



CHROMOSOMAL CHARACTERIZATION OF TAXA  
OF THE GENUS *TRINOMYS* THOMAS, 1921, (RODENTIA: ECHIMYIDAE)  
IN THE STATES OF RIO DE JANEIRO AND SÃO PAULO <sup>1</sup>

(With 3 figures)

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**ABSTRACT:** Ten species of spiny rats of the genus *Trinomys* are currently recognized in eastern Brazil. Although most taxa known in the genus *Trinomys* have been characterized on the basis of craniodental, pelage, and bacular traits, data on chromosomal morphology are available for only four taxa, two from the State of Bahia, one from the State of São Paulo, and one from the State of Espírito Santo. Here we describe the normal chromosomal complement for three additional taxa, namely, *Trinomys graciosus bonafidei* (Fazenda Boa Fê, Teresópolis, Rio de Janeiro, type-locality), *Trinomys eliasi* (Barra de Maricá, Maricá, Rio de Janeiro, type-locality), and *Trinomys dimidiatus* (Rio Bonito, Rio de Janeiro, and Ubatuba, São Paulo). The specimens analyzed here from the locality of Ubatuba were identified on the basis of craniodental, pelage, and bacular traits as *T. dimidiatus*, extending the known range of this species at least 100km south into the State of São Paulo. The three taxa for which chromosomal data are presented differ in their diploid and fundamental numbers and, therefore, can be diagnosed on the basis of their karyotypes. The significance and implications of chromosome numbers and morphology as diagnostic markers are evaluated in the framework of the molecular phylogenetic relationships and of the data on geographic distribution currently available for the genus *Trinomys*.

**Key words:** Echimyidae, karyotypes, Rodentia, spiny rats, taxonomy, *Trinomys*.

**RESUMO:** Caracterização cromossômica de taxa do gênero *Trinomys* Thomas, 1921, (Rodentia, Echimyidae) nos Estados do Rio de Janeiro e São Paulo.

Dez unidades taxonômicas no nível de espécie são atualmente reconhecidas para os roedores do gênero *Trinomys* no leste do Brasil. Embora a maioria dos taxa conhecidos tenham sido caracterizados com base em caracteres do crânio, da dentição, da pelagem e do báculo, a informação sobre a morfologia dos cromossomos limita-se até o momento apenas a quatro taxa, dois provenientes do Estado da Bahia, um de São Paulo e um do Espírito Santo. Neste trabalho são descritos os complementos cromossômicos para mais três taxa, *Trinomys graciosus bonafidei* (Fazenda Boa Fê, Teresópolis, RJ, localidade tipo), *Trinomys eliasi* (Barra de Maricá, Maricá, RJ, localidade tipo) e *Trinomys dimidiatus* (Rio Bonito, RJ, and Ubatuba, SP). Os espécimes analisados neste estudo provenientes de Ubatuba foram identificados como *T. dimidiatus* com base em caracteres craniodentais, da pelagem e do báculo, estendendo a distribuição da espécie pelo menos 100km ao sul na direção do Estado de São Paulo. Os taxa analisados neste trabalho diferem nos seus números diplóide e fundamental e, por conseguinte, podem ser diagnosticados com base nos seus cariótipos. As implicações da variação nos cromossomos para a diagnose dos taxa do gênero *Trinomys* que ocorrem nos estados do Rio de Janeiro e São Paulo são avaliadas no contexto das relações filogenéticas deste grupo, inferidas a partir de seqüências do genoma mitocondrial e da informação disponível sobre a distribuição geográfica de suas espécies.

