

MICROSTRUCTURE OF THE ENAMEL OF THE INCISORS OF SOME CTENOMYID AND OCTODONTID RODENTS (RODENTIA, CAVIOMORPHA).

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ABSTRACT: The microstructure of the enamel of incisors of the rodent families Ctenomyidae and Octodontidae was investigated using scanning electron microscopy. Specimens of *Ctenomys azarae*, *C. australis*, *C. talarum*, *C. mendocinus*, *Tympanoctomys barrerae*, and *Actenomys* sp. were examined in order to establish a relationship between structure of the enamel, dental morphology, and habitat. The results indicated a relation between soil texture and the external enamel layer (EE). No correlation was found between the slope of the Hunter-Shreger Bands (HSB) and incisor function. A greatest slope of the HSB grants an increment to the resistance to cracks; probably the invasion of interprismatic material of the EE layer could contribute to this reinforcement. For some species of *Ctenomys*, the structure of the enamel supports previous statements about its use as digging tools.

RESUMEN: Microestructura del esmalte de los incisivos de algunos Octodontidos y Ctenomidos (Rodentia, Caviomorpha). Los incisivos de los roedores constituyen los órganos adaptativos más destacados del orden. La utilización del MEB permite investigar detalles de la microestructura del esmalte que muestran adaptaciones a los diferentes requerimientos biomecánicos. Las bandas de Hunter-Shreger (HSB) representan el único modelo presente en los mamíferos para fortalecer el esmalte; la microestructura del mismo varía en función de los distintos patrones en la disposición de los prismas de hidroxiapatita. Hasta ahora no se han realizado investigaciones sobre la estructura del esmalte de los incisivos en los integrantes de la familia Octodontidae. En el presente trabajo se adelantan algunas observaciones realizadas en *Ctenomys azarae*, *C. australis*, *C. talarum*, *C. mendocinus*, *Tympanoctomys barrerae* y *Actenomys* sp., para establecer la posible vinculación entre la estructura del esmalte, la morfología dentaria, el hábitat y la modalidad excavatoria de estos animales. De los resultados obtenidos se desprende una relación directa entre la textura del suelo y el grosor de la capa de esmalte externo, corroborando para el caso de algunas especies de *Ctenomys*, que la estructura del esmalte les permite utilizar los incisivos para la construcción de sus galerías.

Key words: Octodontidae, Ctenomyidae, incisors, enamel, microstructure.

Palabras clave: Octodontidae, Ctenomyidae, incisivos, esmalte, microestructura.

INTRODUCTION

The structure of the enamel of mammalian teeth has been of interest to researchers of dental morphology, and has been oriented primarily towards descriptive works that have

been used to investigate systematic and phylogenetic relationships. (Tomes, 1850; Escala and Gallego, 1977). The scanning electron microscope (SEM), allows a more detailed investigation of the microstructure of the

enamel, showing different biomechanical adaptations to the stress they are exposed to (Flynn et al, 1987; Koenigswald, 1986). Koenigswald (1985) defined the inner enamel layer (IE) as composed of one to several prisms, the Hunter-Schreger Bands (HSB) which decussate, and the outer portion (EE) as that one made up of radial enamel. In the latter, the prisms are straight or slightly curved, but never intercross.

The HSB are the only structural elements known in mammals which strengthen the enamel layer. The variation observed in the microstructure is a result of the arrangement of the hydroxiapatite rods. In the most primitive type, radial enamel, the rods are straight and markedly slanted with respect to the enamel-dentin (ED) border line. This arrangement which provides resistance to wear but susceptibility to cracks, is found in Taeniola-boid Multituberculates, Apatemids, and Hyracoids. A second type corresponds to a disposition of the radial enamel in the EE, where the prisms are parallel. The third type in which the prisms are parallel and decussate in the IE is found primarily in mammals with hypsodont incisors.

Finally, the enamel of the incisors may group in packages that intercross, appearing in the outermost layer, as seen in the molariform teeth of the proboscideans.

Incisors are the most conspicuous adaptive organs of the Order Rodentia (Flynn and Wahlert, 1978), since they are used in food gathering, biting, gnawing, and in some species, digging tunnels and burrows (Dubost, 1968).

