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Original investigation

Trinomys mirapitanga, a new species of spiny rat (Rodentia: Echimyidae) from the Brazilian Atlantic Forest

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Abstract

A new species of spiny rat (genus *Trinomys*) from Porto Seguro, state of Bahia in the Atlantic Forest of Brazil is described based on skin, skull, and bacular characters and mitochondrial cytochrome b gene sequences. The new species is the sister to *T. dimidiatus* and *T. iheringi* which forms a monophyletic group together with *T. gratiosus*. It is diagnosed by having a tail less than head and body length that is covered by short hairs, without a brush of elongated hairs on the tail tip, a round post-orbital process of the zygomatic arch that is formed by both the squamosal and jugal, an oval incisive foramen with a well developed maxillary portion of the septum, and a baculum with well developed basal expansion, a median trough on the dorsal surface and ventral flexion.

Key words: Genus *Trinomys*, spiny rats, systematics, neotropics, new species

Introduction

South American spiny rats and tree rats in the family Echimyidae are the most ecologically diverse and speciose group of living caviomorph rodents. Spiny rats of the genus *Proechimys* occur in South and Central America, and are the most abundant mammal in primary and secondary lowland tropical forests where they play important ecological roles as seed dispersers and as prey for large predators. Despite the biological importance of spiny rats their taxonomy and systematics remain poorly known.

In 1921 Thomas divided the genus *Proechimys* into two subgenera: *Proechimys* sensu stricto and *Trinomys*. The former ranges widely from southern Honduras to northern Paraguay, and contains 59 named taxa currently placed in nine species groups (PATTON 1987). In contrast, *Trinomys* has a much more restricted distribution, limited to six eastern states of Brazil. It is also less diverse, with only six species currently recognized, all but one of which is restricted to the Atlantic Forest of coastal Brazil (MOOJEN 1948; PESSÔA, 1992; ROCHA 1995; LARA and PATTON 2000). Diagnosis of species within *Trinomys* has benefited from karyotypic descriptions for some taxa (YONENAGA-YASSUDA et al. 1985; LEAL-MESQUITA et al. 1992) and extensive morphologic and morphometric analyses (PESSÔA 1992; PESSÔA and DOS REIS 1991, 1992 a, 1992 b,

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1993, 1994). Until recently, the most complete systematic treatment was that of MOOJEN (1948).

Recent molecular systematic analyses by LARA and others (LARA 1994; LARA et al. 1996; LARA and PATTON 2000) have resulted in several taxonomic changes and a much deeper understanding of the evolutionary history of spiny rats. LARA (1994) and LARA et al. (1996) demonstrated that the initial diversification of echimyid rodents was rapid and consistent with a hypothesis of adaptive radiation. Furthermore, these authors found that the subgenera *Proechimys* and *Trinomys* were not sisters in a phylogenetic analysis, but were as divergent from one another as either was from other genera within the family Echimyidae. This finding led LARA (1994) to elevate *Trinomys* to generic rank (see also LARA and PATTON 2000). LARA (1994) and LARA et al. (1996) also documented the presence of three divergent clades within *Trinomys*. The divergence among clades within *Trinomys* was equal to or greater than that observed among other genera of echimyids, suggesting that *Trinomys* itself may be composed of as many as three separate genera. However the rapid radiation of echimyid rodents has resulted in a lack of resolution of sister group relationships among most supraspecific taxa, including most currently recognized genera and also the three clades of *Trinomys*. Furthermore, morphological characters are largely uninformative because the extant members of Echimyidae possess shared primitive and uniquely derived morphological characters, with few synapomorphies. Eventhough the three clades within *Trinomys* are so divergent as to possibly warrant recognition as three separate genera, LARA (1994), LARA et al. (1996) and LARA and PATTON (2000) took a more conservative approach and treated *Trinomys* as a monophyletic group. We adopt the same view here and treat the monophyly of *Trinomys* as a working hypothesis justified and based on 1) its unique morphological and cytological characters that seem to be all synapomorphic, and 2) the fact that *Trinomys* is readily diagnosable morphologically from *Proechimys* sensu stricto.

