

Adaptive diversity of incisor enamel microstructure in South American burrowing rodents (family Ctenomyidae, Caviomorpha)

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Abstract

The aim of this study was to analyse the morphofunctional and adaptive significance of variation in the upper incisor enamel microstructure of South American burrowing ctenomyids and other octodontoid taxa. We studied the specialized subterranean tooth-digger †*Eucelophorus chapalmensis* (Pliocene – Middle Pleistocene), and compared it with other fossil and living ctenomyids with disparate digging adaptations, two fossorial octodontids and one arboreal echimyid. Morphofunctionally significant enamel traits were quite similar among the species studied despite their marked differences in habits, digging behaviour and substrates occupied, suggesting a possible phylogenetic constraint for the Octodontoidea. In this context of relative similarity, the inclination of Hunter–Schreger bands, relative thickness of external index (EI) and prismless enamel zone were highest in †*Eucelophorus*, in agreement with its outstanding craniomandibular tooth-digging specialization. Higher inclination of Hunter–Schreger bands reinforces enamel to withstand high tension forces, while high external index provides greater resistance to wear. Results suggest increased frequency of incisor use for digging in †*Eucelophorus*, which could be related to a more extreme tooth-digging strategy and/or occupancy of hard soils. Higher external index values as recurring patterns in distant clades of tooth-digging rodents support an adaptive significance of this enamel trait.

Key words Ctenomyidae; incisor enamel microstructure; morphofunctional significance; Rodentia; tooth-digging adaptations.

Introduction

The family Ctenomyidae includes an assemblage of South American caviomorph rodents diversely adapted to life underground. The morphological disparity observed among the genera and species, at least since the Pliocene, is partly explained by different habits and digging strategies (Reig & Quintana, 1992; Lessa, 1993; Fernández et al. 2000; Verzi, 2002). The latter involve specializations of the forelimbs (scratch-digging) and/or masticatory apparatus (tooth-digging) (Hildebrand, 1985; Stein, 2000). Subterranean habits and digging specializations evolved independently in two different lineages of the family: †*Eucelophorus* (Pliocene – Middle Pleistocene) and *Ctenomys* (late Pleistocene – Recent) (Verzi & Olivares, 2006). A third lineage, †*Xenodontomys* (late Miocene) – †*Actenomys* (Pliocene), does not show clear evidence of such specialization, in

accordance with its inferred fossorial, not strictly subterranean, habits (Fig. 1; Fernández et al. 2000).

Because of the diverse use of incisors as digging tools, characteristics of these teeth provide important adaptive information in ctenomyids (Verzi, 2002). To date, this information comes mostly from gross morphology (Reig & Quintana, 1992; Mora et al. 2003; Vassallo & Mora, 2006), whereas enamel microstructure has only been studied in †*Actenomys priscus* (Owen) and some living *Ctenomys* species (Martin, 1992; Justo et al. 1995; De Santis et al. 2001). As in other caviomorph rodents, the enamel pattern or schmelzmuster (*sensu* Koenigswald, 1980) of ctenomyid incisors comprises an external layer – portio externa (PE) – of radial enamel (RE) and occasionally a zone of prismless enamel (PLEX; Martin, 1992), and an internal layer – portio interna (PI) – formed by multiseriate Hunter–Schreger bands (HSB). In addition, ctenomyids, as well as the remaining members of the superfamily Octodontoidea, possess a particular subtype of multiseriate HSB, in which the interprismatic matrix is arranged perpendicularly to the prisms; this is considered as an octodontoid synapomorphy (Martin, 1992). Within this pattern, variation in relative thickness of enamel types and HSB inclination can be related

