE) SPECIES

Miriam Luz Giannoni[1], Iris Ferrari[2] and Marcos Antonio Giannoni[1]

## ABSTRACT

A cytogenetic study was conducted on four *Turdus* species from the state of São Paulo: *T. leucomelas (Tle), T. rufiventris* (Tru), *T. amaurochalinus* (Tam) and *T. albicollis* (Tal), and on one from North America: *T. migratorius* (Tmi). Bone marrow metaphase preparations were obtained and the chromosomes were measured and classified by standard methods.

Two karyotypic groups, denoted type I and type II, were detected. The first includes the 3 Brazilian species (Tam, Tru and Tal) and the North American species (Tmi), and the second, only the Tle species, which differed from the others mainly in terms of one macroautosome which is telocentric and classified as no. 6 in the type I karyotype, and submetacentric and classified as number 4 in the type II karyotype. The remaining macroautosomes are of similar morphology and size in all species studied. The chromosome number was 2n = 78 in Tal and Tru and 2n = 80 in the other species. The sex pair consists of a metacentric Z, the 4th in size in Tmi, Tam and Tle, and the 3rd in Tru, and a submetacentric W, the 8th in size in Tmi, Tam, Tru and Tle and the 7th in Tal.

By comparing these results with those obtained for two European species of *Turdus, T. pilaris* (Tri) and *T. merula* (Tme), it can be seen that Tri belongs to type I and Tme to type II. Literature data indicate that type II is more frequent for the genus *Turdus*.

## INTRODUCTION

The order Passeriformes is subdivided into two major groups: (1) suborder Suboscine, comprising more than 1300 species widely distributed in Central and

1 Departamento de Melhoramento Genético Animal, Faculdade de Ciências Agrárias e Veterinárias, UNESP, 14870 Jaboticabal, SP, Brasil. Send correspondence to M.L.G.

2 Departamento de Medicina Especializada, Faculdade de Ciências da Saúde, Universidade de Brasília, 70910 Brasília, DF, Brasil.

South America and in the Old World tropics, and (2) Suborder Oscine or Passeres, comprising approximately 4000 species of cosmopolitan distribution and including the only species in this order that have been karyologically analyzed. In this respect, Belterman and De Boer (1984), on the basis of karyotaxonomic information concerning species belonging to 12 different bird orders, proposed representative schemes for the possible evolutionary changes that occurred in these orders. These authors considered the information in the literature and the information obtained by them for Passeriformes to be insufficient for a discussion of their possible karyotypic relationships. According to them, 25 of the 66 Passeriformes families continue to be cytogenetically unknown. The 200 species studied were investigated with deficient techniques which did not include chromosome banding, except for 10 species, 6 of which were analyzed by G-banding and 4 by C-banding, as shown in the most recent review of bird karyology (De Boer, 1984).

The largest Passeriformes family is Muscicapidae, which comprises 254 genera and approximately 1415 species, only 51 of which have been studied cytogenetically (De Boer, 1984). Particularly interesting in this family is the subfamily Turdinae which comprises approximately 6 genera and more than 300 species. Because it involves a large number of transition forms it is preferably considered to belong to the family Muscicapidae (Ripley, 1964a; Grzime, 1973; Morony *et al.*, 1975; Camargo, H.F.A., personal communication), although many authors consider it to belong to the independent family Turdidae (Oliverio Pinto, 1944; Makino and Baldwin, 1954; Udagawa, 1954, 1955a,b, 1966; Tyne and Berger, 1959; Jovanovic and Atkins, 1969; De Lucca, 1974a,b; Ruschi, 1979; Frisch, 1981; Brodokorb, 1986).

In Brazil, the family Muscicapidae is represented by species of the subfamily Turdinae belonging to the genera *Turdus* (10 species), *Platycichla* (1 species), *Catharus* (3 species) and *Myadestes* (1 species). In the state of São Paulo, the species *T. albicollis, T. amaurochalinus, T. leucomelas* and *T. rufiventris* are found in the hinterland, and *P. flavipes* along the coast (Ripley, 1964b). In the U.S. the only representative of the genus *Turdus* is the American robin (*T. migratorius*).

With the objective to contribute to the cytogenetic knowledge of the genus *Turdus*, we analyzed cytologically 5 species of this genus, 4 of which were from the state of São Paulo and 1 from the state of Minnesota, USA. Two European species whose karyotypes were kindly provided by Dr. Hans Ryttman (personal communication) were used for comparison.

## MATERIAL AND METHODS

Table I shows the species, number, sex and site of origin of the animals used in the present study. The Brazilian birds were identified zoologically by Dr. Helio F.A. Camargo, Zoology Museum of the University of São Paulo, and the North

American specimen was identified by Dr. Harrison Tordoff, Bell Museum of Natural History, University of Minnesota.

*Table I - Species, sex and number of the specimens of the genus Turdus investigated.*

| Species | Origin | Latitude Longitude | Male | Female | Brazilian name | English name |
|---|---|---|---|---|---|---|
| *T. leucomelas* | Jaboticabal (SP) | 21º15'S 48°18'W | 5 | 4 | Sabiá branco | Pale-breasted Thrush |
| *T. rufiventris* | Jaboticabal (SP) | | 2 | 3 | Sabiá laranjeira | Rufous-bellied Thrush |
| *T.amaurochalinus* | Jaboticabal (SP) | | 5 | 8 | Sabiá pardo | Creamy-bellied Thrush |
| *T. albicollis* | São J.Rio Preto (SP) | 20º49'S 49°25'W | - | 1 | Sabiá-de-coleira | White-necked Thrush |
| *T. migratorius* | Minn. USA | 45ºN 95°W | - | 1 | - | American Robin |

(SP) São Paulo State, Brazil.

