Incisors as digging tools in molerats (Bathyergidae)

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The angle at which the incisors project forward and the amount of enamel per incisor is greater in molerats that use their incisors for digging (genera *Georychus* and *Cryptomys*), than in those molerats that do not use the incisors for digging (genus *Bathyergus*).

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De Graaff (1981), Smithers (1983) and Skinner and Smithers (1990) follow Roberts (1951) in recognizing the Bathyerginae and Georychinae as subfamilies of the family Bathyergidae. The Bathyerginae accommodates members of the genus *Bathyergus*, which have grooved upper incisors, while the Georychinae include the genera *Georychus*, *Cryptomys* and *Heliophobius*, which have smooth upper incisors. *Heterocephalus* has also been included in the Georychinae (Honeycutt, Allard, Edwards & Slitter 1991; Jarvis & Bennett 1991), although Ellerman, Morrison-Scott and Hayman (1953) suggested that this genus belongs in a different subfamily. However, on the basis of recent phylogenetic studies the subfamily Georychinae is considered absolute, and the placement of *Bathyergus* in a subfamily separate from *Cryptomys*, *Georychus* and *Heliophobius* is regarded as unwarranted (Honeycutt *et al.* 1991; Janecek, Honeycutt, Rautenbach, Erasmus, Reig & Schlitter 1992). These authors recognize two subfamilies within the Bathyergidae, the Heterocephalinae (containing *Heterocephalus*) and Bathyerginae (containing *Bathyergus*, *Georychus*, *Cryptomys* and *Heliophobius*). *Heterocephalus* and *Heliophobius* have no representatives in the southern African subregion. In this study, we have chosen to follow the latter classification.

The family Bathyergidae is endemic to the African continent, with a wide distribution from the Cape Province to north of the equator and westwards to Ghana and West Africa (Skinner & Smithers 1990). With the exception of the genus *Bathyergus*, the prominent incisor teeth are used for burrowing (Ellerman 1956; Jarvis & Bennett 1991; Skinner & Smithers 1990; Woods 1984). In contrast, *Bathyergus* has enlarged and curved front claws used for digging (De Graaff 1964, 1981; Ellerman 1956; Meester, Rautenbach, Dippenaar & Baker 1986). In the other genera, the front feet and claws are not particularly well adapted for digging but are mainly used to move soil loosened by the incisors (De Graaff 1981; Skinner & Smithers 1990).

The Cape dune molerat, *Bathyergus suillus*, is the largest of the bathyergids and the largest subterranean rodent in the world (Skinner & Smithers 1990). The average mass of males is 896 g and that of females, 670 g. The Namaqua dune molerat, *B. janetta*, is about half the size of the Cape dune molerat (average mass of males and females are 468 g and 338 g respectively). The Common molerat, *Cryptomys hottentotus*, is the smallest bathyergid, with an average mass of 61.3 g and 45.3 g for males and females respectively. The average mass of the male Cape molerat, *Georychus capensis*, is 181.8 g and that of the female is 180.0 g (see Skinner & Smithers 1990).

The purpose of the present study is to (i) establish whether there is any difference in the angle at which the incisors project forward in molerats that use them for digging and those that do not and (ii) to determine whether there is any difference in the enamel to dentine ratio of the incisors of the same animals.

Material and methods

A total of 24 molerat skulls was examined. In all cases the largest skulls, and those in the best condition, were collected. With the exception of one Cape dune molerat skull, which was kindly given to us by Jenny Jarvis (Department of Zoology, University of Cape Town, S.A.), the skulls were borrowed from the Transvaal Museum. The 24 skulls comprised six Cape dune molerats, *Bathyergus suillus*; six Namaqua dune molerats, *B. janetta*; six Common molerats, *Cryptomys hottentotus*; and seven Cape molerats, *Georychus capensis*. With the kind permission of the Transvaal Museum, we were allowed to remove the right upper and lower incisor of three skulls of each species for scanning electron microscopy. This was done by submerging the skulls in boiling water, to soften connective tissue and loosen the teeth. Backscatter electron (BSE) micrographs (Figure 1) were used to determine the ratio between the enamel and dentine for each incisor and normal electron microscopy techniques were used in sample preparation. The teeth were embedded in cold mounting powder resin obtained from IMP (Innovative Met Products), cut transversely with a diamond saw at more or less the same level just above the point where the tip of the tooth becomes chisel-shaped (the thickness of both upper and lower incisors are constant from the root up to the point where they become chisel-shaped). The cross sections were prepared with standard polishing techniques and coated with a thin layer of carbon. Samples were examined with a Jeol 840 scanning electron microscope at an accelerating voltage of 15 KV and

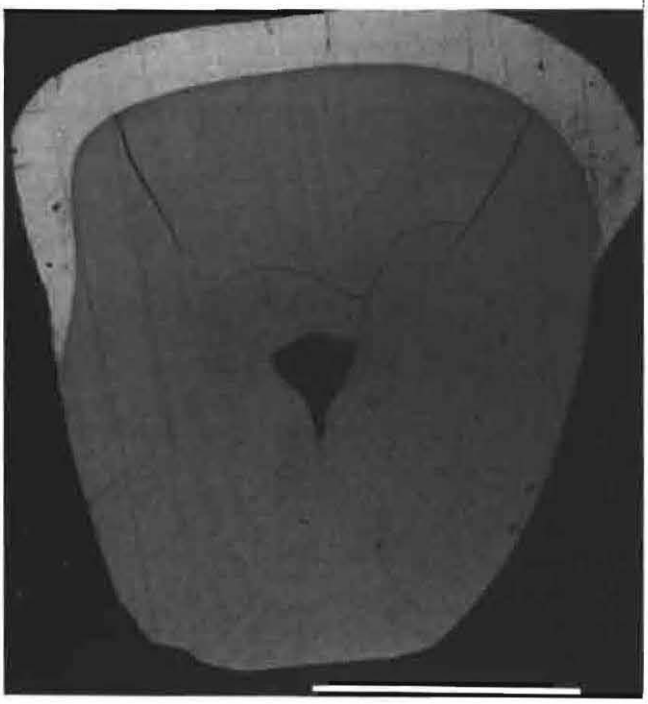

Figure 1 Cross section through the lower incisor of *Georhychus capensis* to show the thin strip of enamel only on the outside (labial) of the tooth. Bar = 1 mm

a working distance of 16 mm. The images were collected with a BSE detector. A Noran image analysis system was used to determine the enamel to dentine ratio.

To calculate the angle at which the incisors protrude forward, the skulls were fixed on their sides on a glass platform and their lateral profiles scanned into a Noran image analysis system with a ccd camera attached to the system. The image analysis system was used to create a binary image of the lateral profiles of the skulls which was then used to measure the angle at which the incisors protrude forwards (Figure 2). On each of these images, a straight line (X–X and Y–Y) was drawn from the centre of the articulation joint between the skull and lower jaw (where the processus articularis of the lower jaw articulates with the fossa glenoidalis of the skull) through the inner base of the incisor where it leaves the skull (Figure 2). A second line (a–a and b–b) was then drawn from the tip of the incisor to cross the line from the articulation joint at the inner base of the incisor where it leaves the skull (Figure 2). This was done for both the skull and the lower jaw. The angle (Xa and Yb) at which the incisors protrude forward was then measured using line X–X and Y–Y as baselines (Figure 2).

Single classification ANOVA and Tukey's Multiple Comparison Test were used to determine whether significant differences existed between the various species examined regarding (i) the angles at which the upper and lower incisors protrude forward and (ii) the enamel/dentine ratio between the upper and lower incisors.

