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Ultrastructure of echimyid and murid rodent spines

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Abstract

Aristiform spines of the rodents *Niviventer fulvescens*, *Maxomys surifer, Hoplomys gymnurus* and 17 species of *Proechimys* (representing both recognized subgenera and all nine species groups) were studied qualitatively using scanning electron microscopy (SEM) and quantitatively by measuring seven linear dimensions. SEM was used to examine spine tips, bases, longitudinal furrows and cross sections. Spines of the murid rodents *N. fulvescens* and *M. surifer* differed from those of the echimyid rodents *H. gymnurus* and *Proechimys* spp. in possessing a smaller base with a longer, narrower neck, scaled rather than ridged longitudinal furrows, and a solid internal core and large lacunae at the spine margins. Spines of *H. gymnurus* differed from those of *Proechimys* spp. in being considerably more robust with a stout neck at the base, an abruptly-tapering tip and a dense inner layer with a series of smaller lacunae at the spine margins. A factor analysis of spine measurements revealed major differences among *N. fulvescens*, *M. surifer*, *H. gymnurus*, the *Proechimys* subgenus *Trinomys* and the nine *Proechimys* species groups within the subgenus *Proechimys*. However, all *Proechimys* species groups clustered closely together. A discriminant function analysis of the nine *Proechimys* species groups provided generally limited discriminatory power. Although spines are distinct at the generic and subgeneric levels, spines may possess limited diagnostic structure at the level of species within the subgenus *Proechimys*.

Key words: *Hoplomys*, *Maxomys*, *Niviventer*, *Proechimys*, hair, spines, ultrastructure

INTRODUCTION

Many species of rodents have hairs that are modified as aristiform spines. Such spines have evolved independently numerous times and are possessed by taxa in at least five families (Heteromyidae, Muridae, Hystricidae, Erethizontidae and Echimyidae). The familiar porcupines (Hystricidae and Erethizontidae) often are covered with elongated spines that clearly function as protection from predators. The structure of those spines has been studied extensively (Schwarz, 1939; Sokolov & Chernova, 1998). By contrast, spinous representatives of the other three families often have less-developed spines whose function and even structure are largely unknown.

Taxonomic characters of mammals commonly include cranial and dental features and pelage. Individual hairs were included in early systematic studies because of their presumably distinctive characteristics (e.g. Cole, 1924; Williams, 1938; Nason, 1948; Noback, 1951; Mayer, 1952), but the utility of individual hairs as diagnostic taxonomic characters has been controversial (Mayer, 1952; Chernova, 2002). Hairs also have been used to identify mammals from both archaeological sites and predator scats (e.g. Brown, 1942; Perrin & Campbell, 1980). Many mammalian systematists no longer consider individual hairs to possess much taxonomic value at the species level. However, many studies of hair features frequently focused on hair colour and texture rather than on microscopic structure (Lyne, 1959). To our knowledge, aristiform spines have not been used in taxonomic studies.

Many genera of mammals contain species that are virtually impossible to identify by external morphology. Of particular note is the Neotropical echimyid genus *Proechimys*. As currently constituted, this genus has 32 species (Woods, 1993) and as many as four species may occur syntopically (Emmons, 1982). The full complement of syntopic species in a given area often is revealed only by destructive sampling and subsequent analysis of cranial, dental and karyotypic materials. If spines have diagnostic features at the species level, then non-destructive sampling of individuals could be performed, thus saving time and reducing the need to kill the animals.

In this report, descriptions are given of the ultrastructure of aristiform spines from 19 species of *Proechimys*, the closely-related *Hoplomys gymnurus* (the sole species of

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Table 1. Numbers of spines examined for each species. Collection locality refers to the original place of capture of the specimens

Genus or species group	Species	No. of specimens examined	Collection locality
Proechimys guyannensis group	*guyannensis*	42	Suriname, S. Venezuela, French Guiana, Central Amazon Basin
Proechimys goeldii group	*goeldii*	22	Amazon Basin, S. Venezuela, Ecuador, E. Peru
	steerei	23	
Proechimys longicaudatus group	*longicaudatus*	9	Bolivia
	brevicauda	43	SW Amazonia, SE Colombia, E. Ecuador, E. Peru, Bolivia
Proechimys simonsi group	*simonsi*	13	Ecuador, E. Peru, SE Colombia
Proechimys cuvieri group	*cuvieri*	22	Suriname, Brazil, French Guiana, Guyana, N. Peru
Proechimys trinitatus group	*trinitatus*	1	Trinidad
	chrysaeolus	1	Colombia
	mincae	1	Colombia
	urichi	1	Venezuela
	guarirae	2	Colombia
	ochraceous	1	Venezuela
Proechimys decumanus group	*decumanus*	14	SW Ecuador, NW Peru
Proechimys canicollis group	*canicollis*	13	NE Colombia
Proechimys semispinosus group	*oconnelli*	9	Colombia
	semispinosus	17	Panama, Costa Rica, Nicaragua, Colombia, Ecuador
Proechimys [*Trinomys*]	*albispinus*	1	Brazil
Proechimys [*Trinomys*]	*iheringi*	2	Brazil
Hoplomys	*gymnurus*	6	Panama
Maxomys	*surifer*	6	Vietnam
Niviventer	*fulvescens*	4	Vietnam

the genus) and two species of murid rodents in the genera *Maxomys* and *Niviventer* using scanning electron microscopy. Also given is a preliminary assessment of the use of spines as diagnostic characters to differentiate cryptic species of *Proechimys*.