Metaphase spreads were obtained by the direct technique of bone marrow chromosome preparation after stimulation with injection of Fleischman yeast as proposed by Lee and Elder (1980) for small rodents. A yeast suspension (1 g Fleischman yeast + 2 g dextrose in 10 ml distilled water incubated for 20-40 minutes in an oven at 41°C) was used at 0.5 ml 100 g live weight. After 24 h, a 0.16% colchicine solution (0.4 ml/100 g live weight) was injected into the abdominal region 30 minutes before killing the animal to remove bone marrow (adult animals weighing 80 to 100 g). The material was submitted to hypotonic treatment (0.075 M KCl) and fixed by standard procedures. Slides for karyotyping were stained with 3% Giemsa for 5 minutes.

Chromosomes were measured biometrically by the technique of Giannoni and Giannoni (1983) and classified by the method of Levan *et al.* (1964).

## RESULTS

Figures 1A and 1B show the metaphase spreads and karyotypes of a male and female specimen Tam (creamy-bellied thrush), respectively. The modal chromosome number observed in 86 metaphases from 13 individuals in this species was 2n = 80. The 20 largest chromosomes (ranging in size from 5.85 to 1.41 μm) were considered macrochromosomes, and the remaining 60, microchromosomes. The macrochromosomes were numbered from 1 to 9, and the sex pair, which was excluded

from the numeration and was placed to the right of the autosomes, consists of a metacentric Z, the 4th in size in the genome, and of a submetacentric W, the 8th in size in the genome. The largest and smallest microchromosome pairs in the karyotype are presented in the Figures.

Figures 2A, 2B and 3A show the karyotypes of female specimens of Tmi, Tru and Tal, which are similar to those of the previous species in terms of macroautosome number and morphology, though the latter two species apparently differ from the others in terms of microchromosome number (58, 2n = 78, FN = 86). Figure 3B shows the karyotype of Tle. In all of the individuals of this species, we observed the presence of a biarmed fourth macroautosome pair classified as sm (AR = 2.37) and the absence of the 7th acrocentric pair, which was present in the remaining species. The two largest microchromosomes differed from the other 4 species, including the North American Tmi, by being clearly submetacentric and for this reason were included in the karyotype. They were considered to be biarmed for the fundamental number of arms count despite the "convention" of considering all microchromosomes as acrocentric when determining this parameter. The modal chromosome number of this species, however, was not reduced, but was 2n = 80, FN = 94 (and FN = 90 if all microchromosomes are considered acrocentric).

The sex chromosomes were similar in size and morphology. The Z chromosomes were classified as metacentric and the 4th in size in the karyotype, and the W chromosomes, although differing slightly in arm ratio (AR = 1.70 to 2.68), were classified as submetacentric and the 8th in size (Levan *et al.*, 1964). The W chromosomes of Tal was slightly larger than those in the remaining species and was 7th in the genome.

Table II shows the mean relative lengths, the arm ratios and classification of the 9 macroautosomes and of the sex pair of the 5 species studied. The means of the 9 macroautosomes and of the Z chromosomes in each metaphase were considered for the calculation of the haploid set, whereas the microchromosomes were excluded.

Table II - Relative length (RL), arm ratio (AR) and morphology of the macrochromosomes of the American species analyzed in the present study.

| Chromosome | | Tle | Tam | Tal | Tru | Tmi |
|---|---|---|---|---|---|---|
| 1 | RL | 18.20 ± 0.66 | 18.23 ± 0.85 | 19.23 ± 1.13 | 18.75 ± 0.32 | 18.51 ± 0.67 |
| | AR | 1.96 | 1.89 | 1.92 | 1.83 | |
| | Class. | sm | sm | sm | sm | |
| 2 | RL | 14.34 ± 1.05 | 15.10 ± 0.88 | 14.59 ± 0.98 | 14.35 ± 0.47 | 13.87 ± 0.73 |
| | AR | 3.32 | 2.66 | 2.59 | 2.70 | 2.80 |
| | Class. | st | sm | sm | sm | sm |

Continua

Table II - Continuação.

