Evolution of morphological adaptations for digging in living and extinct ctenomyid and octodontid rodents

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To examine the evolution of burrowing specializations in the sister families Octodontidae and Ctenomyidae (Rodentia: Caviomorpha), we produced a synthetic phylogeny (supertree), combining both molecular and morphological phylogenies, and including both fossil and extant genera. We mapped morphological specializations of the digging apparatus onto our phylogenetic hypothesis and attempted to match morphological diversity with information on the ecology and behaviour of octodontoid taxa. Burrowing for sheltering and rearing is the rule among octodontids and ctenomyids, and adaptations for digging have been known from the Early Pliocene onward. However, only a few taxa have evolved fully subterranean habits. Scratch-digging is widespread among both semifossorial and fully subterranean lineages, and morphological changes associated with scratch-digging are not restricted to subterranean lineages. By contrast, various adaptations for chisel-tooth digging are restricted to some subterranean lineages and are combined differently in the octodontid *Spalacopus*, the fossil ctenomyid *Eucelophorus*, and some living *Ctenomys*. Some octodontid taxa are able to dig complex burrows in spite of having no substantial changes in musculoskeletal attributes. Hence, we suggest that, during the early evolution of those branches giving rise to fully subterranean ctenomyids and octodontids, a change in behaviour probably preceded the origin of structural adaptations. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **95**, 267–283.

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INTRODUCTION

The Caviomorpha (= South American Hystricognathi) compose the most diverse clade of rodents in terms of ecology, life-history traits, body size, and locomotor habits (Mares & Ojeda, 1982). Cursorial adaptations are present in agoutis (*Dasyprocta*) and maras (*Dolichotis patagonum*); coypus (*Myocastor coypus*) and capybaras (*Hydrochoerus hydrochaeris*) show swimming adaptations, whereas porcupines (e.g. *Erethizon*, *Coendou*) and spiny rats (e.g. *Echimys*, *Dactylomys*) show striking climbing adaptations

(Redford & Eisenberg, 1992; Eisenberg & Redford, 1999; Galewski *et al.*, 2005). Among caviomorphs, living and extinct Octodontidae and Ctenomyidae show a progressive development of evergrowing cheek teeth and other adaptations to open habitats, including the acquisition of burrowing habits, which characterize the evolution of both families from the late Miocene-Early Pliocene onward (Quintana, 1994; Verzi, 2001).

Burrowing is widespread among mammals, even in those species having strict epigeous habitats (Nowak, 1999). In five extant (Geomyidae, Ctenomyidae, Octodontidae, Bathyergidae, and Muridae, including Spalacinae and Rhizomyinae) and at least two extinct (Mylagaulidae and Tsaganomyidae) rodent families,

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fossorial and subterranean habits have evolved independently as a further specialization of that generalized burrowing behaviour, in close association with the emergence of open environments during mid-to-late Cenozoic cycles of increasing aridity (Nevo, 1999; Wang, 2001; Hopkins, 2005). The energetic cost of excavating burrows is 360–3400-fold as great as moving the same distance across the surface (Vleck, 1979). Burrowing requires the capacity to produce and transmit considerable force during long-term activity periods. This functional demand has resulted in profound changes in physiological attributes (McNab, 1979; Luna & Antinuchi, 2007), as well as in the entire architecture of the myoskeletal system of diggers (Lehman, 1963). For example, the enlarged muscles of diggers have their origins and insertions relatively far from the joints they turn, and the distance from the joint to the tip of the digging tool is short (Lessa, 1990). This change in lever arm relationships, which results in an elevated mechanical advantage of corresponding muscles, has appeared in rather different body parts in terms of their original function, such as the chewing apparatus and the extremities (Hildebrand, 1985; Wake, 1993). Digging species have shorter and thicker long bones than epigeous species (Biknevicius, 1993; Casinos, Quintana & Viladiu, 1993). Incisors may show increased procumbency, which provides an adequate angle of attack against the soil (Reig & Quintana, 1992), and changes in enamel composition (Justo, Bozzolo & De Santis, 1995).

These examples suffice to indicate that morphological adaptations to life underground are numerous and relatively well understood (reviewed by Hildebrand, 1985; Nevo, 1999; Lacey, Patton & Cameron, 2000). However, the first appearances of many subterranean lineages in the fossil record already showed numerous advanced features (Cook, Lessa & Hadly, 2000). It has thus become relatively difficult to identify stages and trends in the evolution of subterranean life. The sister families Octodontidae and Ctenomyidae provide a unique opportunity to trace the evolution of morphological adaptations related to digging. Ctenomyids and octodontids encompass a broad array of behavioural and structural adaptations, from surface dwelling to fully subterranean species. Three additional factors make the group an excellent candidate to analyze some relevant issues in evolutionary morphology, such as convergence, structural versatility, and coadaptation of functionally related traits (Gatesy & Dial, 1996; Rose & Lauder, 1996; Galis & Metz, 1998). First, there is well preserved fossil material, including both cranial and postcranial remains, which allows characterization of early stages of adaptation. Second, phylogenetic relationships can be assessed for both extant and extinct taxa due to the

existence of good information on morphological (Verzi, 2001, 2002) and molecular (Castillo, Cortinas & Lessa, 2005) character variation. Third, there is substantial work on functional morphology and behaviour of living taxa, as well as paleobiological analysis of extinct taxa (Reig & Quintana, 1992; Quintana, 1994; Vassallo, 1998; Fernández, Vassallo & Zárate, 2000; Morgan & Verzi, 2006; Verzi & Olivares, 2006; Vassallo & Mora, 2007).

In the present study, we examine the evolution of adaptation to fossorial and fully subterranean life in octodontids and ctenomyids. We begin by obtaining a supertree that combines both fossil and extant genera, making use of published morphological and molecular phylogenies. We then characterize burrow structure, life habits, and morphological features of the skull, mandible, and postcranial skeleton related to digging using a combination of published and original data. Finally, we map character variation and correlation between characters onto the supertree to gain insights into the evolution of digging adaptations and life habits.

MATERIAL AND METHODS
PHYLOGENETIC ANALYSIS

Molecular phylogenetic analyses have confirmed that the superfamily Octodontoidea is a monophyletic group of caviomorph rodents that includes the traditionally recognized families Abrocomidae, Myocastoridae, Capromyidae, Echimyidae, Octodontidae, and Ctenomyidae (Nedbal, Allard & Honeycutt, 1994; Huchon & Douzery, 2001; Honeycutt, Dowe & Gallardo, 2003; Galewski *et al.*, 2005; Opazo, 2005). In line with traditional interpretations based on morphological comparisons (Pascual, Pisano & Ortega, 1965; Woods, 1972), there is a growing consensus that Octodontidae and Ctenomyidae are sister taxa (Opazo, 2005), although some analyses (e.g. certain trees; Honeycutt *et al.*, 2003) suggest alternative arrangements. For our purposes, we assumed that Ctenomyidae and Octodontidae are reciprocally monophyletic taxa. To obtain a working phylogeny that included both extant and extinct octodontids and ctenomyid genera, we built a supertree using PAUP* (Swofford, 1998) on the basis of the morphological phylogenies of Mares *et al.* (2000) and Verzi (2001, 2008), and the molecular phylogenies of Honeycutt *et al.* (2003: fig. 3), Leite & Patton (2002), Gallardo & Kirsch (2001), Slamovits *et al.* (2001), Castillo *et al.* (2005: fig. 3). Nodes in these published trees were encoded as binary discrete characters, and a single supertree was obtained from the resulting matrix using maximum parsimony. Three morphologically divergent species of tuco-tucos (*Ctenomys australis*,

Ctenomys talarum, and *Ctenomys leucodon*) were included, and their phylogenetic relations were taken from Castillo *et al.* (2005: Fig. 3). The extinct taxa included were only those known through both cranial and mandibular remains, and for which phylogenetic information was available. Variation in both ecological and morphological characters was coded as discrete, ordered, unpolarized states and mapped under the maximum parsimony criterion using MacClade, version 3.08 (Maddison & Maddison, 1992). Conservatively, ambiguities over all possible reconstructions were retained. The Echimyidae *Thrichomys apereoides* and *Proechimys poliopus* were used as outgroups in reconstructions of character evolution.