MATERIALS AND METHODS

Specimen collection

Spines were collected from 274 museum specimens of 17 species of *Proechimys* (Table 1) representing the 9 species groups identified by Patton (1987). Spines from 2 species of the subgenus *Trinomys* were collected from museum specimens. *Trinomys* is sometimes elevated to generic status (e.g. Lara, Patton & Hingst-Zaher, 2002), but here the more conservative subgeneric designation is followed (Moojen, 1948; Woods, 1993). Spines were collected from live specimens of *Proechimys semispinosus* (trapped in 1996) and *Hoplomys gymnurus* (trapped in 1997) from the Canal Area and Darien Province of Panama (Adler, Tomblin & Lambert, 1998). Spines from the murids *Maxomys surifer* and *Niviventer fulvescens* were collected in southern Vietnam from live specimens trapped in June 1997 and January 1998 (Adler, Mangan & Suntsov, 1999). Spines from both museum and live specimens were collected only from individuals in full adult pelage. Spine nomenclature and morphology followed Chernova & Kuznetsov (2001) and Chernova (2002).

Table 2. Quantitative variables measured on each spine

Variable	Description
Spine length	Length of spine from basal to distal ends
Spine width	Greatest width of spine from margin to margin
Spine depth	Greatest thickness of spine taken at centre of furrow
Furrow length	Length of furrow from basal to distal ends
Furrow width	Greatest width of furrow
Furrow depth	Greatest depth of furrow taken from a cross-section
Ridge width	Greatest distance between adjacent ridges

Specimen preparation and examination

All spines were collected from the lower left hip area to reduce differences due to pelage variation. Spines were removed gently with a pair of fine-tipped, self-closing forceps that caused no damage to the skin or spines, rinsed in carbon tetrachloride to remove dust and residual oils and air-dried overnight. Spine length and width and width of the longitudinal furrow were measured under a dissecting microscope (Table 2). Some spines were cross sectioned with a razor blade. All spines were mounted on aluminium stubs sputter-coated with *c*. 100 nm of Au/Pd

and viewed in a Hitachi 2460N scanning electron microscope at a standard accelerating voltage and working distance. Measurements were taken of the length of the longitudinal furrow, distance between furrow ridges, depth of the longitudinal furrow and depth of the spine from the resulting electron micrographs (Table 2).

Morphometric analysis

Means and standard deviations of the 7 metric spine variables were calculated for each species. Factor analysis (SAS, 1993) was used to describe spine ultrastructure by using the fewest variables possible. Because spines varied in size and robustness owing to both species-specific differences and individual variation in body size and spine development, such variation was controlled for by dividing spine measurements by either spine length (furrow length) or spine width (remaining 6 variables). Spine length corrected for furrow length was named spine robustness. Thus, 6 spine variables were included in the factor analysis. Principal axes factoring was used and initial communalities inserted as diagonals in an initial factoring (Cureton & D'Agostino, 1983). Resulting factors were subjected to an oblique promax rotation. The number of salient factors retained for further analysis was determined from a scree plot and by calculating the critical minimum eigenvalue as $\lambda_{crit} = N^{0.6}/15$, where N is the number of raw variables (Cureton & D'Agostino, 1983). Thus $\lambda_{crit} = 0.20$. Salient factors were interpreted by examining the factor structure (correlations of the original spine variables with resulting factors). Factor means and standard errors were calculated for each *Proechimys* species group, the *Trinomys* subgenus, *H. gymnurus*, *N. fulvescens* and *M. surifer* and these mean values were plotted in factor space defined by the first 2 factors. This plot graphically depicted the distribution of each species group, subgenus, or species in factor space and assessed the use of spines as diagnostic taxonomic features.

Discriminant function analysis (SAS, 1993) was used to maximize the degree of separation among the *Proechimys* species groups. The analysis was conducted using only the size-adjusted spine measurements. Spines were then classified into species groups based on the discriminant functions and per cent correct classification was calculated for each species group. The species group *P. trinitatus* and the subgenus *Trinomys* were excluded from analysis because of small sample sizes of spines from those 2 groups.

RESULTS

Spine structure

All seven quantitative spine variables showed substantial variability both within and among species (Table 3). Despite this variability, spines of all species of *Proechimys* were superficially similar to each other and yet differed from spines of the other genera. Spines of the two murid species were the shortest and narrowest of the spines investigated. Spines from the echimyds were longer and wider, while those collected from *H. gymnurus* were the widest and longest of all.

Spine tips. The distal tips of *Proechimys* spp. (Figs 1a & 2a), *N. fulvescens* (Fig. 3a) and *M. surifer* (Fig. 4a) spines were morphologically similar both within and among species groups and gradually tapered to a very fine point of between 2 and 20 μm in width. Distal spine tips of *H. gymnurus* were different from those of all other echimyids and the murids examined and abruptly ended at a wide, blunt point (Fig. 5a).