| Chromosome | | Tle | Tam | Tal | Tru | Tmi |
|---|---|---|---|---|---|---|
| 3 | RL | 9.69 ± 0.37 | 10.63 ± 0.92 | 10.45 ± 0.60 | 10.59 ± 0.60 | 10.05 ± 0.51 |
| | AR | 2.04 | 1.94 | 1.79 | 1.91 | 2.13 |
| | Class. | sm | sm | sm | sm | sm |
| 4 | CR (5) | 12.74 ± 0.84 | 12.79 ± 1.48 | 12.24 ± 0.80 | 11.90 ± 0.96 | 12.63 ± 0.87 |
| | RB | ∞ | ∞ | ∞ | ∞ | ∞ |
| | Class. | T | T | T | T | T |
| 5 | RL (6) | 8.58 ± 0.66 | 8.76 ± 0.85 | 9.13 ± 0.32 | 8.98 ± 0.47 | 9.02 ± 0,49 |
| | AR | ∞ | ∞ | ∞ | ∞ | ∞ |
| | Class. | T | T | T | T | T |
| 6 | RL (4) | 8.87 ± 0.45 | 7.21 ± 0.58 | 7.62 ± 0.54 | 7.62 ± 0.65 | 7.79 ± 0.66 |
| | AR | ∞ | ∞ | ∞ | ∞ | ∞ |
| | Class. | T | T | T | T | T |
| 7 | RL | 6.24 ± 0.40 | 5.88 ± 0.40 | 5.84 ± 0.59 | 5.75 ± 0.45 | 6.11 ± 0.30 |
| | AR | ∞ | ∞ | ∞ | ∞ | ∞ |
| | Class. | T | T | T | T | T |
| 8 | RL | 5.22 ± 0.57 | 5.15 ± 0.39 | 5.04 ± 0.56 | 5.03 ± 0.45 | 5.48 ± 0.35 |
| | AR | ∞ | ∞ | ∞ | ∞ | ∞ |
| | Class. | T | T | T | T | T |
| 9 | RL | 4.75 ± 0.45 | 4.39 ± 0.40 | 4.65 ± 0.57 | 4.44 ± 0.41 | 4.97 ± 0.58 |
| | AR | ∞ | ∞ | ∞ | ∞ | ∞ |
| | Class. | m | m | m | m | m |
| Z | RL | 11.43 ± 0.61 | 11.87 ± 0.64 | 11.37 ± 0.40 | 12.54 ± 0.71 | 11.56 ± 0.67 |
| | AR | 1.09 | 1.17 | 1.17 | 1.11 | 1.13 |
| | Class. | m | m | m | m | m |
| W | RL | 7.91 ± 0.78 | 6.88 ± 0.62 | 8.15 ± 1.10 | 6.52 ± 1.05 | 7.09 ± 1.11 |
| | AR | 1.88 | 2.21 | 2.06 | 2.68 | 1.70 |
| | Class. | sm | sm | sm | sm | sm |

(4), (5) and (6) - Numeration according to the classification proposed for this species.
*Tle = T. leucomelas; Tam = T. amaurochalinus; Tal = T. albicollis; Tru = T. rufiventrus; Tmi = T. migratorius.*

Table III presents the numbers and types of macrochromosomes, the number of microchromosomes, the diploid number and the fundamental number of arms for the 5 American species analyzed here and for the 2 species studied by Ryttman (1984) and presented here for comparison.

Figure 4 illustrate the idiograms of Tal and Tle, with the macrochromosomes arranged by centromere.