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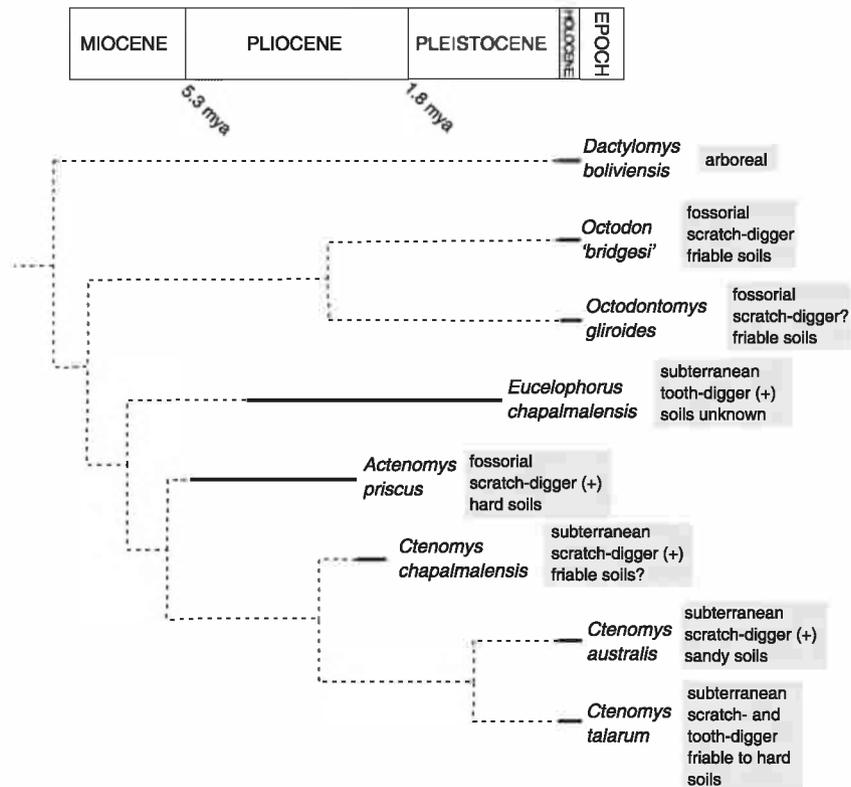


Fig. 1 Known or inferred habits, digging modes and occupied soils of species analysed (after Contreras et al. 1987; Verzi & Alcover, 1990; Reig & Quintana, 1992; Quintana, 1994; Vassallo, 1998; Fernández et al. 2000; Patton et al. 2000; Morgan & Verzi, 2006; Verzi & Olivares, 2006). Phylogenetic relationships (dotted lines) and biochrons (solid lines) after Honeycutt et al. (2003), Opazo et al. (2005) and Verzi (2002). A plus sign indicates the predominant digging mode.

to different functional requirements (Koenigswald, 1985; Flynn et al. 1987; Martin, 1999).

With the goal of assessing enamel variation in ctenomyids and its morphofunctional and adaptive meaning, we provide the first analysis of enamel microstructure of the upper incisors of †*Eucelophorus chapalmalensis* Ameghino and †*Ctenomys* (= *Paractenomys*) *chapalmalensis* (Ameghino), and compare it with that of other related taxa. The former is the only species of †*Eucelophorus* for which cranial remains have been preserved (Kraglievich, 1940). Likewise, †*C. chapalmalensis* is the oldest *Ctenomys* species known through dental and cranial remains. We also revise the enamel microstructure of previously studied ctenomyids, including †*Actenomys priscus*, and two extant *Ctenomys* species, *C. australis* Rusconi and *C. talarum* Thomas, which have disparate digging habits (Justo et al. 1995; Vassallo, 1998; De Santis et al. 2001). Finally, the living fossorial *Octodontomys gliroides* (Gervais & d'Orbigny) and *Octodon 'bridgesi'* (see Díaz & Verzi, 2006: 233) of the sister family Octodontidae (Verzi, 2001; Honeycutt et al. 2003) and the arboreal echimyid *Dactylomys boliviensis* Anthony are included as outgroup in the comparisons; Echimyidae is currently assumed as the sister taxon of Octodontidae + Ctenomyidae (e.g. Leite & Patton, 2002; Honeycutt et al. 2003; Opazo et al. 2005). The results are assessed and discussed in the context of the adaptive diversity of these South American octodontoid species, and compared with data available for other clades of subterranean rodents.