Spine width. Spines of *Proechimys* spp. examined had maximum widths of 0.6 mm (*P. decumanus*, Fig. 1b) to 0.7 mm (*P. semispinosus*, Fig. 2b), whereas *N. fulvescens* and *M. surifer* spines were 0.4 (Fig. 3b) and 0.7 mm (Fig. 4b) wide, respectively. The long, broad *H. gymnurus* spines were *c*. 2.1 mm wide (Fig. 5b).

Spine bases. The bases of all *Proechimys* spp. spines possessed similar insertion points, both in length and width (Figs 1c & 2c). The neck of the spine narrowed rather quickly before meeting the base. By contrast, the bases of the murid spines were smaller with a longer, narrower neck (Figs 3c & 4c). The large, broad *H. gymnurus* spine bases had stout necks (Fig. 5c).

Spines in cross-section. *Proechimys* spp. spines in cross section (Figs 1d & 2d) were thicker than spines of the murid species (Figs 3d & 4d), while *H. gymnurus* spines (Fig. 5d) were the thickest of all. The internal structure (medulla) of the *Proechimys* spp. spines seemed to be of a laminate construction, while the murids had a more solid core and large lacunae at the spine margins. *Hoplomys gymnurus* spines (Fig. 5d) had a dense inner layer with a series of smaller lacunae at the spine margins and underlying the spine furrow.

Spine longitudinal furrows. The longitudinal furrows of the spines of *Proechimys* spp. (Figs 1e & 2e) and *H. gymnurus* (Fig. 5e) exhibited a similar pattern of parallel ridges – termed a terrace-band shaped cuticle by Chernova & Kuznetsov (2001). By contrast, the thin longitudinal furrows of murid spines exhibited strongly ribbed scales (Chernova & Kuznetsov, 2001) rather than a ridged pattern (Figs 3e & 4e).

Spines as diagnostic characters

Factor analysis produced two salient factors (Table 4) that were interpreted as spine depth and furrow depth and width (factor 1) and spine robustness and distance between ridges (factor 2). The plot of mean values of these two factors in factor space showed that the nine *Proechimys* species groups clustered closely together near the centre of the plot, while the other genera were widely separated (Fig. 6). Spines of species of the subgenus *Trinomys* also were distinct from the nine *Proechimys* species groups and

Table 3. Means (and standard deviations) of spine variables for each species

Species	*n*	Spine length (mm)	Spine width (mm)	Spine depth (μm)	Furrow length (mm)	Furrow width (μm)	Furrow depth (μm)	Ridge width (μm)
Hoplomys gymnurus	6	27.3 (4.3)	2.1 (0.6)	182.5 (46.6)	18.9 (4.2)	672.7 (105.5)	180.3 (42.0)	11.3 (2.3)
Maxomys surifer	6	12.3 (0.2)	0.7 (0.1)	98.0 (7.4)	11.0 (6.9)	236.0 (40.9)	200.3 (7.5)	27.6 (3.1)
Niviventer fulvescens	4	13.4 (0.6)	0.4 (0.1)	149.7 (185.5)	5.9 (5.9)	178.2 (18.5)	85.2 (11.8)	21.0 (6.2)
Proechimys [*Trinomys*] *albispinus*	1	28.0	1.0	171.0	25.0	600.0	285.0	13.1
Proechimys brevidauda	43	21.7 (1.5)	0.5 (0.1)	111.3 (27.3)	14.9 (1.5)	243.4 (73.0)	91.7 (39.4)	7.3 (2.2)
Proechimys canicollis	13	22.4 (1.3)	0.5 (0.1)	124.4 (10.1)	13.8 (0.8)	267.4 (42.7)	131.4 (59.0)	12.0 (1.6)
Proechimys chrysaeolus	1	19.0	0.4	128.0	15.5	214.0	157.0	8.5
Proechimys cuvieri	2	22.6 (1.6)	0.9 (0.1)	168.2 (38.3)	15.6 (1.3)	403.4 (54.3)	156.7 (57.2)	7.7 (1.8)
Proechimys decumanus	14	24.6 (2.0)	0.6 (0.1)	154.0 (36.3)	15.7 (1.7)	294.2 (66.9)	119.1 (48.0)	10.3 (2.9)
Proechimys goeldii	22	21.6 (2.8)	0.7 (0.2)	142.9 (39.8)	15.0 (3.6)	353.0 (99.3)	128.3 (53.3)	7.9 (1.6)
Proechimys guairae	2	15.5 (4.9)	0.3 (0.1)	102.5 (3.5)	11.0 (7.1)	121.0 (9.9)	35.5	9.3 (5.0)
Proechimys guyannensis	42	20.9 (2.5)	0.6 (0.2)	125.9 (37.8)	15.8 (2.2)	343.1 (112.5)	123.1 (64.6)	7.1 (1.5)
Proechimys [*Trinomys*] *iheringi*	2	21.2 (3.9)	0.8 (0.5)	149.5 (30.4)	18.5 (4.9)	557.0 (60.8)	228.0 (19.8)	11.9 (4.9)
Proechimys longicaudatus	9	22.2 (1.5)	0.5 (0.1)	100.9 (24.9)	14.8 (1.2)	207.0 (35.4)	89.7 (28.0)	9.3 (1.7)
Proechimys mincae	1	20.0	0.5	185.0	15.0	257.0	128.0	8.2
Proechimys ochracheous	1	20.0	6.0	142.0	16.0	257.0	114.0	10.8
Proechimys oconnelli	9	21.8 (3.7)	0.7 (0.3)	144.1 (48.9)	15.0 (0.9)	275.2 (50.0)	126.3 (41.3)	11.6 (2.3)
Proechimys semispinosus	17	23.9 (2.0)	0.7 (0.2)	174.8 (45.6)	15.8 (1.8)	344.7 (92.3)	145.1 (54.1)	8.8 (1.7)
Proechimys simonsi	13	19.0 (1.4)	0.5 (0.1)	100.2 (45.1)	13.2 (1.3)	209.7 (84.9)	87.4 (59.1)	8.2 (1.8)
Proechimys steerei	23	18.9 (1.6)	0.5 (0.1)	100.6 (29.5)	13.4 (1.5)	210.4 (64.6)	80.3 (47.3)	7.2 (1.9)
Proechimys trinitatus	1	21.0	0.5	114.0	22.0	194.0	100.0	5.4
Proechimys urichi	1	23.0	0.6	142.0	14.0	342.0	185.0	9.1