Results

Significant differences were found in upper incisor angles between the various species ($f = 13.39$; $p<0.001$), but not in the angles of the lower incisors ($f = 0.95$; $p>0.05$). The angle of the upper incisors of those species using them for digging

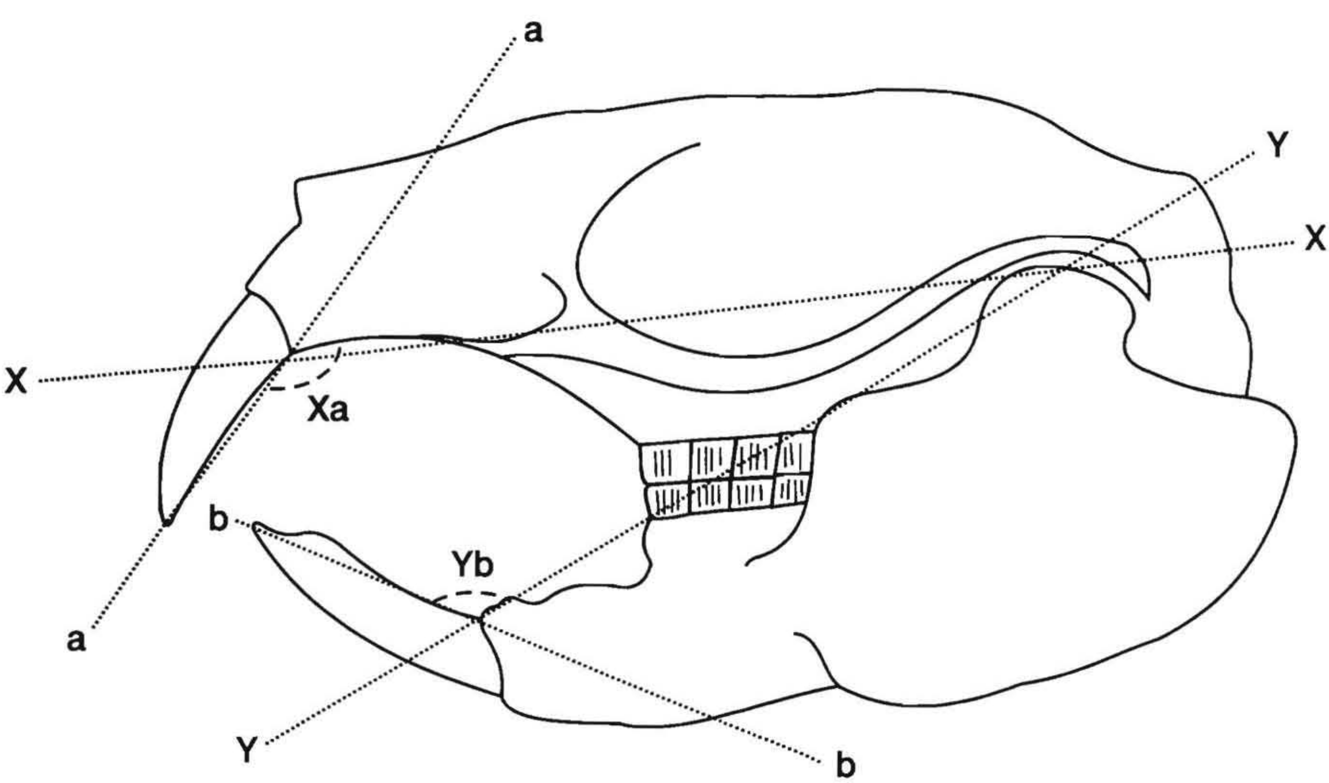

Figure 2 Illustration of the lateral profile of a mole rat skull to illustrate the angles (Xa and Yb) at which the upper and lower incisors (lines a–a and b–b) project forward from the baselines (X–X and Y–Y)

(*C. hottentotus* and *G. natalensis*) was significantly greater than in those species not using them for digging (*B. suillus* and *B. janetta*) (see Table 1 for individual differences). The average angle at which the upper incisors project forward is 13.6° greater in molerats that use their incisors as digging tools (genus *Cryptomys* and *Georychus*) than those who do not (genus *Bathyergus*) (Figure 3). The greatest average difference was 15.1°, between *G. capensis* and *B. janetta*, with the smallest average difference being 12.0°, between *C. hottentotus* and *B. suillus*.