Materials and methods

The materials studied belong to the mammalogical and palaeontological collections of Museo de La Plata (MLP) and Museo de Ciencias Naturales de Mar del Plata 'L. Scaglia' (MMP). Specimen data are presented in the Appendix.

For the study of enamel microstructure, the incisors were embedded in artificial resin and cut in both longitudinal sections and cross-sections. Longitudinal sections were made from the flat medial surface of the incisors. Each tooth was ground to half of its total transverse diameter, to ensure homology of the section plane for all the materials analysed, using sandpaper and 1000-grit powdered silicon carbide. Finally, they were etched for 4–5 s with 10% hydrochloric acid to accentuate topographic detail (Flynn & Wahlert, 1978). After rinsing and drying, samples were sputter-coated with gold. The specimens *C. talarum* MLP 1.I.03.2–6, previously analysed by De Santis et al. (2001), were reprepared following this technique. Photographs of longitudinal sections were taken under a Jeol JSM 6360 LV scanning electron microscope (SEM). The following variables were measured from the photographs: EI, external index (PET/ET ratio); ET, total enamel thickness; HSBi, Hunter–Schreger band inclination; PET, thickness of PE (radial enamel and PLEX); REi, inclination of prisms in radial enamel; RLT, relative enamel thickness (ET/transverse incisor diameter × 100) (Koenigswald, 1985; Wahlert & Koenigswald, 1985; Flynn et al. 1987). Inclination was measured as the angle between

Table 1 Measurements and indexes of the upper incisor enamel of octodontoids examined

	Transv. inc. diam. (mm)	ET (μm)	RLT	PET (μm)	EI	HSBi ($^\circ$)	REi ($^\circ$)
† <i>Eucelophorus chapalmalensis</i>	3.48	230 \pm 4.24 <i>n</i> = 2	6.70	56 \pm 3.25 <i>n</i> = 2	0.24 \pm 0.02 <i>n</i> = 2	45–55 <i>n</i> = 2	67
<i>Ctenomys talarum</i>	2.47 \pm 0.13 <i>n</i> = 3	187.13 \pm 19.6 <i>n</i> = 8	8.35 \pm 0.66 <i>n</i> = 3	31.5 \pm 2.88 <i>n</i> = 8	0.17 \pm 0.01 <i>n</i> = 8	30–45 <i>n</i> = 8	79
<i>Ctenomys australis</i>	3.54 \pm 0.57 <i>n</i> = 3	226.34 \pm 27.1 <i>n</i> = 3	6.43 \pm 0.51 <i>n</i> = 3	31 \pm 3.46 <i>n</i> = 3	0.14 \pm 0.01 <i>n</i> = 3	30–40 <i>n</i> = 3	89
† <i>Ctenomys chapalmalensis</i>	2.61	167	6.40	25	0.15	40	78
† <i>Actenomys priscus</i>	3.27	258 <i>n</i> = 2	7.89	34.5 \pm 0.71 <i>n</i> = 2	0.13 \pm 0.003 <i>n</i> = 2	40–45 <i>n</i> = 2	69
<i>Octodontomys gliroides</i>	1.67	325	19.46	36.1	0.11	0–30	78
<i>Octodon 'bridgesi'</i>	1.94	174	8.97	24.4	0.14	45	80
<i>Dactylomys boliviensis</i>	2.44	225	9.22	24	0.10	40	77

EI, external index; ET, total enamel thickness; HSBi, Hunter–Schreger band inclination; PET, radial enamel thickness; REi, radial enamel inclination; RLT, relative enamel thickness. Values represent mean \pm SD, or range in HSBi and REi. Number of specimens is indicated when more than one was examined.

the HSB and a line perpendicular to the enamel–dentine junction (EDJ) (Korvenkontio, 1934). As no lower incisors of *Eucelophorus* were available for study, our analysis is focused on upper incisors.