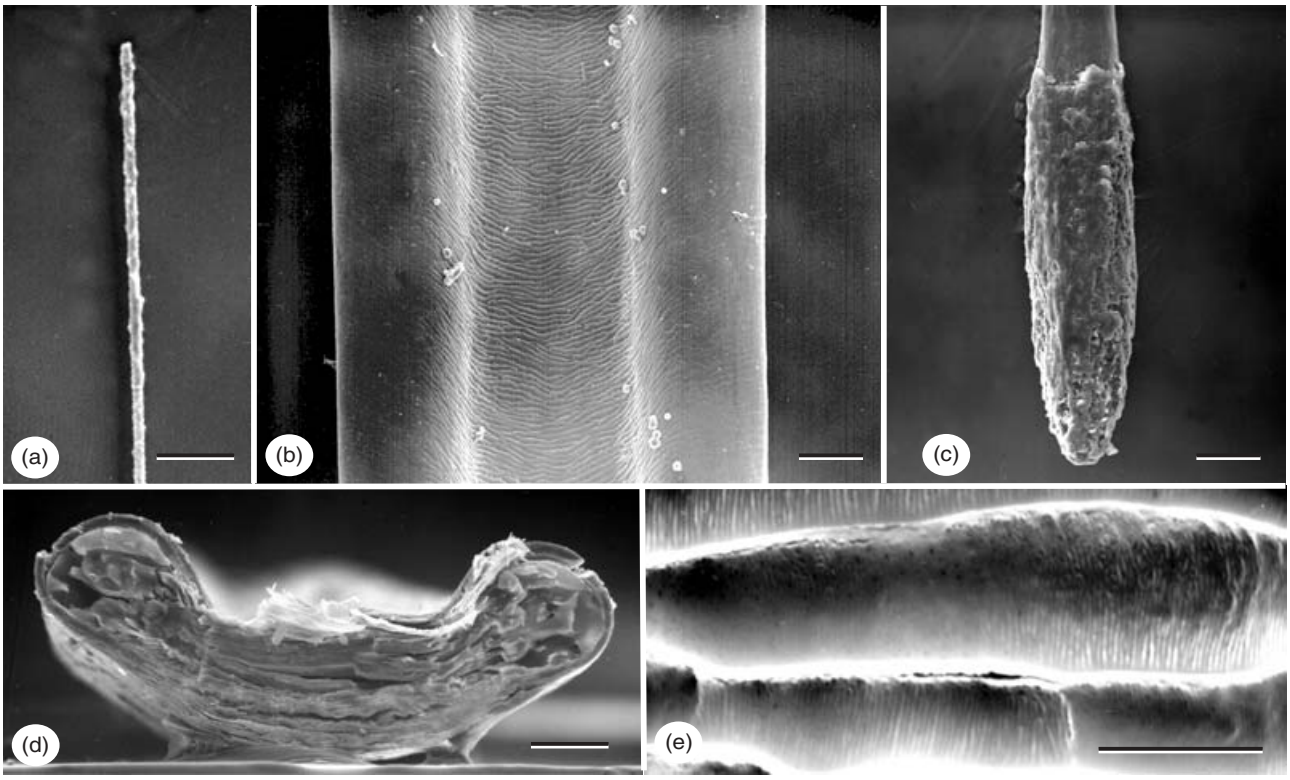

Fig. 1. Architecture of *Proechimys decumanus* spines: (a) tip; (b) medial view of spine showing logitudinal furrow; (c) base; (d) spine in cross section; (e) furrow ridges. Scale bars: (a)–(d) 100 μm; (e) 10 μm.

