Craniometrics Analysis for Ontogenetic Physiognomy and Sexual Dimorphism in Emin's Silvery Mole-Rats (*Heliophobius argenteocinereus emini*: Bathyergidae) from Tanzania

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Abstract

Emin's silvery mole-rat, the *Heliophobius argenteocinereus emini* belongs to a family Bathyergidae. The *Heliophobius argenteocinereus emini* (Noak, 1894) is among the least studied sub-Saharan subterranean rodents. Among others, information on ontogenetic physiognomy and status of sexual dimorphism in *H. a. emini* is missing. The present study intended to fill gaps on ontogenetic characteristics and status of sexual dimorphism in these mole-rats by comprehensively examining 55 skulls. Based on teeth eruption and wear, the dental formula of 1/1, 0/0, 1/1, 3/3 is reported for the first time, and subsequently established eight relative age classes. This information was key to the assessment of ontogenetic variations between sexes and age classes. The multidisciplinary analyses of craniometrics between and within relative age classes showed a sharp increase in sizes of cranial facets from relative age classes III to VIII, which signifies a divergence in the investment of energy for growth between age classes. Within all relative age classes except age classes I and II, females showed smaller craniometrics than males, indicating that sexual dimorphism in *H. a. emini* is well noticeable from the relative age class III. Subsequent analyses of craniometrics revealed that sexual dimorphism in *H. a. emini* is attributed by size.

Keywords: Ontogenetic, *Heliophobius argenteocinereus emini*, craniometrics, sexual dimorphism

Introduction

The Emin's silvery mole-rat (*Heliophobius argenteocinereus emini*) is a solitary subterranean rodent belonging to the family Bathyergidae (Faulkes et al. 2011, Ngalameno et al. 2017). The geographic distributional range of genus *Heliophobius* is Tanzania, Malawi, Zambia, Kenya, Democratic Republic of Congo and Mozambique (Faulkes et al. 2011). Similar to other subterranean rodents, the *H. a. emini* lives in closed burrow systems comprising of a food store, toilet, nest and a bolt hole (Bennett and Faulkes 2000). The Emin's silvery mole-rats feed on underground storage organs of a variety of vegetation (i.e. geophytes) and on a few occasions, they can pull shoots of annual plants to their burrow systems. The *H. a. emini* inhabit agricultural fields and thus becoming agricultural pests because of their feeding and burrow excavations like their counterparts (Katandukila et al. 2014).

Among bathyergids, Emin's silvery mole-rats are the least studied and could be termed a "neglected taxon" although their impacts on farm fields are conspicuous in their geographical range. The existing studies of

H. a. emini focused on the dental structure and peculiarities (Rodrigues et al. 2011, Rodrigues and Šumbera 2015), chronological captive activity pattern (Ackermann et al.2017) and reproductive patterns (Katandukila et al. 2017, Ngalameno et al. 2017). Currently, there is neither report on their ontogenetic characteristics nor the status of sexual dimorphism.

Ontogenetic characteristics refers to the developmental history of an organism from embryo to adulthood with insight that as the organism grows, it changes in size and shape (Badyaev and Martin 2000). Since it is costly to examine embryo-genesis characteristics, most of the ontogenetic studies were conducted from birth to adult-hood (Chimimba et al. 2010). Ontogenetic studies enlighten the sources of variations between individuals within a population (Ernande and Dieckmann 2004). Individuals within a population may have a similar growth pattern as a consequence of equal opportunities in response to stress and acquisition of essential resources including food, space and mate. The divergence of ontogenetic characteristics among individuals within a population has been related to evolutionary consequences on the accessibility of resources or natural selection which is advantageous to survival (Ernande and Dieckmann 2004, Isaac 2005, Huchard et al. 2016).

In rodents, social behaviour has been reported to divert equal acquisition of resources and consequently causes divergence of ontogenetic characteristics between reproductive and non-reproductive (i.e. breeding vs non-breeding) groups (Van Rensburg et al. 2004, Huchard et al. 2016). The divergence of ontogenetic characteristics in solitary species is however, related to pup caring, mate selection, defense of harem and territoriality (Stamps and Krishnan 2001, Chimimba et al. 2010, Katandukila et al. 2017). Species that defend their territory and harem tend to evolve competitive characters that allow the growth of acceptable size or shape to secure more mates or defend their

territory for reproductive success (Huchard et al. 2016).

The ontogenetic variations have been reported in several solitary and social subterranean rodents (Daly and Patton 1986, Van Rensburg et al. 2004, Hart et al. 2007, Chimimba et al. 2010, Katandukila 2017) with none documented on Emin's silvery mole-rat. Since Emin's silvery mole-rats are among the solitary species, they were hypothesized to have significant variations of sizes or shapes between age classes and slight variations within age classes as a consequence of their similar growth trends. The assumption is that acquisition and consumption of energy may differ between age classes but not within the same age classes. The majority of studies in solitary subterranean rodents reported ontogenetic divergence in the female of higher age classes as the consequence of investment of energy for reproductive activities (Katandukila 2017), and therefore enhanced sexual dimorphism. The study hypothesised that silvery mole-rats exhibit sexual-ontogenetic divergence within higher age classes as the consequence of natural selection or investment to competitive adult characters.

