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Morphological affinities of *Proechimys yonenagae* Rocha, 1995 (Rodentia: Echimyidae): Evidence from bacular and cranial characters

Leila Maria Pessôa, Fernando José Von Zuben & Sérgio Furtado dos Reis

Abstract. *Proechimys yonenagae* is a species of spiny rat in the rodent family Echimyidae that was recently described from the Caatingas biome of northeastern Brazil, a geographic area characterized by semi-arid climatic conditions. *P. yonenagae* departs from the remaining taxa in the genus in its habitat in that it inhabits fossil sand dunes. Morphologically, this species diverges from its congeneries by the presence of morphological traits usually associated with life in desert environments, such as a well developed tail brush, large hind feet and an inflated bulla. In the original description, the conjecture was raised, based on a cladistic and biogeographic rationale, that *P. yonenagae* is phyletically close to *P. albispinus*. An alternative hypothesis of affinities is derived here from the perspective of the structure of the morphological variation of qualitative bacular features and quantitative cranial traits. The results indicate that *P. yonenagae* shares closer morphological affinities with taxa in the *P. iheringi* complex than with *P. albispinus*.

Key words. *Proechimys yonenagae*, spiny rats, morphological affinities, bacular and cranial variability, canonical variates analysis, parametric bootstrap.

Introduction

Spiny rats of the genus *Proechimys* J. A. Allen are one of the most diversified and complex mammalian taxa in the Neotropical region (Moojen 1948, Patton 1987). Two subgenera, *Proechimys* and *Trinomys* Thomas, are currently recognized on a morphological basis. They have disjunct distributions, with the former ranging from Honduras in Central America, south through the Amazon basin and central Brazil and the latter being restricted to eastern Brazil (Moojen 1948, Patton 1987). The subgenus *Trinomys*, which is of concern here, currently comprises five species: *Proechimys dimidiatus* (Günther) and *P. moojeni* Pessôa, Oliveira & Reis regarded as monotypic (Moojen 1948, Pessôa & Reis 1990a, 1991a, 1993a, Pessôa et al. 1992); *P. albispinus* (Is. Geoffroy) with three subspecies (Moojen 1948, Pessôa & Reis 1991b, Reis & Pessôa 1995); *P. setosus* (Desmarest) with two subspecies (Moojen 1948); and *P. iheringi* Thomas with seven subspecies (Moojen 1948, Pessôa & Reis 1991c, 1993b, 1994, Reis et al. 1992, Pessôa & Reis 1996).

A new species of spiny rat, *P. yonenagae* Rocha, 1995 belonging to the subgenus *Trinomys* was recently described by Rocha (1995). This species is quite remarkable because it departs, both in its habitat and morphology, from the remaining taxa in the subgenus *Trinomys* (Rocha, 1995). Contrary to most species of the subgenus *Trinomys* that occur in forests, *P. yonenagae* inhabits fossil sand dunes in a restricted area in the left bank of the São Francisco River in the state of Bahia in northeastern Brazil (Rocha 1995, Vivo 1997). This habitat is part of the Caatingas biome and is

characterized by unpredictable rainfall and semi-arid conditions, with vegetation including plants in the families Cactaceae and Bromeliaceae (Ab'Saber 1974). Morphologically, *P. yonenagae* differs from the other species of *Trinomys* by a combination of traits, including a well developed tail brush, large hind feet and an inflated bulla (Rocha, 1995), features usually associated with life in desert environments (Vaughan 1972, Nowak & Paradiso 1983).