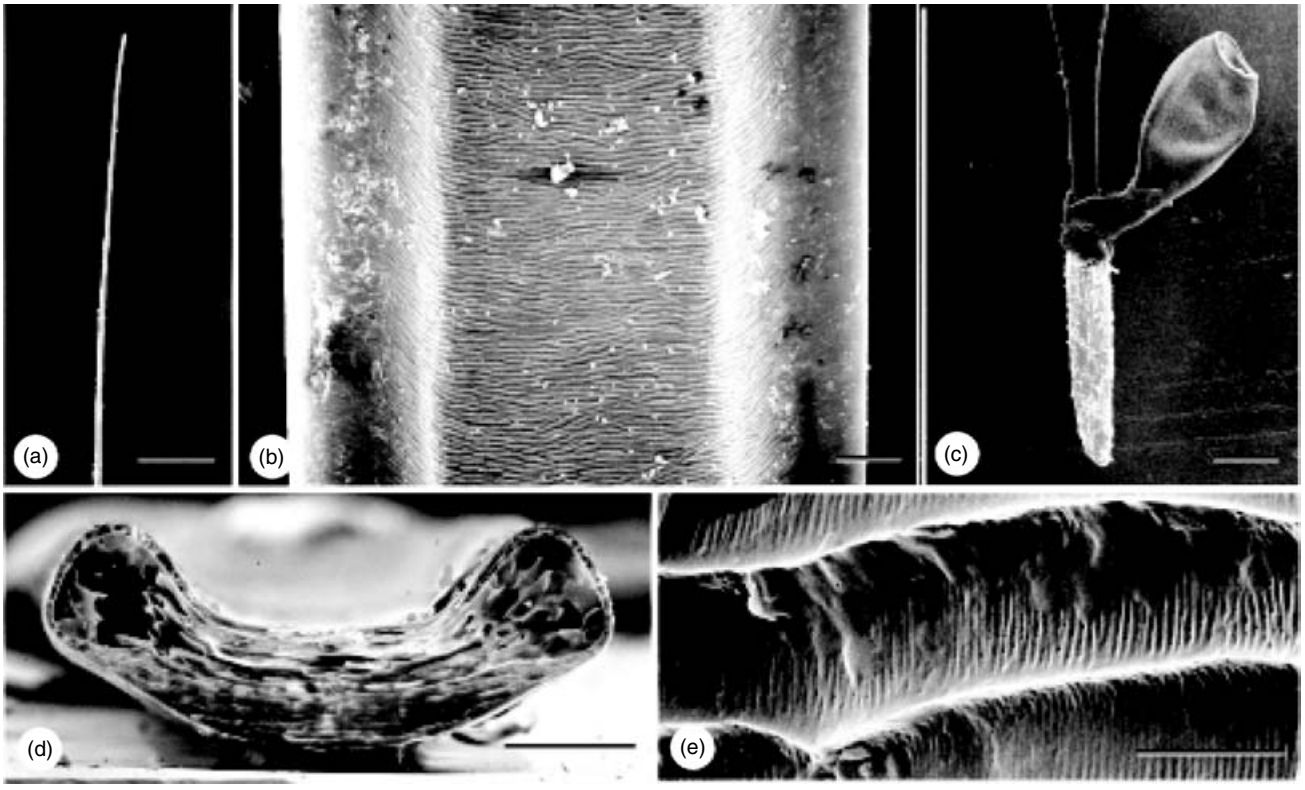

Fig. 2. Architecture of *Proechimys semispinosus* spines: (a) tip; (b) medial view of spine showing longitudinal furrow; (c) base; (d) spine in cross section; (e) furrow ridges. Scale bars: (a)–(d) 100 μm; (e) 10 μm.

