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Title: Patterns of covariation in the masticatory apparatus of hystricognathous rodents: implications for evolution and diversification.

Running head: Patterns of covariation in the masticatory apparatus of hystricognaths

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Abstract

The mammalian masticatory apparatus is a highly plastic region of the skull. In this study, a quantification of shape variation, the separation of phylogeny from ecology in the genesis of shape brings new insights on the relationships between morphological changes in the cranium, mandible, and muscle architecture. Our study focuses on the Ctenohystrica, a clade that is remarkably diverse and exemplifies a rich evolutionary history in the Old and New World. Current and past rodent diversity brings out the limitations of the qualitative descriptive approach and highlights the need for using integrative quantitative methods. We present here the first descriptive comparison of the whole masticatory apparatus within the Ctenohystrica, by combining geometric morphometric approaches with a non-invasive method of dissection in 3D, iodine-enhanced microCT. We used these methods to explore the patterns of covariation between the cranium and the mandible, and the interspecific morphological variation of the skull with regard to several factors such as phylogeny, activity period, type of habitat, and diet. Our study revealed strong phylogenetic and ecological imprints on the morphological traits associated with masticatory mechanics. We showed that, despite a high diversification of lineages, the evolutionary history of Ctenohystrica comprises only a small number of morphotypes for the skull and mandible. The position of the eye was suggested as a key factor determining morphological evolution of the masticatory apparatus by limiting the number of possible pathways and promoting convergent evolution towards new habitats and diets between different clades.

INTRODUCTION

Rodents represent by far the largest mammalian order with more than 2200 species that occupy most of the ecosystems on the planet (Wilson and Reeder, 2005). But despite such diversification, all extinct and extant rodents share one of the most extreme specializations of the masticatory apparatus. Diprotodonty (i.e. the reduction of the upper and lower incisor series to a single pair) is a hallmark of the rodent masticatory apparatus and is accompanied by a reduction of the number of cheek teeth in association with the development of antero-posterior movements of the mandible for gnawing and chewing (Becht, 1953). Despite the apparent versatility of their masticatory apparatus, the order Rodentia has retained only a small number of different morphotypes for the skull and the mandible (Wood, 1965; Hautier et al., 2008, 2009; Cox and Jeffery, 2011). Different phylogenetic histories and selective pressures have moulded the characteristics of these morphotypes, while strong functional constraints affecting mastication have limited the number of possible evolutionary pathways and promoted convergent evolution.

The Ctenohystrica (*sensu* Huchon et al. 2002: Ctenodactylidae+Diatomyidae and Hystricognathi; Fig. 1) exemplifies a rich evolutionary history in the Old and New World and is remarkable in showing multiple examples of parallel evolution. Both molecular (Huchon and Douzery, 2001; Huchon et al., 2007; Montgelard et al., 2008) and morphological analyses (Bugge, 1985; Luckett and Hartenberger, 1985; Woods and Hermanson, 1985; Marivaux et al., 2002) have long supported the monophyly of this major group of rodents. Like the great majority of living rodents, most of the members of Ctenohystrica are omnivorous or herbivorous (Landry, 1970); however, in contrast to this restricted variation in diet, they display a diverse array of ecological types. The South American Caviomorpha is arguably the most successful group of Ctenohystrica. Their fossil record attests for a rapid radiation, most of the modern caviomorph families appearing during the Paleogene (Lavocat, 1976). Because they diversified in complete isolation in South America during part of the Cenozoic period, they were able to fill niches usually occupied by other placental mammals (Elissamburu and Vizcaíno, 2004; Townsend and Croft, 2008). As a consequence, extant and extinct caviomorphs show a high anatomical and ecological diversity, ranging from the pseudo-ungulate maras (*Dolichotis*) to the fossorial tuco-tuco (*Ctenomys*). Interestingly, the differentiation in diet and habitat has occurred independently in two different monophyletic groups (the Cavioidea [Rowe and Honeycutt, 2002] and the Octodontoidea [Honeycutt et al., 2003]), but few studies have depicted the morphological characters of their masticatory apparatus as a whole. Such parallel evolution gives us a unique opportunity to estimate the role of phylogeny and evolutionary selective forces in driving the morphological evolution of the caviomorph skull.

In the present study, we sought to determine whether ecological factors have influenced the evolution of the skull of Ctenohystrica. Hypotheses explaining the adaptive significance of these traits often relate to diet (e.g. Alvarez et al., 2011a, Croft et al., 2011). It is however reasonable to question whether animals subjected to intense predation pressure like rodents may evolve differently in different types of habitat or during different periods of the day. Phylogenetic constraints may have also played an important role in the morphological evolution of the skull precluding the occurrence of particular feeding modes in a given lineage (Claude et al., 2004). Broad cladewide studies combining analyses of cranial and mandibular variations are clearly lacking for rodents. Here, we use geometric morphometrics to explore the morphological variation of the skull of Ctenohystrica in relation to both phylogeny and ecology. Many works have been devoted to describing the morphological variation of the cranium or the mandible (e.g. Renaud and Michaux, 2003; Michaux et al., 2008; Hautier et al., 2009, 2011; Alvarez et al., 2011b), but the patterns of covariation between these two main elements of the masticatory complex have been largely unexplored. Thus, we strive to characterize how the morphological features of the cranium covary with the mandibular morphology, especially by characterizing the interplay between the position of the eye socket and the masticatory musculature.