Finally, LARA and PATTON (2000) revised the species level taxonomy within *Trinomys*. Their criteria for recognizing species included monophyly and degree of divergence in mitochondrial DNA sequences, and the presence of diagnostic morphological traits. Each of the species they recognized has a limited distribution, and several are known only from their type locality, reflecting the general lack of knowledge concerning species distributional ranges. As currently recognized, *T. albispinus* contains three subspecies distributed in the northern portion of the range of *Trinomys* (DOS REIS and PESSÔA 1995) and *T. dimidiatus* is monotypic and is known only from the state of Rio de Janeiro (Fig. 1). The species *T. iheringi*, was conceived by MOOJEN (1948) and all subsequent authors (PESSÔA and DOS REIS 1991, 1992 a, 1993, 1994, 1996; DOS REIS et al. 1992; WOODS 1993; ROCHA 1995) to contain seven described subspecies that replaced each other from north to south. However, LARA (1994) found "*iheringi*" to be a massively paraphyletic, and possibily polyphyletic taxon, and that MOOJEN's (1948) taxonomy did not account for either the phylogenetic diversity nor the phylogenetic relationships among lineages (LARA 1994). To reflect phylogenetic relationships of monophyletic entities, LARA (1994) and LARA and PATTON (2000) revised the taxonomy, elevating four subspecies to specific rank (*T. iheringi*, *T. paratus*, *T. gratiosus* and *T. eliasi*) and reallocating the remaining subspecies to these or other previously recognized species. *Trinomys gratiosus* now contains two subspecies (*T. gratiosus gratiosus* and *T. g. bonafidei*) which occur above 600 meters altitude in the Serra do Mar and Serra da Mantiqueira in eastern Brazil. *Trinomys setosus* previously contained two described subspecies, but LARA and PATTON (2000) placed *T. iheringi denigratus* as a subspecies of *T. setosus*. The three subspecies of *T. setosus* apparently have disjunct distributions; *T. s. denigratus* extends from Bahia to Minas Gerais, *T. s. elegans* ranges from Ala-

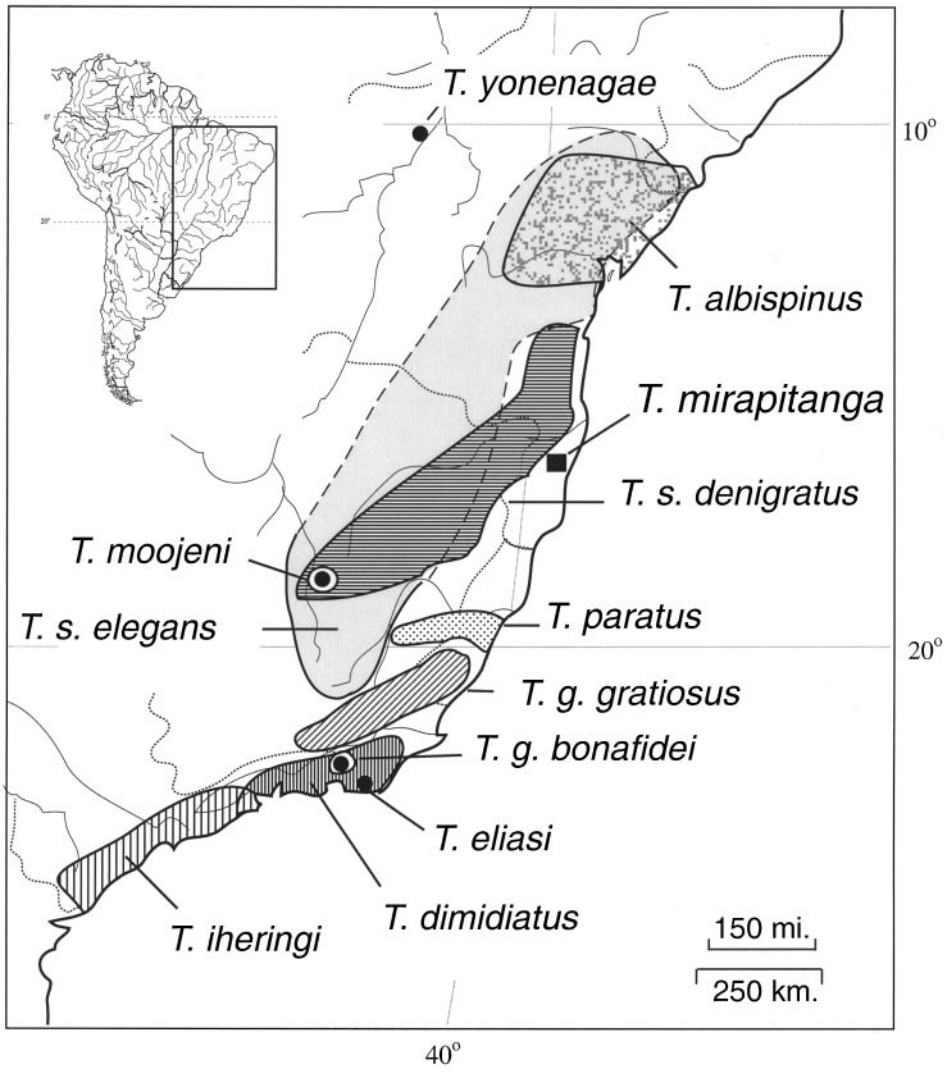

Fig. 1. Map of eastern Brazil showing known distributional range of taxa in the genus *Trinomys,* including type locality of the new species.

goas to Minas Gerais and and *T. s. setosus* is confined to Minas Gerais (see Fig. 1). Following Lara and Patton (2000) *T. iheringi panema* is treated as synomym of *T. g. gratiosus.*

Two additional species have been described recently, both known only from their type localities. *Trinomys yonenagae* was discovered in the dune vegetation along the Rio São Francisco (Rocha 1995), well outside the limits of the Atlantic Forest. The other, *T. moojeni*, is within the broader range of *T. setosus denigratus* and *T. s. elegans* but has yet to be found sympatric with either. Although some taxa show potential overlapping distributions, sympatry has been verified only at the northern most distribution of *Trinomys*, where *T. albispinus* and

T. setosus are sympatric at a single locality (see Fig 1).

Here we present the description of another new species of *Trinomys*, found in the moist tropical forests of the state of Bahia. Its phylogeographic relationships have been described elsewhere where it was treated simply as *Trinomys sp.* (LARA 1994; LARA et al. 1996; LARA and PATTON 2000).

Material and methods

The specimens examined were collected in the moist tropical forest at Porto Seguro, Bahia in 1992 and are housed in the Museu Nacional do Rio de Janeiro (MN). In total we examined 71 individuals representing 12 of the 15 described taxa within *Trinomys*. Morphological diagnosis is based on skin, skull and bacular characters. Pelage is described following MOOJEN (1948); capitalized color terms are from RIDGWAY (1912). Cranial and bacular measurements follow PATTON and ROGERS (1983) and PATTON (1987) and were taken with digital calipers graduated to 0.01 mm. Hypotheses of phylogentic relationships were based on variation of the mitochondrial cytochrome b gene as reported elsewhere (LARA and PATTON 2000). Taxon names follow LARA (1994) and LARA and PATTON (2000).

Results

Trinomys mirapitanga sp. nov.

Holotype: (MN 31460) adult male; skin, skull, baculum and partial skeleton (right fore and hind limbs retained in skin). Collected by ERIKA HINGST-ZAHER on 21 November 1992 (field number EDH33) at Porto Seguro, Bahia, Brazil.

Type Locality: Estação Ecológica do Pau Brasil, 16 km W Porto Seguro, Bahia, Brazil, 16°22′ S 39°11′ W. 40 m alt (see Fig. 1).

Paratypes: Skins, skulls and partial skeletons of one adult female and one young female (MN 31422 and MN 31459, respectively).

Distribution: Known only from the type locality.