The discovery of a new species that differs so noticeably from the remaining taxa in a group immediately raises the question of its phylogenetic relationships. Rocha (1995: 547) surmised that *P. yonenagae* is phylogenetically close to *P. albispinus*. His argument follows two lines of reasoning, one applying cladistic principles to morphological data and the other based on biogeographic data. The hypothesis advanced by Rocha (1995) is based on the following cladistic argument: *P. yonenagae* shares a most recent common ancestor with *P. albispinus* due to the presence in both species of only one counterfold in each molariform tooth, a presumptively shared derived condition (= synapomorphy). However, the presence of only one counterfold in the molariform teeth is not unique to *P. yonenagae* and *P. albispinus* since this condition is also present in *P. setosus* and *P. iheringi denigratus* Moojen (Moojen 1948). From a biogeographic point of view, Rocha (1995) argues that both species are found in the extreme northern range known for the subgenus *Trinomys*. Nevertheless, another taxon, *P. iheringi denigratus*, in reaching the state of Sergipe in northeastern Brazil (Pessôa et al. 1993) ranges even farther north than *P. yonenagae*. Rocha (1995) further argues that *P. yonenagae* and *P. albispinus* are the only species in the subgenus *Trinomys* to occur in open habitats, although it is known that *P. iheringi eliasi* Pessôa & Reis occurs in a similar environment in the coastal sand dunes in the state of Rio de Janeiro (Pessôa & Reis 1993b).

In this paper an alternative assessment of relationships of *P. yonenagae* is offered. Our approach differs from that pursued by Rocha (1995) in that we do not make deductions from the polarity of character states or make use of biogeographic data. The alternative hypothesis of systematic affinities of *P. yonenagae* is developed here from the viewpoint of characters that diagnose and define taxonomic units in the subgenus *Trinomys* as currently understood. Detailed surveys of qualitative morphological characters of the baculum have shown that this structure has features that uniquely diagnose the taxa currently recognized at the specific and subspecific levels in the subgenus *Trinomys* (Pessôa et al. 1992, Pessôa & Reis 1992a, 1993a,b, Pessôa et al. 1996). The baculum has also proven useful in the discovery of new taxa in the subgenus *Trinomys* (Pessôa et al. 1992, Pessôa & Reis 1993b). These results establish the baculum as a valuable morphological marker to define limits of taxonomic variation in the subgenus *Trinomys*, and qualitative bacular features are employed here to evaluate the morphologic affinities of *P. yonenagae*. Morphologic affinities of *P. yonenagae* are also explored from the perspective of cranial metric traits because craniometric data have provided useful quantitative descriptors of patterns of variation in the subgenera *Proechimys* and *Trinomys* (Pessôa et al. 1990, Pessôa & Reis 1991a, b, c, 1992b, 1994, Reis et al. 1992). The term affinity is used throughout this paper strictly in the sense of similarity.

Materials and methods

The specimens used in this study were identified using a combination of pelage and skull characters described by Moojen (1948, see also Pessôa et al. 1992, Pessôa & Reis 1993, Rocha 1995). The methodology for the study of qualitative bacular morphology in the subgenus *Trinomys* is detailed in Pessôa & Reis (1992a) and Pessôa et al. (1996). Briefly, for the study of bacular variation phalli were removed from skins, immersed in water for 24 hours and afterwards the bacula were dissected from surrounding tissues. Bacula were examined under a binocular microscope and morphological features, including shape of the proximal and distal ends, presence of apical wings, presence and location of lateral indentation, dorsoventral curvature and median depression were recorded. Bacular morphology was recorded from the following population samples: *P. dimidiatus* (Floresta da Tijuca, state of Rio de Janeiro: $n = 5$); *P. iheringi eliasi* (Barra de Maricá, state of Rio de Janeiro: $n = 2$); *P. iheringi bonafidei* Moojen (Fazenda Boa Fé, state of Rio de Janeiro: $n = 4$); *P. iheringi iheringi* Moojen (Ubatuba and Juréia, state of São Paulo: $n = 1$ and $n = 3$, respectively); *P. iheringi gratiosus* Moojen (Santa Teresa, state of Espírito Santo: $n = 5$); *P. iheringi panema* Moojen (Campinho, state of Espírito Santo: $n = 1$); *P. iheringi paratus* Moojen (Capela de São Braz, Espírito Santo: $n = 1$); *P. iheringi denigratus* (Itabuna, Bahia: $n = 4$); *P. setosus* (Juiz de Fora, Peti, and Lagoa Santa; state of Minas Gerais: $n = 2$, $n = 1$ and $n = 1$, respectively); *P. albispinus* (Jaguaquara and Jequié, state of Bahia: $n = 1$ and $n = 4$, respectively); *P. moojeni* (Conceição do Mato Dentro, state of Minas Gerais: $n = 1$); *P. yonenagae* (Ibiraba, state of Bahia: $n = 6$).