MATERIAL AND METHODS

Sample composition - The material studied came from the collection of the *Museum national d'Histoire naturelle* in Paris (MNHN, collection *Vertébrés supérieurs Mammifères et Oiseaux*), the Natural History Museum in London (BMNH), the Mahasarakham University Herbarium (MSUT), and of the *Institut des Sciences de l'Evolution de Montpellier 2* (ISE-M). We analysed 177 mandibles and 196 skulls belonging to sciurognathous and hystricognathous rodents of both sexes, representing 41 genera and 16 families of Ctenohystrica (Fig. 1): Abrocomidae, Capromyidae, Cuniculidae, Caviidae, Chinchillidae, Ctenodactylidae, Ctenomyidae, Dasyproctidae, Diatomyidae, Dinomyidae, Echimyidae, Erethizontidae, Hystricidae, Octodontidae, Petromuridae and Thryonomyidae (see list in S1). The Ctenohystrica have the essential assets to fulfil the objectives set here: they are highly diversified, with a wide range of ecomorphological adaptations, and they include a wide range of mandibular morphologies (Hautier et al., 2011).

Geometric morphometric methods – The mandibular and cranial forms were quantified with 23 and 73 anatomical landmarks respectively (Fig. 2). Digital data of all specimens were acquired using a Microscribe 3-D digitizer and using X-ray micro-computed tomography (µCT). Because the mandible of rodents is constituted by a unique dentary bone of relatively simple shape, most of the landmarks taken on the dentary were of type 2 (e.g. maxima of curvature – Fig. 2; Bookstein, 1991). All configurations (sets of landmarks) were superimposed using the Procrustes method of generalized least squares superimposition (GLS scaled, translated, and rotated configurations so that the intralandmark distances were minimized) following the method used by Rohlf (1999) and Bookstein (1991). Subsequently, mandibular and cranial forms of each specimen were represented by centroid size S, and by multidimensional shape vector v in linearized Procrustes shape space. Shape variability of the mandible was analysed by principal components analysis (PCA) of shape (Dryden and Mardia, 1998). Analysis and visualization of patterns of shape variation were performed with the interactive software package MORPHOTOOLS (Specht, 2007; Specht et al., 2007; Lebrun, 2008; Lebrun et al., 2010). Because it was impossible to remove the incisors from the CT scanned mandible, colors are mapped onto the mandibular incisors in all figures even if only two landmarks were actually taken on the incisors (mandible landmarks 1 and 2, Fig. 2). Thus, it is worth noting that the incisor structure is not analyzed by the set of landmarks used here, and no interpretation can be made on a putative link between incisor shape and ecology. A public version is currently being developed (contact renaud.lebrun@univ-montp2.fr for further information). In order to take into account of the potentially confounding effects of size allometry on shape, size-corrected shapes were obtained as follows. Regressions of Procrustes coordinates against the logarithm of centroid size were computed for all families (except for mono-specific families), yielding family-specific allometric shape vectors (*ASVf*). The *ASVf* represent directions in shape space which characterize family-specific allometric patterns of shape variation. A common allometric shape vector (*ASVc*), obtained as the mean of all the *ASVf*, provided a direction in shape space that minimizes potential divergence in mandibular allometric patterns across families (see Lebrun et al., 2010 and Ponce de León and Zollikofer, 2006 for further details concerning this methodology). *ASVc* was then used to decompose the shape of each species-wise mean shape and of each family-wise mean shape into size-related (*vs*) and size independent (*vi*) components.

Furthermore, covariation patterns between the crania and the mandibles were studied using 2-blocks partial least square analysis, as described by Bookstein et al. (2003), only adapted to allow for the use of 3D landmarks. For the N=164 specimens for which both cranial (k=73) and mandibular (l=23) landmarks had been digitized, cranial and mandibular landmark configurations were aligned separately using GLS, yielding a cranial matrix of N* 3k shape coordinates and a mandibular matrix of N *3l shape coordinates. The PLS analysis computed a series of pairs of unit vectors, the singular cranial and mandibular warps (Uc and Um), each being of length 3k and 3l, respectively. These pairs of singular warps maximize the covariance between the two sets of shape coordinates. Cranial and mandibular projection scores of the specimens on the singular warps were subsequently computed.

Multivariate analysis of Variance (MANOVA) and Canonical Variate Analyses were performed on the principal component scores of each species-wise mandibular and cranial mean shapes (*vi*) in order to assess the effects of different factors on mandibular and cranial shape variation: clades (families), activity period (diurnal, nocturnal, and twilit), type of habitat, and diet (Nowak, 1999; Townsend and Croft, 2008). Following Townsend and Croft (2008), five categories of diets were considered: omnivorous, fruit-leaf, fruit-seed, grass, and roots. Four types of habitats were set apart: open areas, woody areas, burrowers, and ubiquists (Nowak, 1999). The terms “type of habitat” and “diet” refer to the usual habitat and principal diet and are given in S1. In order to quantify mandibular shape affinities at the family level, family-wise mean mandibular shapes were clustered using the UPGMA (unweighted pair-group method) on original shape data and shape data corrected for allometry. MANOVAs were performed with STATISTICA v6.0 (StatSoft Ltd., Milton Keynes, UK), Canonical Variate Analyses with MORPHOTOOLS. The UPGMA trees were computed using PHYLIP (Felsenstein, 1989).