External and Skull Dimensions (in mm): Holotype measurements are: total length 410, tail 185, hindfoot 48 (including claw), ear (from notch) 27, greatest length of skull 51.19, zygomatic breadth 25.31, mastoid breadth 20.19, least interorbital constriction 11.40, rostral breadth 8.09, nasal length 17.88, basilar length of Hensel 36.55, palatal length A 16.63, palatal length B 6.48, length of incisive foramen 4.21, diastema length 11.71, alveolar length of upper tooth row 8.20, maxillary breadth 8.86, length of tympanic portion of auditory bulla 9.17, mandibullar length 27.52.

Definition and Diagnosis: *Trinomys* contains three distinct clades (Fig. 2). Clade 1

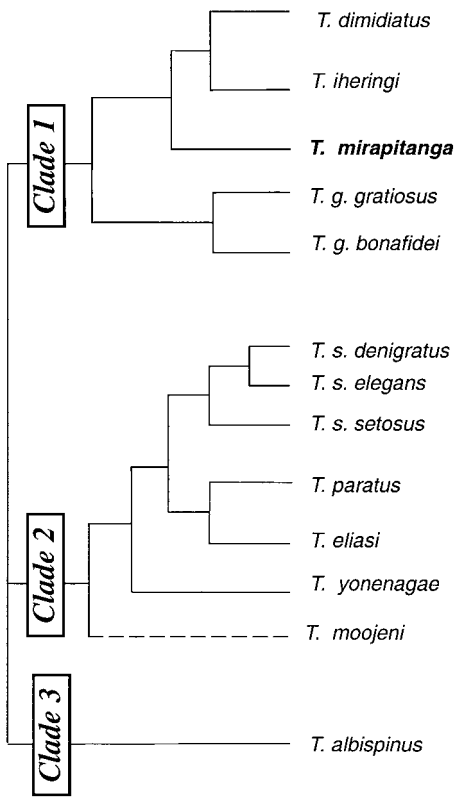

Fig. 2. Phylogenetic relationships of *Trinomys* depicting the three distinct clades as a basal polytomy (see text for details). It reflects species monophyly infered from DNA data and congruence of morphological characters (after LARA 1994). Based on morphology *T. moojeni* (dashed line) is clearly placed within clade 2 but its precise placement is not resolved.

contains *T. dimidiatus*, *T. iheringi*, and *T. gratiosus*; Clade 2 includes *T. yonenagae, T. eliasi, T. paratus* and *T. setosus* (sensu Lara and Patton 2000); and Clade 3 is restricted to *T. albispinus*. These three clades show a striking concordance with the distribution of major vegetation zones in coastal Brazil. Members of clade 1 are distributed along the coastal margins of southeastern Brazil, within the moist tropical forest. Members of clade 2 are found in the semideciduous tropical forest. Clade 3 is found in a more xeric vegetation.

Trinomys mirapitanga is the sister to *T. dimidiatus* and *T. iheringi* in Clade 1 (see Fig. 2). It is readily diagnosed by a tail length less than head and body length (ca. 82%; Fig. 3 A), and a tail covered with short hairs. Post-orbital process of the zygomatic arch is round and formed by both the squamosal and jugal (Fig. 3 C, D). The incisive foramen is oval (Fig. 3 B). Finally, the baculum has a strong ventral flexion and unique medial trough basally on the dorsal surface (Fig. 4 A).

T. mirapitanga differs from *T. setosus*, *T. paratus*, *T. eliasi*, and *T. yonenagae* by: 1) having a tail less than head and body in length and no brush of elongated hairs on the tail tip (not penicilate); 2) a round rather than a spiculate post-orbital process of the zygoma; 3) an oval incisive foramen; and 4) a baculum with both apical and basal expansions. It differs from *T. dimidiatus*, *T. iheringi*, *T. gratiosus* by having: 1) a well developed maxillary portion of the septum in the incisive foramen; 2) a post-orbital process of the zygoma formed by both the jugal and squamosal; 3) a basal expansion of the baculum more developed than the apical; 4) a ventral flexion in the baculum; and 5) a median trough on the dorsal surface of basal portion of the baculum.