Sexual dimorphism has been reported in a number of rodents' species with some evolving shape-sexual dimorphism (Schulte-Hostedde 2007, Abdel-Rahman et al. 2009, Chimimba et al. 2010), while others evolve size-sexual dimorphism (Katandukila 2017). Since the Emin's silvery mole-rats have maternal pup caring, they were also hypothesized to have sexual dimorphism, although it was unknown whether it is caused by size or shape sexual dimorphism. Given the paucity of information on ontogenetic characteristics and the status of sexual dimorphism, the present study has undertaken the analysis of craniometrics of Emin's silvery mole-rat population. Analyses of craniometrics have been used successfully to reveal the variations between groups within a population (Chimimba et al. 2010, Katandukila 2017). The present study also

examined the molar eruption and wear in Emin's silvery mole-rats to assign individuals into relative age classes for easy testing of study hypotheses. The grouping of individuals into age classes is vital for assessing nature and extent of divergence on the growth of typical character as reported in number of small mammals including subterranean rodents (Hench et al. 1984, Taylor 1985, Bennett et al. 1990, Van Rensburg et al. 2004, Hart et al. 2007, Chimimba et al. 2010, Katandukila 2017).

Materials and Methods
Study site
Emin's silvery mole-rats were collected from February to March in the year 2016. They were captured in agricultural fields at Mlali village in the Mvomero District, Morogoro Region, Tanzania. The village is located at 06°57´16.45-48"S, 037°32´05.40-47"E, 1266-1330 metres above sea level. The study site is located in an ecological zone with two rainy seasons with a mean annual rainfall of 600 mm (Morogoro Regional Profile [MRP], 2000). The more extended period of rainfall (i.e. heavy rainfall) in Mlali is experienced from March through May with a mean of 470 mm, whereas a shorter period of rainfall is from October to December with a mean of 130 mm. The average temperature is 23 °C which ranges from 18 to 30 °C (MRP 2000).

Animal capturing and housing
The study animals were captured in agricultural fields after burrow excavation (Katandukila et al. 2014). Fifty-five animals were collected in which 28 animals were females and 27 animals were males. Animals were kept singly in a bucket aligned with wood shaving to avoid wetting before transportation to the laboratory. In both collecting buckets (where they were kept after capture) and laboratory, the animals were fed with pieces of carrots and potatoes that are their staple food since they feed on underground storage organs of a variety of vegetation (i.e. geophytes) (Bennett and Faulkes 2000).

Specimen preparation
Animals were euthanized with an acceptable dose of chloroform, and subsequently, measurements and characteristics were recorded including sex, head-body length, tail length, and hind legs length. The head was cut and labelled accordingly and soaked in a 10% solution of potassium hydroxide (KOH) for the digestion of cranial muscles. After complete digestion of muscles, skulls were rinsed with double distilled water (DDW) and subsequently dehydrated in series of concentrations of glycerine, i.e., 30%, 60% and 100% for final fixation and then dried for storage and further analysis.

Assessment of relative age classes
The assessments of age classes were based on the degree of molar eruption and wear of the dental formula within the family Bathyergidae, which is 1/1, 0/0, 2-3/2-3, 2-3/2-3. Protocols for assigning relative age classes were similar to the previous studies of small mammals (Hench et al. 1984, Taylor et al. 1985, Chimimba and Dippenaar 1994, Zuri and Terkel 2001, Van Rensburg et al. 2004, Hart et al. 2007, Abdel-Rahman et al. 2009, Chimimba et al. 2010, Katandukila 2017). These studies supported and recommended molar eruption and wear as an appropriate method in the determination of relative age classes within the rodents taxa.

Selection of craniometrics
The criteria for selection of cranial facets in Emin's silvery mole-rats were based on the standard protocol of cranial assessment as reported in parallel studies of small mammals (Van Rensburg et al. 2004, Chimimba et al. 2010, Katandukila 2017) with little modifications (Figure 1). The lengths of selected cranial facets were measured to the nearest 0.05 mm using a Mitutoyo digital caliper (Mitutoyo American Corporation, Aurora, Illinois, U.S.A.).

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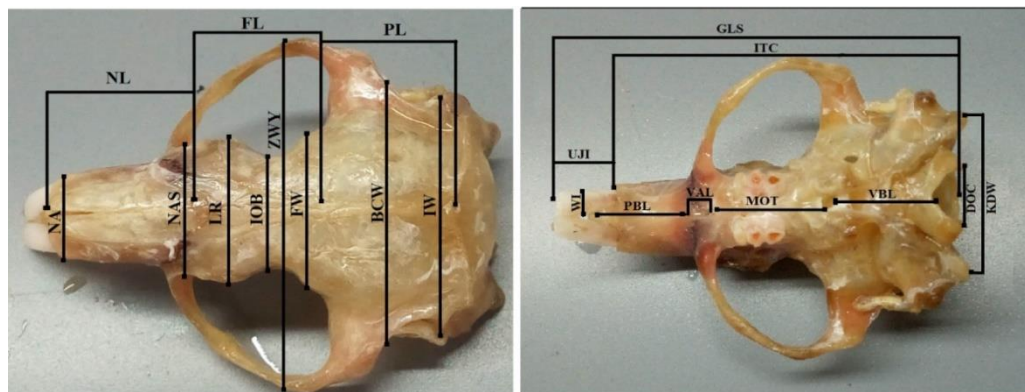
Figure 1: Selected cranial facets for investigation of ontogenetic physiognomy and sexual dimorphism of *Heliophobius argenteocinereus emini* (animals collected in February 2016).

Meaning of abbreviations on Figure 1: 1) BCW = Brain case breadth, 2) DOC = Distance between right and left occipital condyle, 3) FL = Frontal bone length (sagittal border length of frontal bone), 4) FW = Frontal bone width, 5) GLS = Length from incisor to condyle (including incisor), 6) IOB = Least breadth of interorbital constriction, 7) ITC = Length from incisor to condyle (excluding incisor), 8) IW = Interparietal bone width, 9) KDW = Distance between left and right paroccipital process, 10) LR = Distance between left and right anterolateral corner of frontal bone 11) MOT = