Morphological adaptations of incisors in the subterranean Gansu zokor, *Myospalax cansus* (Rodentia, Spalacidae)

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Abstract. The incisor morphology of rodents varies a good deal among different genera and each structure may have a special evolutionary significance. Some basic and lateral profile measurements of upper and lower incisors which may reflect morphological adaptations of the Gansu zokor (*Myospalax cansus*, a typical subterranean rodent in northern Asia) and the brown rat (*Rattus norvegicus*, a typical aboveground rodent that has close body size to the Gansu zokor) were analyzed. GIS (Geographic Information System) software and nonlinear regression were used to analyze incisor lateral profile, allowing the incisors to be viewed as circular arcs with a high degree of accuracy. The results show that: i) zokors have more robust (i.e. larger anteroposterior diameter and transverse diameter values), heavier and longer upper as well as lower incisors than rats; ii) zokors show a significantly higher level of sexual dimorphism (male dominant) than rats on the incisor morphology (including basic and lateral profile measurements) and iii) the upper incisor is heavier than lower incisor in rats, as opposed to zokors, in which the lower incisor is heavier than the upper incisor, indicating that more resources must have been allocated to lower incisors of zokors.

Key words: subterranean rodent, incisor morphology, adaptation, GIS software

Introduction

Teeth play an important role in the daily life of animals and the morphological structure of teeth will reflect adaptations to different lifestyles (Gordon & Illius 1988, Van Valkenburgh 1989, Janis 1995, Pan 2006, Christiansen 2008, Samuels 2009). The highly derived, ever-growing rodent incisors are very effective tools for food processing, gnawing, and burrowing and may have significantly contributed to the great success of the Rodentia (Landry 1970, Samuels 2009, Van Daele et al. 2009).

Subterranean rodents are a widely distributed group of rodent species that live primarily underground and show strong adaptation to that environment (Lacey et al. 2000). They do a large amount of digging underground to forage for food, escape from predators, and mate. Among subterranean rodents, three digging types have been recognized based on the methods of breaking up soil, i.e. head-lift digging, chisel-tooth digging and scratch digging (Hildebrand et al. 1985). The former two types depend heavily on the incisors for digging activities; and while the scratch diggers may depend more on their forelimbs, in some species the incisors are also used during digging (Lacey et al. 2000).

Previous studies on the morphology of subterranean rodent incisors have found remarkable examples of ecological adaptation. Landry (1957) suggests that the procumbency of rodent upper incisors is related to their specific life style, e.g. subterranean genera such as *Thomomys* and *Cryptomys* have more procumbent and more proodont upper incisors, an adaption to their obligatory subterranean life-style. Even between sympatric species of the same genus the procumbency of rodent upper incisors could be different e.g. within *Ctenomys* which is related to habitat segregation (Vassallo 1998). Palestine mole-

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rats (*Spalax ehrenbergi*), which are aggressive and solitary subterranean rodents, use their lower incisors mainly to excavate their tunnel systems. Zuri et al. (1999) found that the lower incisors of these animals grow significantly faster than the upper incisors, while the upper and lower incisors of males grow significantly faster than incisors of females.

As typical subterranean rodent species mainly distributed in North Asia, zokors (*Myospalax spp.*) live their whole lives underground (Chu et al. 2007). They possess stocky and strong forelimbs and laterally flattened claws frequently supported by a bony phalanx extending into them (Begall et al. 2007). The forelimbs are always used for digging; they belong to the scratch digging group of Lacey et al. (2000). However, the incisors are also frequently used for breaking up highly compact soils or cutting the roots of plants when digging their burrows (Fan & Gu 1981, Su 1992). We performed a comparative morphological study of the incisors of the Gansu zokor (*Myospalax cansus*) and brown rats (*Rattus norvegicus*, a typical and one of the most common aboveground rodents that has close body size to the Gansu zokor). The aim is to answer whether and, if, how the zokors have built up morphological incisor adaptations for their subterranean life-style.

Material and Methods

Incisor preparation and measurement selection

Skulls of adult zokors and rats of known sex (ten males and ten females of each species) and body mass were selected and boiled in water for about two hours. Both upper and lower incisors were pulled out carefully using forceps and oven dried at 80°C. Two kinds of measurements were taken: 1. the basic measurements: incisive mass (IM), anteroposterior diameter (AD), transverse diameter (TD); 2. the lateral profile measurements: radius of curvature (r), arc angle (θ), arc length (l).