Description

Pelage: As usual for this genus, *Trinomys mirapitanga* has a marked difference in color between the white ventral and the darker dorso-lateral pelage. The lateral dorsal surface has lighter aristiforms and setiforms. Aristiforms are much darker along the medial dorsal region, forming a dark cape on the middle of the back that sharply contrasts with the lateral lighter hairs (see Fig. 3 A). Aristiforms in the medial dorsal

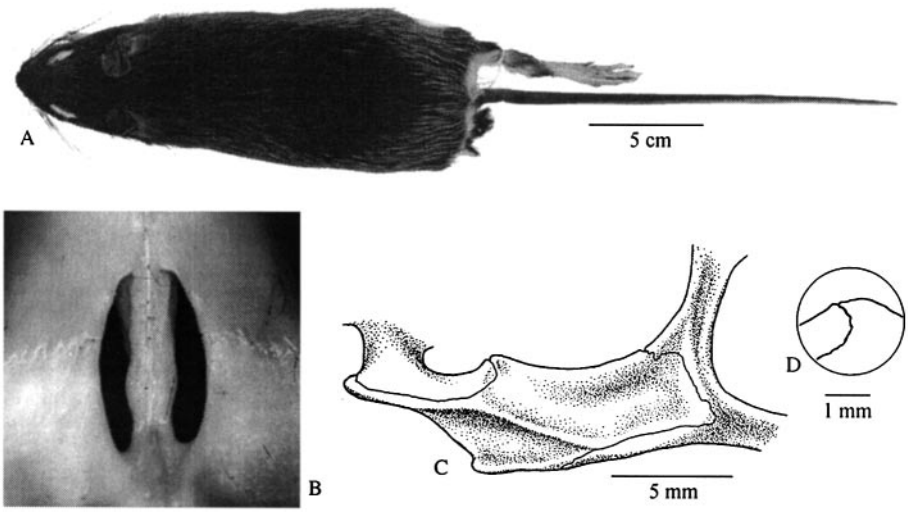

Fig. 3. Dorsal view of skin (A), incisive foramem showing a well developed maxillary portion of the septum (B), and zygomatic arch with a round post-orbital process formed by both the jugal and squamosal (C and D) of the holotype of *Trinomys mirapitanga* (MN31460).

