



Taxonomic implications of morphological variation in three species of *Trinomys* (Rodentia: Echimyidae) from eastern Brazil

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Abstract

Trinomys is a genus of terrestrial spiny rats from the Atlantic Forest, and three species occur in the state of Espírito Santo, eastern Brazil: *T. graciosus*, *T. paratus*, and *T. setosus*. The levels of morphological variation within and among these species are virtually unknown, and their geographic ranges have not been properly assessed. These three species are externally very similar, hampering their identification in surveys and ecological studies that are not based on voucher specimens. We evaluated 162 specimens of *Trinomys* spp. from eastern Brazil, especially from the state of Espírito Santo, and used data from skulls, skins, and bacula to examine morphological variation and its taxonomic implications. We found extensive morphological variation in the skins and skulls even when diagnostic characters were examined, such as the number of dental lophs and bones contributing to the postorbital process. We also found variation in bacular shape among and within species, including polymorphism among individuals from the same population. The geographic range of each species in Espírito Santo was well defined: *T. setosus* occurred on the left (north) bank of the Doce River, and the other two species, *T. graciosus* and *T. paratus*, occurred on the right (south) bank of this river; however, *T. graciosus* was found at altitudes above 500 m, whereas *T. paratus* occurred below 580 m. Despite difficulties in species identification, the results of morphological and morphometric analyses are compatible with the current classification of these three species. In addition, the level of morphological variation found in specimens identified as *T. g. panema*—including types—falls within the range of *T. g. graciosus*, confirming the taxonomic status of the former as a junior synonym of the latter.

Key words: Atlantic Forest, Eumysopinae, geographic distribution, morphology, species limits

Introduction

Trinomys Thomas is a rodent genus of terrestrial spiny rat mainly associated with the Atlantic Forest of eastern Brazil (Attias *et al.* 2009). *Trinomys* was described by Thomas (1921) as a subgenus of *Proechimys* J. A. Allen restricted to eastern Brazil, whereas *Proechimys* (*Proechimys*) comprised species from Central America, throughout the Amazonia, and in the Cerrado of central Brazil. Moojen (1948) reviewed the genus *Proechimys* and maintained *Trinomys* as a subgenus, but Lara *et al.* (1996) and Lara & Patton (2000) considered *Trinomys* as a full genus because it did not form a monophyletic group with *Proechimys* in molecular phylogenetic analyses. Furthermore, *Trinomys* has dental characters supporting its monophyly and distinctiveness (Carvalho & Salles 2004). Several important studies addressing intraspecific variation (Pessôa & Reis 1994; Pessôa *et al.* 1996; Pessôa & Strauss 1999), geographic distribution (Attias *et al.* 2009) and the description of new species (Pessôa *et al.* 1992; Pessôa & Reis 1993; Lara *et al.* 2002) have been published. Lara & Patton (2000) studied the evolutionary relationships of *Trinomys* species and proposed taxonomic changes based on a molecular phylogeny, and Iack-Ximenes (2005) examined type specimens, analysed morphological variation, and suggested taxonomic adjustments. Here we followed Pessôa *et al.* (2015), who considered both Lara & Patton (2000) and Iack-Ximenes (2005) in their taxonomic arrangement of *Trinomys* species.

Pessôa *et al.* (2015) indicated three *Trinomys* species occurring in the state of Espírito Santo: *Trinomys graciosus* (Moojen), *Trinomys paratus* (Moojen), and *Trinomys setosus* (Desmarest). *Trinomys graciosus* and *T. setosus* are polytypic, and the subspecies *Trinomys graciosus graciosus* (Moojen) and *Trinomys setosus setosus*

The absence of *Trinomys* in areas above 1300 metres (Bonvicino *et al.* 1997, Geise *et al.* 2004; Attias *et al.* 2009) indicates a low tolerance to the lower temperatures that occur in these areas. Another observation that supports this idea is the low abundance of *Trinomys* in the subtropical areas of southern Brazil; the southernmost occurrence of this genus was recorded at a latitude of 25° south in the state of Paraná (Cerboncini *et al.* 2014).