The analysis of cranial affinities was based on seventeen cranial traits defined in Patton & Rogers (1983). Measurements were taken with digital calipers accurate to 0.01 mm interfaced to a microcomputer, as follows: greatest skull length, basilar length, palatal length A, palatal length B, upper tooth row, diastema, rostral length, nasal length, least interorbital constriction, rostral breadth, skull depth, rostral depth, maxillary breadth, zygomatic breadth, bulla length, post-palatal length, length of incisive foramen and mandible length. The following population samples were examined: *P. iheringi denigratus* (Itabuna, state of Bahia: $n = 8$); *P. iheringi panema* (Campinho, state of Espírito Santo: $n = 5$); *P. iheringi paratus* (Capela de São Braz and Cariacica, state of Espírito Santo: $n = 4$ and $n = 6$, respectively); *P. iheringi gratiosus* (Santa Teresa, state of Espírito Santo: $n = 12$); *P. iheringi bonafidei* (Teresópolis, state of Rio de Janeiro: $n = 10$); *P. iheringi eliasi* (Barra de Maricá, state of Rio de Janeiro: $n = 6$); *P. iheringi iheringi* (Casa Grande, Boracéia, Island of São Sebastião and Iporanga, state of São Paulo: $n = 10$, $n = 14$, $n = 6$, $n = 8$, respectively); *P. albispinus* (Jequié, state of Bahia: $n = 24$); *P. yonenagae* (Ibiraba, state of Bahia: $n = 17$). Patterns of craniometric ordination and affinities amongst taxa of *Proechimys* were investigated using canonical variate analysis (CVA), a multivariate technique designed to display morphometric relationships among groups (Krzanowski 1988). CVA is used in systematic and evolutionary biology primarily as an exploratory procedure (e.g. Brown & Pérez-Mellado 1993, How et al. 1996), but since our interest is in the inference of craniometric affinities we incorporate to CVA resampling procedures that allow for the statistical inference of variability. Inferential information on the expected bounds of craniometric variability was added to CVA by superimposing confidence regions on the plotted centroids in the canonical diagram, following a theory recently developed by Ringrose (1996). Ninety-five percent confidence regions around centroids for each population sample were constructed using estimates of variances obtained by parametric bootstrapping (Ringrose 1996). The replicate data matrices were generated from the $N_p(\bar{x}_p, \Sigma)$ distribution, where p is the number of variables, \bar{x}_i is the vector of the i -th group means and Σ is the within-group variance-covariance matrix (formulae in Ringrose 1996). All computations were carried out with MatLab (Moler et al. 1987).

All specimens examined in this study are deposited in the Museu Nacional, Rio de Janeiro and Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Results and discussion

In what follows we will describe the morphology of the baculum in the taxa allocated to the genus *Trinomys* and discuss the morphologic affinities of *P. yonenagae* from

the perspective of qualitative bacular traits. The morphological affinities of *P. yonenagae* will then be further evaluated from the viewpoint of quantitative cranial traits.

The baculum in the subgenus *Trinomys* is an elongate and narrow structure with a straight shaft (fig. 1). In *P. albispinus*, the baculum has a dorsoventral curvature and slightly tapered lateral indentations near the mid-shaft. The proximal end is paddle-shaped and pointed. The distal end has well-developed apical wings with a pronounced median depression. The shaft of the baculum in *P. moojeni* has a slight dorsoventral curvature and a tapered lateral indentation near the mid-shaft.