The families Octodontidae and Ctenomyidae include a relatively small group of related autochthonous and endemic South American hystricognaths, which are partially scansorial to strictly subterranean (Reig, 1981, 1986). Both are known from the Oligocene. The Ctenomyidae includes the extant genus *Ctenomys*. The family Octodontidae contains six extant genera, *Octomys*, *Octodontomys*, *Spalacopus*, *Tympanoctomys*, *Octodon*, and *Aconaemys*. Among the extinct genera, *Actenomys* (family Ctenomyidae) is widely represented in Pliocene sediments and has

been proposed as an ancestor of *Ctenomys*. The latter, with numerous living species, is endemic to South America south of 15° S, is fossorial and has strict preferences regarding the soil type where it digs its burrows (Contreras and Reig, 1965; Comparatore et al., 1992).

The monotypic genus *Tympanoctomys* has a distribution restricted to the arid regions of central Argentina (Justo et al., 1985; Ojeda et al, 1989). Like the other living octodontids, it is known only by the extant taxa.

We present some observations made for *C. azarae*, *C. australis*, *C. talarum*, and *C. mendocinus*. In order to evaluate the possible link between enamel structure, dental morphology, and the habits of these rodents, comparisons were made with *Tympanoctomys barrerae* and *Actenomys* sp.

MATERIALS AND METHODS

Sections of teeth were prepared following the guidelines of Flynn and Wahlert (1978), with the exception that carborundum powder and water sandpapers were used.

Sections were photographed, using the SEM, at 200x, 350x, 500x, 750x, 1000x, and 2000x magnifications. Photomicrographs where the enamel and dentin layers were seen most clearly were selected. Demarcation lines were drawn between the EE and IE layers, external border, and EE-IE boundary and ED joint; lines perpendicular to these and the axes of each enamel band also were drawn. Over these lines, measures of the band width of EE, IE, and the inclination bands were taken following García et al. (1975). All materials are deposited at the Cátedra de Anatomía Comparada, Museo de La Plata.

RESULTS

Ctenomys talarum: Measurements were taken on photomicrograph 3616 (Fig. 1a, 200x), fitting on the frame a section where a complete band is recognized. Band slope was measured from photomicrograph 3621 (750x). At this magnification the radial prism of enamel of the EE layer is seen; at 1000x (in photo 4803), details of the interprismatic

framework are observed.

Ctenomys australis: (Fig. 1b, photomicrograph 4807, 500x) The ED border is absent or obsolete; thus IE was not measured. Also not observed is the radial deposition of the enamel prism.

Ctenomys azarae: (Fig. 1c; photomicrograph 4801, 350x). In photomicrographs 4800 and 4802 (Fig. 2a), the prisms of enamel seen in the EE layer are oblique relative to the surface because the photograph was taken at the distal extreme of the incisor. At 2000x, photomicrograph 4799 (Fig. 2b), the interprismatic material and the hollow prisms of enamel corresponding to a HSB are seen.

Ctenomys mendocinus: Measurements were taken on photomicrograph 3614 (Fig. 2c; 200x). HSB slope was not recorded. At 750x (photo 3615) the radial disposition of the prisms can be seen in the EE layer.

Actenomys sp.: (Fig. 3a; photomicrograph 3613, 200x). At a magnification of 750x (photo 4805) the oblique prism in the EE layer is observed, and at 1000x (photo 4805), the inclination of the bands were measured (Fig. 3b).

Tympanoctomys barrerae: Microphotographs could not be taken in the sagittal plane; only the radial disposition of the enamel prisms is indicated. The slope was measured at 1000x (Fig. 3c; photomicrograph 4808).

DISCUSSION

A number of investigators (e.g. Flynn et al., 1987; Buza-Stephens and Dalquist, 1991) have suggested that one must use enamel microstructure cautiously in determining phylogeny. Alternatively, Martin (1993) proposed that enamel microstructure is an effective tool for assessing phylogenetic relationships among rodents.

Coincidence exists about the ecological adaptation of enamel structure, indicating that enamel thickness itself is beneficial for digging. Development of two layers in the outer enamel may reflect a digging function (Flynn et al., 1987).

The spatial distribution of subterranean ro-

dents reflects the texture of the soil. For example, species of *Ctenomys* inhabiting the same region show a differential use of the soils. Contreras and Reig (1965) studied populations of *C. australis* and *C. talarum* along the coast of Buenos Aires Province. *C. australis* inhabited the coastal dunes while *C. talarum* was found on the firmer inland soils with abundant vegetation. *C. australis* is the largest species examined in our study. *C. talarum* is the smallest, with a slender appearance.