Conclusions

Morphological variation across multivariate space allowed us to confirm the occurrence of three species of *Trinomys* in the state of Espírito Santo: *T. g. gratiosus*, *T. paratus* e *T. s. setosus*. These species can be differentiated in the field using external morphological characters, and their geographic distribution in the state of Espírito Santo has clear limits. *Trinomys g. gratiosus* occurs only in areas above 500 meters and to the south of the Doce River. *Trinomys s. setosus* and *T. paratus* are often found in the lowlands, but *T. s. setosus* is distributed only to the north of the Doce River while *T. paratus* is found to the south of that river.

We found no evidence of sexual dimorphism in skull morphometry of *T. paratus*. The morphological characters of *T. g. panema* fall within the variation detected in *T. g. gratiosus*, corroborating that the former is a junior synonym of the latter. Some of diagnostic characters of these three species of *Trinomys* reported in the literature are polymorphic, and a set of morphological characters is necessary for species level identification.

There are at least three forms of baculum for each species of *Trinomys* analysed, indicating the high diversity of this structure and its failure as a source of diagnostic features. Part of the morphological variation (e.g., bullar size, coronoid and articular processes of mandible, glans penis) is coherent with the basal phylogenetic relationships of the species in the genus. Topography and possibly rivers influenced the diversification and distribution of *Trinomys* species in the state of Espírito Santo. There is still need to review the validity of some subspecies and species in the genus to determine its true diversity, and to refine our knowledge about its distribution and evolution.

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References

- Agrizzi, J. (2012) *Filogeografia comparada de Trinomys spp. (Rodentia: Echimyidae) na região central da Mata Atlântica*. Universidade Federal do Espírito Santo, Vitória, 29 pp.
- Atchley, W.R. & Hall, B.K. (1991) A model for development and evolution of complex morphological structures. *Biological Reviews*, 66, 101–157.
<http://dx.doi.org/10.1111/j.1469-185x.1991.tb01138.x>
- Atchley, W.R. (1993) Genetic and developmental aspects of variability in the mammalian mandible. *In*: Hankenand, J. & Hall, B.K. (Eds.), *The Skull: Development. Vol. 1*. The University of Chicago Press, Chicago, pp. 207–247.
- Attias, N., Raíces, D.S.L., Pessoa, F.S., Albuquerque, H., Jordão-Nogueira, T., Modesto, T.C. & Bergallo, H.G. (2009) Potential distribution and new records of *Trinomys* species (Rodentia: Echimyidae) in the state of Rio de Janeiro. *Zoologia (Curitiba)*, 26 (2), 305–315.
<http://dx.doi.org/10.1590/s1984-46702009000200013>
- Bonvicino, C.R., Langguth, A., Lindbergh, S.M. & De Paula, A.C. (1997) An elevational gradient study of small mammals at Caparaó National Park, southeastern Brazil. *Mammalia*, 61 (4), 547–560.
- Candela, A.M. & Raisa, L.L. (2012) Tooth morphology of Echimyidae (Rodentia, Caviomorpha): homology assessments, fossils, and evolution. *Zoological Journal of the Linnean Society*, 164, 451–480.
<http://dx.doi.org/10.1111/j.1096-3642.2011.00762.x>
- Carvalho, G.A.S. & Salles, L.O. (2004) Relationships among extant and fossil echimyids (Rodentia: Hystricognathi).