**Palavras-chave:** Echimyidae, cariótipos, Rodentia, taxonomia, *Trinomys*.

## INTRODUCTION

In his monograph "Speciation in Brazilian spiny rats (Genus *Proechimys*, Family Echimyidae)", MOOJEN (1948) established the foundations for the study of the taxonomy of spiny rats of the

genus *Proechimys* Allen, 1899, distributed in Brazil. MOOJEN (1948) assessed morphological variation in craniodental and pelage traits and used this evidence to define taxa at the subgeneric, specific, and subspecific levels. Based primarily on the condition of the mainfold

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in the molariform teeth and on the patterns of geographic distribution, MOOJEN (1948) recognized two subgenera, *Proechimys*, distributed in the Amazon and Central Brazil, and *Trinomys* Thomas, 1921, distributed in eastern Brazil. Within each subgenus, taxa at the species and subspecies levels were characterized by a combination of traits in cranial character complexes, involving mainly the shape and configuration of the postorbital process of zygoma and the incisive foramen and patterns of pelage color. MOOJEN (1948) constructed his taxonomic structure on the basis of overall morphological similarity, following the prevailing theoretical paradigm of his time (SIMPSON, 1961) and, therefore, no phylogenetic information content should be expected or inferred from his taxonomic structure. MOOJEN's (1948) taxonomic structure and the diagnoses at the morphological, organismal level have served as the primary source for the identification of spiny rats in eastern Brazil and also as the basis for the discovery of new taxa (PESSÔA, OLIVEIRA & REIS, 1992; PESSÔA & REIS, 1993; REIS & PESSÔA, 1995; ROCHA, 1995; LARA, PATTON & HINGST-ZAHER, 2002).

Recently, evidence from molecular sequences sampled from the mitochondrial genome indicated that the subgenera *Trinomys* and *Proechimys*, as conceived and defined by MOOJEN (1948) on the basis of dental traits and distribution patterns, do not share a most recent common ancestor (LARA, PATTON & SILVA, 1996; LARA & PATTON, 2000; LEITE & PATTON, 2002). As a corollary to the molecular approach, the subgenera *Proechimys* and *Trinomys* were granted genus status. Furthermore, the specific and infraspecific taxonomic structure for *Trinomys* is currently based on the phylogenetic relationships of haplotype lineages, derived from 726 base pairs of the cytochrome *b* gene in the mitochondrial genome (LARA & PATTON, 2000). Three major clades are recognized in the molecular taxonomic structure (LARA & PATTON, 2000): the first clade includes the monotypic taxa *Trinomys dimidiatus* (Günther, 1877), *Trinomys iheringi* Thomas 1911, *Trinomys mirapitanga* Lara, Patton & Hingst-Zaher, 2002, and the polytypic *Trinomys graciosus* Moojen, 1948; the second clade includes the monotypic *Trinomys yonenagae* Rocha, 1995, *Trinomys paratus* Moojen, 1948, *Trinomys eliasi* Pessôa and Reis, 1993, and the polytypic *Trinomys setosus* Desmarest 1817; and the third clade is represented only by *Trinomys albispinus* (Is.

Geoffroy, 1838). These molecular clades also have morphological cohesion as defined in LARA & PATTON (2000). One taxon originally described in MOOJEN's (1948) taxonomic structure, *Proechimys iheringi panema* Moojen, 1948, and another described more recently, *Proechimys moojeni* Pessôa, Oliveira & Reis, 1992, have not been sampled for molecular sequences.

Whereas data on morphological and molecular variation have become available for most taxa in the genus *Trinomys*, information on chromosomal variation has been available only for four taxa of *Trinomys*, namely, *T. albispinus* (LEAL-MESQUITA *et al.*, 1992), and *T. yonenagae* (LEAL-MESQUITA *et al.*, 1992) from Bahia, *T. iheringi* (YONENAGA-YASSUDA *et al.*, 1985) from São Paulo, and *T. graciosus graciosus* Moojen, 1948 (ZANCHIN, 1988) from Espírito Santo. Here we focus our attention on chromosome morphology and characterize the chromosomal complement of additional three taxa of the genus *Trinomys* from Rio de Janeiro and São Paulo. We identified the taxa of interest by diagnostic features of the postorbital process of zygoma, incisive foramen, and pelage (MOOJEN, 1948; PESSÔA & REIS, 1992a) and of the baculum (PESSÔA & REIS, 1992b; PESSÔA, REIS & PESSÔA, 1996). The entities thus defined bear names in the morphological taxonomic structure (MOOJEN, 1948), which we then mapped onto names in the current molecular taxonomic structure (LARA & PATTON, 2000). Finally, we use the names and implied relationships available in the molecular taxonomic structure to convey information on chromosomal morphology and variation. The primary aim is to evaluate whether chromosomal morphology can be useful as markers in the diagnosis of taxa of spiny rats of eastern Brazil.