Ctenomys azarae, *C. talarum* in La Pampa, and *C. mendocinus* in Mendoza follow a similar distribution pattern based on soil type and the size of the species. *C. talarum* lives in soils with a superficial obscure horizon containing a considerable amount of organic matter, a relatively compact texture, and that support an underlying horizon with calcareous materials, brunizem or molisols (Justo, 1992).

The typical vegetation of this area (La Pampa), "caldenal", is composed of *Prosopis caldenia* on the lower areas, slopes, and grassy plain ranges. Meanwhile, *C. azarae*, lives in poor soils. The parental materials are only slightly altered and are of poor structure; the soil is sandy, without calcareous horizon, from the orders of the regosols or entisols. The vegetation of this area is composed by psamophitic grassland species.

Ctenomys mendocinus lives in arid regions of central and western Argentina, mainly in the phytogeographic province known as the Monte. The prevailing soils are aridisols; the principal plants are low scrubs and hard grasses.

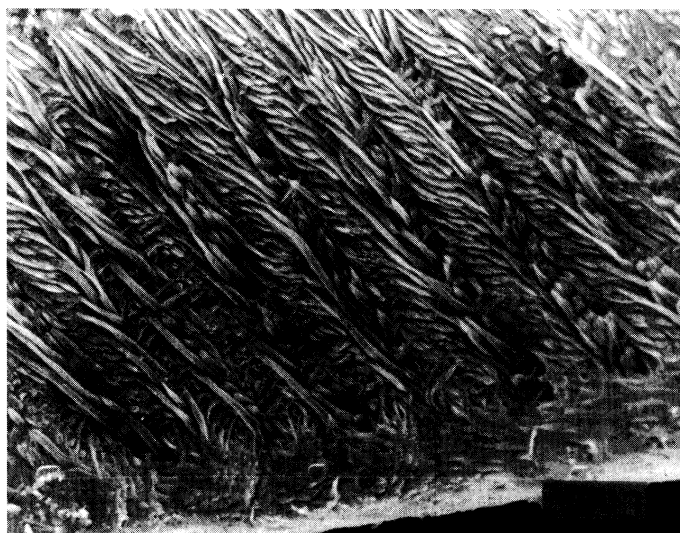
A relationship between the texture of the soil and the width of the EE layer can be seen from the data presented in Table 1. This correlation also is reflected in the values derived from the respective EI indexes.

It is generally assumed that *Ctenomys* digs exclusively with the forelegs. Hickman (1985) observed the digging behavior (especially surface-mound formation) of *Ctenomys fulvus*.

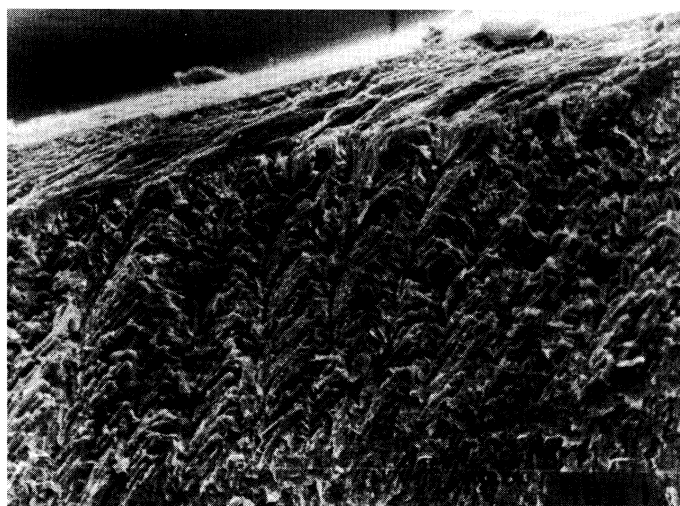
The use of the incisors as a secondary digging instrument by *Ctenomys* is mentioned



a)



b)



c)

Fig. 1: Teeth sections photographed using the SEM of the Museo de La Plata. a) *Ctenomys talarum*: (photogram 3616, 200x). b). *Ctenomys australis*: (photogram 4807, 500x). c) *Ctenomys azarae*: (photogram 4801, 350x).