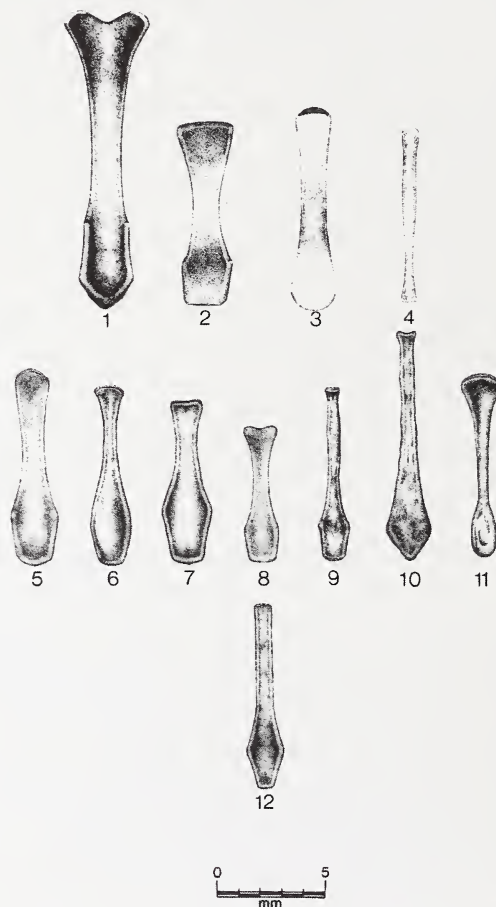


Fig. 1: Ventral view of bacula in the taxa of the subgenus *Trinomys*. The distal end is at the top. 1. *P. albispinus*, 2. *P. moojeni*, 3. *P. dimidiatus*, 4. *P. setosus*, 5. *P. iheringi denigratus*, 6. *P. iheringi panema*, 7. *P. iheringi graciosus*, 8. *P. iheringi bonafidei*, 9. *P. iheringi eliasi*, 10. *P. iheringi paratus*, 11. *P. iheringi iheringi*, 12. *P. yonenagae*.

Proximal end straight and paddle-shaped. The distal end has weakly developed apical wings. In *P. dimidiatus*, there is no dorsoventral curvature but there is a lateral indentation near the mid-shaft. The proximal and distal ends are evenly round, and the latter shows no development of apical wings or median depression. The baculum in *P. setosus* has no dorsoventral curvature and has a lateral indentation near the posterior tip. The proximal end is slightly paddle-shaped and the distal end is square with no development of apical wings or median depression. In *P. iheringi denigratus* and *P. iheringi panema*, the shaft has a dorsoventral curvature in the proximal, the proximal end is broad and round and the distal end is convex. The lateral indentation is near the middle of the shaft in the former and in the distal third in the latter subspecies. In *P. iheringi graciosus* the shaft has an accentuated dorsoventral curvature in the proximal third and a lateral indentation near the distal end. The distal end has a weak median depression. In *P. iheringi bonafidei* and *P. iheringi eliasi*, the shaft has a slight dorsoventral curvature in the proximal third, although they differ in the lateral indentation which is located near the middle in the former and in the proximal third in the latter. The distal end has an accentuated median depression in *P. iheringi bonafidei*. The baculum in *P. iheringi paratus* and *P. iheringi iheringi* has no dorsoventral curvature or lateral indentation. The distal end is concave and shows a slight median depression and the proximal end is broad and pointed in *P. iheringi paratus*. The distal and proximal ends are round in *P. iheringi iheringi*. Apical wings are present only in *P. iheringi bonafidei*. In *P. yonenagae*, the baculum is elongate and narrow with a straight shaft. Shaft with a slight dorsoventral curvature and a tapered lateral indentation in the proximal third. Proximal end paddle-shaped and the distal end has no apical wings or median depression. Table 1 summarizes the main qualitative morphological features of the baculum that in combination allow the identification of the taxa of the subgenus *Trinomys*.

The morphological features of the baculum surveyed above are sufficient to identify taxa currently recognized in the subgenus *Trinomys* of the genus *Proechimys*. The diagnostic features of the baculum that uniquely identify the taxa at the species and subspecies level include the shape of proximal and distal ends, the presence and degree of development of apical wings and the location of the lateral indentation in the shaft (fig. 1, Table 1; Pessôa & Reis 1992a, b, Pessôa et al. 1996). Although bacular morphology is not known to vary in *P. albispinus*, *P. moojeni*, *P. dimidiatus* and *P. setosus* (see Pessôa & Reis 1992 a, b, Pessôa et al. 1992), it becomes quite clear from the above descriptions that bacular morphology varies extensively within *P. iheringi*, mainly in the shape of the proximal and distal ends and in the dorsoventral curvature (fig. 1). It is also evident that the bacula in *P. i. iheringi* and *P. i. paratus* have quite distinct morphologies (fig. 1). These findings in association with craniometric data suggest that *P. i. iheringi* and *P. i. paratus* may actually be isolated at the specific level and *P. iheringi* in fact may represent a species complex (Pessôa & Reis 1994, Pessôa et al. 1996).