## MATERIAL AND METHODS

### MORPHOLOGICAL DIAGNOSES OF *TRINOMYS* TAXA

All specimens karyotyped in this study were deposited as skins and skulls as vouchers in the mammal collection of Museu Nacional - Rio de Janeiro (MN). Morphological diagnoses provided below for the *Trinomys* taxa are based on MOOJEN (1948), PESSÔA & REIS (1992a,b) and PESSÔA, REIS & PESSÔA (1996).

*Proechimys dimidiatus* – Maxillary part of vomerine septum wide and strong, vomer not visible ventrally; postorbital process of zygoma formed entirely by squamosal; proximal and distal ends of



baculum round, lateral indentation on mid-shaft; setiforms on mid-dorsal region gradually blackening toward tip but interrupted by Ochraceous-Buff subapical zone, setiforms on outer thighs white on basal half then gradually becoming gray on middle part and finally Light Ochraceous-Buff on distal third, or with tip blackish and Ochraceous-Buff subapical zone. The name *P. dimidiatus* in the morphological taxonomic structure (MOOJEN, 1948) maps onto *Trinomys dimidiatus* in the molecular taxonomic structure (LARA & PATTON, 2000). The following specimens of *T. dimidiatus* were analyzed: Rio Bonito, Rio de Janeiro (MN67553, MN67554), and Ubatuba, São Paulo (MN67550-67552).

*Proechimys iheringi bonafidei* – Maxillary part of vomerine septum long and thin, vomer not visible ventrally; post-orbital process of zygoma formed mostly by squamosal; proximal end of baculum square and distal end convex, lateral indentation on mid-shaft; setiforms on mid-dorsal region gradually blackening toward tip but interrupted by Ochraceous-Buff subapical zone, setiforms on outer thighs gray basally, gradually blackening toward the tip but interrupted by Ochraceous-Buff subapical zone, only a short blackened tip, setiforms on outer thighs gray basally gradually blackening toward tip, but interrupted by a Cinnamon-Buff subapical zone. The name *P. iheringi bonafidei* in the morphological taxonomic structure (MOOJEN, 1948) maps onto *T. gratosus bonafidei* in the molecular taxonomic structure (LARA & PATTON, 2000). The following specimens of *T. gratosus bonafidei* from Fazenda Boa Fé, Rio Bengalas, Teresópolis, Rio de Janeiro, were analyzed (MN43807, MN43821 and MN54153).

*Proechimys iheringi eliasi* – Maxillary part of vomerine septum narrow and short, vomer visible ventrally between the premaxillary and maxillary parts of vomerine septum; post-orbital process of zygoma formed mostly by jugal; proximal end of baculum tapered and distal end straight, lateral indentation on proximal third of shaft; setiforms on mid-dorsal region gradually blackening toward tip but not interrupted Ochraceous-Buff subapical zone. The name *P. iheringi eliasi* in the morphological taxonomic structure (MOOJEN, 1948) maps onto *T. eliasi* in the molecular taxonomic structure (LARA & PATTON, 2000). One specimen of *T. eliasi* from Restinga da Barra de Maricá, Rio de Janeiro, was analyzed (MN43822).

#### CHROMOSOMAL ANALYSIS

The nine specimens of *Trinomys* listed earlier in the text were studied morphologically and cytogenetically. A total of 446 metaphase cells were analyzed.

Cytogenetic analyses were done on mitotic metaphase chromosomes from bone marrow according FORD & HAMERTON (1956) with modifications. The chromosomes were stained with Giemsa and classified following LEVAN, FREDGA & SANDBERG (1964). The metacentric and submetacentric chromosomes are considered biarmed and subtelocentric and acrocentric ones are uniarmed.