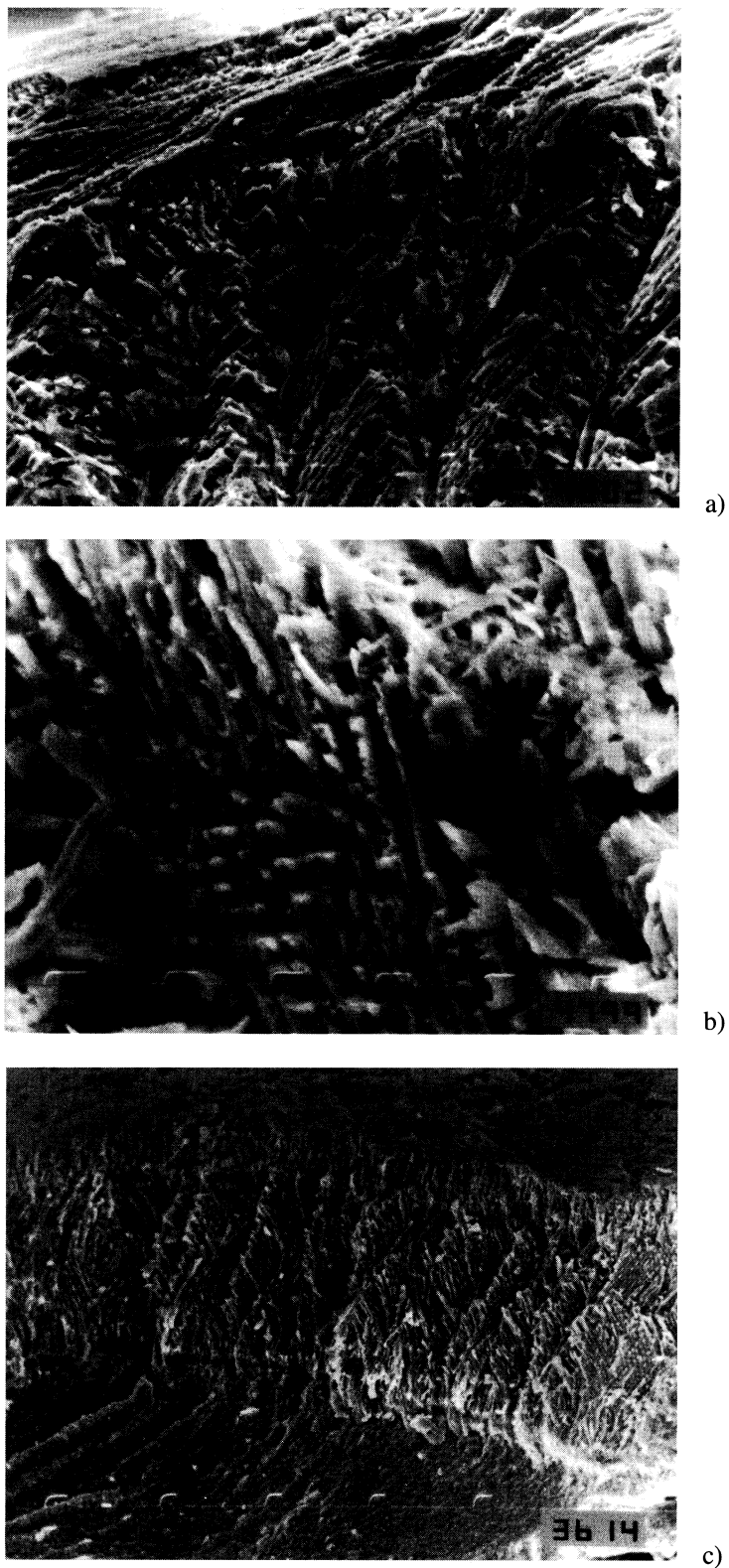
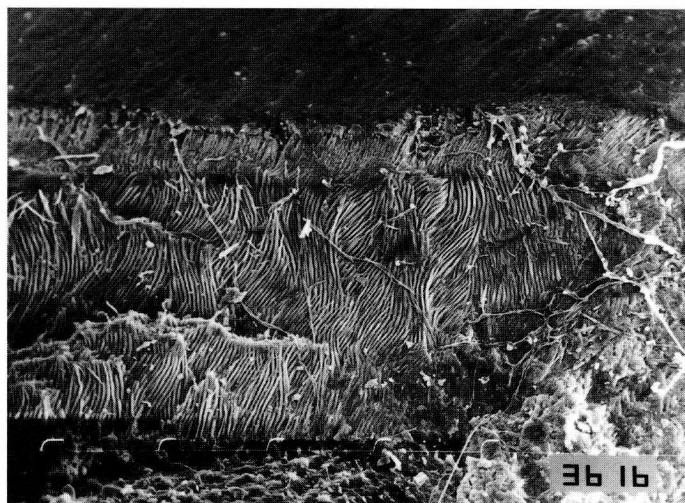
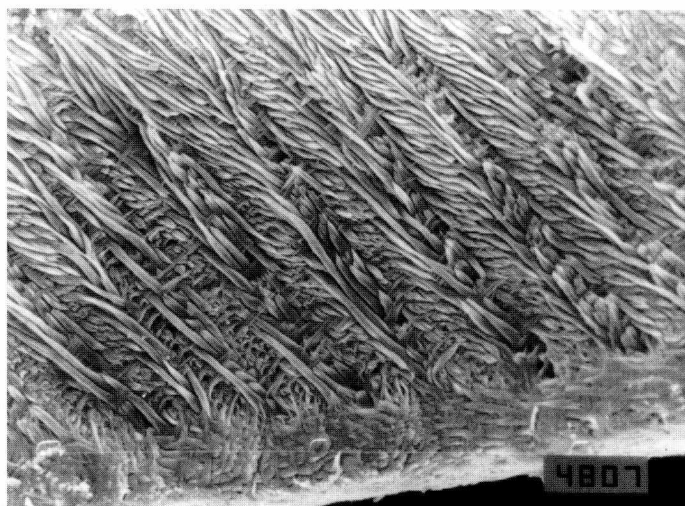