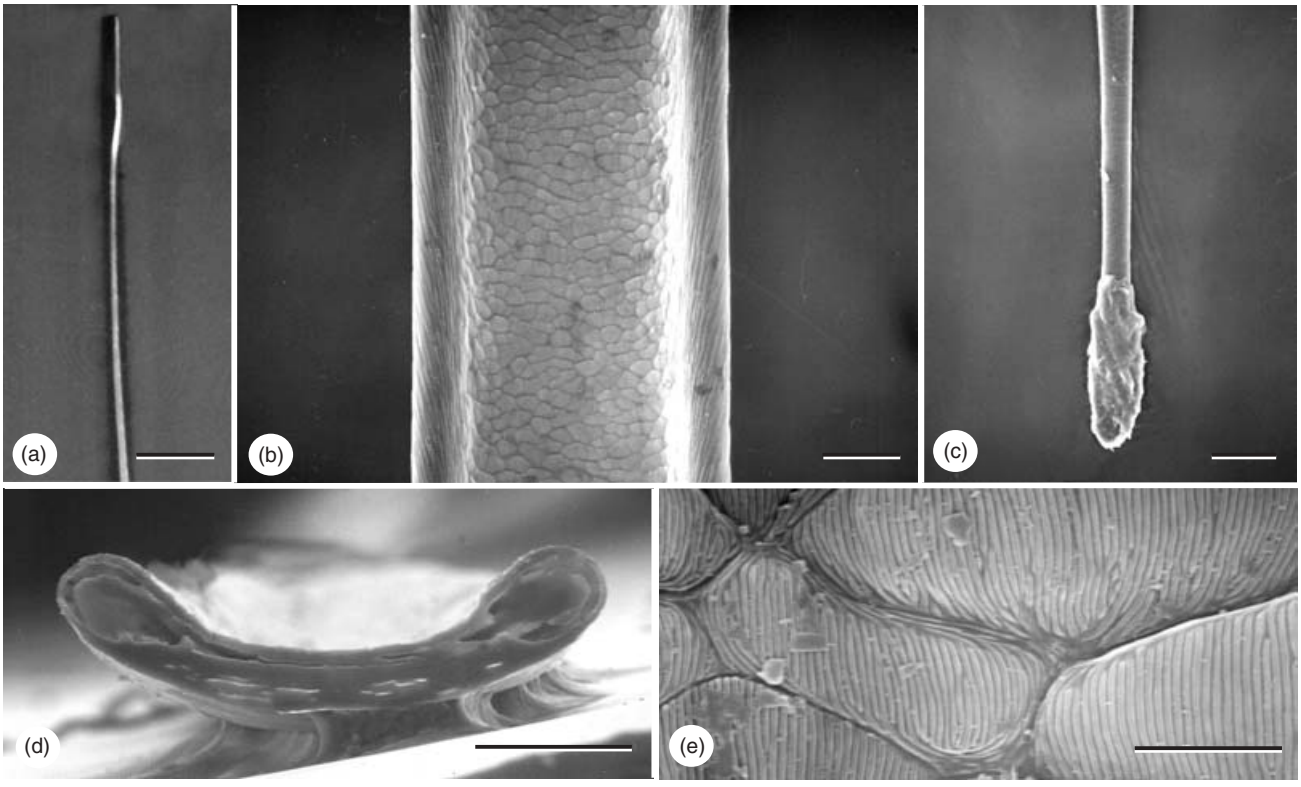

Fig. 3. Architecture of *Niviventer fulvescens* spines: (a) tip; (b) medial view of spine showing longitudinal furrow; (c) base; (d) spine in cross section; (e) furrow ridges. Scale bars: (a)–(d) 100 μm; (e) 10 μm.