Imaging and reconstruction - In order to reveal detail of both soft tissue and bony anatomy, formalin-fixed heads of *Cavia porcellus* and *Proechimys cuvieri* (representatives of the Cavoidea and Octodontoidea respectively) were imaged using the new technique of contrast-enhanced microCT (Jeffery et al., 2010). The specimens were supplied post-mortem by Biomedical Services, University of Liverpool, and François Catzeflis, Institut des Sciences de l’Evolution de Montpellier, respectively. The specimens were stained by immersion in an approximately 10% solution of iodine potassium iodide (I_2KI) over a number of weeks. The stained specimens were then scanned with the Metris X-Tek custom 320kV bay system at the EPSRC funded Henry Moseley X-ray Imaging Facility, University of Manchester. Voxel resolutions were 0.08 mm (*Cavia*) and 0.04 mm (*Proechimys*). Three-dimensional reconstructions of the skull, mandible, masticatory muscles and orbital contents (eye globe, extraocular muscles and lacrimal gland) were then created using the segmentation function of Amira 5.3.3 (Visage Imaging Inc., San Diego, CA, USA).

RESULTS

Phylogenetic constraints and allometric patterns – A MANOVA indicates highly significant morphological differentiation of the crania and mandibles between rodents relative to phylogeny (mandible F=3.71, p<0.001, dl=11; skull F=9.39, p<0.001, dl=11). The families are well discriminated in the morphospace defined by the two first principal components (Fig. 3). Differentiation is also well expressed at the super-familial level especially for the Cavioidea and Octodontoidea members that occupy distinct positions in the morphospace of the mandibles and crania. However, this phylogenetic differentiation seems to be weaker on the mandibles, almost certainly due to the fact that the lower jaw comprises a single bone that can be characterized by few landmarks (most of them of type II). We have already demonstrated that a continuity of morphologies exists between the two extreme mandibular morphotypes (i.e. cavioid and octodontoid; Hautier et al., 2009). Here, we show that such continuity is not visible for the crania that appear to be clearly differentiated at a familial level.

Compared to other rodent groups, living Ctenohystrica are characterized by a rather high variation in body size, from 170 g in the gundi (*Ctenodactylus*) to 50 kg in the capybara (*Hydrochoerus* - Nowak, 1999). A multivariate regression of the shape component on size, estimated by the logarithm of centroid size, was highly significant (mandible: F=16.5, p <0.001, dl=105; skull: F=66,7, p <0.001, dl=95). As such, allometry therefore explains a substantial part of shape variation, and plays an important role in determining the pattern of morphological diversification of both mandible and skull. A regression of the first principal component on centroid size (Fig. 4) shows that the largest mandibles are characterized by a slight and elongated symphysis, a shallow horizontal ramus, a slight ascending ramus, a low condyle, ventrally oriented incisors, and a distally positioned angular process; whereas the smallest mandibles show a robust symphysis, curved incisors, a deep horizontal ramus, a robust ascending ramus, a high condyle, and a reduced angular process. The biggest crania display a narrow basicranium, posteriorly positioned orbits and elongated, convergent tooth rows; whereas the smallest crania are characterized by a wide basicranium, anteriorly positioned orbits and short, parallel tooth rows.

Morphological variation and environment - Mandibular shapes in relation to the type of habitat (Fig. 5) can be completely discriminated ($F=1.51$, $p<0.001$, dl=3). The first discriminant axis (53.3% of total shape variation, Fig. 5A) separates mandibles with a deep horizontal ramus, a robust ascending ramus, a wide condyle, and a reduced angular process, from mandibles characterized by a shallow horizontal ramus, a slight ascending ramus, a narrow condyle, and a distally positioned angular process. Hence, this axis distinguishes between rodents living in open and woody areas. The second discriminant axis (27.9 % of total shape variation) mainly separates mandibles having widely spaced tooth rows, and reduced angular and coronoid processes, from mandibles showing close tooth rows, and distally positioned and highly divergent angular processes. This axis discriminates the burrowers from other rodents.

A MANOVA indicates a highly significant morphological differentiation of the crania between rodents of different environmental preferences ($F=2.06$, $p<0.001$, dl=3). The direction of shape change is dominated by the relative position of the orbits, the relative development of the basicranium, and the relative size of the cheek tooth rows. The first discriminant axis (50.9 % of total shape variation, Fig. 5B) is strongly associated with the opening of the environment. The crania of rodents living in open areas are characterized by a wide basicranium, posteriorly positioned orbits and elongated, convergent tooth rows; whereas rodents living in woody areas display a narrow basicranium, anteriorly positioned orbits and short, parallel tooth rows. The second discriminant axis (39.5 % of total shape variation) mainly separates ubiquist rodents that exhibit high robust crania with larger posteriorly positioned orbits and narrow basicrania. A consensus of cranial and mandibular morphologies associated with different environments is presented in S2.