A comparison of the qualitative features of the baculum of *P. yonenagae* and that of the remaining forms in the subgenus *Trinomys* reveals that bacular morphology in this species has an overall shape similar to that found in taxa of the *P. iheringi* complex (fig. 1). In particular, the baculum in *P. yonenagae* shares characters with that of *P. i. denigratus*, *P. i. panema*, *P. i. graciosus*, *P. i. bonafidei* and *P. i. eliasi*.

The similarity in bacular morphology between *P. yonenagae* and these forms of *P. iheringi* is due to the presence of a dorsoventral curvature, the proximal end square or evenly round, and a lateral indentation in the shaft. The baculum of *P. yonenagae* is quite distinct in morphology from that of *P. albispinus*, whose bacular morphology is the most divergent amongst taxa in the subgenus *Trinomys* (fig. 1). The distinctiveness of bacular morphology in *P. albispinus* is due to the presence of well-developed apical wings with a pronounced median depression and a paddle-shaped proximal end (fig. 1; Pessôa & Reis 1992a). The qualitative analysis of bacular morphology indicates that, as evidenced by the overall shape of the baculum, *P. yonenagae* has affinities with taxa in the *P. iheringi* complex and not with *P. albispinus* as suggested by Rocha (1995).

We proceed now with a quantitative analysis of cranial affinities of these taxa. The simple question is whether *P. yonenagae* is craniometrically more similar to *P. albispinus* or to taxa in the *P. iheringi* complex. Figure 2 shows results obtained from 1,000 replications of the parametric bootstrap. Centroids for each taxon are indicated by a dot and the estimated bounds of craniometric variability are represented by ellipses derived from the parametric bootstrap. The confidence region for *P. yonenagae* overlaps completely with those of *P. iheringi* along the first canonical variate. On the other hand, *P. yonenagae* and *P. iheringi* ellipses are completely separated from *P. albispinus* along this axis, which alone accounts for more than half (56.62 %) of the variation in the seven canonical variates. This result suggests that *P. yonenagae* is craniometrically more similar to taxa in the *P. iheringi* complex than to *P. albispinus*. The inference of expected craniometric variability afforded by the construction of confidence regions allows us to further investigate

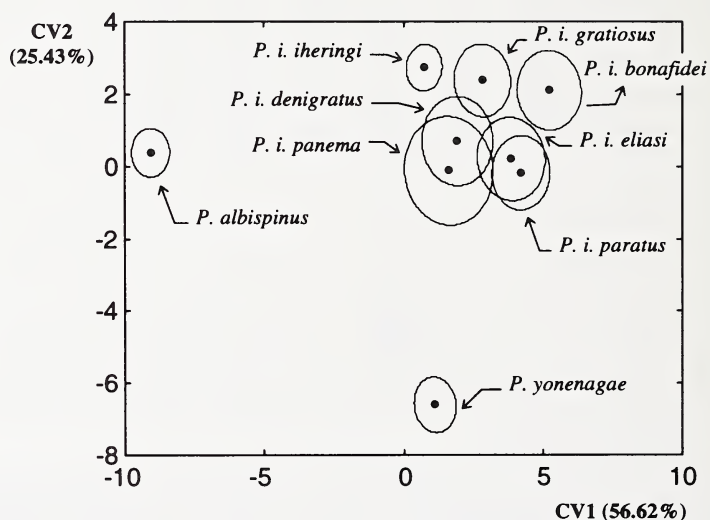


Fig. 2: Bivariate plot of centroids, indicated as dots, and 95 % parametric bootstrap confidence regions derived from a canonical variate analysis for *P. yonenagae*, *P. albispinus* and taxa in the *P. iheringi* complex.