Basic measurements

The upper/lower incisor of each individual was weighed with an electronic analytical balance (0.0001 g, Metter Toledo Inc.). The anteroposterior diameter and transverse diameter were measured according to the definitions in Millien & Jaeger (2001) to 0.01 mm using vernier calipers. The greatest skull length (GSL), which was a relatively stable index for representing body size of mammals (Yom-Tov et al. 2003, Liao et al. 2006), was also measured to correct the measurements for intersexual and intraspecific comparisons.

Lateral profile measurements

The lateral profile of rodent incisors varied a good deal among different genera and each structure form has its own special evolutionary significance (Landry 1957). The methods as well as indices used to determine lateral profile were however not well established. For example, most of previous studies were usually with a basic assumption that the incisors could be viewed as circular arcs (Landry 1957, Kerley 1976, Akersten 1981) but no objective tests on this assumption have been done yet. According to the geometry, if the lateral profile of incisors does form a circular arc structure, relevant general indices can easily be computed with coordinate information of the two tips (Landry 1957). Inversely, we can also test whether the lateral profile could be viewed as a circular arc by using Nonlinear Regression analysis, if we know the coordinates of enough points along the lateral profile. Based on our daily observations, the lateral profile of incisors shows good symmetrical vaulted structure, indicating that we can at least assume it is an elliptic arc. GIS (geographic information system) software is generally developed for the management of large scale digital maps and georeferenced data. Numerous GIS systems are nowadays available and their powerful functions on geospatial data handling can easily be applied to treat 'small scale' images. In this study we introduced ArcGIS (ESRI Inc.) to analyze lateral profile of incisors.

A semicircle frame with a horizontal diameter and a vertical radius intersecting to three intersecting points (M, N and L, see Fig. 1) was drawn in ArcMap and printed. The image of each incisor was taken using a Ricoh Caplio R7 digital camera (Tokyo, Japan) within

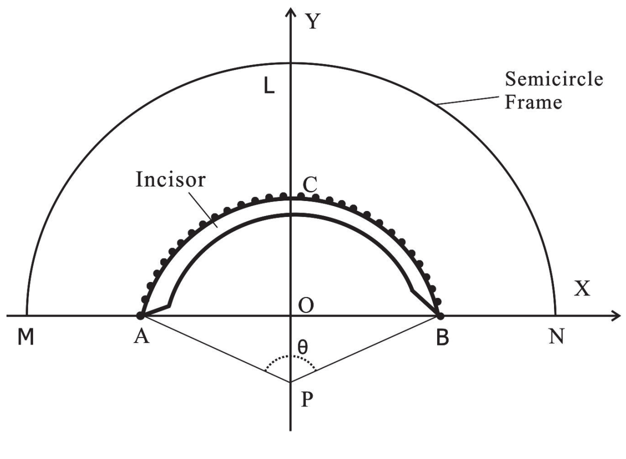

Fig. 1. *Sketch map for incisor image preparation and index estimation (The dots show arbitrary sketching points).*

the frame and was adjusted with Georeferencing Module tools with M, N and L as control points. A point shapefile was created in ArcCatalog and about 30 points (determined by preliminary analysis) along the lateral profile of incisors were drawn at roughly regular intervals with Sketch Tools. The XY coordinates of the points were then automatically written into a dbf file in the folder where the point shapefile using Add XY Coordinates tool is placed.

Nonlinear Regression was executed in SPSS 15.0 with elliptic function. The default Levenberg-Marquardt estimation method and related settings were used. The curvature (long-radius/short-radius) and the arc angle (θ) were calculated based on the estimated elliptic parameters. Since the value of curvature was near perfectly 1.0 (see below), indicating both upper and lower incisors of the two species could be viewed as circular arcs, we could easily calculate the radius (r) and the arc length (l) based on circle function.

Data analysis

All analyses were performed in SPSS 15.0. All the basic and lateral profile measurement data were corrected by greatest skull length (GSL). Means between species (male zokors vs. male rats; female zokors vs. female rats) as well as between sexes within each species were compared by Independent-Samples T Test. Means between upper and lower incisors of each sex were compared by Paired-Samples T Test.

Results

Basic measurements

Table 1 lists the body size (GSL) and uncorrected basic measurements of incisors of zokors and rats. No significant body size differences were found between male rats and male zokors as well as between female rats and female zokors. Interestingly however, all the size (GSL) corrected basic measurements (IM, AD, TD) of upper and lower incisors of male and female zokors were significantly larger than those of rats ($df = 18$, $P < 0.0001$).