Results

Measurements and indexes illustrating observed enamel variation are presented in Table 1. The overall disparity in enamel microstructure was low among the studied taxa (Fig. 2), but interesting differences in indexes and traits were recorded. Enamel thickness (measured as RLT) of *O. gliroides* was more than double that of the other taxa studied. Among the latter, RLT values were always lower in ctenomyids, although some of the differences were slight (cf. *C. talarum* and *O. 'bridgesi'*). Relative thickness of the PE (external index, EI) was highest in the subterranean †*E. chapalmalensis*. In the remaining taxa this index showed a weak gradient from the subterranean *C. talarum* to the lowest values in the fossorial *O. gliroides* and the arboreal *D. boliviensis*. Among ctenomyids, the fossorial †*A. priscus*, and the subterranean †*C. chapalmalensis* and *C. australis* showed similar EI values as the fossorial octodontid *O. 'bridgesi'* (Table 1; Fig. 3A). Inclination of the Hunter–Schreger bands (HSBi) was lowest in *O. gliroides*, and highest in †*E. chapalmalensis*, while the remaining taxa showed intermediate values (Figs 2 and 3B). All the taxa examined showed high REi (angle $>$ 55 $^\circ$ according to Martin, 1999). PLEX occurred in the enamel of all the taxa examined except *Octodontomys*; this layer was approximately twice as thick in †*Eucelophorus* as in the other taxa.

These quantitative results agree only partially with those obtained by Martin (1992) for *O. gliroides*, Justo et al. (1995) for *C. australis*, *C. talarum* and †*A. priscus*, and De Santis

et al. (2001) for *C. talarum*. These dissimilarities could be reflecting actual variability; however, the strong influence of the data acquisition process precludes reliable comparisons among results. Quantitative differences between the data in Justo et al. (1995) and De Santis et al. (2001) were due to methodological issues (De Santis et al. 2001: 12; L. J. M. De Santis, personal communication). Likewise, the reanalysis of materials studied by De Santis et al. (2001) showed that their results were not comparable with ours due to different orientation of the tooth sections (E.C.V., personal observations).

Discussion

The primary functional requirements of dental enamel are resistance to abrasive wear and prevention of the propagation of internal fractures (Pfretzschner, 1988; Koenigswald & Pfretzschner, 1991). Thus, morphological changes in enamel microstructure frequently reflect these requirements. A thick layer of external RE increases resistance to abrasion, because the orientation of the closely packed prisms with respect to the forces minimizes wear rates (Rensberger & Koenigswald, 1980; Boyde & Fortelius, 1986). Notwithstanding this mechanical advantage of RE, the trade-off of its parallel arrangement of prisms is greater vulnerability to interprismatic fractures created by tensional forces (Koenigswald, 1985, 1986; Pfretzschner, 1988). In this regard, HSB are interpreted as an adaptation to strengthen the enamel when chewing stress is increased (Koenigswald et al. 1987; Pfretzschner, 1988; Rensberger, 1997). HSB, which are formed by decussating prism layers, are able to stop fractures by dissipating tensional stresses. An increasing inclination of the bands, so that they tend to lie in the same direction as the applied forces, enhances their efficiency