To investigate hypotheses of character correlation of discrete variables in a phylogenetic context, we used the method of phylogenetic pairwise comparison developed by Maddison (2000) and implemented in the pairwise module in the program MESQUITE (Maddison & Maddison, 2006). The one pair option of the program was used to choose pairs of taxa that differ in the state of one character (e.g. fossoriality) to examine its correlation with a second variable (e.g. burrow structure). Analyses of correlated evolution among continuous characters were carried out using phylogenetically independent contrasts (Felsenstein, 1985). The data were converted to phylogenetically independent contrasts using the PDAP package (Midford, Garland & Maddison, 2003). Standardization tests in PDTREE indicated that Grafen's branch length transformation (Grafen, 1992) was the appropriate method for assigning arbitrary branch lengths (Garland, Harvey & Ives, 1992). This method assumes a gradual Brownian motion model of evolution, and the height of each node is proportional to the number of species derived from it.

BEHAVIOURAL AND MORPHOLOGICAL CHARACTERS

A matrix of two behavioural and eight morphological characters was generated (see Appendix, Table A1). To this aim, we reviewed the literature on fossil and living octodontoids, and added novel unpublished data from specimens belonging to the collections of Museo de La Plata (La Plata, Argentina), Facultad de Ciencias Exactas y Naturales (UNMdP) and Museo Lorenzo Scaglia (Mar del Plata, Argentina) (see Appendix). The characters are listed below, in conjunction with their behavioural or functional/adaptive connotation.

Behavioural characters
Character 1. Burrow structure: Genise (1989) recognized five, increasingly complex types of burrows among octodontoid rodents, from simple burrows used mainly as shelters to the complex burrows of fully

subterranean species. We adopted this proposal to assign particular character states to octodontoid species in our study, using additional information from more recent studies such as Antinuchi & Busch (1992), Ojeda *et al.* (1996), Begall & Gallardo (2000), and R. Ojeda and L. Ebensperger (pers. comm.).

The character states and taxa were: (1) simple burrows, which consist of a slight alteration of a pre-existing crevice, hollow or natural refuges (*Proechimys*, *Thrichomys*); (2) simple burrows excavated starting from pre-existing refuges (*Octodontomys*; *Octomys*); (3) complex burrows which consist mainly of oblique tunnels connecting the surface to the nest, with several branches and openings (*Octodon*, *Aconaemys*, and *Tympanoctomys*); (4) complex burrows, which consist of horizontal tunnels (largely parallel to the soil surface) followed by oblique tunnels with several branches and openings connecting the surface to the nest (*Actenomys*); and (5) complex burrows which consist mainly of horizontal foraging tunnels; with several branches and openings. In one or two points an oblique, relatively short tunnel branches off from the foraging tunnel to a deeper nest or nests (*Ctenomys*, *Spalacopus*) (Fig. 1).

Character 2. Fossoriality: Fossorial species (state 1) spend a substantial fraction of their lives outside their burrows. Above-ground excursions to collect food consist of relatively long trips, lasting several minutes. Sometimes, fossorial species use runways across vegetation (e.g. *Aconaemys*, *Octodon*). After burrow construction, burrowing activities are sporadic. By contrast, subterranean species (state 2) conduct the vast majority of their life underground (*Ctenomys* spend less than 1% of total time outside their burrows). Foraging excursions are usually limited to the vicinity of burrow openings (in the order of 0.3–4 m). Subterranean species perform regular, usually daily digging activities (see Appendix, Table A1).

Functional morphological characters
Functional morphological characters were sometimes expressed as ratios in relation to another measure to standardize for size differences among taxa. For example, we used basicranial axis length as a conservative measure of size that changes little when other skull characters change (Radinsky, 1985).

Character 3. Teres major process: The posterior angle of the scapula may be small (state 1) or enlarged (state 2), providing both a greater area of origin and greater in-lever arm for *musculus teres major*, a flexor muscle of the shoulder (Lehman, 1963; Vassallo, 1998; Fernández *et al.*, 2000).
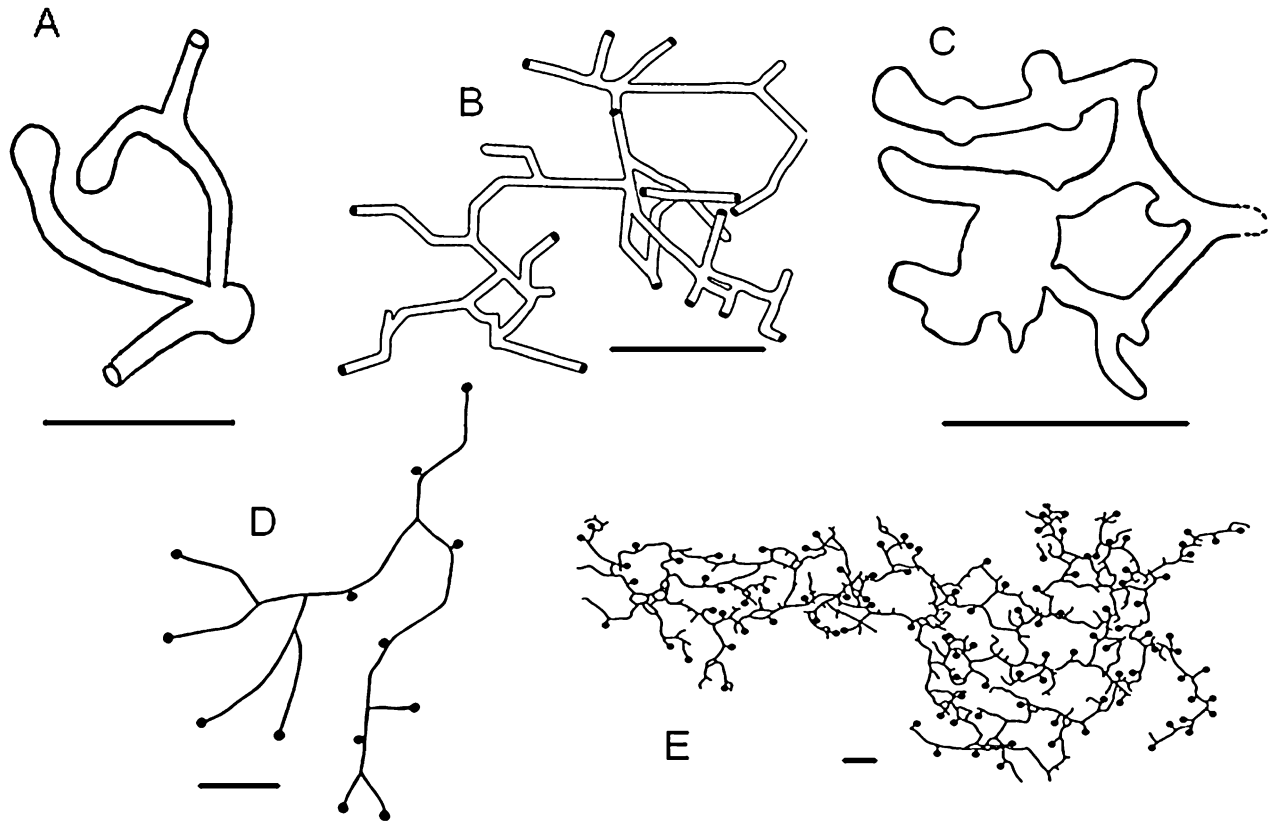
Figure 1. Burrows of some octodontid and ctenomyid rodents. A, *Octodon degus* (from Fulk, 1976). B, *Tympanoctomys barrerae* (from Ojeda *et al.*, 1996). C, *Actenomys priscus* (from Genise, 1989). D, *Ctenomys talarum* (Antinuchi & Busch, 1992). E, *Spalacopus cyanus* (from Begall & Gallardo, 2000). Scale bars = 1 m.