Sexual dimorphism of the skull (based on GSL) was evident in both zokors and rats (male dominant, $df = 18$, $P < 0.01$). Moreover, all the size corrected basic measurements (IM, AD, TD) of upper and lower incisors of males were significantly larger than those of females ($df = 18$, $P < 0.01$) in zokors. However, only the lower incisor weight showed significant difference between sexes (male > female).

Paired-Samples T Test showed that AD and TD of upper incisors were significantly larger ($df = 9$, $P < 0.0001$) than lower incisors in both sexes of the two species. For the IM index however, the upper incisors of male and female rats were heavier than lower incisor, as opposed to zokors, in which the lower incisors were heavier than upper incisors ($df = 9$, $P < 0.01$).

Lateral profile measurements

Table 2 lists the curvature and uncorrected r, θ and l values of zokor and rat incisors. For each sex, both upper and lower incisors from zokors had significantly ($df = 18$, $P < 0.001$) longer radius and arc lengths than those from rats. The upper incisor from male or female zokor had significantly ($df = 18$, $P < 0.01$) larger θ values than those from rats; however, the lower incisors from female zokor had significantly ($df = 18$, $P < 0.05$) smaller θ values than those from female rats, while no significant difference was found

Table 1. *Basic measurements of incisors and body size (sample means ± SD) of* Myospalax cansus *and* Rattus norvegicus.

Index	*M. cansus*		*R. norvegicus*	
	male	female	male	female
UI-IM/g	0.2115 ± 0.0574	0.1294 ± 0.0237	0.0866 ± 0.0088	0.0780 ± 0.0063
LI-IM/g	0.2536 ± 0.0580	0.1758 ± 0.0315	0.0782 ± 0.0057	0.0688 ± 0.0040
UI-AD/mm	3.41 ± 0.34	2.84 ± 0.18	2.68 ± 0.11	2.56 ± 0.11
LI-AD/mm	2.95 ± 0.26	2.53 ± 0.16	2.13 ± 0.09	2.04 ± 0.07
UI-TD/mm	2.81 ± 0.32	2.34 ± 0.21	1.51 ± 0.04	1.43 ± 0.04
LI-TD/mm	2.23 ± 0.21	1.90 ± 0.15	1.33 ± 0.05	1.24 ± 0.03
GSL/mm	46.34 ± 2.25	43.43 ± 1.99	46.16 ± 1.57	44.16 ± 0.88

UI, upper incisor; LI, lower incisor; IM, incisor mass; AD, anteroposterior diameter; TD, transverse diameter; GSL, greatest skull length. n = 10 for each category.

between the θ value from male zokors and male rats. Male rats had smaller θ values in their upper incisors than females ($df = 18$, $P < 0.01$), while no significant differences were found between sexes in other indices. As to zokors, males had smaller θ values but larger l values in their upper incisors than females ($df = 18$, $P < 0.05$); males had larger r values in their lower incisors than females.

Paired-Samples T Test showed that all of the species-sex groups (male zokors, female zokors, male rats and female rats) showed significant differences between upper and lower incisors, i.e. the upper incisors had larger θ values but smaller r and l values than lower incisors ($df = 9$, $P < 0.001$). The lower incisors of male and female rats were 16.45% and 18.43% longer than the upper incisors, while in zokors the lower incisors of male and female could be 33.69% and 36.18% longer than the upper incisors, respectively.

Table 2. *Sample means ± SD of the curvature and the commonly used indices (r, radius; θ, arc angle; l, arc length) for lateral profile of incisors of rat and zokor.*

Category	curvature	r/mm	θ/°	l/mm
RUM	1.0094 ± 0.0104	6.7623 ± 0.2383	206.6572 ± 3.1758	24.3763 ± 0.8717
RUF	1.0173 ± 0.0101	6.4631 ± 0.1479	208.8350 ± 3.9405	23.5496 ± 0.8462
RLM	0.9895 ± 0.0107	11.9446 ± 0.5042	136.3049 ± 3.3989	28.3870 ± 1.0161
RLF	0.9841 ± 0.0108	11.7948 ± 0.4018	135.6424 ± 5.1791	27.8897 ± 0.9183
ZUM	1.0379 ± 0.0131	7.7158 ± 0.4984	221.4051 ± 6.1686	29.8181 ± 2.3115
ZUF	1.0350 ± 0.0099	7.0231 ± 0.4586	218.1350 ± 7.3273	26.7245 ± 1.9191
ZLM	1.0265 ± 0.0315	17.0901 ± 0.8715	133.8378 ± 9.0242	39.8653 ± 2.9051
ZLF	0.9992 ± 0.0164	16.6290 ± 0.6849	125.4685 ± 6.6911	36.3947 ± 2.3865

RUM, male rat upper incisor; RUF, female rat upper incisor; RLM, male rat lower incisor; RLF, female rat lower incisor; ZUM, male zokor upper incisor; ZUF, female zokor upper incisor; ZLM, male zokor lower incisor; ZLF, female zokor lower incisor. n = 10 for each category.