craniometric affinities by plotting the centroids of *P. yonenagae* and *P. albispinus* on the morphometric space defined by the *P. iheringi* complex. We have done so by performing a canonical variate analysis including only the data for the *P. iheringi* complex and then projecting the centroids of *P. yonenagae* and *P. albispinus* onto the canonical axes defined for the *P. iheringi* data set. The confidence regions for the centroids of *P. yonenagae* and *P. iheringi* were calculated using Ringrose's results on simplified confidence regions (1996: 578; formula 4). These regions can be obtained in a closed form and do not depend on bootstrap resampling and can be used in this case because the data for *P. yonenagae* and *P. iheringi* were not used to calculate the canonical axes, and, therefore, are independent of them. Figure 3 shows the centroids for *P. yonenagae* and *P. albispinus* projected onto the morphometric space defined by the taxa in the *P. iheringi* complex. It can be seen that the centroid and confidence region for *P. yonenagae* fall well within the 95 % confidence region of the subspecies of *P. iheringi*, reinforcing the pattern of morphometric affinities described above. Since this result reflects the projection of the first two canonical variates alone, it was checked by computing the Mahalanobis D^2 distances (Mardia et al. 1979: 31) between centroids in all taxa in the space defined by the seven canonical variates (Table 2). Mahalanobis D^2 distances separating *P. yonenagae* and taxa in the *P. iheringi* complex are smaller (3.4965–5.5363) than the distance between *P. yonenagae* and *P. albispinus* (8.4645), confirming that *P. yonenagae* is craniometrically closer to taxa in the *P. iheringi* complex.

The results obtained using qualitative features of the baculum and quantitative traits of the skull indicate that *P. yonenagae* has morphological affinities with taxa in the *P. iheringi* complex and not with *P. albispinus*. As emphasized earlier, the

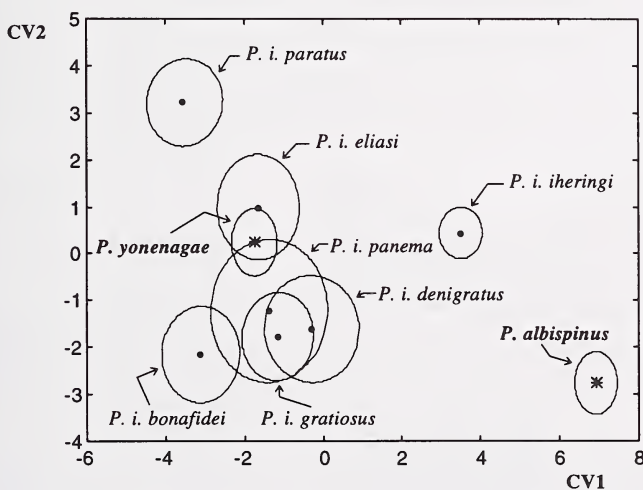


Fig. 3: Bivariate plot of centroids, indicated as dots, and 95 % parametric bootstrap confidence regions derived from a canonical variate analysis for the *P. iheringi* complex. The centroids for *P. yonenagae* and *P. albispinus* are indicated as asterisks. The 95 % confidence ellipses for *P. yonenagae* and *P. albispinus* were constructed using the approach described in Ringrose (1996: 578; formula 4).

Table 1: Diagnostic qualitative features of the bacular morphology in *P. albispinus*, *P. moojeni*, *P. dimidiatus*, *P. setosus*, the subspecies of *P. iheringi* and *P. yonenagae*. Morphological features include the shape of the proximal and distal ends, presence or absence of apical wings and location of the lateral indentation in the shaft of the baculum.