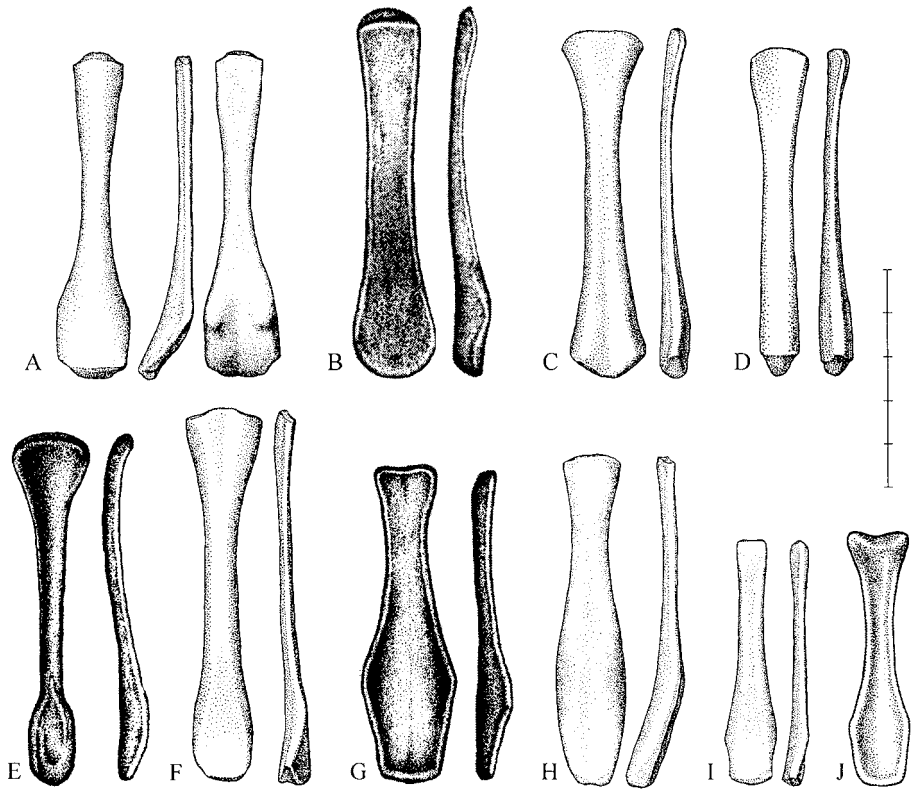

Fig. 4. Ventral and lateral views of bacula of taxa of *Trinomys* in Clade 1. A) *T. mirapitanga* (MN31460, holotype) – includes ventral, lateral, and dorsal views; B), C) and D) *T. dimidiatus* (MN10373, EDH68, and MN31414, respectively); E) and F) *T. iheringi* (no identification available and ML43, respectively); G) and H) *T. g. gratiosus* (M101 and MN31426, respectively); I) and J) *T. g. bonafidei* (MAN487 and LMP82, respectively). Scale = 5 mm.
(B, E, G are after PESSÔA (1992) and J after PESSÔA et al. (1996) and are presented as originally published).

region are Pale Smoke-Gray basally turning Black towards the distal third of the hairs. These aristiforms are very long (mean 24.9 mm) and average 1.49 mm wide. Aristiforms in the lateral region are smaller (mean length: 19.5 mm, mean width: 1.25 mm), Smoke-Gray basally, with a transitional Light Ochraceous-Buff in the middle and Dresden-Brown at the tip. The hands and feet have White hairs dorsally. Setiforms in the lateral region are Pale Drab-Gray basally, turning into Smoke-Gray, then an Ochraceous-Buff subapical zone and Black at the tip.

Skull: Skull large (Fig. 7), bulla large and smooth, post-orbital process of the zygomatic arch is round (never forming a sharp spine) and formed by the squamosal and jugal. Incisive foramen is oval and large (see Fig. 3 B). Median palatal ridge is moderate with posterolateral margins flanged. Premaxillary portion of the septum extends well over one-half the length of the foramen. The maxillary portion is well developed, always in direct contact with the premaxillary portion. The vomer does not contribute to the ventral aspect of the septum. The mesopterygoid fossa extends to anterior one half of M2.

Teeth: Teeth of holotype (MN 31460) relatively unworn; upper molariform teeth with three primary folds (rudimentary fourth

fold on posterior of M3), with first fold isolating an anteroloph in each; lower teeth with three folds, the first smaller than the remaining.

Baculum: Baculum of holotype and only known male is 7.91 mm, which is smaller than the average size for other species in the genus. Bacula size ranges from the largest in *T. albispinus*, *T. s. denigratus*, and *T. s. setosus* (11.4 mm, 10.2 mm, 10.1 mm respectively; Fig. 5 and Fig. 6) to the shortest in *T. g. bonafidei* (5.8 mm; Fig. 4 I, J). Baculum of holotype is short with both apical and basal expansions, the former weakly developed. Basal portion with larger and more developed expansion and a strong ventral flexion. Dorsal surface of the basal portion with a median trough (see Fig. 4 A).

Bacular morphology alone diagnoses the species of *Trinomys*. Two previous studies on bacular variation in *Trinomys* (Pessôa and dos Reis, 1992; Pessôa et al. 1996) deal