Morphological variation and diet – A MANOVA indicates significant morphological differentiation of the mandible between rodents of different diets ($F=3.09$, $p<0.001$, $dl=5$). Morphological groups reflecting distinct types of diet are displayed along the first discriminant axis (26.9% of total shape variation - Fig. 6A). This axis mainly discriminates grass eaters from other types of diet by separating robust mandibles with a strong symphysis, short parallel tooth rows, a thin angular process, and a posteriorly positioned condyle, from mandibles showing a slender symphysis, elongated and convergent tooth rows, a distally positioned angular process, and an anteriorly positioned condyle. In terms of shape variation, the second discriminant axis (25.6% of total shape variation) separates mandibles that show an elongated angular process and a low condyle relative to the alveolar plane, from mandibles having a reduced angular process associated with a higher position of the condyle. This axis mainly discriminates rodents that eat fruit and seeds from other groups.

This morphological differentiation relative to diet was also detected in the cranial morphology ($F=4.96$, $p<0.001$). The first discriminant axis (27.7% of total shape variation, Fig. 6B) separates crania characterized by a wide basicranium, posteriorly positioned orbits and elongated convergent tooth rows, from crania with a narrow basicranium, anteriorly positioned orbits as well as short and parallel tooth rows. The second discriminant axis (26.2% of total shape variation) mainly discriminates high robust crania exhibiting larger posteriorly positioned orbits and a narrow basicranium, from gracile crania that exhibit relatively smaller orbits and a wide basicranium (Fig. 6B). CV1 well discriminates grass eaters from other types of diet whereas CV2 tends to separate seed-eating species. A consensus of cranial and mandibular morphologies associated with different diets is presented in S3.

Morphological variation and activity pattern – A MANOVA indicates a significant morphological differentiation of the mandibles between rodents of different activity patterns ($F=1.51$, $p<0.001$). However, a weak differentiation is observable on the two first discriminant axes (Fig. 7). The first discriminant axis explains 42% of total shape variation (Fig. 7A). The morphological differentiation depicted by this axis is dominated by a change in the shapes of the angular, coronoid, and condylar processes and the relative differences in the sizes of cheek tooth rows. In the positive direction, the mandibles are gracile and exhibit a slender symphysis, elongated and convergent tooth rows, a distally positioned angular process, and an anteriorly positioned, low condyle. In the negative direction, mandibles are robust with a strong symphysis, short parallel tooth rows, a thin angular process, and a distally positioned, high condyle. The second discriminant axis explains a small amount of variation (Fig. 7A, 31.8 % of total shape variation) among taxa of different activity patterns; it partly separates crepuscular rodents from nocturnal and diurnal forms.

The cranial shape differences associated with nocturnality and diurnality are significant ($F=2.06$, $p<0.001$). The crania of nocturnal rodents present positive scores along the first discriminant axis (43,1 % of total shape variation). This direction of shape change is dominated by crania with a narrower basicranium, anteriorly positioned orbits, and shorter, parallel tooth rows (Fig. 7B). In the negative direction, crania of diurnal species are characterized by a wider basicranium, posteriorly positioned orbits, and elongated, convergent tooth rows. The crepuscular rodents occupy the same morphospace as diurnal forms. The second discriminant axis (Fig. 7B, 37.3 % of total shape variation) does not allow the detection of morphological differentiation between diurnal, nocturnal, and crepuscular species. A consensus of cranial and mandibular morphologies associated with different activity patterns is presented in S4.

Covariation between the skull and the mandible - PLS analysis was performed using both landmark datasets in order to assess the morphological features that covary between the skull and the mandible (Fig. 8). As expected, the skull and mandible show strong morphological covariation. The association of mandibular features highly depends on the position of eyes, the length of the tooth rows, and the shape of the basicranium on the cranium. More precisely, we observed that mandibles with a deep horizontal ramus, a robust ascending ramus, a high condyle, curved incisors, and a reduced angular process are associated with skulls that display a narrow basicranium, anteriorly positioned orbits and short, parallel tooth rows. In contrast, mandibles with a shallow horizontal ramus, a slight ascending ramus, a low condyle, ventrally oriented incisors, and a distally positioned angular process appear to be associated with skulls characterized by a wide basicranium, posteriorly positioned orbits and elongated, convergent tooth rows (Fig. 8). It is worth noting here that the specimens tend to group according to their environment on the first three singular warps, especially on SW2 (Fig. 8).

Orbital contents – In order to assess the effect of orbital morphology on cranial and mandibular morphology, the orbital contents of a member of the Cavioidea and Octodontoidea (*Cavia* and *Proechimys* respectively) were reconstructed from contrast-enhanced microCT scans (Fig. 9). Both specimens suffered considerable shrinkage of the tissues due to the effects of the paraformaldehyde in which they had been stored, and the iodine potassium iodide with which they were stained. This is particularly noticeable in the eye of *Cavia* (Fig. 9A). However, shrinkage notwithstanding, it can be seen that the eyes of both *Cavia* and *Proechimys* are supported in the orbit by a mass of soft tissue – largely the lacrimal gland (Cooper and Schiller, 1975).