The angle at which the lower incisors project forward does not differ much amongst the various species examined, although it was slightly larger in favour of those using their incisors for digging (Figure 3). The average difference between those using their teeth for digging and those who do not was 2.2°. The greatest average difference was 4.3° between *C. hottentotus* and *B. suillus*, and the smallest difference 0.1° between *C. hottentotus* and *B. janetta* (Figure 3).

Significant differences were found in the enamel/dentine ratio of the various species in both the upper incisors ($f = 63.11$; $p<0.001$) and lower incisors ($f = 69.56$; $p<0.001$). Although the sample size is very small (due to the scarcity and value of the skulls), Figure 4 shows a clear difference in the enamel to dentine ratio (for both upper and lower incisors), between those using their incisors for digging (*C. hottentotus* and *G. natalensis*) and those who do not (*B. suillus* and *B. janetta*) (see Table 1 for individual differences).

The average percentage enamel per upper incisor in the

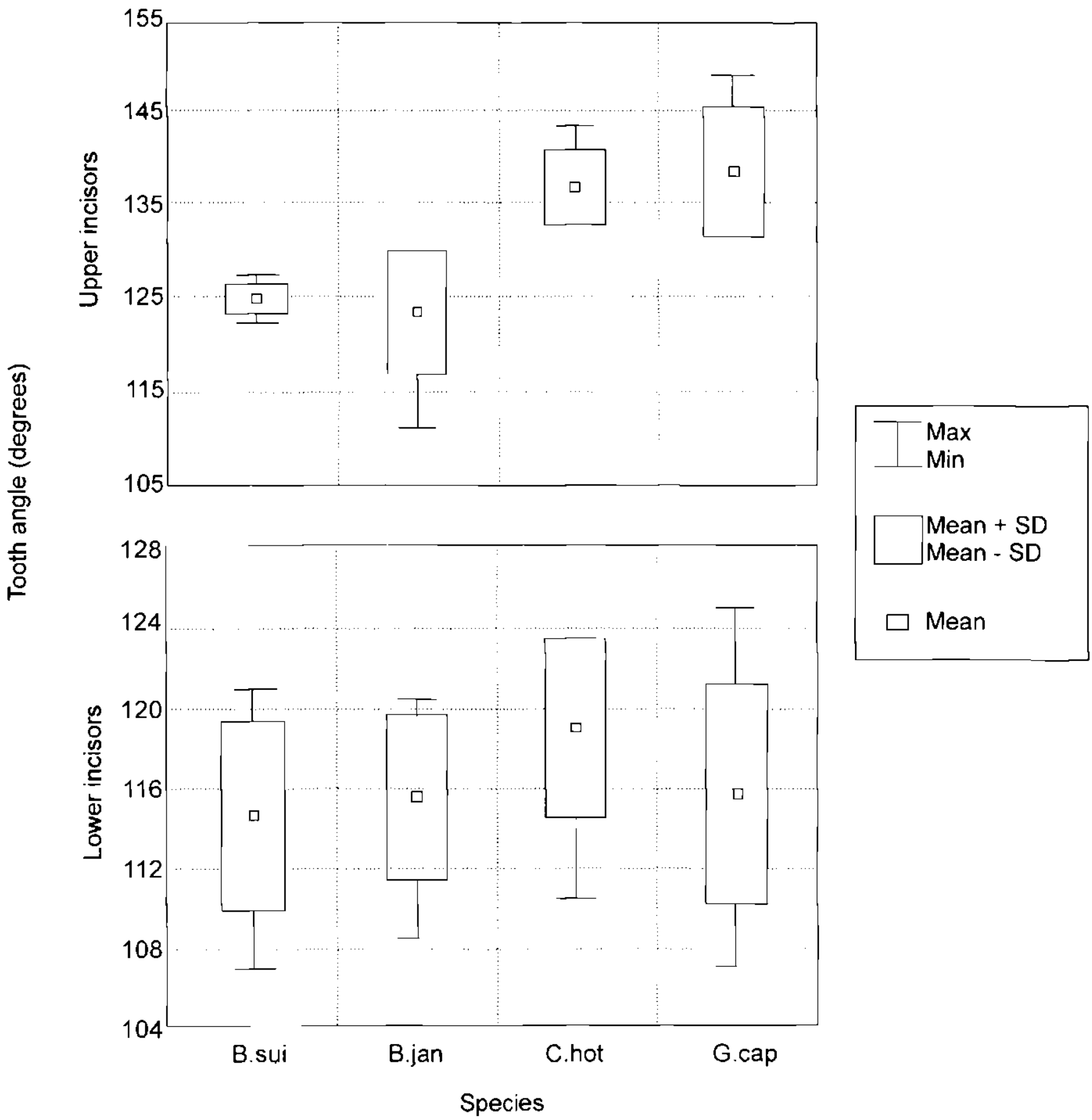

Figure 3 Degree to which the angle of the upper and lower incisors differ between the genus *Bathyergus* and the genus *Cryptomys and Georychus*)

Table 1 Mean (± standard error) and sample sizes of upper and lower incisor angles and enamel/dentine ratios in the various molerat species

Incisors	*B. suillus*	*B. janetta*	*C. hottentotus*	*G. capensis*
Angle	124.92 (±0.66)[a]	123.50 (±2.76)[a]	136.92 (±1.62)[b]	138.57 (±2.63)[b]
upper	n = 6	n = 6	n = 6	n = 7
Angle	114.67 (±1.94)[a]	115.50 (±1.71)[a]	119.00 (±1.84)[a]	115.64 (±2.10)[a]
lower	n = 6	n = 6	n = 6	n = 7
Enamel	10.77 (±0.09)[a]	13.83 (±0.24)[b]	17.63 (±0.74)[c]	17.23 (±0.20)[c]
upper	n = 3	n = 3	n = 3	n = 3