- Zoological Journal of the Linnean Society*, 142, 445–477.
<http://dx.doi.org/10.1111/j.1096-3642.2004.00150.x>
- Cerboncini, R.A.S., Rubio, M.B.G., Bernardi, I.P., Braga, T.V., Roper, J.J. & Passos, F.C. (2014) Small mammal community structure and vertical space use preferences in nonfragmented Atlantic Forest. *Mammalia*, 78 (4), 429–436.
<http://dx.doi.org/10.1515/mammalia-2013-0128>
- Fabre, P.H., Galewski, T., Tilakand, M.K. & Douzery, E.J.P. (2012) Diversification of South American spiny rats (Echimyidae): a multigene phylogenetic approach. *Zoologica Scripta*, 42 (2), 117–134.
<http://dx.doi.org/10.1111/j.1463-6409.2012.00572.x>
- Fonseca, G.A.B. & Kierulff, M.C.M. (1989) Biology and natural history of Brazilian Atlantic forest small mammals. *Bulletin of the Florida Museum of Natural History*, 34 (3), 99–152.
- Galewski, T., Mauvrey, J.F., Leite, Y.L.R., Patton, J.L. & Douzery, E.J.P. (2005) Ecomorphological diversification among South American spiny rats (Rodentia; Echimyidae): a phylogenetic and chronological approach. *Molecular Phylogenetics and Evolution*, 34, 601–615.
<http://dx.doi.org/10.1016/j.ympev.2004.11.015>
- Gardner, A.L. & Emmons, L.H. (1984) Species groups in *Proechimys* (Rodentia, Echimyidae) as indicated by karyology and bullar morphology. *Journal of Mammalogy*, 65, 10–25.
<http://dx.doi.org/10.2307/1381195>
- Geise, L., Pereira, L.G., Bossi, D.P.E. & Bergallo, H.G. (2004) Pattern of elevational distribution and richness of non volant mammals in Itatiaia National Park and its surroundings, in southeastern Brazil. *Brazilian Journal of Biology*, 64 (3B), 599–612.
<http://dx.doi.org/10.1590/s1519-69842004000400007>
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4 (1). Available from: http://palaeo-electronica.org/2001_1/past/issue1_01.htm. (accessed 20 December 2012)
- Iack-Ximenes, G.E. (2005) *Revisão de Trinomys Thomas, 1921 (Rodentia, Echimyidae)*. Universidade de São Paulo, São Paulo, 265 pp.
- Jaeger, J.J. (1989) L'évolution de la pentalophodontie chez les rongeurs caviomorphes (Mammalia, Rodentia). *Geobios*, 22, 235–244.
[http://dx.doi.org/10.1016/s0016-6995\(89\)80025-7](http://dx.doi.org/10.1016/s0016-6995(89)80025-7)
- Lara, M.C. & Patton, J.L. (2000) Evolutionary diversification of spiny rats (genus *Trinomys*, Rodentia: Echimyidae) in the Atlantic Forest of Brazil. *Zoological Journal of the Linnean Society*, 130, 661–686.
<http://dx.doi.org/10.1111/j.1096-3642.2000.tb02205.x>
- Lara, M.C., Patton, J.L. & Hingst-Zaher, E. (2002) *Trinomys mirapitanga*, a new species of spiny rat (Rodentia: Echimyidae) from the Brazilian Atlantic Forest. *Mammalian Biology*, 67, 233–242.
<http://dx.doi.org/10.1078/1616-5047-00034>
- Lara, M.C., Patton, J.L. & da Silva, M.N.F. (1996) The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution*, 5 (2), 403–413.
<http://dx.doi.org/10.1006/mpev.1996.0035>
- Lavocat, R. (1976) Rongeurs caviomorphes de l'Oligocène de Bolivie II. Rongeurs du Bassin Déséadien de Salla-Luribay. *Paleovertebrata*, 7, 15–90.
- Lay, D.M. (1972) The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents. *Journal of Morphology*, 138, 41–120.
<http://dx.doi.org/10.1002/jmor.1051380103>
- Leite, Y.L.R. & Patton, J.L. (2002) Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. *Molecular Phylogenetics and Evolution*, 25, 455–464.
[http://dx.doi.org/10.1016/s1055-7903\(02\)00279-8](http://dx.doi.org/10.1016/s1055-7903(02)00279-8)
- Lewontin, R.C. (2000) The problems of population genetics. In: Singh, R.S. & Krimbas, C.R. (Eds.), *Evolutionary genetics: from molecules to morphology*. Cambridge University Press, Cambridge, pp. 5–23.
- Liao, J., Zhang, Z. & Liu, N. (2007) Effects of altitudinal change on the auditory bulla in *Ochotona daurica* (Mammalia, Lagomorpha). *Journal of Zoological Systematics and Evolutionary Research*, 45 (2), 151–154.
<http://dx.doi.org/10.1111/j.1439-0469.2006.00401.x>
- Monteiro, L.R. & Reis, S.F. (2005) Morphological evolution in the mandible of spiny rats, genus *Trinomys* (Rodentia: Echimyidae). *Journal of Zoological Systematics and Evolutionary Research*, 43 (4), 332–338.
<http://dx.doi.org/10.1111/j.1439-0469.2005.00323.x>
- Moojen, J. (1948) Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). *University of Kansas Publications, Museum Natural History*, 1, 303–401.
- Nicola, P.A., Monteiro, L.R., Pessôa, L.M., Von Zuben, F.J., Rohlf, F.J. & Reis, S.F. (2003) Congruence of hierarchical, localized variation in cranial shape and molecular phylogenetic structure in spiny rats, genus *Trinomys* (Rodentia: Echimyidae). *Biological Journal of the Linnean Society*, 80, 385–396.
<http://dx.doi.org/10.1046/j.1095-8312.2003.00245.x>
- Patterson, B.D. & Wood, A.E. (1982) Rodents from the Deseadan Oligocene of Bolivia and the relationships of the