Character 4. Deltoid process of the humerus: The deltoid process is the site of insertion of the *musculus deltoideus* and *musculus pectoralis*, two flexor muscles of the forearm. The position of the deltoid crest was expressed by the quotient between the distance from the head of the humerus to the tip of the deltoid process/total length of the humerus (Fig. 2). This index reflects the mechanical advantage of the muscles *m. deltoideus* and *m. pectoralis* (Fernández *et al.*, 2000).

Character 5. Width of humerus across epicondyles: The medial epicondyle of the humerus is an origin of digital and carpal flexors and of the pronator, whereas the lateral epicondyle is an origin of carpal extensors and supinator. A flaring medial epicondyle also increases the effective force of flexors by altering their line of action. A larger humerus width across epicondyles provides a broader area of origin for these muscles (Hildebrand, 1985; Vassallo, 1998). This character was expressed as ratio relative to the total length of the humerus (Fig. 2).

Character 6. Length of the olecranon process of the ulna: The olecranon process is the site of insertion, and the in-lever arm of extensors muscles of the forearm, such as *musculus triceps* and *musculus dorsoepitrochlearis*. The medial surface of the olecranon process is also an origin of digital and carpal flexors. This character was expressed relative to the total length of the ulna, and reflects the mechanical advantage of forearm extensors (Fernández *et al.*, 2000).

Character 7. Upper incisor procumbecy: This character was measured as the 'angle of Thomas' (Reig, Contreras & Piantanida, 1965). In a lateral view of the skull, this angle is delimited by the grinding plane of the molariforms and the straight line going through the tip of the incisor and the posterior ridge of its alveolus. Variation in this character (Fig. 3) changes the angle of attack of the upper incisors in chisel-tooth digging (Lessa, 1990).

Character 8. Upper incisor roots: A long root provides the condition for an adequate dissipation of the forces
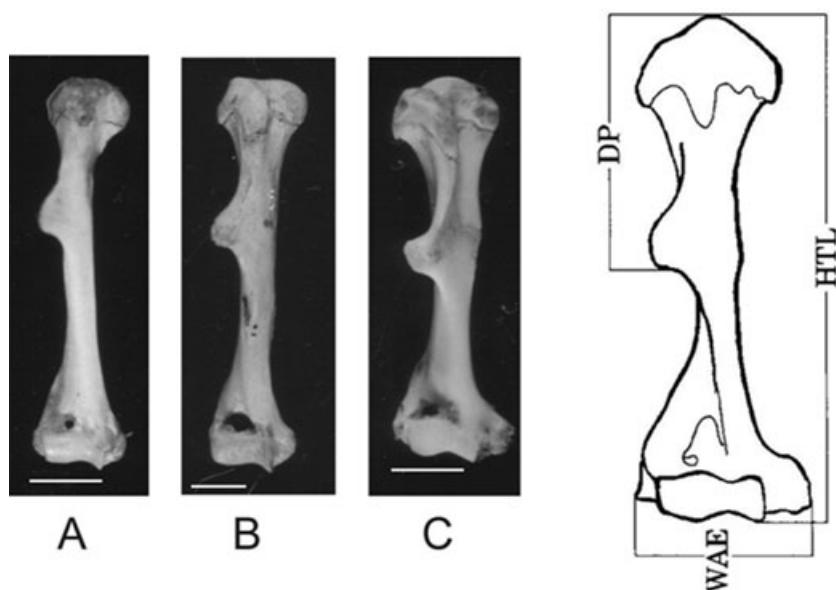
Figure 2. Position of deltoid crest and development of the epicondyles in the humerus. The figure on the right shows the linear variables used to estimate functional indexes of the humerus (see Material and Methods). HTL: humerus total length; DP: distance from the head of the humerus to the tip of the deltoid process; WAE: width of humerus across epicondyles. A, *Actenomys priscus*. B, *Octodon* sp. C, *Ctenomys talarum*. Scale bars = 0.5 cm.

exerted at the tip of incisors during excavation (Landry, 1957). The position of the posterior end of the incisor root was expressed in relation to the maxillary cheek teeth. (1) root reaching the posterior end of diastema; (2) root reaching the premolar; and (3) root reaching or posterior to the first molar.

Character 9. Upper incisor cross section: An enlarged incisor cross section provides resistance to bending and shearing stress during chisel-tooth digging (Bacigalupe, Iriarte-Díaz & Bozinovic, 2002; Mora, Olivares & Vassallo, 2003). This character was expressed as a ratio of incisor cross section/length of upper diastema.

Character 10. Mandible width across masseteric crest: Because the angle of the mandible and the masseteric crest are the site of insertion of *musculus masseter superficialis* and *musculus masseter lateralis*, the mandible width across masseteric crest is an indicator of overall masseter development (Mora *et al.*, 2003; Olivares, Verzi & Vassallo, 2004; Fig. 4). This character was expressed relative to basicranial length.

RESULTS

A single most parsimonious tree (Fig. 5A), with a consistency index of 0.80 resulted from the supertree analysis, suggesting that there is substantial congruence among trees built from seemingly disparate datasets, including external (Mares *et al.*, 2000) and skeletal morphological characters (Verzi, 2001, 2008), immunological distances (Gallardo & Kirsch, 2001), and mitochondrial and nuclear DNA sequence data (all other trees). Conservatively focusing on unambiguous changes only, character evolution shows the following overall patterns (Fig. 5A): (1) the lineage leading to *Spalacopus* is inferred to have accumulated, approximately 2.2 Mya, a large number of both behavioral and morphological changes in the context of a rather conservative octodontid clade and (2) the ctenomyids show much greater dispersion of changes, including an accumulation of character transformations at the root of this clade (8–15 Mya), and a mosaic of subsequent variation broadly distributed across lineages.

BEHAVIOURAL CHARACTERS (FIG. 5B, C)