#### RESULTS

Cytogenetic analyses of one female and one male of *T. dimidiatus* collected in Rio Bonito and two females and one male collected in Ubatuba, revealed a diploid number of  $2n=60$  and  $FN=116$ . This karyotype comprises 29 pairs of metacentric and submetacentric autosomes. Pair 10 has a secondary constriction on the long arm, probably coincident with the nucleolar organizer regions (NORs). The X chromosome is a large submetacentric (corresponding to the second pair of the complement) and the Y is a metacentric intermediary to pairs 20 and 21 (Fig. 1a, b).

One female and two males of *T. g. bonafidei* collected in Teresópolis had a diploid number of  $2n=56$  and  $FN=108$ . The karyotype comprises 27 pairs of metacentric and submetacentric autosomes. Pair 10 showed a secondary constriction on the long arm, probably coincident with the NORs. The X-chromosome is a large submetacentric (corresponding to the second pair of the complement) and the Y is a metacentric intermediary to pairs 20 and 21 (Fig. 2).

Cytogenetic analyses of one male of *T. eliasi* collected in Maricá showed a diploid number of  $2n=58$  ( $FN=112$ ) with 28 pairs of metacentric and submetacentric autosomes. Pair ten also had a secondary constriction on the long arm, probably coincident with the NORs. The X chromosome is a large submetacentric (corresponding to the second pair of the complement) and the Y is a metacentric intermediary to pairs 21 and 22 (Fig. 3). Diploid and fundamental numbers are summarized in table 1.



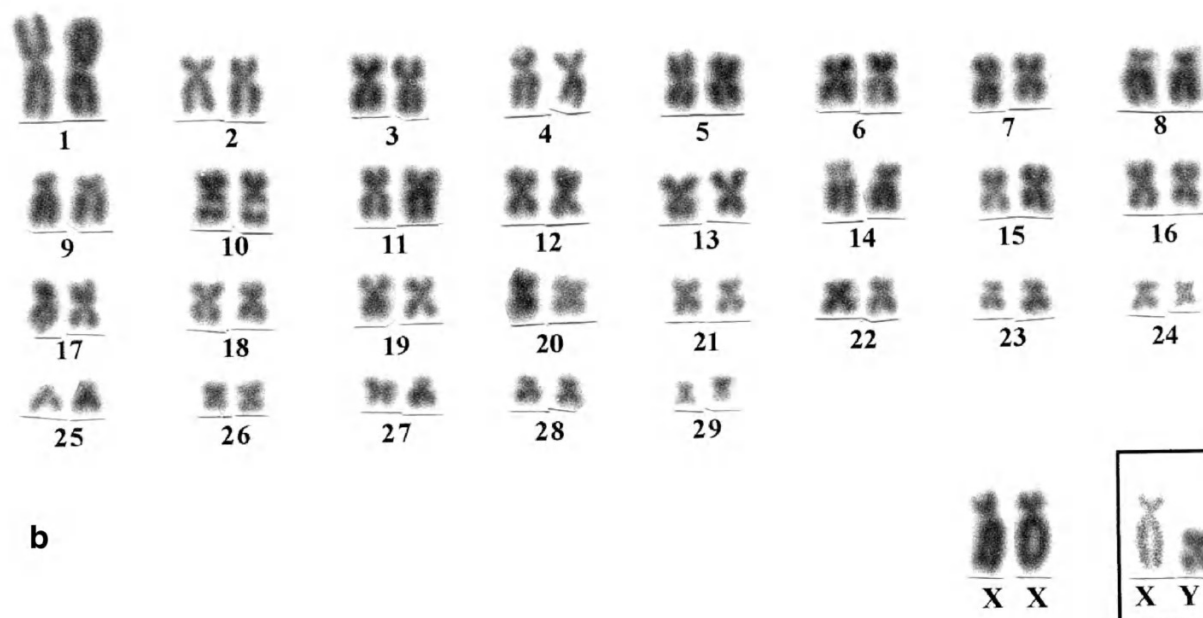
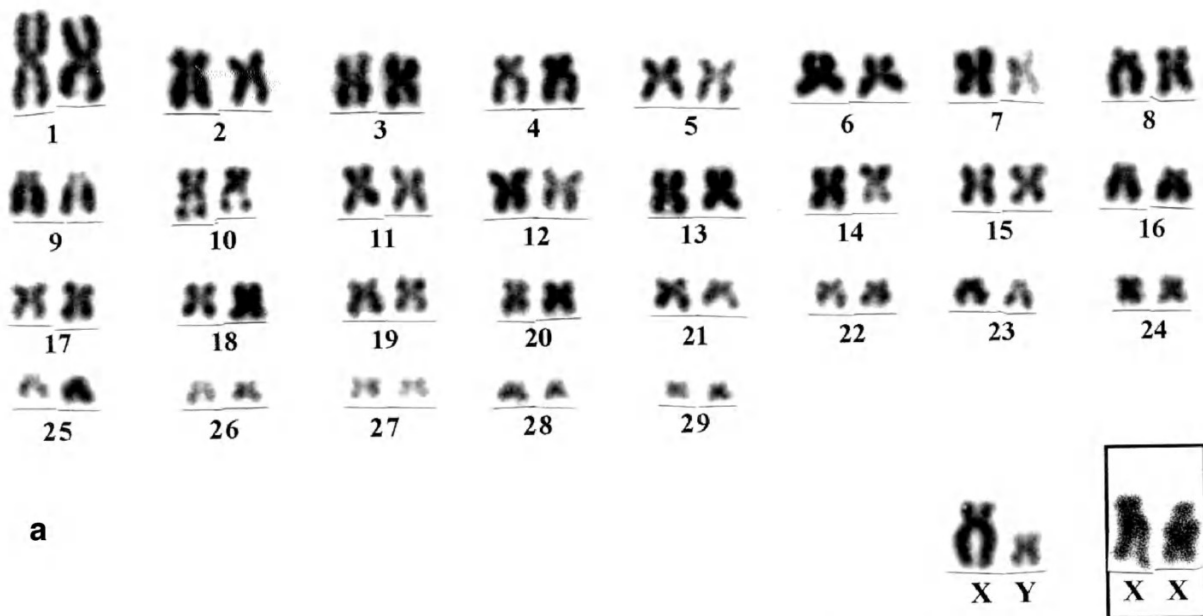