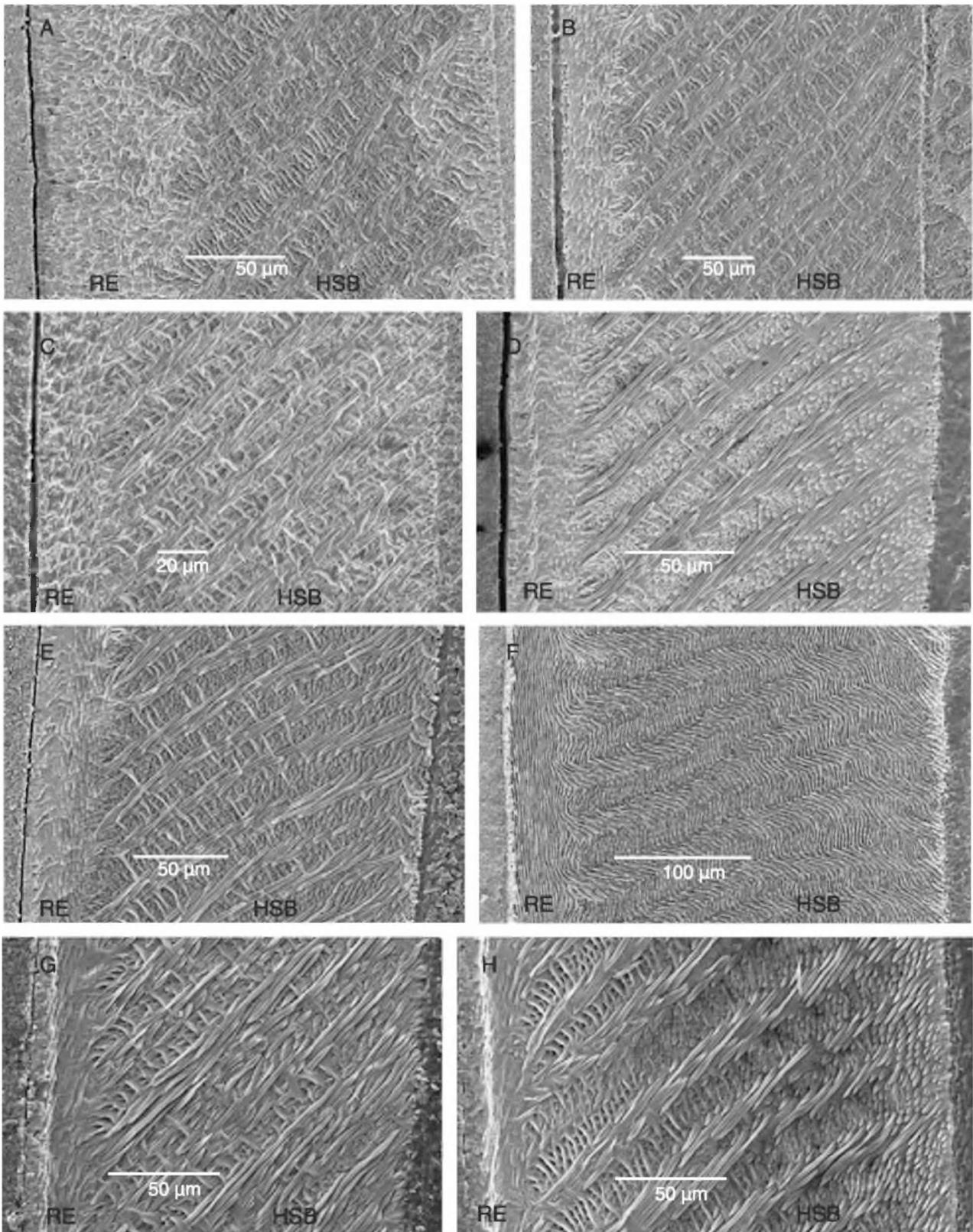


Fig. 2 SEM photographs of enamel microstructure of upper incisors (longitudinal sections, outer tooth surface at left, enamel–dentine junction at right, and occlusal tip down): A, †*Eucelophorus chapalmalensis*; B, †*Actenomys priscus*; C, †*Ctenomys chapalmalensis*; D, *Ctenomys talarum*; E, *Ctenomys australis*; F, *Octodontomys gliroides*; G, *Octodon 'bridgesi'*; H, *Dactylomys boliviensis*. RE, radial enamel; HSB, Hunter–Schreger bands.