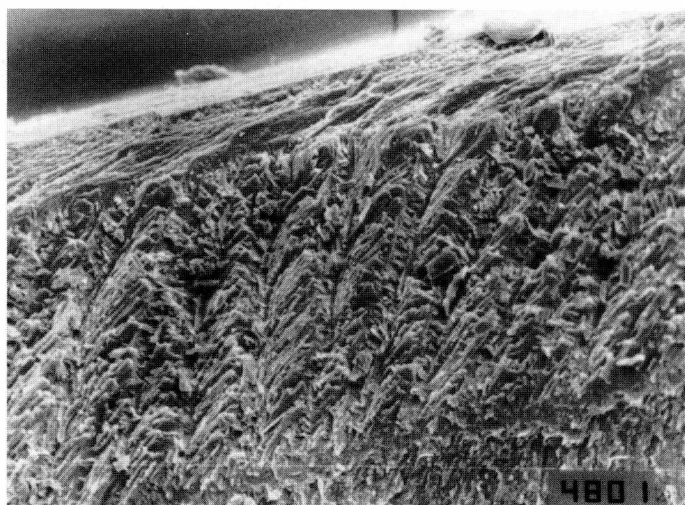
Fig. 2: Teeth sections photographed using the SEM of the Museo de La Plata. a) *Ctenomys azarae*: the prisms of enamel are seen in the EE layer oblique to the surface. b) *Ctenomys azarae*: (2000x, photo 4799). c) *Ctenomys mendocinus*: (photogram 3614; 200x).



a)



b)