With the notable exception of the fossil burrows in *Actenomys* (Genise, 1989; Fernández *et al.*, 2000), no direct data exist on burrow complexity or degree of fossoriality in fossil ctenomyids. This introduces uncertainty in the reconstruction of the evolution of these characters. However, our analyses show that, although there are several possible reconstructions, burrow structure among octodontids must have evolved similar levels of complexity independently in several lineages. Among ctenomyids, the phylogenetic position of *Actenomys* contributes to suggest a rela-
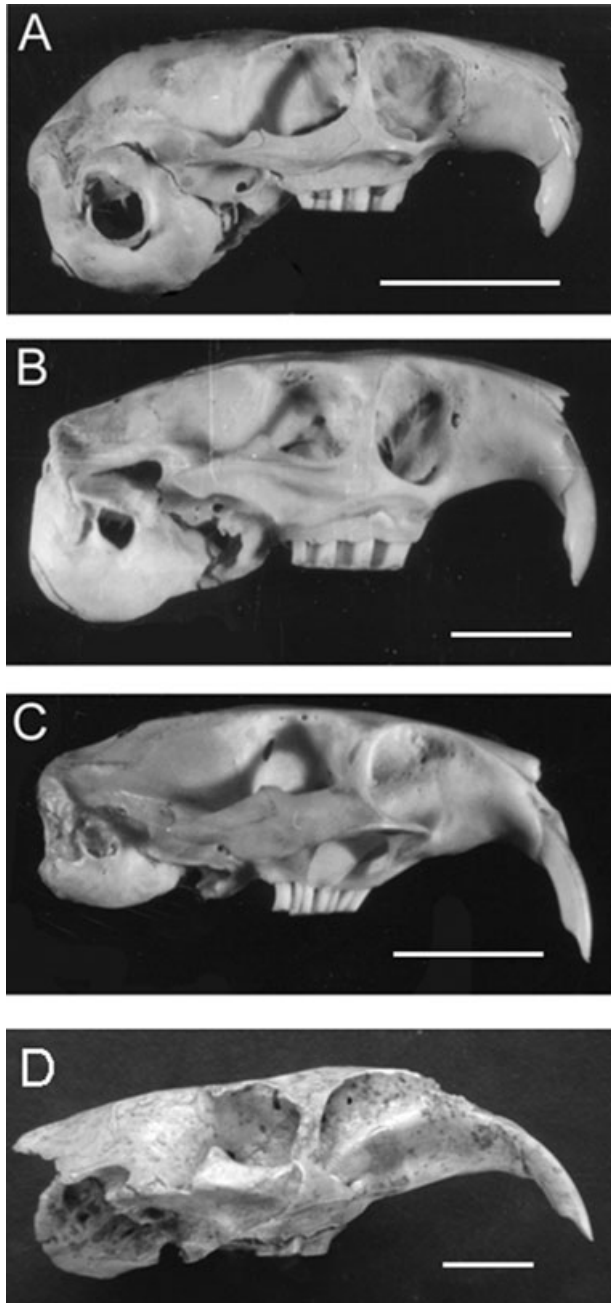
Figure 3. Lateral view of the skull of octodontid and ctenomyid rodents; numbers in parenthesis indicate their character states in upper incisor procumbency (see Appendix, Table A1). A, *Octodontomys gliroides* (1). B, *Ctenomys australis* (2). C, *Spalacopus cyanus* (4). D, *Eucelophorus zaratei* (4). Scale bars = 1 cm.

tively early appearance of its fairly complex burrows. The fossil ctenomyid genera *Praectenomys* and *Xenodontomys* are inferred to have had burrows at least as complex as those of *Actenomys*. In summary, although the most complex burrows are restricted to fully sub-

terranean *Ctenomys* and *Spalacopus*, the association of these two characters is surprisingly varied, both in terminal taxa and, by inference, across the phylogeny. Quantitatively, we found no significant correlation between fossoriality and burrow complexity ($P > 0.25$; pairwise comparison; one pair method), although missing data on these characters in most fossils obviously limit the power of this assessment.

FORELIMB CHARACTERS (FIG. 6)

Expanded olecranon and epicondylar processes characterize subterranean *Spalacopus* and *Ctenomys* and, by inference, their exclusive ancestors. Other forelimb adaptations for digging, however, are more broadly distributed. In particular, an expanded *teres major* process is inferred to have characterized all ctenomyids, with the exclusion of the branch leading to *Eucelophorus*, in which this trait is unknown. Similarly, moderately distal position of the deltoid process is inferred to have characterized all ctenomyids, and was independently acquired by *Spalacopus*. However, fully distal deltoid processes are only found in *C. talarum*. Overall, we found a pattern of correlated change in forelimb attributes, as indicated by the statistically significant correlation among characters of the ulna and humerus using independent contrasts (Fig. 7A, B). Both the enlargement of digital and carpal flexors, and the change of the deltoid process to a distal position onto the humerus accompanied the evolution of a large olecranon process.

UPPER INCISORS (FIG. 8A, B, C)

Highly procumbent incisors and posteriourly displaced incisor capsules appeared early in the radiation of ctenomyids, and independently in *Spalacopus*. Early ctenomyine lineages, such as *Eucelophorus*, had extremely procumbent incisors. All octodontids, including *Spalacopus*, have slender incisors (small cross-sectional areas) regardless of their procumbency. In contrast, ctenomyids show great variation, and generally increased cross-sectional areas, especially among procumbent taxa. Overall, we found no significant correlation between incisor procumbency and incisor cross section (Fig. 7C).

MANDIBLE (FIG. 8D)

The hypertrophy of the masseteric musculature characterized also the early evolutionary history of ctenomyids, as indicated by the flaring mandibular angle and masseteric crest seen in basal, extinct taxa. This is reflected in large mandibular widths in *Euce-*
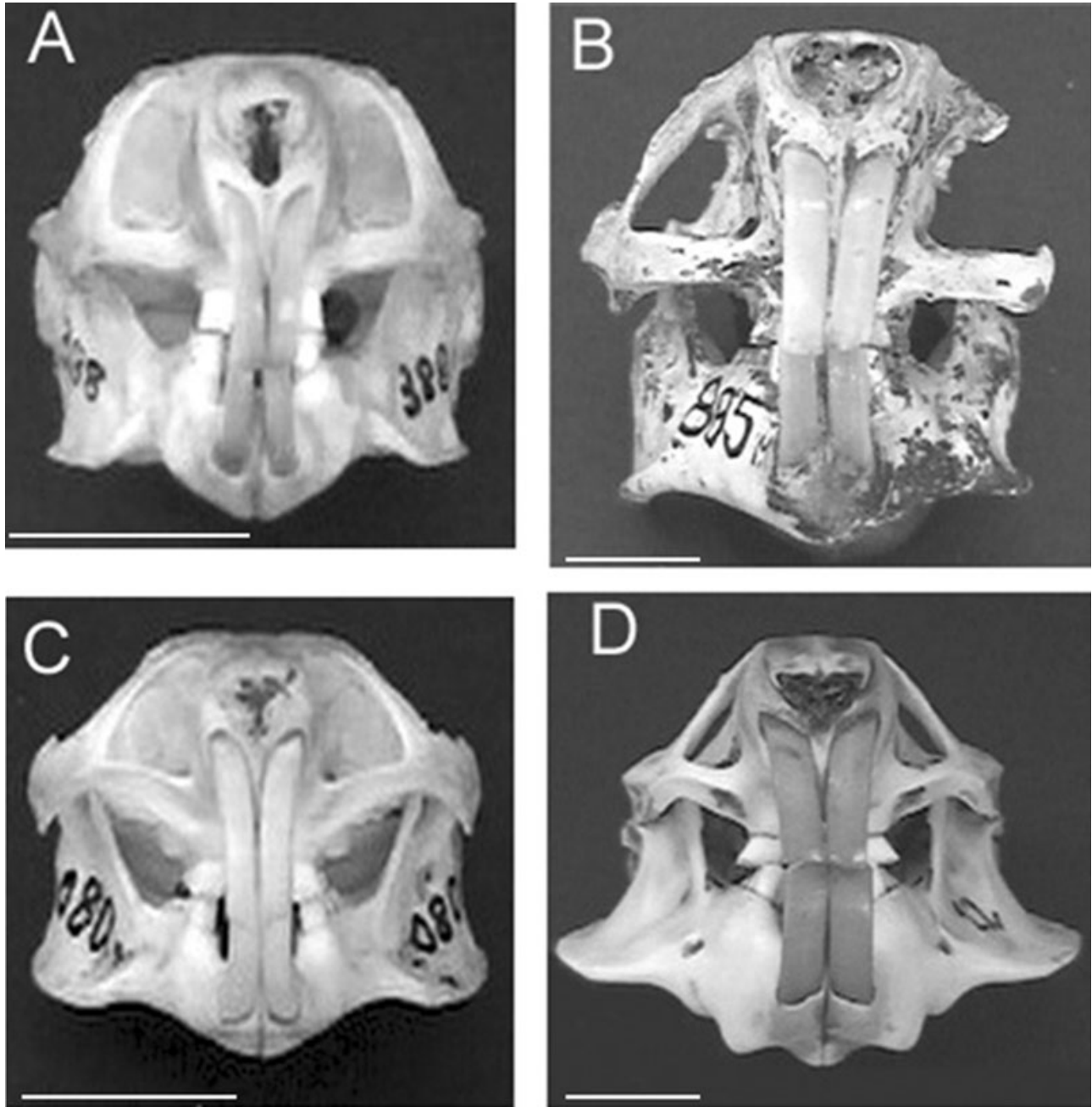
Figure 4. Anterior view of skulls and jaws of selected octodontids and ctenomyids; numbers in parenthesis indicate their character states in mandible width, as an indicator of overall masseter development (Appendix, Table A1). A, *Octomys mimax* (1). B, *Actenomys priscus* (2). C, *Spalacopus cyanus* (2). D, *Ctenomys australis* (3). Scale bars = 1 cm.