Discussion

Zokors vs. rats

From the analyses on AD and TD measurements, our results showed that zokors had higher robustness on both upper and lower incisors than rats, which was consistent with previous studies (Nevo 1999, Lacey et al. 2000). Since heavier incisors mean more resources and energy that animals should spend; if using the weight as a resource allocation index, zokors allocated obviously more resources than rats to their incisors. According to the Resource Allocation Theory, there are life-history trade-offs caused by the allocation of limited resources among competing traits or organs within an organism (Rauw 2008). The relatively heavier incisors in zokors than in rats suggest that, the zokors incisors have been strengthened at the morphological level to deal with the greater functional demands. It is suggested that, the greater the pressure applied to the tip of an incisor, the more advantageous is length, for a long incisor gives greater surface inside the alveolus to increase the friction of the tooth against the alveolar wall (Landry 1957). The results in our study thus indicate that, also consistent with previous studies on other subterranean rodents (Nevo 1999, Lacey et al. 2000), the subterranean life style has forced the zokors to have long (i.e. deeply rooted) incisors for massive digging activities.

It should be mentioned that the properties of the foods animals eat likely play an important role in the structure of their incisors (Samuels 2009). Zokors feed predominantly on roots, bulbs, and rhizomes underground (Nowak 1999), which is likely harder and more fibrous than the dietary categories consumed by rats. Therefore, like their use in digging, the more robust, heavier and longer upper as well as lower incisors in zokors than in rats may also reflect the greater functional demands to treat the foods.

Males vs. females

The body size (GSL) as well as basic measurements and, to some degree the lateral profile measurements, showed that both species had male dominant sexual dimorphism. However, zokors had an obviously higher sexual dimorphism level on the incisor morphology.

A previous study on the aggressive and solitary subterranean rodent species, the Palestine mole-rats, showed that intersexual behavioral differences could cause intersexual differences in their incisor growth and incisor plus maxillary bone densities (Zuri et al. 1999). Like the Palestine mole-rats, zokors are also aggressive and solitary rodents. Our personal observations revealed that males were obviously more aggressive than females. Moreover, males generally had larger home ranges and excavated longer tunnels than females (Zhou & Dou 1990). We suggest that male zokors, like the Palestine mole-rats, have developed stronger incisors which were used more extensively in digging and fighting than those of females. We can also conclude that the length, rather than the arc angle or radius, was the final and direct indicator for incisor adaptation at the lateral profile level.

Upper vs. lower incisors

Zokors had heavier lower incisors while the upper incisors of rats were much heavier. This was mainly due to the severely prolonged lower incisors in zokors. Zuri et al. (1999) found that the lower incisors of *Spalax ehrenbergi* (head-lift diggers) grow significantly faster than the upper incisors and attributed this to the fact that they use their lower incisors mainly to excavate their tunnel systems. The especially longer and heavier lower incisors in zokors thus showed that, although zokors were more likely scratch diggers, this species also depends more on their lower incisors than upper incisors in their daily lives.

Curvature & GIS method

The Nonlinear Regression showed that over 99% (R^2) of variables could be explained by the estimated function for each incisor. This meant that our method was powerful in predicting the incisor lateral profile. As shown in Table 2, the curvatures of upper as well as lower incisors of female and male of the two rodent species were nearly 1.0. One-Sample T Test showed that all the curvatures of the eight categories were significantly ($P < 0.001$) larger than 0.95 while smaller than 1.05, indicating that the incisors could be viewed as circular arcs at the 5% confidence range.

The powerful functions on geospatial data handling in GIS software facilitate us to revise the distortions in the image as well as other fine-tuning such as rotating and shifting, and finally minimize the systematic error. Most importantly, GIS systems can output the coordinates of sketched points in batches and this make it feasible to analyze the lateral profile of rodent incisors using nonlinear regression methods. In this study, we had only used a very small part of the functions available in ArcGIS; we suggested that, the GIS software, although originally having been developed for 'large scale' geographic analysis, can also be used in many other "small scale" biological studies (e.g. see Evans et al. 2007).

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