Enamel	18.53 (±0.50)[a]	10.87 (±1.04)[a]	17.47 (±0.35)[b]	18.93 (±0.09)[b]
lower	n = 3	n = 3	n = 3	n = 3

Superscript letters: means in the same row with the same superscript letter do not differ significantly at p = 0.05 (Tukey's Multiple Comparison Test).

genus *Cryptomys* and *Georychus* is 5.1% greater than in the genus *Bathyergus*. The greatest average difference was 6.8%, between *G. capensis* and *B. suillus* and the smallest average difference was 3.4%, between *C. hottentotus* and *B. janetta*.

For the lower incisors the differences are even more remarkable. The average percentage of enamel per lower incisor for the genus *Cryptomys* and *Georychus* is 8.6% greater than in the genus *Bathyergus*. The greatest difference was 10.5% between *C. hottentotus* and *B. suillus* with the smallest difference being 6.6% between *G. capensis* and *B. janetta*. In *C. hottentotus* and *G. capensis* the enamel to dentine ratio is very similar between the upper and lower incisors. In this study, the average percentage enamel of the lower incisors was 0.8% higher than in the upper ones. However, in the genus *Bathyergus*, the average percentage of enamel in the upper incisors is 2.7% higher than in the lower ones.

Discussion

One of the notable characteristics of rodents is that they possess a pair of upper and lower incisors that grow persistently throughout life (Fekete 1941; Hickman 1961; Romer 1963; Shani 1984). Therefore, the tips must wear away continuously to keep pace with growth (Hickman 1961). The incisor has enamel only on its anterior (labial) surface (Figure 1) and thus maintains a cutting edge (Hickman 1961; Storer & Usinger 1957; Von Koenigswald 1984). The gnawing action of the upper and lower incisors against one another maintains a chisel edge.