lophorus and *Ctenomys*. Intermediate values are found in the clade formed by *Spalacopus* and *Aconaemys* among octodontids, and independently in *Actenomys*. There is uncertainty in the reconstruction of this character in several ctenomyid lineages, but it is inferred to have been at least as developed as in *Aconaemys* early in the ancestry of ctenomyids. Overall, incisor cross-section and mandibular width are positively correlated using independent contrasts (Fig. 7D).
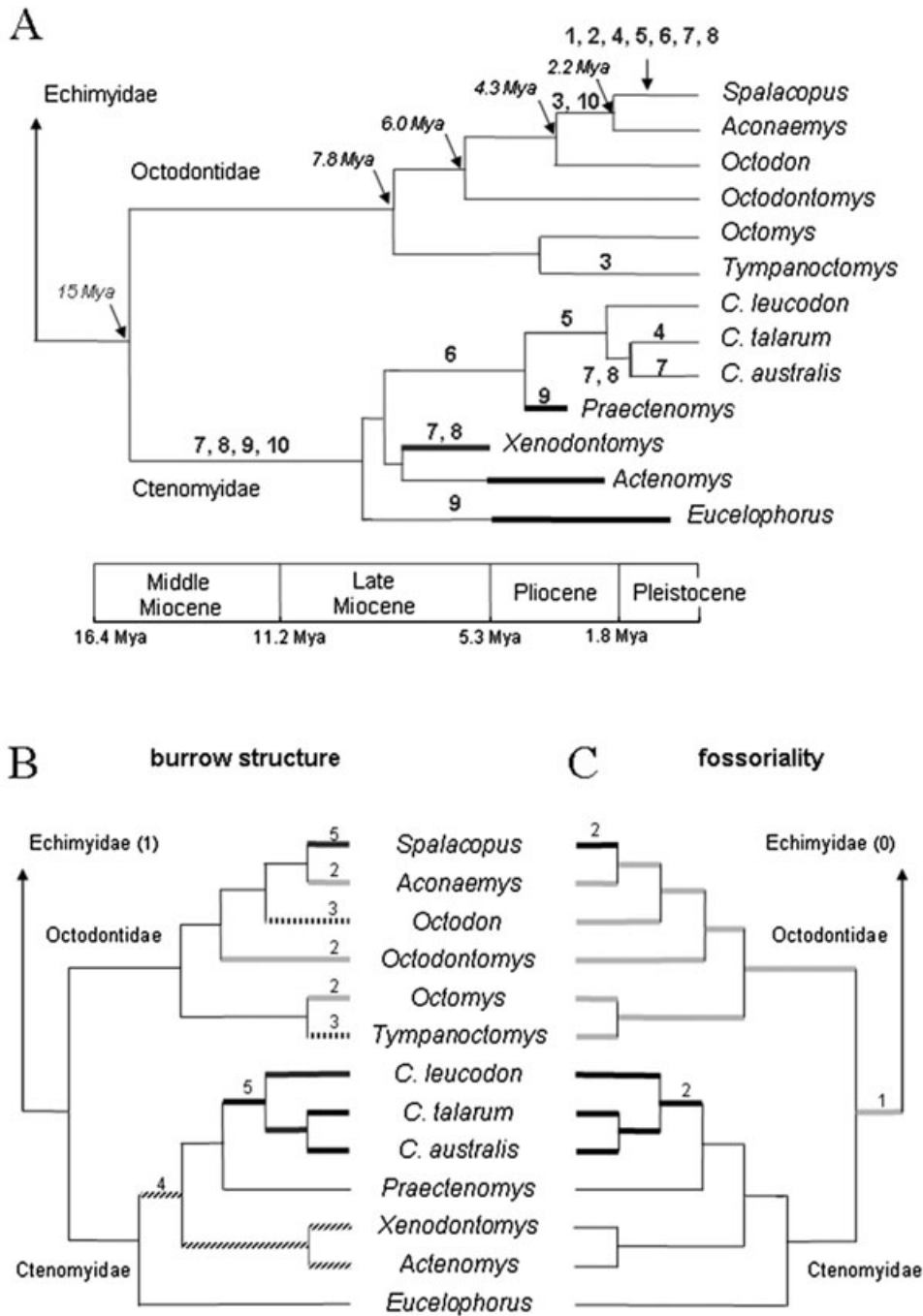
Figure 5. A, time scale for the evolution of morphological adaptations for digging in living and extinct ctenomyid and octodontid rodents. Numbers in bold indicate behavioural or morphological characters that unambiguously changed on indicated branches (numbers indicate characters as listed in the Material and Methods and Table A1 in the Appendix). Estimated times of divergence of families and living genera are taken from Opazo (2005) and the chronology of extinct taxa from Verzi (2002). B, reconstruction of the evolution of burrow structure. C. levels of fossoriality. Unambiguous states are indicated by shadings of tree branches and numbered on selected branches (ambiguous states are indicated by thin branches).
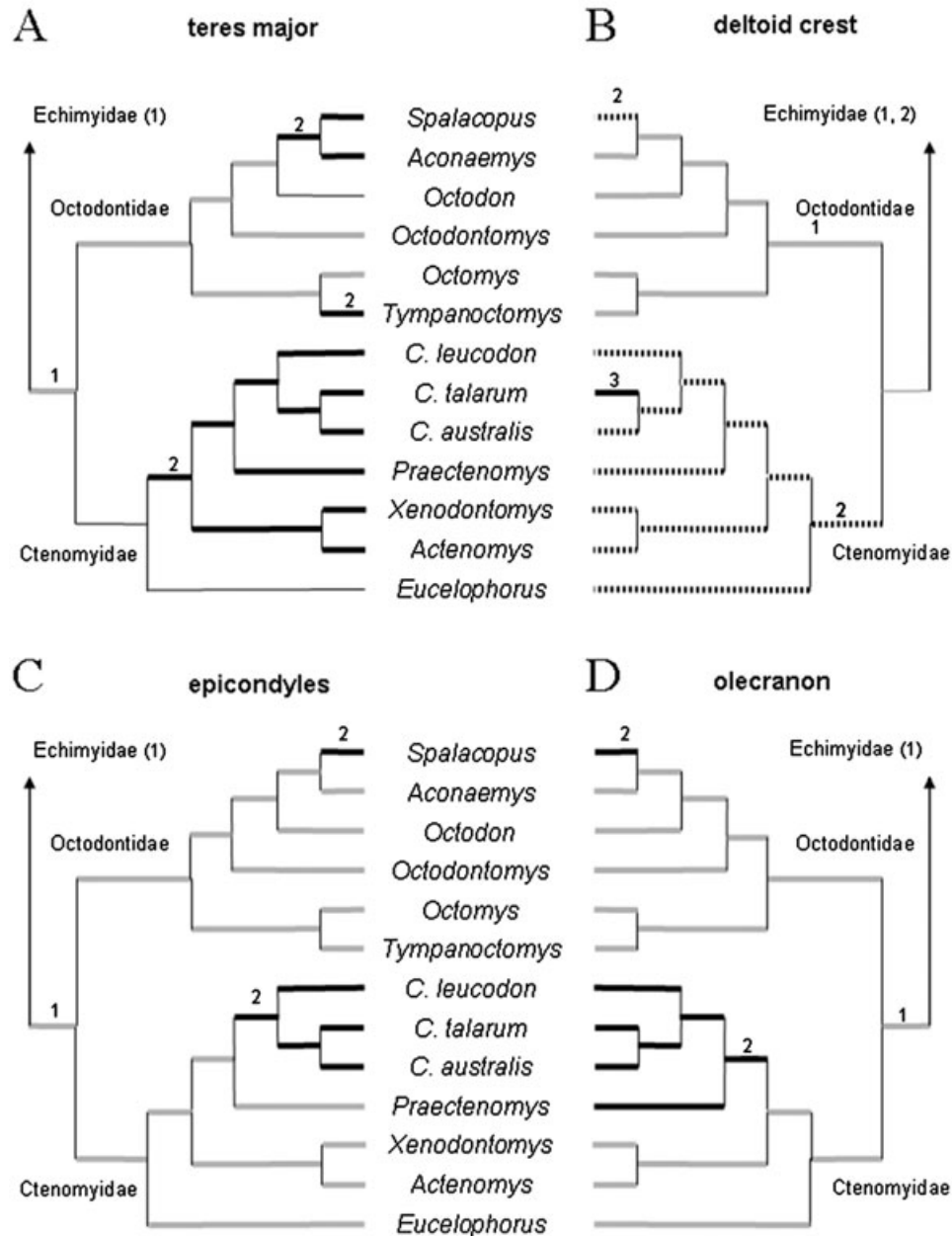
Figure 6. Reconstruction of the evolution of characters of the forelimb. Unambiguous states are indicated by shadings of tree branches and numbered on selected branches; ambiguous states are indicated by thin branches. A, relative development of the *Teres major* process. B, relative position of the deltoid crest. C, relative width of epicondyles. D, relative length of the olecranon process.