Fig.1- (a) karyotype of male (MN67553) *Trinomys dimidiatus* ( $2n=60$ , FN=116) from Rio Bonito, RJ. Pair ten shows a secondary constriction. In the inset, sex chromosomes of a female (MN 67554); (b) karyotype of female (MN67551) *T. dimidiatus* ( $2n=60$ , FN=116) from Ubatuba, SP. Pair ten shows a secondary constriction. In the inset, sex chromosomes of a male (MN67552). Scale bars =  $10\mu\text{m}$ .



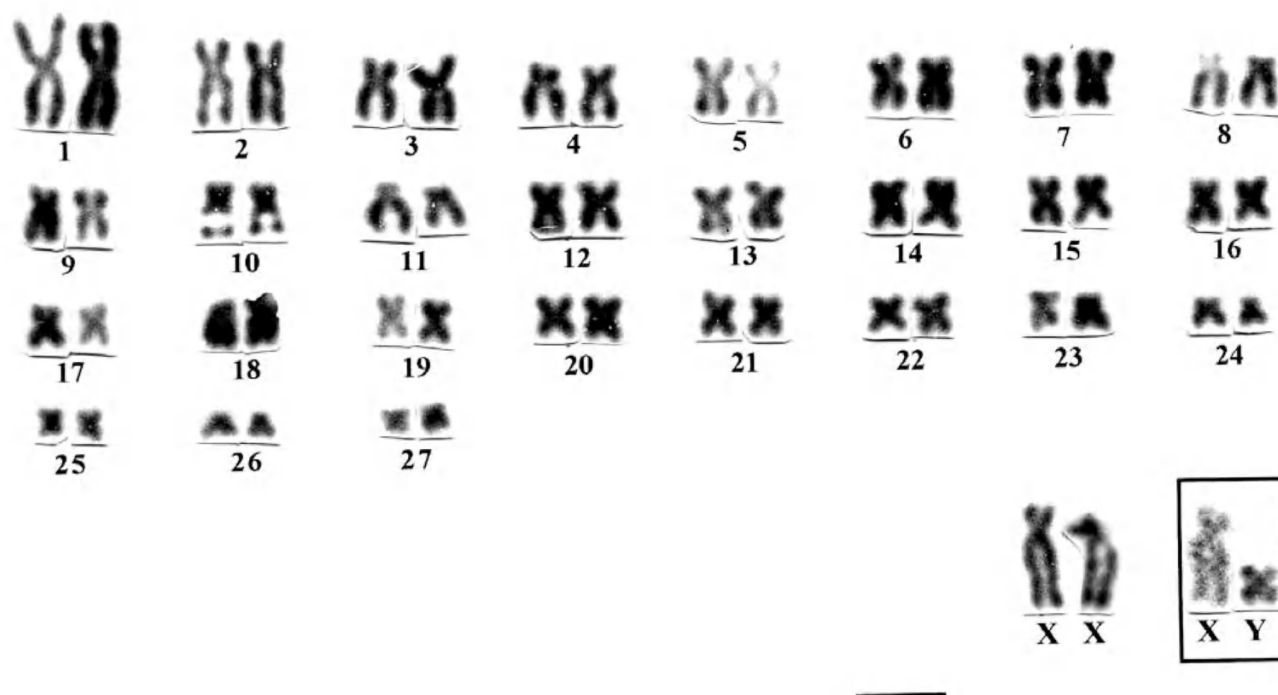


Fig.2- Karyotype of female (MN43807) *Trinomys gratus bonafidei* ( $2n=56$ ,  $FN=108$ ) from Teresópolis, RJ. Pair ten shows a secondary constriction. In the inset, sex chromosomes of a male (MN54153).