As in most other mammals, *Cavia* has six extraocular muscles (Fig. 9A). The superior, inferior, medial and lateral rectus muscles all arise from a tendinous ring around the optic nerve as it emerges through the optic foramen. Because of the postero-ventral position of the optic foramen in the rodent orbit, the radial pattern of the four rectus muscles is rotated (by about 20°) relative to the more familiar human condition (Oyster, 1999), in which the medial and lateral rectus sit on a plane orthogonal to the midsagittal plane of the skull. As a consequence, the actions of the extraocular muscles are as follows: the superior rectus pulls the eye dorso-laterally, the inferior rectus pulls ventro-medially, the medial rectus pulls dorso-medially, and the lateral rectus pulls ventro-laterally. The same situation is seen in the extraocular muscles of *Proechimys* (Fig. 9B), but with an even greater rotation of approximately 30° from vertical. Thus, compared to *Cavia*, the superior rectus of *Proechimys* has an increased lateral component to its pull direction, the inferior rectus has an increased medial component, the medial rectus has an increased dorsal component, and the lateral rectus has an increased ventral pull.

The superior and inferior oblique muscles complete the set of six extraocular muscles. The inferior oblique originates from the anterior part of the orbital wall – near the dorsal margin of the infraorbital foramen in *Cavia*, more postero-ventral in

Proechimys – and runs back to insert on the inferior surface of the eyeball. It forms an approximate 40° with the midline (in dorsal view) and thus acts to extort the eye. The superior oblique shows greater variation between the two species. In *Proechimys*, the superior oblique lies in a similar orientation to the inferior oblique and acts to rotate the eye inwards. However, the superior oblique of *Cavia* acts at a much greater angle to the midline, approximately 70° (similar to that measured by Simpson and Graf, 1981), and hence this muscle tends to elevate the eye to a greater degree.

DISCUSSION

Morphological variation and adaptation - Our results demonstrate strong phylogenetic and ecological imprints on the morphological traits associated with masticatory mechanics in hystricognathous rodents. Though all members of Hystricognathi are supposed to be characterized by a hystricognathous mandible and hystricomorphous infraorbital foramen, these morphological features, used for establishing long-standing classifications (Brandt, 1855; Tullberg, 1899), were shown to be highly variable among our dataset. We have already demonstrated that the morphological variation of the mandible is great within the extant shapes of hystricognathous jaws and noticed a significant morphological differentiation of the hystricognathous mandibles between rodents of different diet or habitat (Hautier et al., 2011). We show here that similar variations and differentiations are also observable in the crania of Hystricognathi especially regarding the position of the eye socket, the shape of the basicranium, the zygomatic arch, and the palate and tooth rows. Whatever the factor considered (habitat, diet, or activity patterns), the cranium always showed a clearer differentiation than the mandible (Figs. 5, 6, and 7). It is highly likely that the number and type of landmarks used to digitalize the mandible had a strong influence on the results, especially if we consider the strong covariation observed between the areas of muscle insertions on the mandible and their cranial counterparts. This methodological artefact should be taken into consideration before using the mandible as a proxy for ecological interpretations.

The different clades of Ctenohystrica are well differentiated especially with regard to cranial morphology (Fig. 3B). Alvarez et al. (2011b) studied the relative influence of phylogeny and ecology on the mandibular variation of caviomorph rodents. They found that phylogenetic constraints were more important than ecological factors for interpreting the morphological variation of the mandible. On the one hand, our results suggest an evident persistent phylogenetic effect upon the morphology of the masticatory apparatus. On the other hand, we showed that rodents living in the same habitat still display an overall convergence in their skull shape. The fact that both Octodontoidea and Cavioidea clades evolved parallel adaptations in their masticatory apparatus with other members of Ctenohystrica implies that phylogenetic constraints did not prevent the skull evolving similarly in a certain type of environment. Among the three discriminant analyses, diet and habitat come foremost in shaping the rodent skull whereas a lower discrimination was obtained for activity patterns (Fig. 7). Roll et al. (2006) proposed that phylogeny strongly constrains the evolution of activity patterns in rodents. However, no conspicuous morphological convergence for the cranium and the mandible was detected between species sharing similar activity patterns. Rodents living in open and woody areas tend to be more diurnal and nocturnal respectively, which could explain some similarities observed between the spatial distribution of the two discriminant analyses involving habitat and activity patterns. However, no clear rule can be generalized, and some exceptions exist, like the Abrocomidae and Thryonomyidae that are nocturnal and live in open areas, or the Dasyproctidae that are diurnal and live in forest habitats.

We observed similar morphological evolution towards new habitats and diets between these different clades, which mirrors previous results showing that specialized dietary adaptations can be recognized in the rodent masticatory apparatus (Michaux et al., 2007; Hautier et al., 2009; Samuels, 2009). Rodents living in open habitats such as guinea pigs are distinguished from other rodents by a suite of derived morphological features, including upward-facing eyes, a wide basicranium, and elongated convergent tooth rows. Rodents living in woody areas such as spiny rats further differ from these forms by displaying more laterally facing orbits, a narrow basicranium, and short parallel tooth rows. Interestingly, the same associations of features were found to differentiate grass-eating rodents from other herbivorous and omnivorous rodents. In fact, such a result was highly expected because the environment (open *vs* woody areas) necessarily has profound effects upon the type of diet, as rodents living in open habitat are more likely to present a diet including grass and thus show correlated adaptive traits. As a matter of fact, an enlarged tooth area (Samuels, 2009) in association with the development of propalinal movements (Vassalo and Verzi, 2001) has long been recognized as a feature of herbivorous rodents and mammals as a whole, and we found this association of morphological features in different groups of rodents living in open areas. Except for omnivorous rodents that appear highly adaptable, habitats seem to impede the morphological evolution toward a type of diet. Among the species living in woody areas, rodents feeding on hard food items (fruit-seed) clearly depart from the remaining trophic categories (Fig. 6).