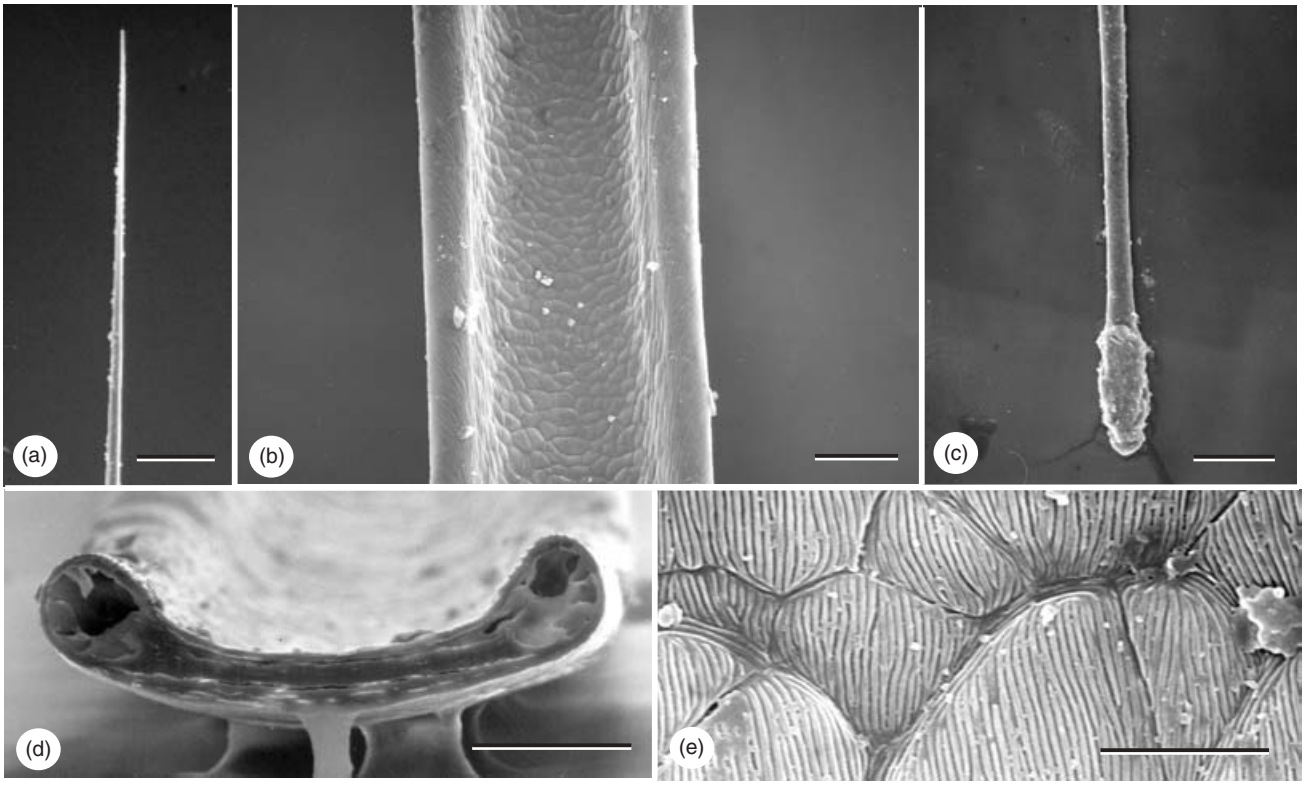

Fig. 4. Architecture of *Maxomys surifer* spines: (a) tip; (b) medial view of spine showing longitudinal furrow; (c) base; (d) spine in cross section; (e) furrow ridges. Scale bars: (a)–(d) 100 μm; (e) 10 μm.

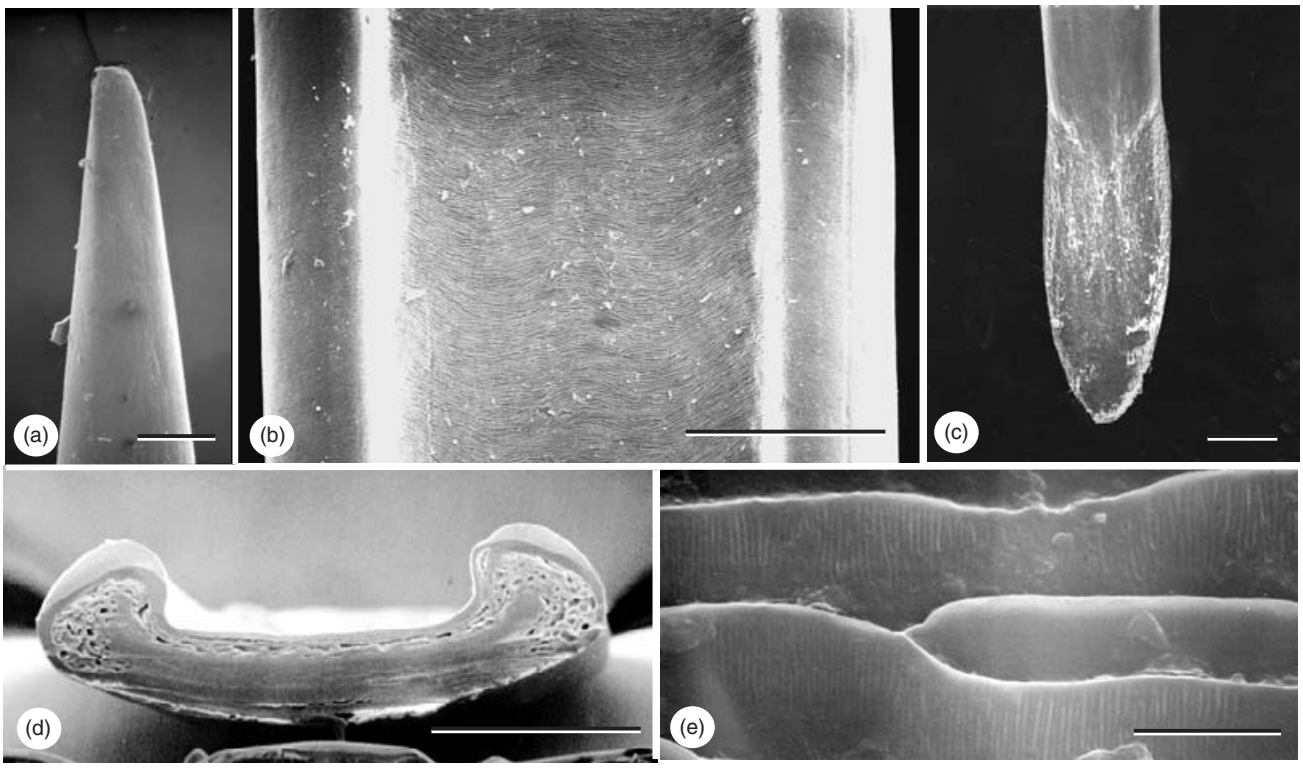

Fig. 5. Architecture of *Hoplomys gymnurus* spines: (a) tip; (b) medial view of spine showing longitudinal furrow; (c) base; (d) spine in cross section; (e) furrow ridges. Scale bars: (a) 250 μm; (b)–(d) 500 μm; (e) 10 μm.