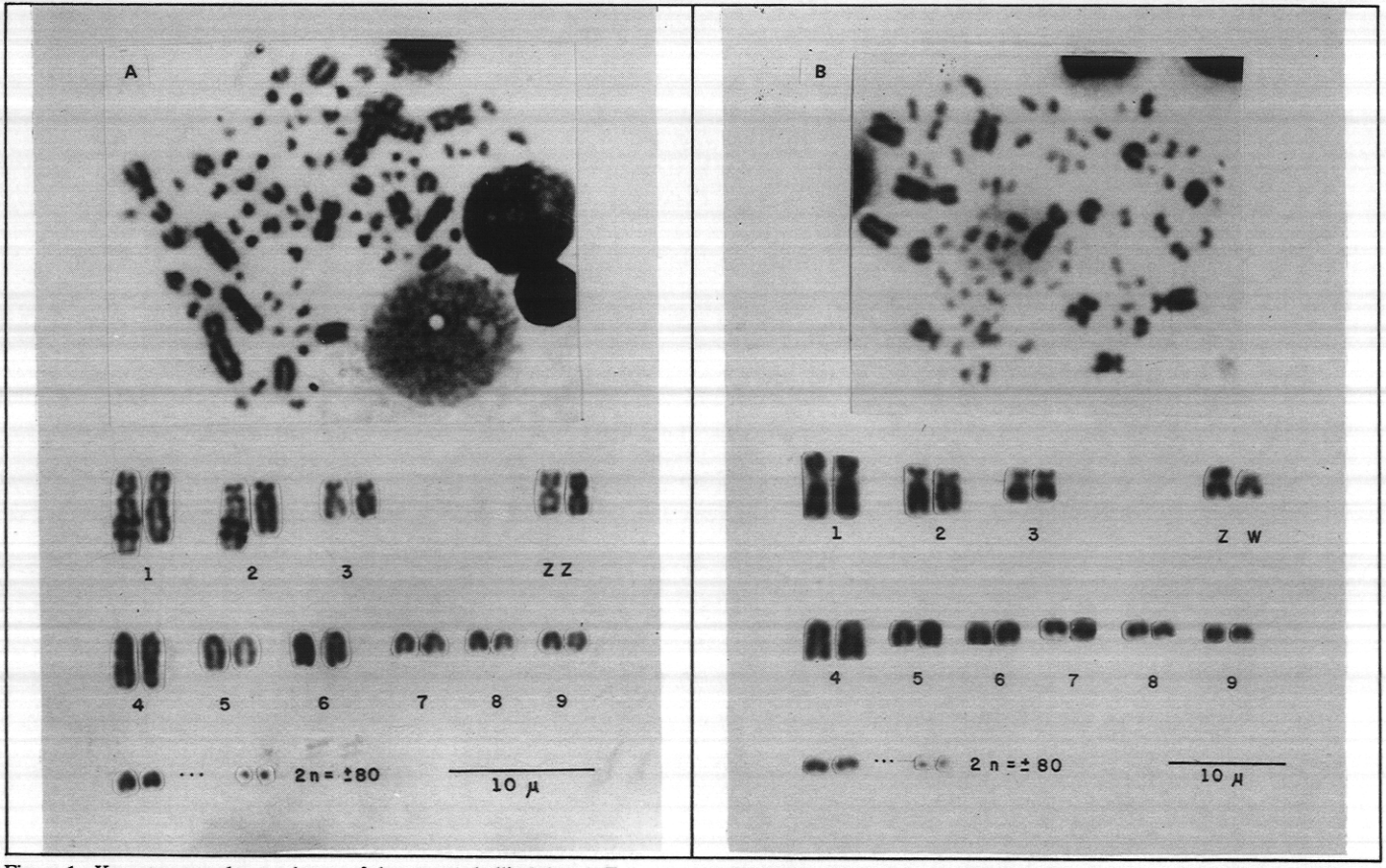



Figure 1 - Karyotypes and metaphases of the creamy-bellied thrush *T. amaurochalinus* obtained from bone marrow cells and stained with Giemsa; (A) male and (B) female, respectively.

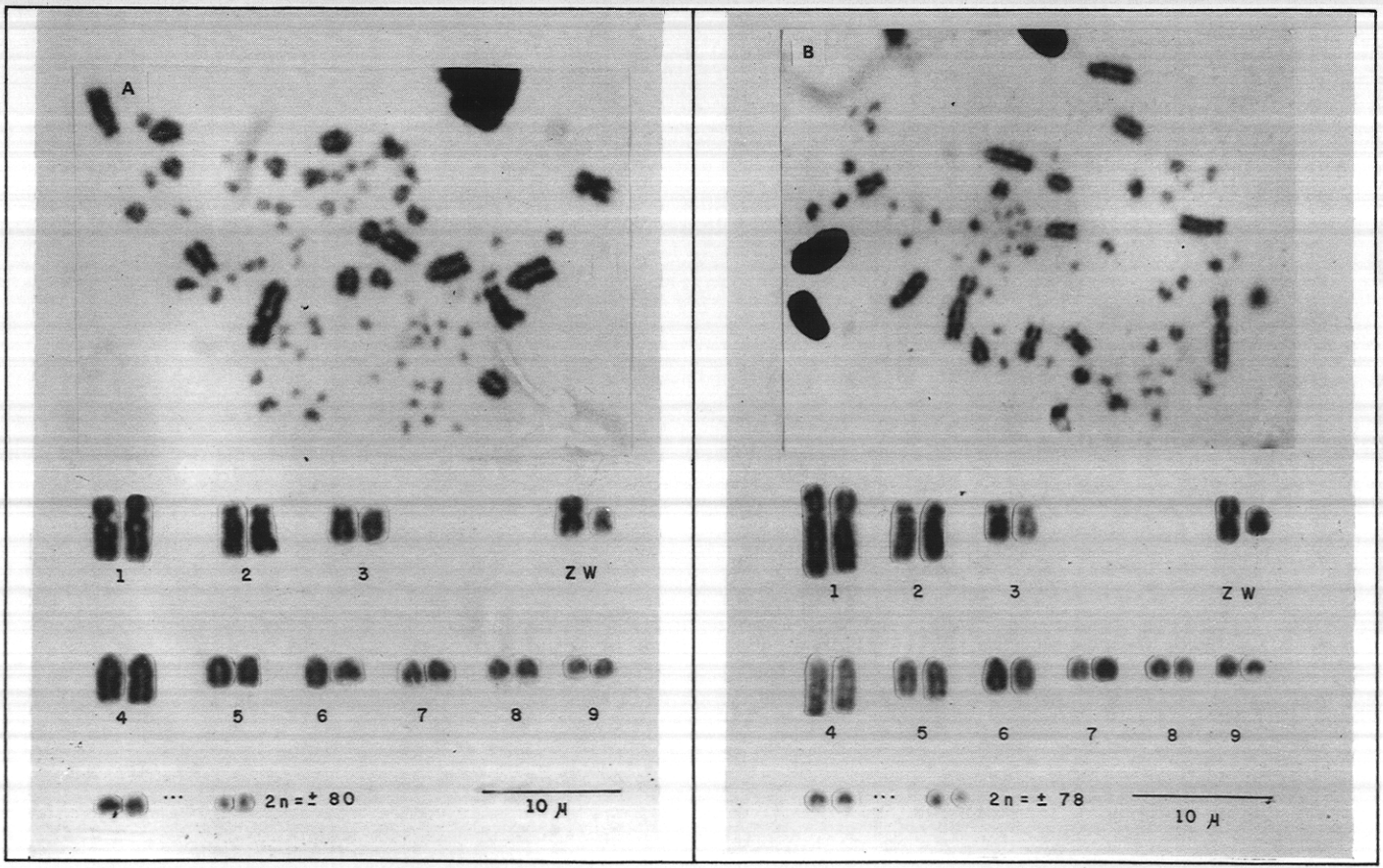



Figure 2 - Karyotypes and metaphases of a female American robin (*T. migratorius*), 2n = 80, FN = 88 (A); and of a rufous-bellied thrush (*T. rufiventris*), 2n = 78 and FN = 86 (B).