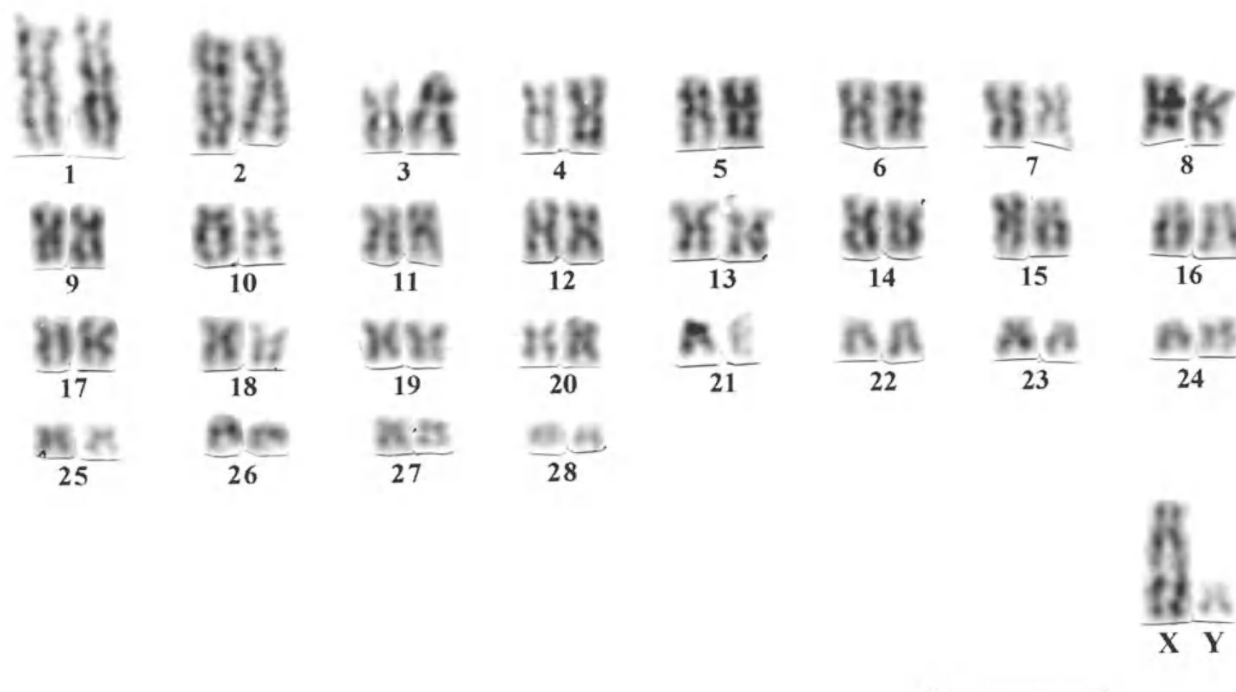


Fig.3- Karyotype of male (MN43822) *Trinomys eliasi* ( $2n=58$ ,  $FN=112$ ) from Maricá, RJ. Pair ten shows a secondary constriction. Scale bars =  $10\mu m$ .



Table 1. Taxa of the genus *Trinomys*, mitochondrial clades, diploid and fundamental numbers, and localities of specimens examined.

SPECIES	MITOCHONDRIAL CLADES	2n	FN	LOCALITY	REFERENCE
<i>T. dimidiatus</i>	Clade 1	60	116	Ubatuba-SP	Present study
<i>T. dimidiatus</i>	Clade 1	60	116	Rio Bonito-RJ	Present study
<i>T. graciosus</i>	Clade 1	56	108	Venda Nova	ZANCHIN, 1988
<i>T. g. bonafidei</i>	Clade 1	56	108	Teresópolis-RJ	Present study
<i>T. iheringi</i>	Clade 1	61-65	116	4 localities-SP	YONENAGA-YASSUDA <i>et al.</i> , 1985
<i>T. eliasi</i>	Clade 2	58	112	Maricá-RJ	Present study
<i>T. albispinus</i>	Clade 3	60	116	Morro do Chapéu-BA	LEAL-MESQUITA <i>et al.</i> , 1992

## DISCUSSION

As outlined in the introduction, our primary aim was to evaluate whether chromosomal morphology provides markers that contribute to the diagnosis of taxa in the genus *Trinomys*. The specimens analyzed were identified on the basis of craniodental, pelage, and bacular traits as, *T. g. bonafidei*, *T. eliasi* and *T. dimidiatus*, and it was demonstrated here that these taxa do differ in their diploid and fundamental numbers and, therefore, can be diagnosed on a chromosomal basis. The implications and relevance of these new data on chromosomal morphology for the taxonomy and systematics of *Trinomys* must be evaluated in the context of the implied relationships derived from the molecular taxonomic structure and of the limited information available on distribution records.