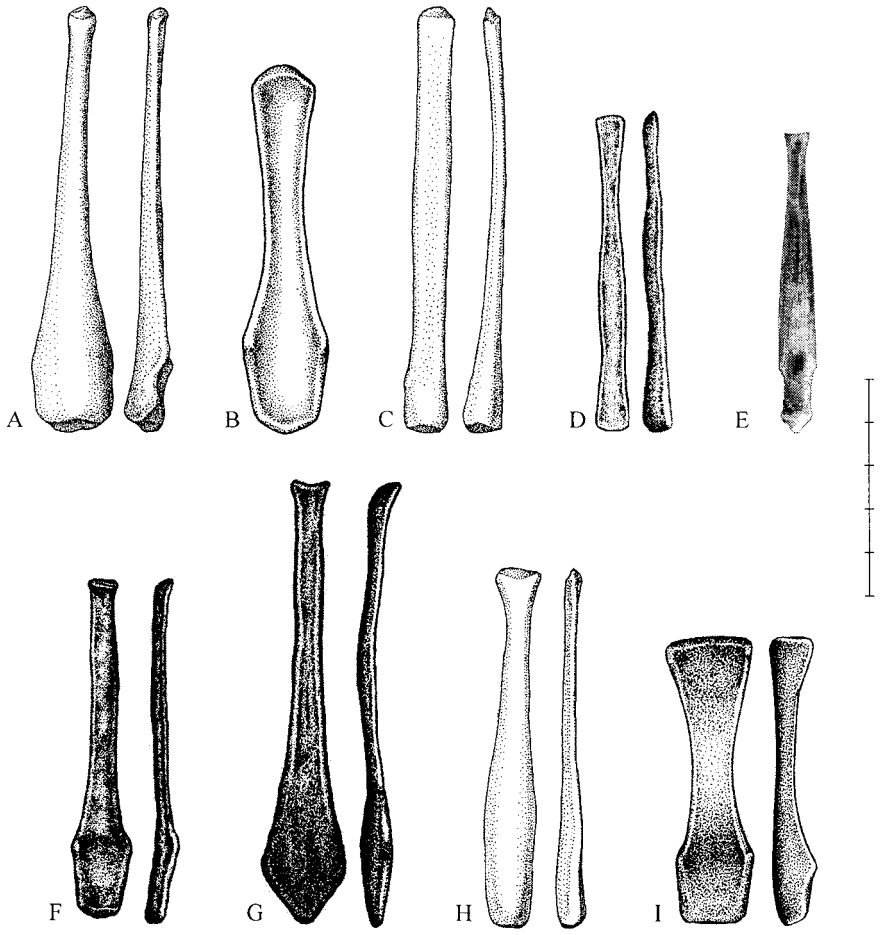

Fig. 5. Ventral and lateral views of bacula of the taxa in Clade 2. A) and B) *T. s. denigratus* (MN31441 and UFPB776); C) and D) *T. s. elegans* (MN31449 and UZM82); E) *T. yonenaga* (MZUSP28933); F) *T. eliasi* (MN30524); G) and H) *T. paratus* (MN5455 and MN31406); I) *T. moojeni* (MN13379). Scale = 5 mm.
(B after Pessôa et al. (1996), D, F, and G after Pessôa (1992), E after Rocha (1995), and I after Pessôa et al. (1992) are presented as originally published).

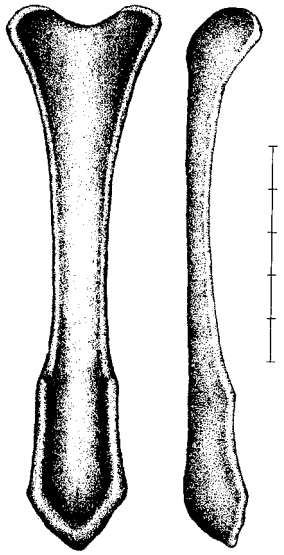

Fig. 6. Ventral and lateral views of baculum of *T. albispinus* representing Clade 3 (no. 2J58, Serviço Nacional da Peste, after PESSÔA 1992). Scale = 5 mm.

with interspecific qualitative features. Here we document variation within species as well as among species by assembling all published illustrations and descriptions of bacula (Figs. 4, 5, and 6). The age class of the specimen is critical, since it is clear that the baculum grows substantially (STRANEY 1990) and an understanding of the overall shape variation across different ontogenetic stages is important. Although all the bacula were drawn from adult specimens, information discriminating among young adult, adult and senile individuals (age classes 8, 9, and 10; see PATTON and ROGERS 1983) is not available. Ontogenetic growth might account for the shape variation seen in *T. g. gratiosus* (Fig. 4 G, H) and *T. s. elegans* (Fig. 5 C, D). However, the bacular variation in *T. dimidiatus* (Fig. 4 B, C, D) and *T. s. denigratus* (Fig. 5 A, B) is extreme by comparison and may not reflect solely ontogenetic differences.