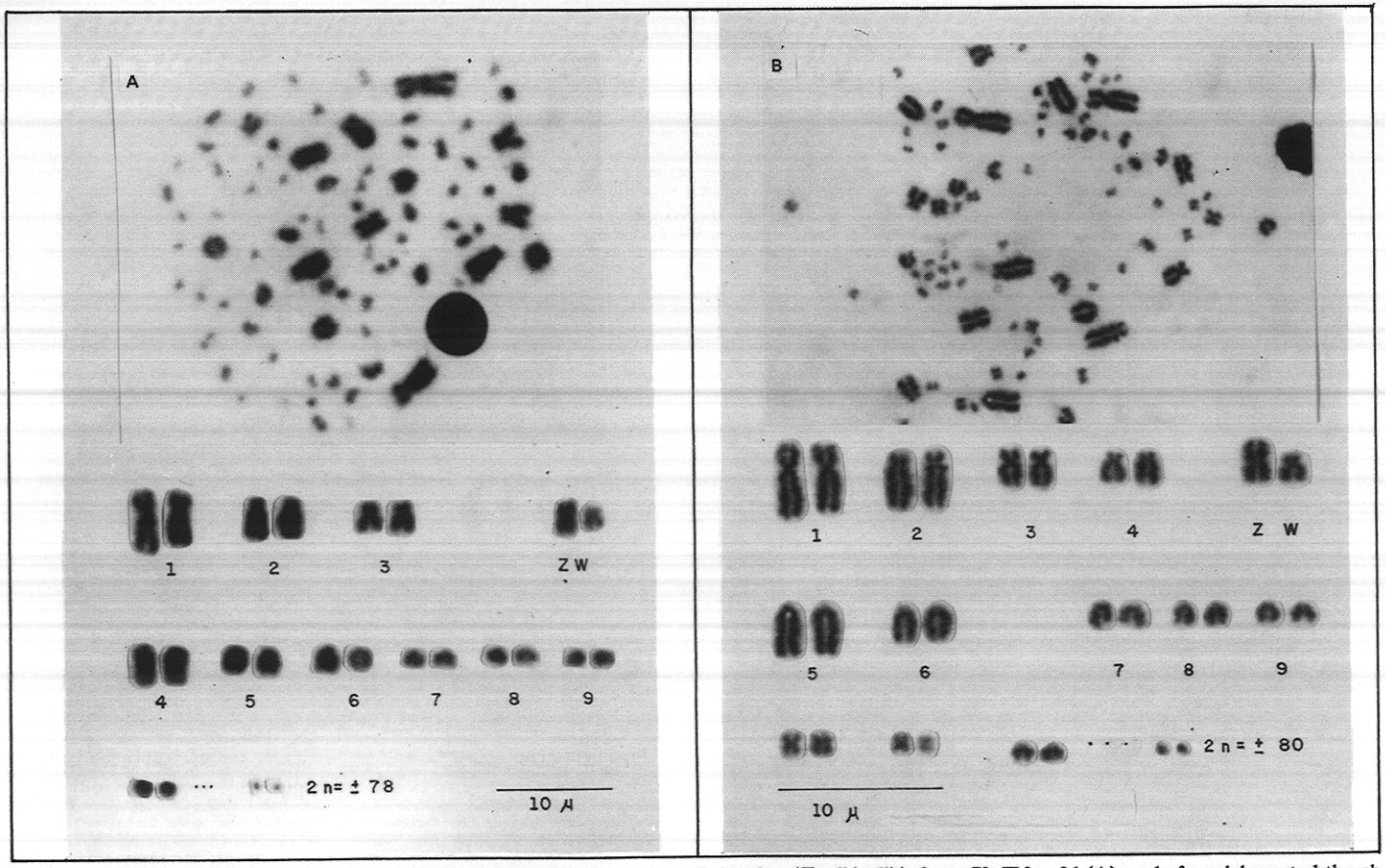



Figure 3 - Karyotypes and metaphases of female white-necked thrushes or "cat" thrushes (*T. albicollis*), 2n = 78, FN = 86 (A), and of a palebreasted thrush (*T. leucomelas*), 2n = 80, FN = 94 (B).

Table III - Types of macro- and microchromosomes, fundamental number of arms and diploid chromosome numbers of the species investigated.

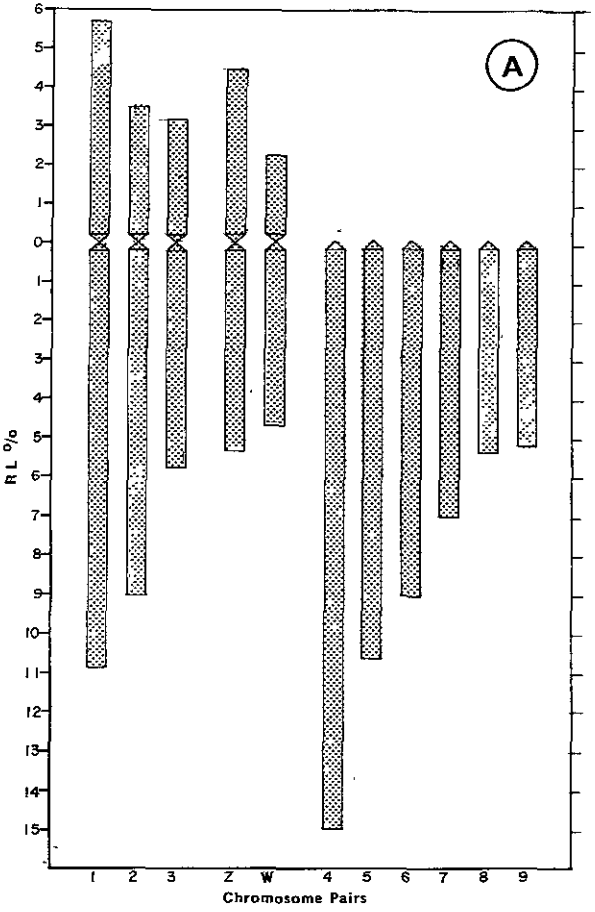
| Species | 2n | Macrochromosome types | | | | Micro-chromosome number | FN |
|---|---|---|---|---|---|---|---|
| | | m | sm | st | T | | |
| *T. leucomelas* | 80 | 1 | 7 | 2 | 10 | 60 | 94 |
| *T. migratorius* | 80 | 1 | 7 | - | 12 | 60 | 88 |
| *T. amaurochalinus* | 80 | 1 | 7 | - | 12 | 60 | 88 |
| *T. albicollis* | 78 | 1 | 7 | - | 12 | 58 | 86 |
| *T. rufiventris* | 78 | 1 | 7 | - | 12 | 58 | 86 |
| *T. merula* | 80 | 1 | 9 | - | 10 | 60 | 90 |
| *T. pilaris* | 80 | 1 | 7 | - | 12 | 60 | 88 |