Subterranean mammals are specialized for burrowing and living underground in burrow systems. This subterranean ecotope is relatively simple, stable, specialized, low in productivity, predictable and discontinuous (Nevo 1979). Three orders of mammals have completely subterranean representatives, namely rodents, insectivores, and marsupials (Ellerman 1956; Nevo 1979). Whether related or not, all share certain characteristics. These include anatomical peculiarities, such as short limbs, thickset and somewhat sausage-shaped bodies and a progressive reduction of the eyes, ears and tail which have completely disappeared in most species (Ellerman 1956). In the case of subterranean rodents, it might be acceptable to substitute the term 'structural reduction' with 'vestigial structure' (Prout 1964), the latter applies to reduced organs that have basically lost their function. This structural reduction in certain organs, however, is accompanied by the development of others such as the incisors, forelimbs, pectoral girdle, claws, and sense organs, which complement each other to optimize burrowing capacities and efficiency in a subterranean existence (Nevo 1979).

Rodent incisors are important tools. Their use ranges from processing food to digging dens (Von Koenigswald 1984). The majority of molerats depend on their incisors for digging in their subterranean environment. In molerats, the skull is stoutly built with large incisors that project outside the mouth (De Graaff 1981). This proodoncy makes the incisors more independent of the oral cavity, thus efficiently protecting it from the incoming earth and the nostrils from friction against the ground (Agrawal 1967). Due to intensive use, the incisors are liable to undergo rapid attrition, which has led to the dentinal pulps becoming more active and deep rooted (Agrawal 1967). In the genera *Cryptomys* and *Georychus*, the incisors of the upper jaw are exceptionally long, curving in an almost complete semicircle past the orbit and rooting posterior to the molars in the pterygoid region (De Graaff 1981; Meester *et al.* 1986; Rosevear 1969; Skinner & Smithers 1990; pers. obs.). This adaptation adds additional strength to the incisors which are used to break down the soil when tunnelling (Rosevear 1969). In the genera *Cryptomys, Georychus* and *Heliophobius* (no southern African species) the front claws are not enlarged because the major share of digging is done by means of the incisors rather than by the front appendages (De Graaff 1981; Meester *et al.* 1986). In the genus *Bathyergus*, however, the roots of the upper incisors lie above the molar teeth (Skinner & Smithers 1990; pers. obs.), reaching only the infraorbital foramen (Meester *et al.* 1986). In this genus the front claws are much enlarged and adapted for digging (De Graaff 1981; Meester, *et al.* 1986). The incisors of the lower jaw in all the genera discussed traverse the whole of the mandible, rooting almost at the condylar knob itself (Rosevear 1969). Although Rosevear (1969) regarded rooting of the incisors posterior to the molars as an adaptation to add additional strength when burrowing, another explanation may be to increase the degree of proodoncy so that the upper incisors can operate better as scrapers. Since the incisors curve in an almost complete semicircle (De Graaff 1981; Meester *et al.*