Table 4. Factor loadings resulting from a factor analysis of spine metric variables. Variation in spine size was controlled by dividing spine measurements by either spine length (furrow length) or spine width (remaining variables). Spine length divided by furrow length was named spine robustness

Variable	Factor 1	Factor 2
Spine robustness	0.35	0.57
Furrow width	0.58	0.28
Distance between ridges	0.40	0.52
Spine depth	0.61	0.49
Furrow length	−0.04	−0.28
Furrow depth	0.61	0.22
Eigenvalue	1.38	1.03

Table 5. Correct classification (%) of spines into *Proechimys* species groups derived from discriminant function analysis

Species group	Correct classification
P. canicollis	84.62
P. cuvieri	77.27
P. decumanus	21.43
P. goeldii	20.00
P. guyannensis	61.90
P. longicaudatus	40.38
P. semispinosus	26.92
P. simonsi	15.38

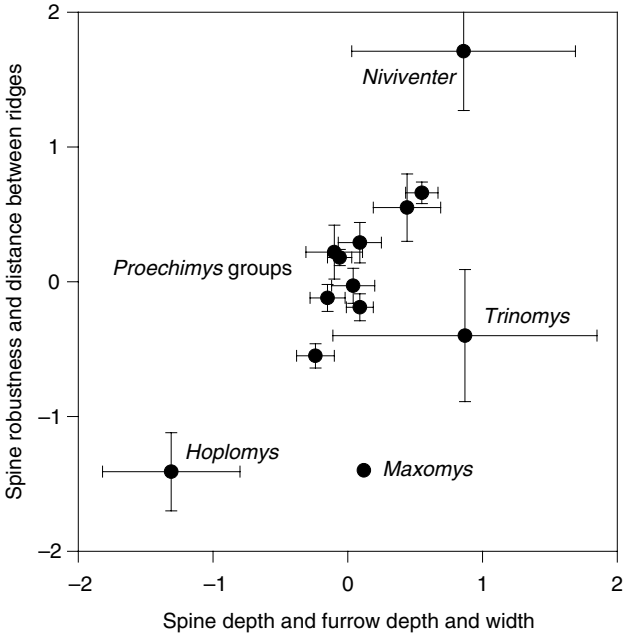

Fig. 6. Plot of mean factor scores (with error bars) of spines of *Niviventer fulvescens*, *Maxomys surifer, Hoplomys gymnurus*, subgenus *Trinomys* and nine species groups of *Proechimys* in factor space defined by the first two factors derived from factor analysis of spine measurements.

differed along factor 1 (spine depth and furrow depth and width).

Discriminant function analysis correctly classified spines into species groups ranging from only 15.38% to 84.62%; < 50% of spines from five out of eight species groups were correctly classified (Table 5).

DISCUSSION

Spines confer an obvious adaptive advantage to species such as porcupines (Hystricidae and Erethizontidae) that are well-protected against predators. However, the function of spines of species in other families (Heteromyidae, Muridae and Echimyidae) is unkown. Spines of species in those families are insufficiently rigid to provide much protection against predators and a wide variety of predators, including snakes, birds and mammals, are known to prey heavily on many spinous species. It has been suggested that spines may protect rodents against rain, thus keeping insulating and guard hairs dry (e.g. Lekagul & McNeely, 1977). Indeed, *H. gymnurus* has the largest and best-developed spines among the echimyids and this species is among the most abundant rodents in the wettest lowland forests of the Neotropics (e.g. Gonzales-M. & Alberico, 1993; Tomblin & Adler, 1998).

Spines of all examined species of *Proechimys* were qualitatively similar and had similar tips, longitudinal furrows and insertion points. The ridge structure within the longitudinal furrows was also similar. Spines of *H. gymnurus*, although considerably more robust than those of *Proechimys* spp., were also qualitatively similar. The only major difference was evident at the tip, where the spines of *H. gymnurus* tapered abruptly to a blunt point, while those of *Proechimys* spp. tapered gradually to a very fine point. By contrast, the spines of the two murid species were qualitatively different from those of echimyids, having a scaled rather than ridged longitudinal furrow and an extremely fine tip that tapered abruptly. These differences suggest an origin of echimyid spines that was independent of murid spines.

Spines of the studied taxa were so distinct that they were easily differentiated at the generic level. Spines of the murid taxa were both qualitatively and quantitatively distinct from the echimyid taxa, while spines of *H. gymnurus* were quantitatively distinct from those of *Proechimys* spp. Although such differences are interesting from an evolutionary standpoint, they provide little systematic use because those genera are distinguished quite readily by other gross morphological criteria such as body and tail measurements and cranial and dental characters. However, sufficient material may not be available in some ecological studies such as analysis of carnivore diets based on scats. In such cases, spines may provide a useful means by which different syntopic genera may be distinguished.

Within the genus *Proechimys*, spines were qualitatively similar, but those of species in the subgenus *Trinomys* were sufficiently distinct quantitatively to separate those species from species of the subgenus *Proechimys*. In particular, spines of the *Trinomys* species were separated from all other *Proechimys* spp. in the factor analysis, despite their qualitative similarities, by having a relatively greater spine depth and furrow depth and width. Thus, spines may serve as diagnostic characters to separate *Proechimys* at the subgeneric level, particularly when used in concert with cranial, molar and bacular characters. However, multivariate analysis generally failed to find systematic differences that could serve as diagnostic features within the subgenus *Proechimys*, even among species groups. Discriminatory power of spines was so poor at the level of species groups within that subgenus that no further analyses to discriminate among individual species were conducted. If spines possess systematic use at the level of individual species within the subgenus *Proechimys*, a more robust analysis that incorporates additional quantitative measurements will be necessary.

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