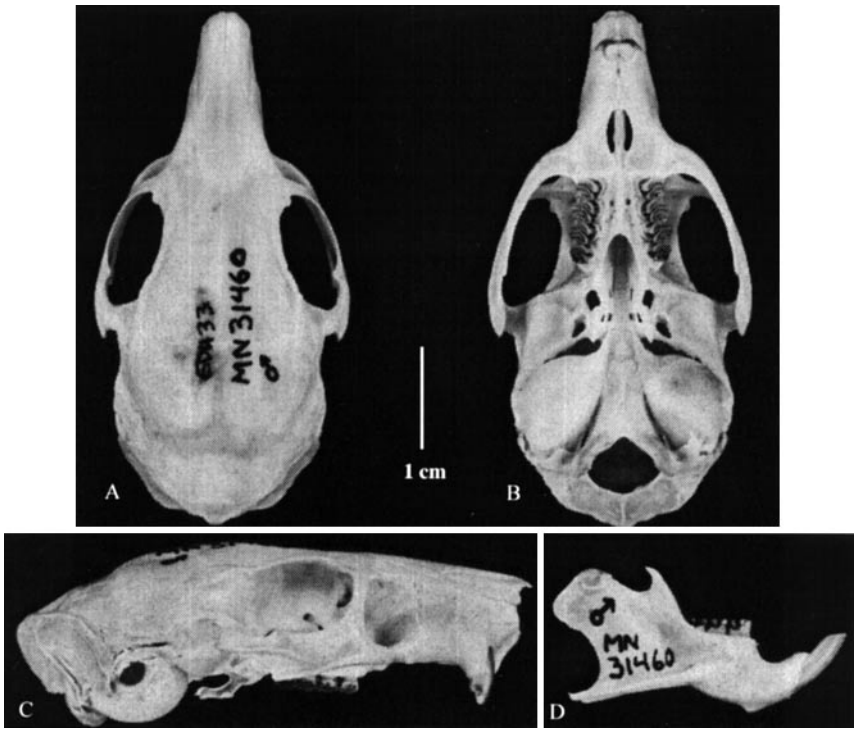

Fig. 7. Dorsal, ventral, and lateral views of the skull and mandible of the holotype of *Trinomys mirapitanga* (MN31460).

Etymology: We chose the specific name to denote its type locality, which is a biological reserve established to protect one of the largest remaining stands of pau-brasil. Pau-brasil is a hardwood tree (*Caesalpinia echinata*) that was exploited during colonial times for its bark, used for red dye in the European fabric industry. Only very few patches of this large leguminous tree remain. The name mirapitanga means pau-brasil in Tupi, the aboriginal language of the region. The Tupi occupied more than half of Brazil at the time of European colonization. Tupi language, with additions from other indigenous languages and Portuguese, was known as the "general language" because of its widespread common use and power to translate the ecologic system of both Atlantic and Amazonian forest regions (Leontsinis, 1992). Even today, despite the fact that few Tupi people remain, many common names of the Brazilian fauna and flora are Tupi.

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Zusammenfassung

Trinomys mirapitanga, eine neue Art der Stachelratte (Rodentia: Echimyidae) aus dem atlantischen Regenwald in Brasilien

Basierend auf Merkmalen der Haut, des Schädels und des Baculum sowie auf mitochondrialen Cytochrom b Sequenzen wird eine neue Art der Stachelratte (Gattung *Trinomys*) aus Porto Seguro im Bundesstaat Bahia im atlantischen Regenwald von Brasilien beschrieben. Die neue Art ist eine Schwesterart von *T. dimidiatus* und *T. iheringi*, welche gemeinsam mit *T. gratiosus* eine monophyletische Gruppe bilden. Die Diagnose der neuen Art erfolgt anhand ihres mit kurzen Haaren bedeckten Schwanzes, dessen Länge unter der der Kopf-Rumpf-Länge liegt, und dem ein terminaler Pinsel fehlt. Weitere Kennzeichen sind ein runder post-orbitaler Fortsatz am Jochbein, ein ovales Foramen incisivum mit einem gut entwickelten maxillaren Teil des Septums, und ein Baculum mit einer ausgeprägten basalen Erweiterung sowie einer medianen Furche entlang der dorsalen Oberfläche und einer ventralen Flexion.

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