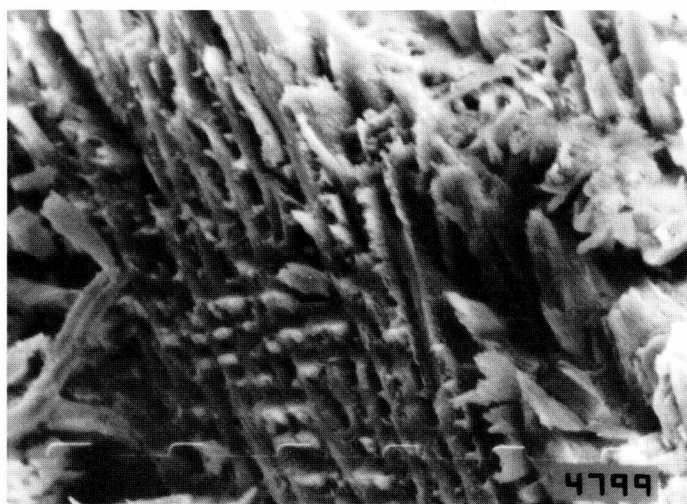


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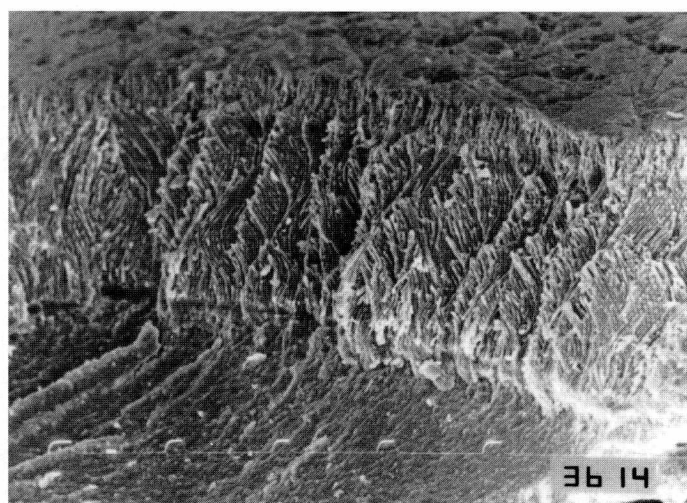
Fig. 1: Teeth sections photographed using the SEM of the Museo de La Plata. a) *Ctenomys talarum*: (photogram 3616, 200x). b). *Ctenomys australis*: (photogram 4807, 500x). c) *Ctenomys azarae*: (photogram 4801, 350x).



a)

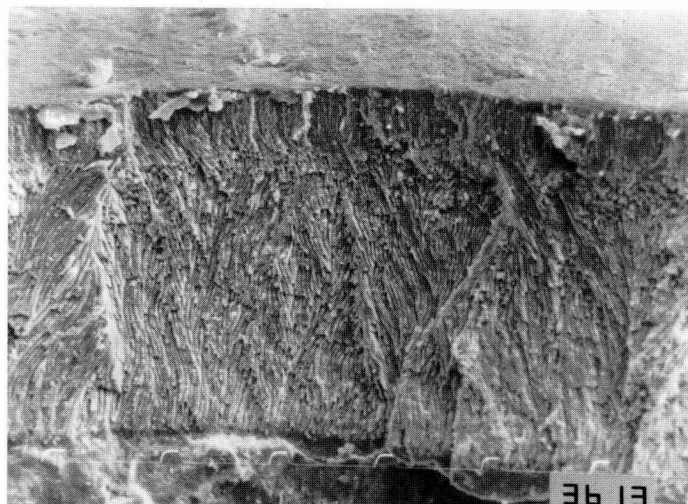


b)

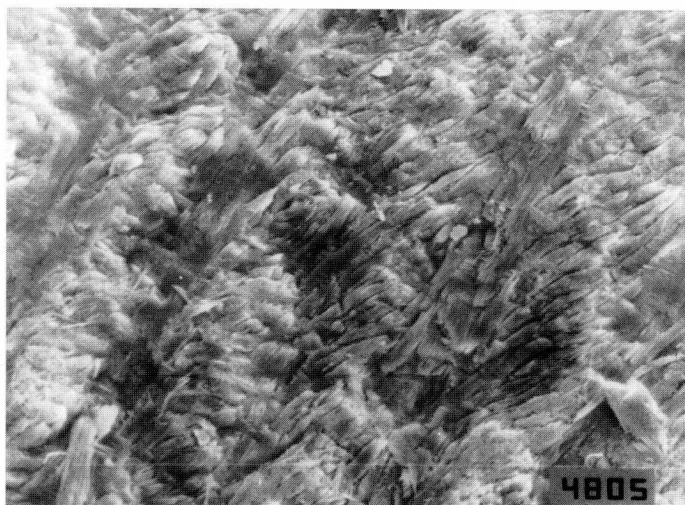


c)

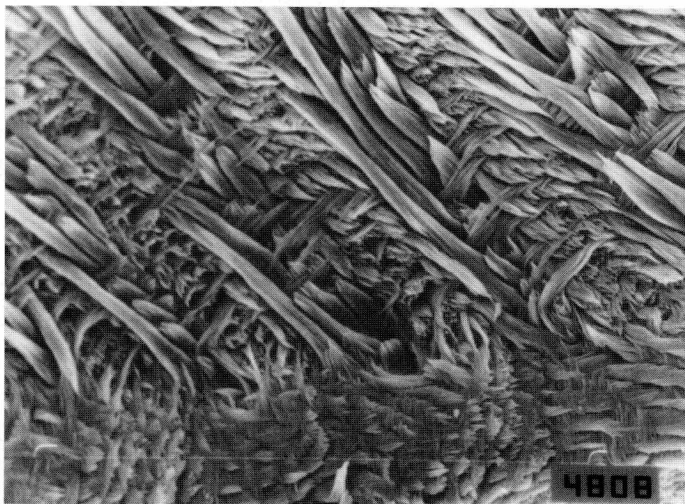
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a)



b)



c)