Considering the versatility of their feeding apparatus, Landry (1970) hypothesized that rodents should share an omnivorous common ancestor. Hystricognath rodents are mainly herbivorous and frugivorous (Townsend and Croft, 2008), but almost all rodents will opportunistically incorporate meat in their diet (Landry, 1970). Among a broad cladewide taxonomic sampling, Samuels (2009) showed that a set of moderate characters (e.g. relatively short and narrow rostrum, narrow incisor blades, and moderate tooth row lengths) usually characterizes omnivorous rodents. In our dataset, only the Capromyidae (*i.e.* hutias) and Hystricidae (*i.e.* Old World porcupines) have been considered as true omnivores. Although capromyid rodents do share some morphological features with the omnivorous morphotype defined by Samuels (2009), such as a relatively short rostrum or narrow incisors, on the other hand porcupines display a very different array of characters, including a dome-shaped skull, and a longer rostrum and tooth rows. In fact, both families were most similar to rodents whose diet is dominated by fruits and leaves according to a discriminant analysis on the cranium and the mandible (Fig. 6).

In his precise study of the cranial morphology and dietary habits of rodents, Samuels (2009) differentiated generalist herbivores (diet composed primarily of soft leafy vegetation and seeds) from specialist herbivores (diet composed mostly of fibrous or difficult to process plants). He showed that, compared to insectivorous, carnivorous, and omnivorous rodents, all herbivores share a more massive skull characterized by a wider rostrum, larger temporal fossae, thicker and broader zygomatic arches, broader incisor blades, and longer tooth rows with larger molar occlusal surfaces. Our results can only partially confirm these observations because a great majority of the Ctenohystrica examined here are herbivorous. However, like

Samuels (2009), we found different degrees of specialization of the masticatory apparatus between both types of herbivore among our dataset. In particular, the rodents with a diet composed primarily of fruits and seeds show skulls distinct from all the other groups in that both the zygomatic arch and the skull roof are relatively narrow and the nuchal region and basicranium are moderately developed. This diet, mainly composed of soft food items, should require reduced masticatory processing. When compared to other dietary groups, the graminivorous rodents show the most important morphological differences (Fig. 6), especially regarding the height of the mandibular condyle, the length of the rostrum and tooth rows, the breadth of the zygomatic arches, and the width of the nuchal region and temporal fossae. These consistent craniomandibular characteristics reflect changes in the origin and insertion of the masticatory muscles and in the masticatory mechanics as a whole. A diet composed primarily of grass demands a greater occlusal pressure, and could explain an enlargement of the areas of origin and insertion of the masseter and the temporalis (Greaves, 1991; Satoh, 1997; Michaux et al., 2007). As a matter of fact, the masseter and temporalis muscles show a greater development in the guinea pig compared to the spiny rat (Fig. 9). In that case, a larger masseter will promote the propalinal movement of the mandible (Turnbull, 1970) in association with an increase of the cheek tooth areas, a result previously confirmed by an analysis of the direction of chewing movement in Caviomorpha (Vassalo and Verzi, 2001). Croft et al. (2011) indicated that the incisor morphology is related to diet. Grass eaters are characterized by long, mesiodistally broad incisors; fruit-seed eaters have short, buccolingually deep incisors; and fruit-leaf eaters have long buccolingually deep incisors. The incisors are only used for cropping in grass-eaters like the guinea pigs or chinchillas, whereas they need to better resist the higher forces necessary to penetrate hard food in fruit-seed eaters (Croft et al., 2011). Thus, the enlargement of the temporalis is unlikely to correspond to an increase of the mechanical advantage of the incisor bite, but instead may mainly facilitate the stabilization of the mandible during the chewing stroke (Greaves, 1980). The association of morphological features observed in graminivorous rodents seem to be also highly linked to the acquisition of hypsodont cheek teeth, which facilitates the processing of a more fibrous diet (Janis, 1988; Vianey-Liaud, 1991; Samuels, 2009). A similar array of morphological characters evolved independently in the extinct family Theridomyidae (Hautier et al., 2010) and was associated with a drastic cooling in the Late Eocene and a subsequent Oligocene aridification (Vianey-Liaud, 1991). Samuels (2009) considered the enlargement of the nuchal region of specialized herbivores as reflecting the development of the neck musculature used in head stabilization in more fossorial rodents. Nonetheless, it should be kept in mind that the development of the basicranium, characterizing rodents living in open areas, may have in turn influenced the evolution of the whole back of the skull.