## DISCUSSION

Even though the techniques initially employed to obtain metaphases spreads in cytogenetic studies of the genus Turdus were precarious (Unger, 1936; Pogossianz, 1937; Yamashina, 1951; Udagawa, 1954, 1955a,b, 1956), diploid chromosome values very close to those obtained later with more efficient techniques (Hammar, 1966; Jovanovic and Atkins, 1969; De Lucca, 1974a,b) and in the present study were detected, i.e. 2n = 78-80 chromosomes.

The American robin (Tmi) was investigated cytogenetically by Jovanovic and Atkins (1969) using metaphase spreads obtained from liver and kidney cells. Even though there was agreement with respect to chromosome number (2n = 80), the karyotype of the specimen collected in Minnesota differs in chromosome morphology and size from that studied by Javanovic and Atkins (1969), who classified the 1st, 2nd, 4th and 7th pairs as metacentric, the 3rd, 5th, 6th, 8th and 9th pairs as subacrocentric, the 10th and 11th pairs and most of the microchromosomes as acrocentric, and the sex chromosomes as metacentric, with the Z being 3rd or 4th in size, and the W 5th or 7th. The most obvious differences concern the 7th submetacentric pair and the large size of the W which were not observed in the specimen analyzed in the present study (Figure 2A).

To explain these divergences, in addition to the different methodologies used, we may propose the occurrence of interpopulation chromosome heteromorphism. The existence of plumage heteromorphism among the robin populations from different regions of the US (Ripley, 1964b), which have not yet been analyzed cytogenetically or karyotypically, leads us to propose the possibility of the occurrence of subspecies.



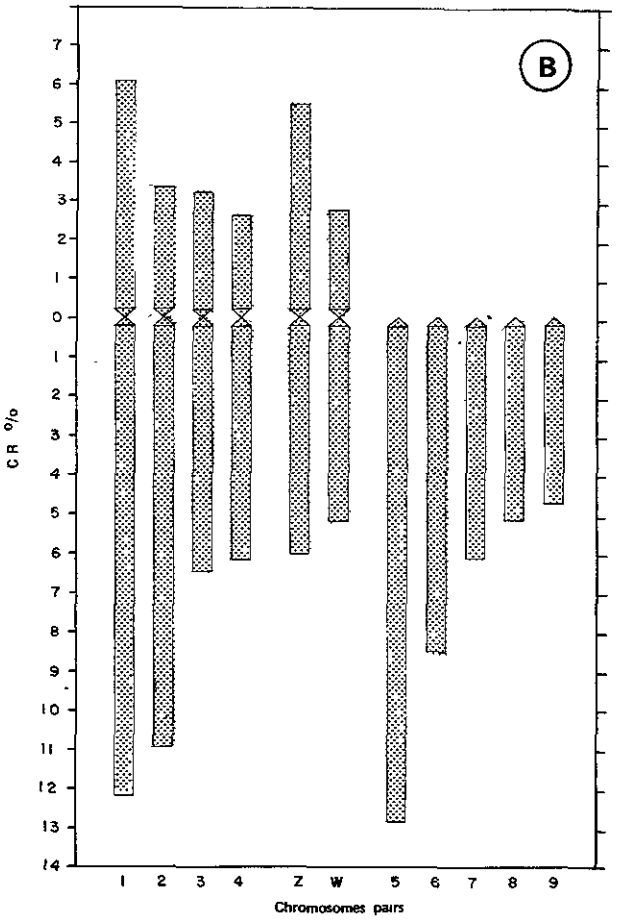




Figure 4 - Idiogram of (A) *T. amaurochalinus* and (B) *T. leucomelas*.

Cytogenetic information on Brazilian *Turdus* is scarce, since of the 23 species and subspecies populating the country (Ruschi, 1979), only 3 have been studied in terms of conventional karyotype and biometric data. They are Tam (reported by De Lucca, 1974a), Tle and Tru (De Lucca, 1974b), all of them from the region of Botucatu, SP (280 km from Jaboticabal).

The morphology and real size of some autosomes and sex chromosomes reported by De Lucca differ from those observed in the present study, probabily because of the different methodologies employed. Of the three species analyzed by De Lucca (1974a,b), the one showing the greatest differences when compared to the present study was Tle (pale-breasted thrush). In the specimens studied here, the 3rd pair in size (5th by the present classification) was a characteristic telocentric (Figure 3B), whereas in the specimen studied by De Lucca it was considered submetacentric, with an arm ratio of 3.0. Less divergence was observed in the classification of pair number 4 and of the sex chromosome, which differed both in size and morphology. Population studies on *T. leucomelas* specimens from different regions may detect possible chromosome polymorphisms. This aspect is reinforced by the observation made by Santos (1979) about the wide geographic distribution of these animals, which show many intermediate forms whose characteristics vary with geographical area.