*Trinomys dimidiatus* is included in clade 1 of the molecular taxonomic structure (LARA & PATTON, 2000) and has so far been thought to be restricted in distribution to the State of Rio de Janeiro (MOOJEN, 1948). The specimens analyzed here from the locality of Ubatuba were identified on the basis of craniodental, pelage, and bacular traits as *T. dimidiatus*, extending the range of this species by at least 100km south into the State of São Paulo. *Trinomys dimidiatus* and *T. iheringi* mitochondrial haplotypes share a most recent common ancestor as indicated by the molecular phylogeny (LARA & PATTON, 2000). The normal complement of *T. dimidiatus* (2n=60 and FN=116) from the localities of Rio Bonito (Rio de Janeiro) and Ubatuba (São Paulo) is identical to that of *T. iheringi* described from the localities of Casa Grande, Ubatuba, and

Iguape in the State of São Paulo (YONENAGA-YASSUDA *et al.*, 1985). The normal complements are therefore not useful as a marker to diagnose either taxon. On the other hand, the Y chromosome was shown here to be metacentric in *T. dimidiatus* whereas it is submetacentric in *T. iheringi* (YONENAGA-YASSUDA *et al.*, 1985). Furthermore, individuals of *T. iheringi* in the populations sampled so far always show variable numbers (from 1 to 5) of supernumerary chromosomes (YONENAGA-YASSUDA *et al.*, 1985). Thus in this case, the morphology of the Y submetacentric chromosome and the presence of supernumerary chromosomes are useful markers to differentially diagnose *T. dimidiatus* and *T. iheringi*.