Allometric patterns and adaptation – Allometry is also a well-known factor to intervene in the evolution of morphological features (Frankino et al., 2005), especially in rodents (Samuels, 2009; Wilson and Sánchez-Villagra, 2009). Wilson & Sánchez-Villagra (2009) showed that convergent morphology, rather than evolutionary history, has played a major role in the generation of allometric patterns during the evolution of muroid and hystricognathous families and explains the disparate structure of their allometric space. The mandibular allometric trends described here reflect in some way broad adaptive patterns. On the mandible, positive allometry was found for tooth row and symphyseal lengths, while negative allometry characterized the height of the condyle and the corpus breadth. For Satoh (1997), an increasing weight of the mandible implies an increase of the area of insertion of the masticatory muscles (especially the masseter). Thus, an increase in size will have profound biomechanical implications and be accompanied by an increase of the overall robustness of the mandible, modifying the lever arm of the masseter and biting efficiency as a result. If the proportion of the skull did not change with the size, larger skulls would be selectively disadvantaged in displaying smaller occlusal surface and pressure (Emerson and Bramble, 1993; Satoh, 1997; Michaux et al., 2007).

Cranial allometric patterns are more difficult to interpret in terms of adaptive signal. The cranium shows a positive allometry for the length of the snout and tooth rows accompanied by a posteriorly located orbit, and a negative allometry for the width of the basicranium. Most of the bigger genera (e.g. *Hydrochoerus*, *Lagostomus*, or *Myocastor*) live in open areas and display caudally displaced orbits, a relatively longer snout, longer tooth rows, and a narrow basicranium; whereas the medium-sized rodents sharing the same type of habitat are characterized by well-developed tympanic bullae and a wide basicranium. Enlarged tympanic bullae allow the rodent to detect a predator by increasing the amplification of sounds (Squarcia et al., 2007). To some extent, selective pressures should act differently on the evolution of sensory systems of bigger rodents like capybaras, notably because they interact with types of predators other than the common birds of prey. However, the morphology of the tympanic bullae per se is not enough to demonstrate conspicuous modifications of their hearing abilities, and further investigations are needed notably on the morphology of the middle and inner ears.

Covariation patterns and ecomorphology of orbit orientation – Relatively high, convergent orbits characterize predatory mammals that use vision to target and track their preys (Cartmill, 1972). In contrast, animals subject to heavy predation like artiodactyls or rodents display narrow fields of binocular overlap and large panoramic visual fields (Heesy, 2004). Divergent orbits are associated with panoramic visual fields while convergent orbits are associated with larger binocular visual fields (Heesy, 2008). Heesy (2008) stated that arboreality does not explain the variance in orbital convergence among non-primate eutherians. However, most of the species studied were gliding taxa (16 out of 26) and few of them were truly terrestrial rodents (4 out of 26). Gliding rodents generally show more convergent orbits, and arboreal rodents usually show less convergent orbits than terrestrial species. Given the limited taxonomic and ecological sampling of these previous studies (Heesy, 2004, 2008), further investigations are needed to test whether there is a relationship between orbit convergence and ecology in rodents. We clearly showed that substrate preference is a significant factor explaining the evolution of the skull in hystricognathous rodents (Fig. 5). Our results demonstrate that rodents living in woody areas have significantly more laterally facing orbital margins. Moreover, we showed that the morphology of the mandible covaries strongly with the morphology of the cranium, especially regarding the position of the eye socket. Although morphological features of the mandible have historically been linked to different diets, the distribution of covariate traits (Fig. 8) suggests that the position of the eye has played a major role in the morphology of masticatory apparatus during the course of hystricognath evolution.

We propose that there is a link between orbit orientation and mode of life. Achieving such a morphological transformation calls for major myological reorganization. One of the most conspicuous morphological specializations involves the arrangement of the extraocular musculature. The comparison of the gross anatomy between two rodents of the octodontoid and cavioid types demonstrated that the superior oblique acts to rotate the eye inwards in *Proechimys*, whereas this muscle tends to elevate the eye to a greater degree in *Cavia*. This may reflect the open habitats in which *Cavia* lives, compared to the more closed, woody areas of *Proechimys*. As a matter of fact, it has been suggested that the medial and the lateral extraocular muscles influence the position of the rotational axis of the eye and help maintain its linear position (Demer et al., 2000; Demer, 2002; Heesy, 2005). Indeed, it seems that the extraocular muscle system can partly compensate small-scaled eye movements caused by the contraction of the temporalis and pterygoid muscles (Heesy, 2003; Heesy, 2005; Heesy et al., 2008). Contractions of the masticatory musculature, especially the temporalis muscle, could likely distort the lateral orbital margin (Cartmill, 1970) and probably disrupt oculomotor precision (Heesy, 2005). For animals such as rodents with large panoramic visual fields, and for which masticating represents one of their main activities, the necessity of locating approaching predators remains essential in order to survive. We hypothesize that the areas of origin and insertion of the temporalis muscles might have been displaced to insulate the eye from its action during mastication and maintain oculomotor stability (Cartmill, 1980; Ross, 1996, 2000; Heesy, 2005). Following this reasoning, the position of the eye is likely to constrain the size and the shape of the two main protractor muscles (i.e. the masseter and temporalis muscles), and to limit the number of possible pathways then promoting convergent evolution as a result.