Cytogenetic analysis revealed great similarities in chromosome size and in centromere position between the North American species Tmi and the three São Paulo species Tru, Tam and Tal. Small differences existed in chromosome W, but they were not sufficient to interfere with classification, which was sm for all species.

A karyotype similar to those of these four species has been described by Ryttman (Ryttman, H., personal communication) for the European *T. pilares*, which was classified as type I.

The widest karyotypic variation was observed in Tle whose karyotype was classified here as type II and was characterized by the presence of the 4th macroautosome pair and of 2 pairs of the largest microchromosomes having 2 arms. A small difference was detected in pair 2, which had an arm of shorter length and was classified as st, while pair 2 is sm in the type I karyotype. The two kinds of karyotypes observed in the species investigated here are shown in Figure 5. The karyotype described by Ryttman (Ryttman, H. personal; communication) for *T. merula* is of type II with respect to the macrochromosomes, with an apparent absence of the 2 metacentric microchromosome pairs.

Information reported in the literature leads us to propose that the type II karyotype may be the primitive one, i.e. having a submetacentric 4th pair (RL = 8.87, 0.45 and AR = 2.37 in Tle), and that the occurrence of a pericentric inversion and the possible loss of a small DNA portion resulted in the telocentric pair no. 6 (RL = 7.45 as the mean value for the 4 species Tal, Tru, Tam and Tmi).

Cytogenetic research on birds has indicated that chromosome conservatism is greater with respect to the sex chromosome Z than to the W. In 25 species of the

Family Muscicapidae analyzed by Bulatova (1981), the Z sex chromosomes were similar in size and morphology, while the W chromosomes varied. These facts were confirmed in the species studied here (Figure 6).

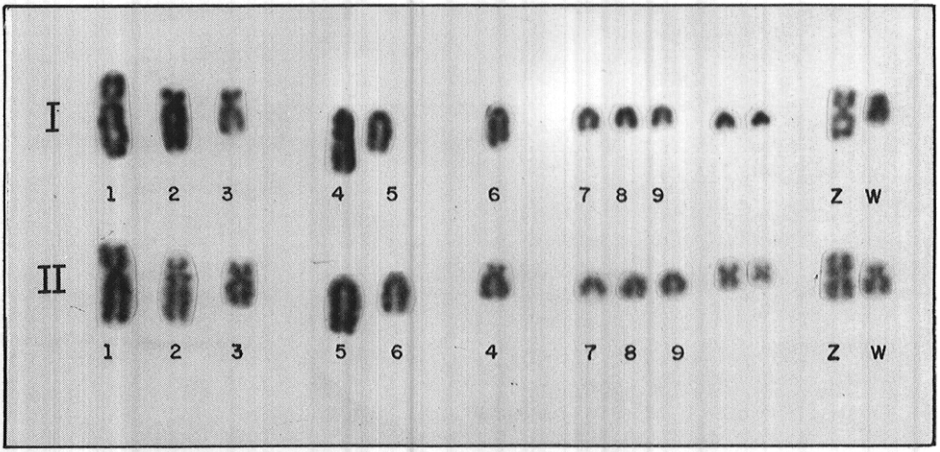



Figure 5 - Type I and type II karyotype constitutions of the macrochromosomes and sex pairs observed in the species investigated.

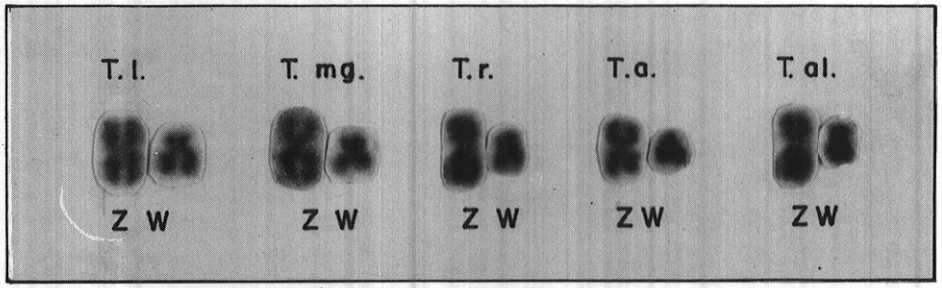



Figure 6 - Z and W sex chromosomes of the species investigated.

## ACKNOWLEDGMENTS

Publication supported by FAPESP.

## RESUMO

Foram estudados citogeneticamente 4 espécies de *Turdus* do Estado de São Paulo, a *T. leucomela* (Tle), *T. rufiventris* (Tru), *T. amaurochalinus* (Tam), *T. albicollis* (Tal) e uma da América do Norte a *T. migratorius* (Tmi). Foram utilizadas técnicas convencionais para obtenção de metáfases de células de medula óssea, para biometria e classificação dos cromossomos.

Verificou-se a existência de 2 grupos cariotípicos, denominados tipo I e II. No primeiro estão incluídas as 3 espécies brasileiras (Tam, Tru e Tal) e a espécie norte americana (Tmi) e no segundo grupo a espécie Tle cuja diferença principal diz respeito ao macroautossomo telocêntrico de número 6 no tipo I e submetacêntrico (e de número 4 pela classificação proposta) no tipo II. Quanto aos demais macroautossomos, estes são semelhantes em morfologia e porte em todas as espécies analisadas. Observou-se 2n = ± 78 nas espécies Tal e Tru verificando-se nas demais 2n = ± 80. O par sexual constitui-se de Z metacêntrico, o 4º em porte na Tmi, Tam, Tal e Tle e o 3º na Tru, o W, submetacêntrico e o 8º na Tmi, Tam, Tru e Tle e 7º, quanto ao tamanho, na Tal.