The second taxon for which chromosomal data are provided here, *T. g. bonafidei*, is known only from the type locality at Fazenda Boa Fé and a few other nearby sites in the locality of Teresópolis, State of Rio de Janeiro. This taxon shares recency of common ancestry with mitochondrial haplotypes of several geographical populations of *T. g. graciosus* (LARA & PATTON, 2000), and together with the sister taxa *T. dimidiatus* and *T. iheringi* comprise clade 1 of the molecular taxonomic structure (LARA & PATTON, 2000). *Trinomys g. bonafidei* and *T. dimidiatus* both occur in Teresópolis in the State of Rio de Janeiro, although apparently each taxon locally occurs at different altitudes and is associated with distinct plant communities (MOOJEN, 1948). Both taxa can be uniquely diagnosed on a chromosomal basis since *T. g. bonafidei* has a chromosomal complement of 2n=56 and FN=108 and the *T. dimidiatus* complement is 2n=60 and FN=116.

The third taxon sampled for chromosomal data is



*T. eliasi* from the type locality, which is included in clade 2 of the molecular taxonomic structure (LARA & PATTON, 2000). *Trinomys eliasi* was originally described from the coastal sand dunes in the locality of Maricá in the State of Rio de Janeiro (PESSÔA & REIS, 1993). Until recently, *T. eliasi* was known only from the type locality and this evidence might suggest that this species is strictly associated with coastal sand dunes. Nevertheless, *T. eliasi* was later found to occur inland in the locality of Silva Jardim in the State of Rio de Janeiro, where the habitat is lowland seasonal forest (specimens deposited in the Museu Nacional; L.M.PESSÔA, personal data). Both of the localities, Maricá and Silva Jardim, where *T. eliasi* is currently known to occur are close (ca.30km) to Rio Bonito where one of our samples of *T. dimidiatus* was collected. Again, both taxa can be diagnosed on the basis of the normal chromosomal complement, as *T. eliasi* has 2n=58 and FN=112 and *T. dimidiatus* has 2n=60 and FN=116.

Since Moojen's seminal publication, significant progress has been made towards the understanding of the taxonomy and systematics of spiny rats of eastern Brazil. New taxa have been described and new information has become available regarding cranial quantitative variation and bacular morphology for most taxa (PESSÔA & REIS, 1992a,b; PESSÔA, OLIVEIRA & REIS, 1992; PESSÔA & REIS, 1993; REIS & PESSÔA, 1995; ROCHA, 1995; LARA, PATTON & HINGST-ZAHER, 2002). In addition, molecular data have allowed the inference of phylogenetic relationships (LARA & PATTON, 2000). Chromosomal information was limited however to very few taxa. Chromosomal information is now available for *T. dimidiatus*, *T. gratosus bonafidei*, *T. eliasi* (this study) and also for *T. gratosus gratosus* (ZANCHIN, 1988), *T. albispinus* (LEAL-MESQUITA *et al.*, 1992), *T. yonenagae* (LEAL-MESQUITA *et al.*, 1992), and *T. iheringi* (YONENAGA-YASSUDA *et al.*, 1985). Furthermore, chromosomal data for *T. moojeni* and *T. setosus* are being presented in this volume by CORRÊA *et al.* (2005).

Given the availability of detailed information on morphological variation, the data on chromosomal complements and the molecular taxonomic structure, attention must now be directed to the definition of distribution limits of each taxon. Unfortunately, knowledge of the geographic range and distribution limits of recognized taxa has not experienced much progress and many of taxa characterized or described by MOOJEN (1948), and

those described after his review, are known only from the type locality and few studies have extended the distribution of known taxa (see PESSÔA *et al.*, 1993, and present study). Evidently, detailed knowledge and characterization of the geographic range and distribution limits of recognized natural units are of fundamental importance to understand the processes that generated the observed patterns of diversity. We hope that the data presented in the present paper will contribute to this endeavor.

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