- Caviomorpha. *Bulletin of the Museum of Comparative Zoology*, 149, 371–543.
- Patterson, B.D. (1983) Baculum-body size relationships as evidence for a selective continuum on bacular morphology. *Journal of Mammalogy*, 64 (3), 496–499.
<http://dx.doi.org/10.2307/1380362>
- Patton, J.L. & Rogers, M.A. (1983) Systematic implications of the non-geographic variation in spiny rats *Proechimys* (Echimyidae). *Zeitschrift für Säugetierkunde*, 48, 363–370.
- Pessôa, L.M. & Strauss, R.E. (1999) Cranial size and shape variation, pelage and bacular morphology, and subspecific differentiation in spiny rat *Proechimys albispinus* (Is. Geoffroy 1838), from northeastern Brazil. *Bonner Zoologische Beiträge*, 48, 231–243.
- Pessôa, L.M. & Reis, S.F. (1993) A new subspecies of *Proechimys iheringi* Thomas (Rodentia: Echimyidae) from the state of Rio de Janeiro, Brazil. *Zeitschrift für Säugetierkunde*, 58, 181–190.
- Pessôa, L.M. & Reis, S.F. (1994) Systematic implications of craniometric variation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae). *Zoologischer Anzeiger*, 5/6, 181–200.
- Pessôa, L.M., Zubenand, F.J. & Reis, S.F. (1998) Morphological affinities of *Proechimys yonenagae* Rocha, 1995 (Rodentia: Echimyidae) evidence from bacular and cranial characters. *Bonner Zoologische Beiträge*, 48 (2), 167–177.
- Pessôa, L.M., Oliveira, J.A. & Reis, S.F. (1992) A new species of spiny rats genus *Proechimys* subgenus *Trinomys* (Rodentia: Echimyidae). *Zeitschrift für Säugetierkunde*, 57, 39–46.
- Pessôa, L.M., Reis, S.F. & Pessôa, M.F. (1996) Bacular variation in subspecies taxonomy of the Brazilian spiny rat *Proechimys (Trinomys) iheringi*. *Studies on Neotropical Fauna and Environment*, 31, 129–132.
<http://dx.doi.org/10.1076/snfe.31.3.129.13339>
- Pessôa, L.M., Tavares, W.C., Oliveira, J.A. & Patton, J.L. (2015) Genus *Trinomys* Thomas, 1921. In: Patton, J.L., Pardiñas, U.F.J. & D'Elía, G. (Eds), *Mammals of South America. Vol. 2. Rodents*. University Of Chicago Press, Chicago. [in press]
- Smith, K.K. (1997) Comparative patterns of craniofacial development in eutherian and metatherian mammals. *Evolution*, 51, 1663–1678.
<http://dx.doi.org/10.2307/2411218>
- Tavares, W.C. & Pessôa, L.M. (2010) Variação morfológica em populações de *Trinomys* (Thomas, 1921) de restingas e matas de baixada no estado do Rio de Janeiro. In: Pessôa, L.M., Tavares, W.C. & Siciliano, S. (Eds.), *Mamíferos de restinga e manguezais do Brasil, Série Livros: 1*. Sociedade Brasileira de Mastozoologia, Museu Nacional, Rio de Janeiro, pp. 127–154.
- Thomas, O. (1921) XIII.—On spiny rats of the *Proechimys* group from South-eastern Brazil. *Journal of Natural History*, 8 (43), 140–143.
<http://dx.doi.org/10.1080/00222932108632569>
- Vucetich, M.G. & Verzi, D. (1994) Las homologías em los diseños oclusales de los roedores Caviomorpha: un modelo alternativo. *Mastozoologia Neotropical*, 1, 61–72.
- Webster, D.B. & Webster, M. (1972) Kangaroo rat auditory thresholds before and after middle ear reduction. *Brain, Behavior and Evolution*, 5, 41–53.
<http://dx.doi.org/10.1159/000123736>