Fig. 3: Teeth sections photographed using the SEM of the Museo de La Plata. a) *Actenomys* sp.: (photogram 3613; 200x). b) *Actenomys* sp.: (photogram 4805; 1000x). c) *Tympanoctomys barrerae*: (photograph 4808; 1000x).

by De Santis (1986) and Altuna et al. (1993). Like the North American pocket gophers (*Thomomys*, *Geomys*, and *Crateogeomys*), all have forelegs with well developed claws, different grades of pelvic morphology (Lessa, 1993) and a two-layered enamel ultrastructure.

Beyond other functional considerations, we suggest that the enamel microstructure in the species of *Ctenomys* studied allows us to corroborate the use of incisors as digging tools.

The HSB does not permit the propagation of the superficial cracks in the enamel while increasing the resistance to forces acting over it. Of the six species studied, four show HSB slanting from right to left, two of them inversely. No relationship could be demonstrated between band slope and function, although stress resistance may be enhanced by increasing the slope of the prisms. In *Tympanoctomys barrerae* and *C. australis* the slope is significantly lower than in the other species studied (Table 1).

A greater HSB slope grants an increment to the resistance to cracks. The invasion of interprismatic material in the EE layer (Fig. 1b, 4809 and 4807) could contribute to this reinforcement. Reig (1970), Reig et al. (1990), Reig and Quintana (1992) compared *Ctenomys leucodon* with *Eucelophorus chapadmalensis* and *Spalacopus cyanus* (Molina). They suggested that the prominent procumbent incisors seen in the three genera reflected their

excavatory-teeth habits.

The comparison between *Actenomys*, *Tympanoctomys*, and *Ctenomys*, allowed us to establish that although they show a diverse grade of procumbency, these genera share a similar arrangement of the enamel bands in the incisors, allowing their use as digging tools.

These observations are similar to those made by Reig et al. (1990) and Lessa (1993) about the secondary function of the incisors in these rodents.

We conclude that, in addition to the biomechanical characteristics found in the enamel layers of incisors, in the ctenomyid and octodontid species these teeth studied may be used as complementary tools for excavation and transport, and possibly in moving obstacles in the tunnels.

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Table 1: Incisor Enamel and Features of the studied species and type of soils where the species live. EE (outer enamel layer); IE (inner enamel layer); EI (enamel index) and the Hunter- Schreger Bands (HSB).

Species	EE width	EE/IE	IE width	EE+IE	EI width	HSB slope	soil type
<i>C. australis</i>	33.33	—	—	—	—	60	entisol
<i>C. azarae</i>	37.50	19.73	190	227.50	16.8	72	entisol
<i>Tympanoctomys</i>	41.83	—	—	—	—	40-45	aridisol
<i>C. mendocinus</i>	58.93	23.63	249.33	308.26	19.1	—	aridisol
<i>Actenomys</i>	47.06	23.28	330.93	408.02	18.8	68-73	—
<i>C. talarum</i>	81.60	26	312.80	394.40	20.6	74-75	molisol