Taxon	Qualitative bacular features			
	Proximal end	Distal end	Apical wings	Lateral indentation
<i>P. albispinus</i>	paddle-shaped	concave	present (well-developed)	middle
<i>P. moojeni</i>	paddle-shaped	concave	present (weak)	middle
<i>P. dimidiatus</i>	evenly round	evenly round	absent	middle
<i>P. setosus</i>	paddle-shaped	square	absent	absent
<i>P. iheringi denigratus</i>	round	concave	absent	middle
<i>P. iheringi panama</i>	round	concave	absent	distal third
<i>P. iheringi gratiosus</i>	tapered	convex	absent	distal third
<i>P. iheringi bonafidei</i>	square	convex	present (weak)	middle
<i>P. iheringi eliasi</i>	tapered	straight	absent	proximal third
<i>P. iheringi paratus</i>	pointed	convex	absent	absent
<i>P. iheringi iheringi</i>	round	concave	absent	absent
<i>P. yonenagae</i>	paddle-shaped	straight	absent	proximal third

Table 2: Mahalanobis D^2 distances between centroids of subspecies of *P. iheringi*, *P. yonenagae* and *P. albispinus*. Distances calculated in the space defined by the seven canonical variates.

	<i>P. i. denigratus</i>	<i>P. i. panama</i>	<i>P. i. paratus</i>	<i>P. i. gratiosus</i>	<i>P. i. bonafidei</i>	<i>P. i. iheringi</i>	<i>P. i. eliasi</i>	<i>P. yonenagae</i>
<i>P. i. panama</i>	1.3843							
<i>P. i. paratus</i>	2.1363	2.1448	1.8341					
<i>P. i. gratiosus</i>	1.3155	1.6990	1.7164	1.9398				
<i>P. i. bonafidei</i>	2.9419	2.9882	3.3487	2.0875	3.9016			
<i>P. i. iheringi</i>	1.6094	2.3460	3.3487	1.5588	1.9965	2.8038		
<i>P. i. eliasi</i>	1.5714	2.1259	1.0064	4.7710	5.5363	4.7552	4.0375	
<i>P. yonenagae</i>	3.7675	3.4965	4.1205	9.0257	10.8398	7.5739	9.7655	
<i>P. albispinus</i>	8.3231	8.0995	10.0327					8.4645

approach followed here was based on the structure of taxonomic variation uncovered from qualitative bacular morphology and cranial metric traits for taxa in the subgenus *Trinomys* as a whole. The primary intent of this note was to inquire into the possible morphologic affinities of the new species, *P. yonenagae*, and the pattern that emerged should be perceived solely as an alternative view of relationships. Further understanding of morphological evolution in *P. yonenagae* will have to be framed in the context of independently derived hypotheses of phylogenetic relationships such as those generated by molecular markers.

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Zusammenfassung

Proechimys yonenagae gehört zu den Stachelratten innerhalb der Nagerfamilie Echimyidae. Kürzlich wurde ihr Vorkommen im Caatingas-Biom in Nordbrasilien, einer Region mit semi-aridem Klima, beschrieben. *P. yonenagae* weicht im Habitat von den übrigen Taxa der Gattung ab, da sie fossile Sanddünen bewohnt. Morphologisch unterscheidet sich diese Art durch Merkmale, die üblicherweise das Leben in Wüstengebieten charakterisieren, z. B. eine ausgeprägte Schwanzbürste, lange Hinterbeine und aufgewölbte Ohrblasen. In der Originalbeschreibung wurde aus kladistischen und biogeographischen Gründen die Vermutung ausgesprochen, das *P. yonenagae* phylogenetisch *P. albispinus* nahesteht. Hier wird eine alternative Hypothese dargestellt, die von der morphologischen Variation qualitativer Merkmale des Baculums und quantitativer Schädelmerkmale ausgeht. Die Ergebnisse zeigen, daß *P. yonenagae* morphologisch den Taxa des *P. iheringi*-Komplexes nähersteht als *P. albispinus*.

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Dr. Leila Maria Pessôa, Departamento de Zoologia, IB, Universidade Federal do Rio de Janeiro, 21941-590 Rio de Janeiro, RJ, Brazil. — Dr. Fernando José Von Zuben, Departamento de Computação e Automação, FEEC, Universidade Estadual de Campinas, 13083-970 Campinas, SP, Brazil. — Dr. Sérgio Furtado dos Reis, Departamento de Parasitologia, IB, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970 Campinas, SP, Brazil.

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