DISCUSSION

The present study provided three major findings regarding the evolution of adaptations to digging in octodontids and ctenomyids. First, the construction of complex burrow structures is not restricted to subterranean species but is also found among fossorial lineages and does not appear to require substantial

morphological change. Second, the digging apparatus of octodontids and ctenomyids shows significant structural flexibility; in particular, adaptations for chisel-tooth digging appear to be recurrent, but show two rather different combinations of traits. Third, the phylogenetic and chronological distribution of adaptations for subterranean life in ctenomyids and octodontids appears to have followed very different
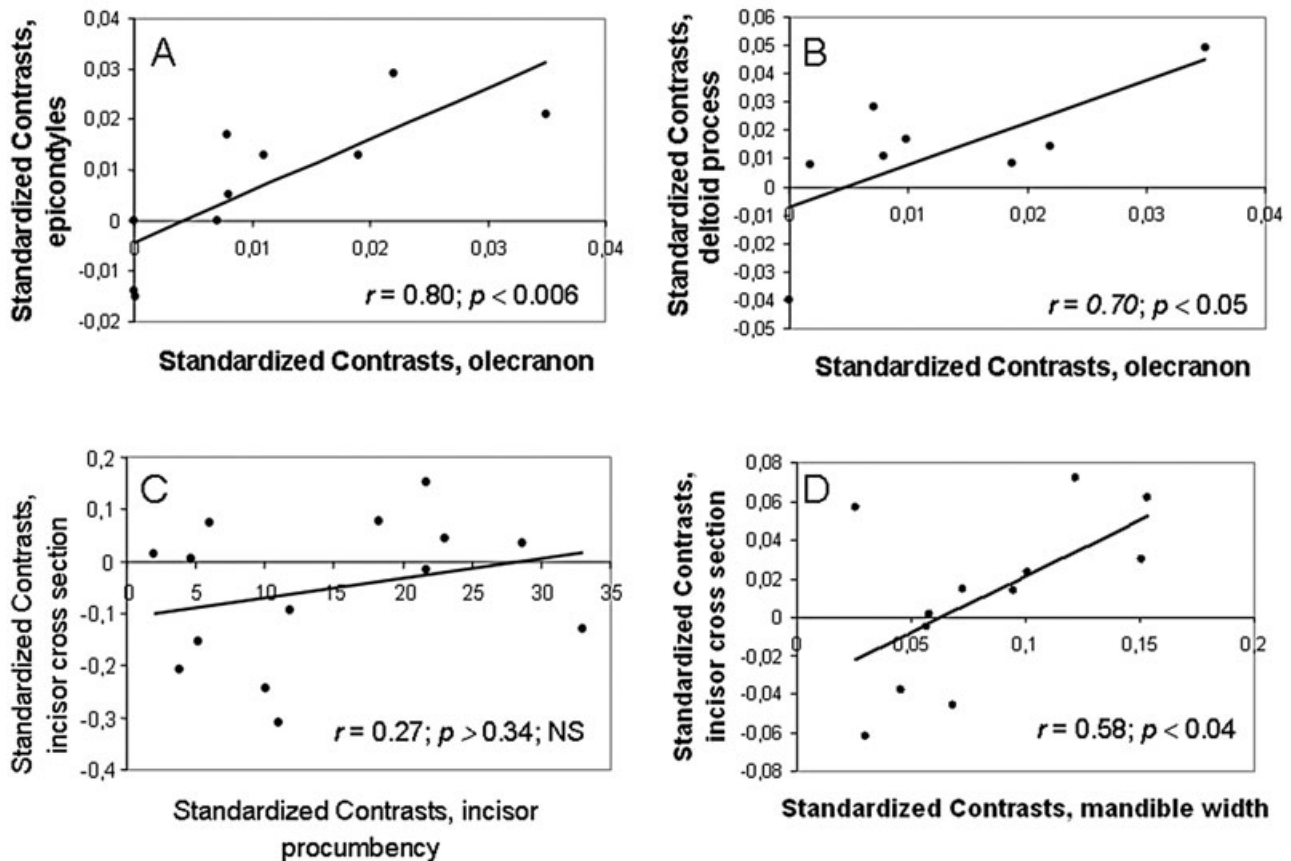
Figure 7. Analyses of character correlation using standardized contrasts on the basis of the phylogeny in Fig. 5. A, relative development of the epicondyles versus relative olecranon length. B, relative position of the deltoid process versus relative olecranon length. C, upper incisor cross section versus upper incisor procumbency. D, upper incisor cross section versus mandible width.

patterns. These findings are discussed below, and conclude that, whereas some of the observed trends were to be expected on the basis of earlier studies, others are less conventional and lead to new research questions and directions of work.

BURROW COMPLEXITY RELATIVE TO BEHAVIOURAL AND MORPHOLOGICAL SPECIALIZATION

A remarkable finding of the present study was that some octodontid taxa that are capable of excavating relatively complex burrows show no substantial modifications in musculoskeletal attributes. This is the case of *Octodon* and *Tympanoctomys*, which posses narrow humeral epicondyles, poorly developed olecranon processes, and nonprocumbent incisors (Figs 1, 6). This strongly suggests that, during the early evolution of subterranean octodontids, behavioural change preceded, and possibly promoted subsequent adaptive change. Interestingly, a recent analysis

of adaptations for digging in *Arvicola terrestris* (Cubo, Ventura & Casinos, 2006) reaches a similar conclusion.

Mayr (1963) advanced the idea that a shift into a new niche or adaptive zone is almost without exception initiated by a change in behaviour, an hypothesis further developed by Wyles, Kunkel & Wilson (1983). However, few analyses offer empirical evidence to test the role of behaviour during the occupation of novel niches and ulterior anatomical evolution (but, for cases in cetaceans and hominids, respectively, see also Stanley, 1992; O'Leary & Uhen, 1999).