However, the position of the eyes cannot itself explain all morphological characteristics of the hystricognathous masticatory apparatus, and several other constraints, development for instance, may have as well influenced the orbit orientation. Rodents living in woody areas such as spiny rats associate a mandible characterized by a high condylar process and a narrow angular process distinctly lateral to the plane defined by the alveolus of the incisors, with laterally facing orbital margins, and gracile zygomatic arches. Rodents living in open habitats such as guinea pigs differ from these forms in displaying a mandible characterized by a weakly individualized, low condylar process and a distally positioned angular process (Hautier et al., 2009), as well as upward-facing eyes with more convergent orbits and robust zygomatic arches. In metatherians, the morphology of the zygomatic arch, which forms the inferior margin of the orbit, shows an allometric relationship with the orbital convergence (Derby et al., 2003). An increase in the robustness of the zygomatic arches is then likely to induce a higher orbital convergence (Derby et al., 2003). We observed a similar allometric trend among our dataset. The robustness of the zygomatic arch in rodents was usually linked to the development of the masseteric complex, and rodents like the guinea pigs generally display robust zygomatic arches (Fig. 9). The orbital convergence observed in these groups could be partly due to a greater development of the area of origin and insertion of the masticatory muscles in rodents that show a bigger size and/or feed on harder food items.

This study illustrates how a holistic approach allows an objective study of the morphological variation of a highly plastic region such as the masticatory apparatus, in reflecting the multiple evolutionary paths followed during the evolution of rodents. Comparative data and fossil evidence (Alvarez et al., 2011a) suggested that early differentiation of the mandibular morphology in caviomorph rodents could reveal the existence of constrained evolutionary diversification. Our analysis provides the first broad cladewide quantified account of the morphological covariation exhibited by the mandible and the cranium. We showed that the demand of evolving in different habitats partly explains the cohesive suite of morphological, ecological and behavioural traits observed in these rodents. We also characterized the interplay between the position of the eye socket and the masticatory musculature, and we suggested the orbit orientation as a key factor constraining the mechanics of the masticatory apparatus and thus promoting convergent evolution as a result. The patterns observed here are of primary importance for interpreting the morphological diversification of early hystricognath rodents.

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Figure legends

Figure 1. A phylogenetic tree of the rodent clade Ctenohystrica derived from molecular analyses (Huchon et al., 2002, 2007; Opazo, 2005). Blue, Ctenohystrica; green, mouse relative clade; red, sciurid relative clade. Dashed lines highlight the sample composition. Original artwork by Laurence Meslin, © Laurence Meslin – CNRS.

Figure 2. Landmarks digitized on the mandible and the skull. Lateral (A) and anterior (B) views of the mandible; lateral (C) and ventral (D) views of the skull.

Figure 3. Principal component analyses and associate patterns of morphological transformation for the mandible (A) and cranium (B) among Ctenohystrica of different habitats. Colors indicate the relative amount of change in local area necessary to attain that shape, with reference to the consensus shape. Yellow and violet code for increases and decreases in surface area respectively. White indicates isometry. Scale unit: local area/same local area of the reference shape.

Figure 4. Regression of the first principal component on the centroid size.

Figure 5. Canonical variate analyses and associated patterns of morphological transformation for the mandible (A) and cranium (B) among Ctenohystrica of different habitats. Symbols indicate different clades: open stars, Diatomyidae; bars; Petromuridae; open circles, Thryonomyidae; crosses, Hystricidae; open triangles, Octodontoidea; open diamonds, Cavioidea; open squares, Chinchilloidea; trifid crosses, Erethizontoidea; "plus" symbol, Ctenodactylidae. Colors indicate the relative amount of change in local area necessary to attain that shape, with reference to the

consensus shape. Yellow and violet code for increases and decreases in surface area respectively. White indicates isometry. Scale unit: local area/same local area of the reference shape.

Figure 6. Canonical variate analyses and associated patterns of morphological transformation for the mandible (A) and cranium (B) among Ctenohystrica of different diet. Same legend as Figure 5.

Figure 7. Canonical variate analyses and associated patterns of morphological transformation for the mandible (A) and cranium (B) among Ctenohystrica of different activity patterns. Same legend as Figure 5.

Figure 8. First three singular warp mandibular and cranial scores and associated mandibular and cranial co-variation patterns for the subset of specimens for which the crania and the mandibles had been digitized. Note how specimens tend to group according to their environment on the first three singular warps.

Figure 9. Right lateral view of 3D reconstructions of the skull, mandible and masticatory muscles of (A) guinea pig *Cavia porcellus*, (B) spiny rat *Proechimys cuvieri*. *Abbreviations*: eom, extra orbital muscles; iozm, infraorbital part of zygomaticomandibularis; pdm, posterior deep masseter; pm, posterior masseter; sm, superficial masseter; t, temporalis. Scale bars: 5mm.

Supporting Information

S1. List of measured specimens. *Abbreviations:* MNHN: Museum National d'Histoire Naturelle, Paris. Collection Vertébrés supérieurs Mammifères et Oiseaux; BMNH: Natural History Museum in London; MSUT: Mahasarakham University Herbarium; UMC: Montpellier University Collection.

S2. Consensus cranial and mandibular morphologies associated with different environments. A, burrowers; B, open areas; C, ubiquists; D, woody areas.

S3. Consensus cranial and mandibular morphologies associated with different diets. A, fruit-seed; B, grass; C, fruit-leaf; D, omnivorous; E, roots.

S4. Consensus cranial and mandibular morphologies associated with different activity patterns. A, crepuscular; B, diurnal; C, nocturnal.