LITERATURE CITED

- ALTUNA, C.A., G. IZQUIERDO and B. TASSINO. 1993. Análisis del comportamiento de excavación en dos poblaciones del complejo *Ctenomys pearsoni* (Rodentia: Octodontidae). Boletín de la Sociedad de Zoología del Uruguay, 2a. época, 8:275-282.
- BUZAS-STEPHENS, P. and W. DALQUAST. 1991. Enamel ultrastructure of incisors, premolars and molars in *Thomomys*, *Cratogeomys* and *Geomys* (Rodentia: Geomyidae). The Texas Journal Science, 43(1):65-74.
- COMPARATORE, V.M., M. AGNUSDEI and C. BUSCH. 1992. Habitat relations in sympatric populations of *Ctenomys australis* and *Ctenomys talarum* (Rodentia, Octodontidae) in a natural grassland. Zeichrift Saugetierkunde, 57:47-55.
- CONTRERAS, J.R. and O.A. REIG. 1965. Datos sobre la distribución del género *Ctenomys* (Rodentia, Octodontidae) en la zona costera de la provincia de Buenos Aires comprendida entre Necochea y Bahía Blanca. Physis xxv, (69):169-186.
- DE SANTIS, L.J.M. 1986. Estudio comparado del aparato masticatorio de los Ctenomyinae (Rodentia, Octodontidae) fósiles y vivientes. Tesis Doctoral de la Universidad Nacional de La Plata, 64 pp., 100 lám.
- DUBOST, G. 1968. Les mammiferes souterrains. Revue d'Ecologie et Biologie du Sol, 5:99-197.
- ESCALA, M. and L. GALLEGGO. 1977. Systematic usefulness of lower incisor enamel in Muridae (Rodentia). Journal of Mammalogy, 58(1):25-31.
- FLYNN, L. and J. WAHLERT. 1978. SEM study of rodent incisors: preparation and viewing. Curator 21 (4):303-310.
- FLYNN, L.J., E. NEVO and G. HETH. 1987. Incisor enamel microstructure in blind mole rats: adaptive and phylogenetic significance. Journal of Mammalogy, 68(3):500-507.
- GARCIA, M., M. ESCALA and L. GALLEGGO. 1975. Microestructura del esmalte en los incisivos de Roedores. I. Variaciones con la edad. Doñana Acta Vertebrata, 2(2):241-252.
- HICKMAN, G.C. 1985. Surface-mound formation by the Tuco-tuco, *Ctenomys fulvus* (Rodentia: Ctenomyidae), with comments on earth-pushing in other fossorial mammals. Journal of Zoology, London, (A) 205:385-390.
- JUSTO, E. 1992. *Ctenomys talarum occidentalis*: una nueva subespecie de tuco-tuco (Rodentia: Octodontidae) en La Pampa. Neotrópica, 38(99):35-40.
- JUSTO, E., C. MONTALVO and L. DE SANTIS. 1985. Nota sobre la presencia de *Tympanoctomys barrerae* (Lawrence, 1941) en La Pampa. Historia Natural, 5(28):243-244.
- KOENIGSWALD, W. VON. 1985. Evolutionary trends in the enamel of rodent incisors. In: Evolutionary relationships among rodents: a multidisciplinary analysis (W. Luckett and J. Hartenberger, eds.) Plenum Press, pp. 403-442.
- KOENIGSWALD, W. VON. 1986. Enamel modification in enlarged front teeth among mammals of the various possible reinforcements of the enamel. In: Teeth revisited. Proceeds of the VII International Symposium of Dental Morphology, Memory Museum Natural History, Paris C, 53:147-167.
- LESSA, E. 1993. Patrones de evolución morfológica en roedores subterráneos americanos. Boletín de la Sociedad de Zoología del Uruguay, 2a. época, 8:37-46. Martin, T., 1993. Early Rodent Incisor Enamel Evolution: Phylogenetic Implications. Journal Mammalian Evolution, 1(4):227-254.

- MARTIN, T. 1993. Early rodent incisor enamel evolution: phylogenetic implication. *Journal of Mammalian Evolution*, 1:227-254.
- OJEDA, R.A., V. ROIG, E. CRISTALDO and C. DE MOYANO. 1989. A new record of *Tympanoctomys* (Octodontidae) from Mendoza Province, Argentina. *The Texas Journal of Science*, 41(3):333-336.
- REIG, O.A. 1970. Ecological notes on the fossorial, octodont rodent *Spalacopus cyanus* (Molina). *Journal of Mammalogy*, 51:592-601.
- REIG, O.A. 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Museo Municipal de Ciencias Naturales "Lorenzo Scaglia". *Monographie Naturae*, 1:1-162.
- REIG, O.A. 1986. Diversity patterns and differentiation of high Andean rodents. *In: High altitude tropical biogeography* (I.Villeumer and M.Monasterio, eds.) Oxford University Press, pp. 404-439.
- REIG, O.A., C. BUSCH, M. ORTELLS and J. CONTRERAS. 1990. An overview of evolution, systematics, population biology and speciation in *Ctenomys*. *In: Evolution of Subterranean Mammals at the Organismal and Molecular Level* (E. Nevo & O.A. Reig, eds.). A.R. Liss, New York, pp. 71-96.
- REIG, O.A. and C. QUINTANA. 1992. Fossil Ctenomyine rodents of the Genus *Eucelophorus* (Cavimorpha: Octodontidae) from the Pliocene and Early Pleistocene of Argentina. *Ameghiniana*, 29(4):363-380.
- TOMES, J. 1850. On the structure of the dental tissues of the Order Rodentia. *Philosophical Transactions of the Royal Society, London*, pp. 529-567.