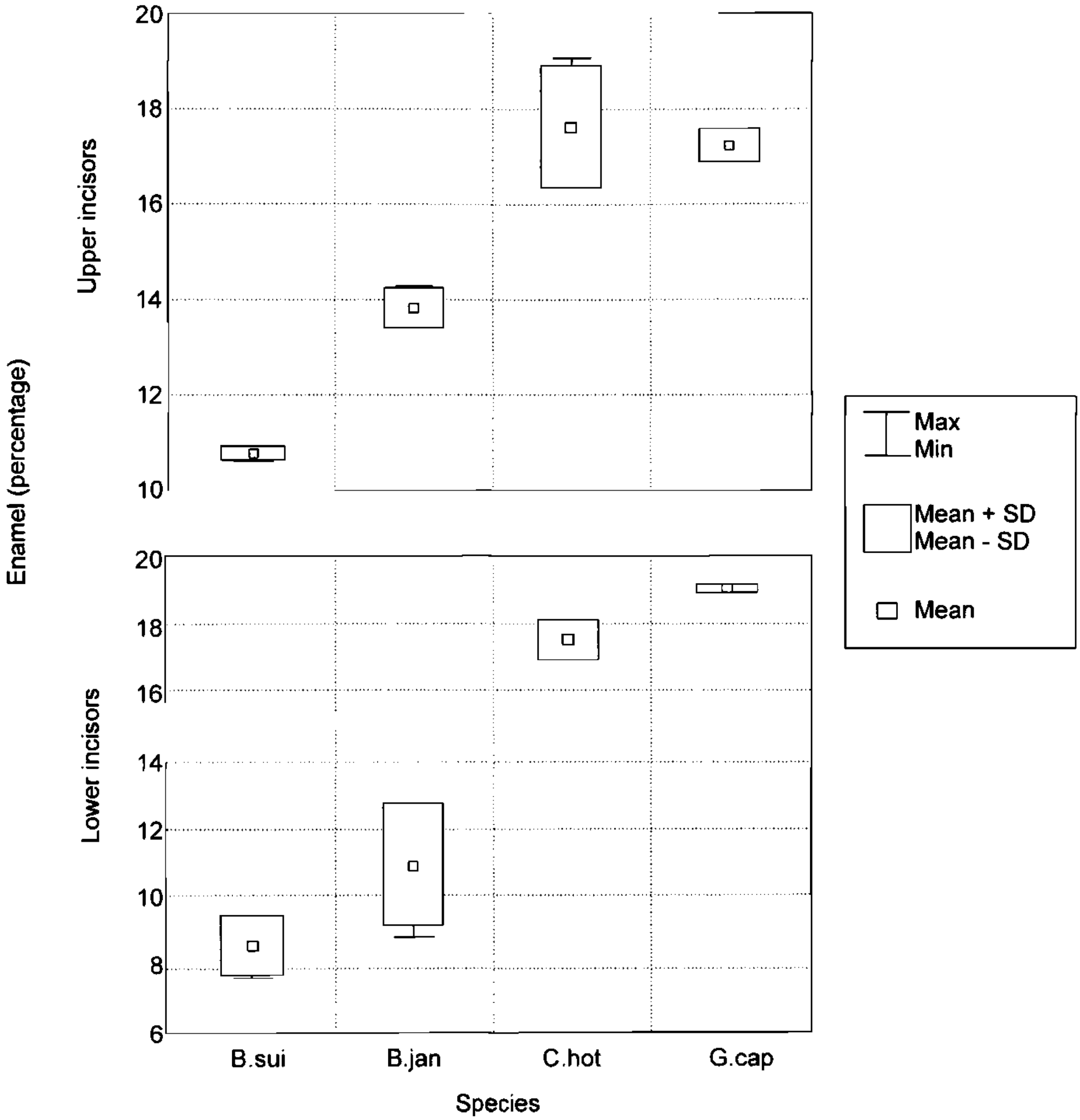

Figure 4 Degree to which the percentage enamel (in a cross section) of the upper and lower incisors differ between the genus *Bathyergus* and the genus *Cryptomys and Georychus.*

1986; Rosevear 1969; Skinner & Smithers 1990; pers. obs.), it is expected that incisors rooted behind the molars would result in a wider curvature (semicircle) than when the incisors are rooted above the molars, especially when reaching only the infraorbital foramen (see Meester *et al.* 1986). A wider curvature should promote proodoncy, which would be beneficial for scraping the soil. However, such an arrangement would not be necessary for those using the front claws for digging. It would also appear that the main digging force is exercised by the upper incisors, with the lower ones following through the bite. Such digging behaviour is suggested by the fact that the angle of curvature of the upper incisors of scrapers differs significantly from those of non-scrapers (genus *Bathyergus*), while very little difference occurs between the angles of the lower incisors in all four species. This argument is further supported by the findings of Jarvis and Bennett (1991) where individuals of both *G. capensis* and *C. hottentotus* had upper incisors worn to the gums within 3–5 days, in an attempt to avoid capture. A thicker enamel layer on the surface of the incisors of scrapers will also be beneficial, because it will increase resistance against tooth wear. Although the sample sizes are very small, the present study indicates a definite trend for a higher percentage enamel for both upper and lower incisors in scrapers compared to those of non-scrapers.

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