Scratch-digging appears to be the norm among fossorial mammals (Vassallo, 1998; Fernández *et al.*, 2000), as well as in any other mammals that only dig occasionally. It thus appears that fossorial habits might easily develop, preceding and promoting subsequent adaptations, although general descriptions of the array of adaptations found among digging mammals may give a different impression. For
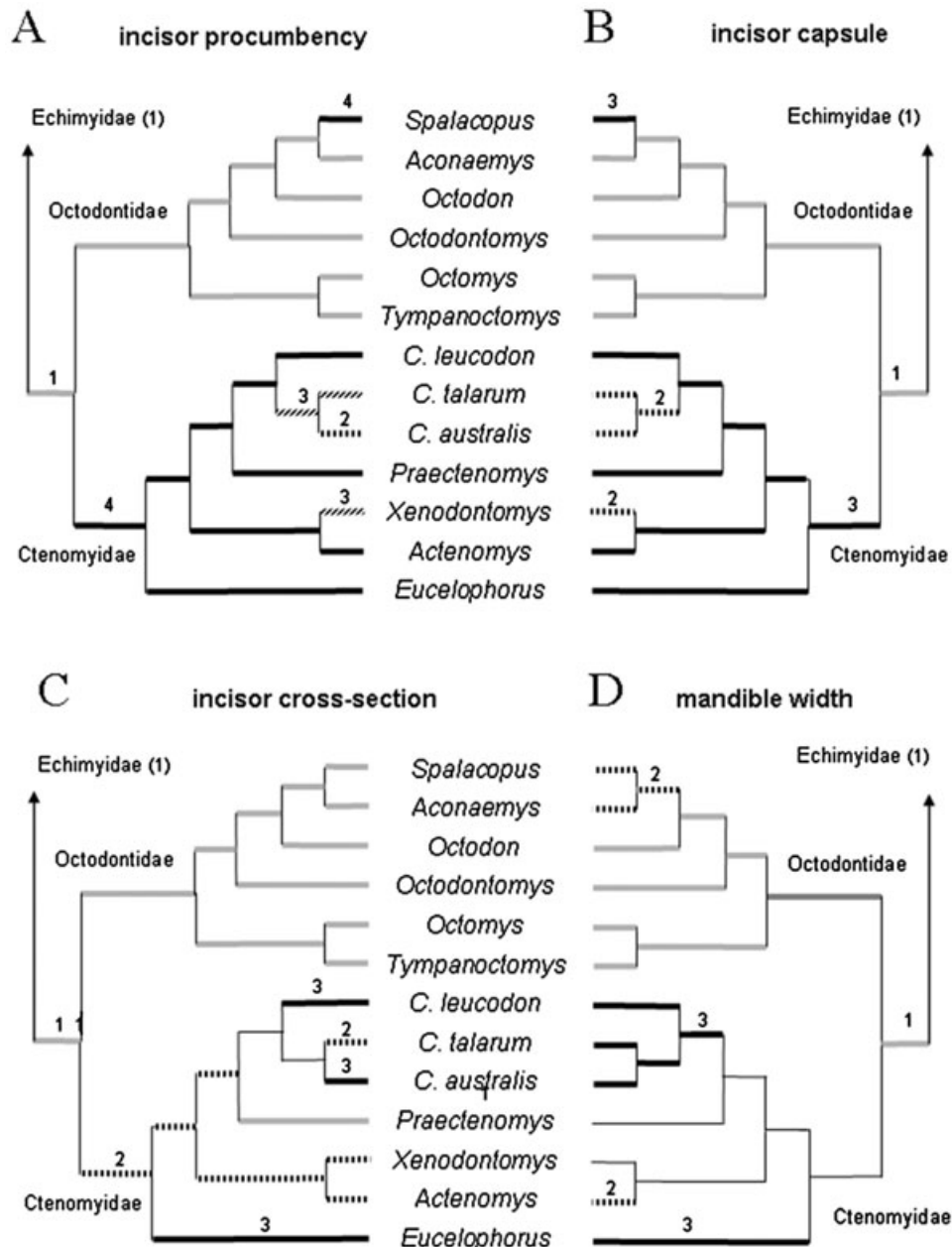
Figure 8. Reconstruction of the evolution of cranial, mandibular and dental characters. Unambiguous states are indicated by shadings of tree branches and numbered on selected branches; ambiguous states are indicated by thin branches. A, degree of procumbency of upper incisors. B, position of upper incisor capsule. C, cross-sectional area of upper incisors. D, mandible width, as an indicator of overall masseter development.

example, Hildebrand (1985) stated that 'most fossorial vertebrates are much modified for their mode of life'. However, organisms are often capable of performing varied behaviours, seemingly overcoming restrictions imposed by a particular morphology (Smith & Redford, 1990).

In summary, we suggest that during the early evolution of lineages giving rise to fully subterranean ctenomyids and octodontids, a change in behaviour probably preceded the origin of structural adaptations. Furthermore, this may be the rule, rather than the exception, in the early evolution of fossoriality among diverse tetrapod lineages. The continuous, often daily remodeling of burrows typical of fully subterranean lineages, may entail substantial adaptations, but the mere construction of complex, stable burrows may not.

STRUCTURAL FLEXIBILITY IN THE EVOLUTION OF THE DIGGING APPARATUS

Previous studies have shown that representatives of octodontids and ctenomyids, such as North American pocket gophers, excavate with both claws (scratch-digging) and incisors (chisel tooth-digging) (Dubost, 1968; Camín, Madoery & Roig, 1995; Vassallo, 1998; Stein, 2000). The dual nature of the digging apparatus in these lineages may explain why specialization say, for example, chisel-tooth digging, is found in species that show only limited specialization for the alternative strategy (for a discussion, see Lessa & Thaeler, 1989). Additionally, these two components of the digging apparatus may be subjected to rather different structural constraints. Thus, Lessa & Patton (1989) suggested that incisor procumbency is constrained by the position of the upper incisor roots. In pocket gophers, upper incisor roots are anterior to the molariforms in most taxa, but are located between the premolar and the first molar in the subgenus *Megascapheus* (Thaeler, 1980), which is the only taxon that includes specialized chisel-tooth diggers. Lessa & Stein (1992) proposed additional morphological constraints of chisel-tooth digging, in contrast with a seemingly more flexible structure of the forelimbs. In conjunction with these observations, Lessa (1990) suggested that chisel-tooth digging was restricted to specialized subterranean lineages, and entailed elongation of the rostrum and slender, procumbent incisors. The reasoning behind this suggestion was that there were limits to obtaining mechanical advantages for the masseteric muscles due to requirements of chewing, so that thinner incisors might be able to turn limited out-forces into high pressures at their tips, as required to penetrate the soil. More recent analyses, as well as our results, reinforce some of these hypotheses, but suggest alternatives to others.

In general, our analyses are in agreement with the suggestions of relatively unconstrained adoption of scratch digging by both fossorial and subterranean rodents. In octodontids and ctenomyids, incisor capsules are lateral to the toothrow, a feature that should allow greater flexibility for the evolution of procumbency. Indeed, incisor capsules are displaced posteriorly to various extents in procumbent ctenomyids and in *Spalacopus*. Mora *et al.* (2003) showed that several species of *Ctenomys*, belonging to different clades within that genus show highly procumbent incisors (angles > 100°). Our larger scale phylogenetic reconstructions (Fig. 8) suggest that high procumbency may have appeared rather early in the history of ctenomyids.

However, our analyses indicate that the association of procumbency with slender incisors, as well as the suggested limitations for increasing the masseteric muscles (Lessa & Stein, 1992) need to be reconsidered. The incisors of *Spalacopus* are both procumbent and slender, but ctenomyids are often characterized by thick incisors in conjunction with increased procumbency (Fig. 8) and strikingly developed masseteric muscles (Figs 4, 8D). Increased mechanical advantages of the masseteric muscles in *Ctenomys* had already been indicated by Mora *et al.* (2003); Verzi & Olivares (2006) described variations in the mandibular joint of ctenomyids in relation to chisel-tooth digging.

These observations suggest that, at least among octodontids and ctenomyids, morphological adaptations for chisel-tooth digging are more varied and complex than anticipated by Lessa (1990). In particular, rather robust incisors, if accompanied by greatly expanded and more advantageously inserted masseteric muscles, may offer a viable alternative to the slender incisors observed in *Spalacopus* and certain pocket gophers.

It should be noted that the three tuco-tuco species included in the present study offer a very limited view of the morphological diversity in *Ctenomys*. Tuco-tucos certainly offer a unique opportunity to examine the set of hypothesis concerning chisel-tooth digging outlined above. Substantial variation in the humeri of ctenomyids (Fig. 2; see also Morgan & Verzi, 2006) suggests that concomitant variation in scratch-digging should be found as well.

As a caveat, our inference of high procumbency appearing early in the history of ctenomyids may be, in part, an artefact of the use of rather late *Eucelophorus* in our analyses. Unfortunately, known earlier representatives of this genus are too fragmentary to be included in this study. Additionally, tuco-tucos are known to have great variation in sociality and, at least in territorial species, incisors are used in agonistic behaviour (Zenuto, Vassallo & Busch, 2001). This may possibly result in an additional source of selective pressure on the evolution of dental and myological attributes of the head of tuco-tucos.

PATTERNS OF EVOLUTION OF ADAPTATIONS TO SUBTERRANEAN LIFE

The evolution of subterranean life and associated morphological variation has been strikingly different in octodontids and ctenomyids. Among octodontids, the lineage leading to *Spalacopus* evolved to fully subterranean life and acquired numerous morphological changes in some 2.2 Ma (Fig. 5). *Aconaemys* is closely related to *Spalacopus*, and some analyses (Gallardo & Kirsch, 2001) even suggest that the former may be paraphyletic with respect to the latter. Information regarding burrow structure and behaviour in *Aconaemys* is rather limited, but our results

suggest that an analysis of the *Spalacopus–Aconaemys* clade would offer a significant opportunity to further elucidate our understanding of the evolution of subterranean life.

By contrast with octodontids, ctenomyids have accumulated changes associated to subterranean life in a mosaic fashion along several lineages, in a process that has taken at least 8 Ma. As indicated above, morphological and behavioural variation among tuco-tucos is also poorly known and offers additional opportunities to study the evolution of subterranean life.

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APPENDIX

Table A1. Functional morphological and behavioral characters related to digging used in this study (see Material and Methods)

Taxa	1. Burrow structure	2. Fossoriality	3. Teres Major process	4. Deltoid process	5. Epicondylar width	6. Olecranon process	7. Incisor procumbency (degrees)	8. Incisor roots	9. Incisor cross section	10. Mandibular width
Aconaemys fuscus	2	1	2	1 (0.38)	1 (0.26)	1 (0.14)	1 (89.7)	1	1 (0.41)	2 (1.81)
Spalacopus cyanus	5	2	2	2 (0.45)	2 (0.29)	2 (0.19)	4 (115.3)	3	1 (0.40)	2 (1.93)
Octodon degus	3	1	1	1 (0.40)	1 (0.25)	1 (0.13)	1 (81.8)	1	1 (0.31)	1 (1.60)
Octodontomys gliroides	2	1	1	1 (0.33)	1 (0.24)	1 (0.13)	1 (89.6)	1	1 (0.43)	1 (1.59)
Octomys mimax	2	1	1	1 (*)	1 (0.22)	1 (0.13)	1 (85)	1	1 (0.46)	1 (1.35)
Tympanoctomys barrerae	3	1	2	1 (*)	1 (0.22)	1 (0.13)	1 (88)	1	1 (0.47)	1 (1.43)
Ctenomys leucodon	5	2	2	2 (0.46)	2 (0.31)	2 (0.19)	4 (118)	3	3 (0.78)	3 (2.38)
Ctenomys australis	5	2	2	2 (0.46)	2 (0.32)	2 (0.20)	2 (94.6)	2	3 (0.85)	3 (2.38)
Ctenomys talarum	5	2	2	3 (0.50)	2 (0.32)	2 (0.21)	3 (102.4)	2	2 (0.59)	3 (2.06)
Eucelophorus zaratei	?	?	?	2 (†)	1 (†)	?	4 (122)	3	3 (0.79)	3 (2.05)
Xenodontomys ellipticus	?	?	?	?	?	?	3 (101)	2	?	?
Actenomys priscus	4	?	2	2 (0.44)	1 (0.25)	1 (0.15)	4 (115.2)	3	2 (0.63)	2 (1.83)
Praectenomys rhombidens	?	?	?	2 (‡)	1 (‡)	2 (0.18)	4 (117.0)	3	1 (0.42)	?
Proechimys poliopus	1	0	1	1	1	1	1	1	?	1
Thrichomys apereoides	1	0	1	2	1	1	1	1	1	1

Original values of the character are shown in parenthesis and discrete character states are indicated by numbers.
*Morgan, unpublished drawing.
†From drawings in Reig & Quintana (1992).
‡From drawings in Quintana (1994).

TAXA AND SPECIMENS EXAMINED

Museo de Historia Natural, Santiago, Chile (MHNC); Laboratorio de Ecofisiología, Universidad Nacional de Mar del Plata, Argentina (LEMP); Museo Municipal de Historia Natural 'Lorenzo Scaglia', Mar del Plata, Argentina (MMP); Museo de La Plata, La Plata, Argentina (MLP).

Octodontidae
Octodon bridgesi MLP: 12.VII.88.1; 12.VII.88.2; 12.VII.88.3; 12.VII.88.4; 12.VII.88.5; 12.VII.88.6; 12.VII.88.7.

Octodon degus MHNC 913; 914; 915; 921; 951; 955; 956; 957.

Aconaemys sagei MLP 17.II.92.8; 17.II.92.10.

Spalacopus cyanus MMP 3807; 3583; 3585; 3590; 3591. MHNC 702; 704. MLP 10.XI.95.5, 30.XI.93.1.

Octodontomys gliroides MMP 755; 2200; 2532; 3057; 3557; MLP 12VII88.10.

Octomys mimax MMP 388.

Tympanoctomys barrerae MMP 3199.

Ctenomyidae
Actenomys priscus MMP 411-M; 497-M; 1567-M; 208-S; 586-S.

Xenodontomys ellipticus MLP: 63-VI-10-49; 60-X-4-1.

Ctenomys australis LEMP P: 1; 4; 8; 9; 10; 12; 14; 16; 17; 18; 23; 31; 33; 35; 38; 39; 41; 42; 46. CA: 2; 4; 5; 6. MMP: 3236; 82.240.

Ctenomys leucodon LEMP 4999; 5793.

Ctenomys talarum LEMP: CT4; CT5; CT5D7; CT(14)19; CT(20)13; CT(15)1; CT16(8); CT19; CT7D(9); CT2.87; CT4FA.88; CT7.87; CT8FA.88; CT9FA.88; CT11FA.88; CT20.87; CT21.87; CT25.87; CT44.87; CT54.88; CT56.88; CT57.88; CT59.88; CT65.88; CT74.88; CT79.88; CT80.88; CT94.88; CT103.88; CT107.88; CT111.88; CT118.88; CT121.88; CT.FA 88(SA).

Echimyidae
Proechimys poliopus MLP: 22.II.00.7; 22.II.00.8.

Thrichomys apereoides MMP: 542.