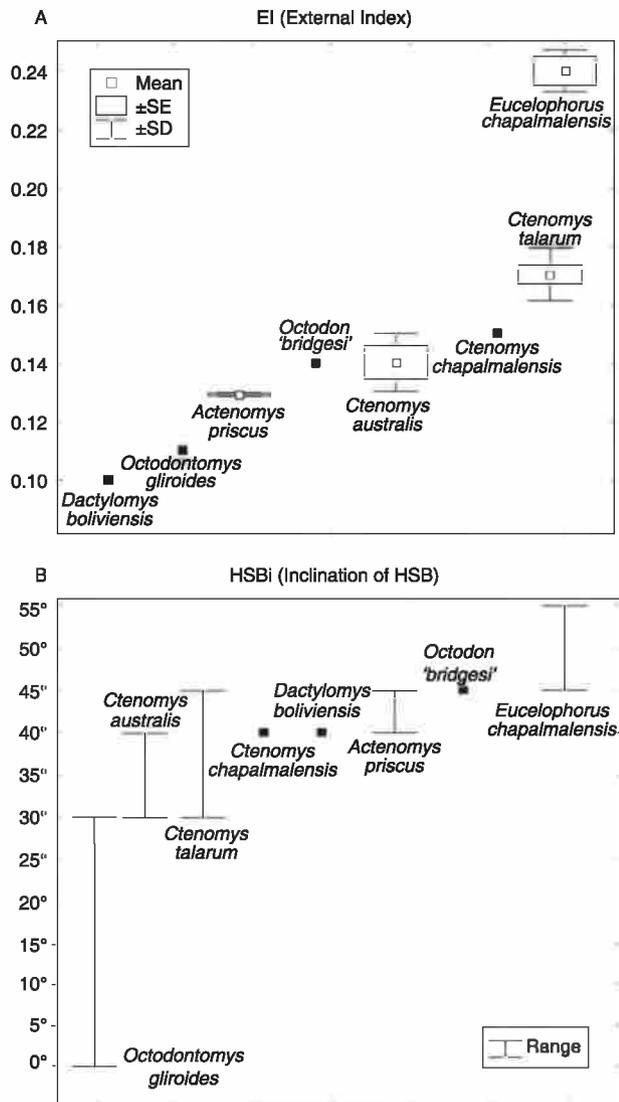


Fig. 3 Boxplots of: A, EI (external index); B, HSBi (Hunter–Schreger band inclination) for the taxa studied. A full square indicates a single measurement.

for fracture detention (Rensberger & Koenigswald, 1980; Martin, 1999). Additionally, Flynn et al. (1987) have suggested that the possession of PLEX could be a specialization to further resist abrasion and relieve digging stresses on the surface of the incisor in tooth-digging rodents.

These morphofunctionally significant enamel traits were quite similar among the species studied, even though these taxa differ markedly in digging behaviour and substrates occupied (Fig. 1; Table 1). The relatively homogeneous HSBi and EI values in ecologically and behaviourally dissimilar taxa suggest a possible phylogenetic constraint in Octodontoidea. Remarkably, similar values of EI occurred in the adaptively disparate species *Octodon 'bridgesi'* and *C. australis*.

Within such a conservative pattern, even slight differences may provide significant information. In this context, the