Comparando os resultados com 2 espécies de *Turdus* européias e analisadas por Ryttman (1984) verifica-se que o cariótipo da *T. pilaris* enquadra-se no Tipo I e o da *T. merula* no tipo II. Dados de literatura indicam ser mais frequente o tipo II para o gênero *Turdus*.

## REFERENCES


Belterman, R.H.R. and De Boer, L.E. (1984). A karyological study of 55 species of birds, including karyotypes of 39 species new to cytology. *Genetica 65*: 39-82.

Brodkorb, P. Apud: Sibley, C.G. and Ahlquist, J.E. (1986). Reconstructing bird phylogeny by comparing DNA's. *Sci. Am. 254*: 68-78.

Bulatova, N.S. (1981). A comparative karyological study of Passerine birds. *Acta Sc. Nat. Brno. 15*: 1-44.

De Boer, L.E.M. (1984). New developments in vertebrate cytotaxonomy. VIII. A current list of references on avian karyology. *Genetica 65*: 3-37.

De Lucca, E.J. (1974a). Cariótipos de 8 espécies de Aves. *Rev. Bras. Biol. 34*: 387-392.

De Lucca, E.J. (1974b). Cariótipos de 14 espécies de Aves das ordens Cuculiformes, Galliformes, Passeriformes e Tinamiformes. *Rev. Bras. Pesq. Med. Biol. 7*: 253-263.

Frisch, J.D. (1981). *Aves Brasileiras.* Dalgas-Ecoltec. Ecologia Técnica e Comércio, São Paulo.

Giannoni, M.L. and Giannoni, M.A. (1983). Cytogenetic analysis of the species *Porzana albicollis* ("Saracura-Sanã" or sora). *Rev. Brasil. Genet. 6*: 649-665.

Grzimek, B. (1973). *Grzimek's Animal Life Encyclopedia*. Van Nostrand Reinhold, New York, pp. 272-309.

Hammar, B. (1966). The karyotypes of nine birds. *Hereditas 55*: 367-385.

Jovanovic, V. and Atkins, L. (1969). Karyotypes of four passarine birds belonging to the families Turdidae, Mimidae and Corvidae. *Chromosoma 26*: 388-394.

Lee, M.R. and Elder, F.F.B. (1980). Yeast stimulation of bone marrow mitosis for cytogenetic investigations. *Cytogenet. Cell. Genet. 26*: 36-40.

Levan, A., Fredga, K. and Sandberg, A.A. (1964). Nomenclature for centromeric position on chromosomes. *Hereditas 52*: 201-220.

Makino, S. and Baldwin, P.H. (1954). The chromosomes of the American blackbirds, *Agelaius phoeniceus* and *Xanthocephalus xanthocephalus* (Family Icteridae). *Cytologia 19*: 217-224.

Morony, J.J., Jr., Bock, W.J. and Farrand, J.J., Jr. (1975). *Reference List of the Birds of the World.* American Museum of Natural History, New York.

Oliverio Pinto, O.M. (1944). *Catálogo das Aves do Brasil.* Departamento de Zoologia da Secretaria de Agricultura Indústria e Comércio de São Paulo, São Paulo, p. 2.

Pogossianz, H. (1937). Karyotypes of some representatives of Passeres (*Passer domesticus* L., *Coloeus monedula* L., *Turdus pilares* L.). *Biol. Zh. 3*: 665-668.

Ripley, S.D. (1963a). Muscicapidae. In: *Check-list of Birds of the World.* (Mayr, E. and Paynter, R.A., Jr., eds.). Mus. Comp. Zool. vol. 10, pp. 13-227.

Ripley, S.D. (1964b). Thrush. In: *A New Dictionary of Birds.* (Thomsowed, A.L., eds.). Thomas Nelson, London, pp. 817-818.

Ruschi, A. (1979). *Aves do Brasil.* Ed. Rios, São Paulo.

Santos, E. (1979). *Pássaros do Brasil.* 4ª ed. Ed. Itatiaia, Belo Horizonte.

Tyne, J. Van and Berger, A. (1959). *Fundamentals of Ornithology.* John Wiley & Sons, London.

Udagawa, T. (1954). Karyogram studies in birds. IV. The chromosomes of four Passeres and two colombine species. *Annot. Zool. Japon. 27*: 208-214.

Udagawa, T. (1955a). Karyogram studies in birds. V. The chromosomes of five passerine birds. *Annot. Zool. Japon. 28*: 19-25.

Udagawa, T. (1955b). Karyogram studies in birds. VI. The chromosomes of five species of the Turdidae. *Annot. Zool. Japon. 28*: 256-261.

Udagawa, T. (1956). Karyogram studies in birds. VIII. The chromosomes of some species of the Turdidae and Troglodytiidae. *Jap. J. Zool. 12*: 105-111.

Unger, H. (1936). Beitrage zur Chromosomenforschung der Vogel. *Z. Zell Forsch. 25*: 476-500.

Yamashina, Y. (1951). Studies on the chromosomes of 25 species of birds. *Pap. Coord. Commt. Res. Genet. 2*: 27-38.

**(Received June 6, 1989).**