highest values of HSBi, and especially EI, observed in †*Eucelophorus*, coupled with the thick PLEX of this taxon, become eloquent because they could represent adaptive responses to biomechanical requirements. The enamel specializations of †*Eucelophorus*, which increase resistance to both fractures and abrasion, agree with its tooth-digging specializations, unique among South American rodents (Verzi & Olivares, 2006). The latter include deeply implanted and highly procumbent upper incisors (highest procumbency among caviomorphs) that provide better angles for soil contact as well as enhance dissipation of forces, and deep fossae and strong cranial ridges for the attachment of massive masseter muscles responsible for production of powerful bite-forces at the incisors (Reig & Quintana, 1992; Mora et al. 2003). In addition, EI values of the remaining taxa showed a slight gradient from lowest values in the arboreal *Dactylomys* and the fossorial *Octodontomys* to highest in the subterranean *C. talarum*. In particular, the higher value of EI of *C. talarum* compared with *C. australis* agrees with the occupancy of harder soils requiring higher frequency of incisor use in the former (Vassallo, 1998). The acquisition of digging specializations has been linked to increasing burrowing frequency derived from increased underground performance of biological functions (Genise, 1989; Stein, 2000; E. P. Lessa, in litt.), and also to substrate characteristics (Mora et al. 2003). Indeed, both aspects could be related, as shown by the above-mentioned data for two equally subterranean *Ctenomys* species. If enamel reinforcement against wear is also related to increased frequency of incisor use, the specialized enamel of †*Eucelophorus* suggests a more extreme tooth-digging strategy compared with the remaining octodontoids studied. Higher frequency of incisor use could have been determined by occupancy of hard soils. Moreover, this latter factor by itself could have promoted the tooth-digging specialization of *Eucelophorus*, but no data are currently available on substrate occupied by this ctenomyid.

Beyond phylogenetic constraints associated with enamel microstructure (Koenigswald, 1985; Martin, 1992, 1993, 1994a,b, 1997), similar requirements of greater resistance to abrasion could be a recurring feature in distant clades of subterranean rodents. The enamel of tooth-digging species of the families Rhizomyidae, Bathyergidae and Spalacidae shows high EI (higher than in †*Eucelophorus*), but with low-inclination HSB, and both traits have been considered as possible tooth-digging adaptations in these taxa (Flynn et al. 1987; Tables 1 and 2). Likewise, among geomyids, higher EI (see Buzas-Stephens & Dalquest, 1991) is positively correlated with greater tooth-digging specialization, from the primarily scratch-digger *Geomys* to the relatively more specialized tooth-diggers *Cratogeomys* and especially *Thomomys* (Lessa & Thaeler, 1989).

Further exploration of the variability of enamel traits in additional taxa of fossorial and subterranean rodents will contribute to test if there is a more widespread positive

correlation between enamel traits and tooth-digging specialization.

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Appendix

Materials examined

†*Eucelophorus chapalmalensis* MLP 97-II-1-60, left upper incisor, Balneario Los Angeles (Buenos Aires province, Argentina), Pleistocene; MLP 91-IV-25-82, Punta Negra (Buenos Aires province), PN8-PN9 levels (from Bidegain et al. 2005), Early Pleistocene. †*Actenomys priscus* MLP 99-XI-5-1, left upper incisor, and MLP 99-XII-5-52, Paso Otero (Buenos Aires province), Pliocene. †*Ctenomys chapalmalensis* MMP 1225-M, right upper incisor, Punta San Andrés (Buenos Aires province), San Andrés Formation, Late Pliocene. *Ctenomys australis* (Recent) MLP 15.VIII.97.1, right upper incisor, Monte Hermoso (Buenos Aires province); MLP 16.V.01.22, left upper incisor, Claromecó (Buenos Aires province); MLP 7.XI.95.11, left upper incisor, Laguna Sauce Grande (Buenos Aires province). *Ctenomys talarum* (Recent) MLP 26.VIII.01.13, left upper incisor, and MLP 26.VIII.01.16, left upper incisor, Punta Indio (Buenos Aires province); MLP 1.I.03.1, right upper incisor, Santa Teresita (Buenos Aires province); MLP 1.I.03.2, right upper incisor, MLP 1.I.03.3, left upper incisor, MLP 1.I.03.4, right upper incisor, MLP 1.I.03.5, right upper incisor, MLP 1.I.03.6, right upper incisor, Mar Azul (Buenos Aires province). *Octodontomys gliroides* (Recent) MLP 5.X.99.10, right upper incisor, Corral Grande (Salta province, Argentina). *Octodon 'bridgesi'* (Recent) MLP 22.II.00.5, left upper incisor, Aluminé (Neuquén province, Argentina). *Dactylomys boliviensis* (Recent) MLP 8.V.95.6, left upper incisor, Echarate (La Convención province, Cusco, Peru).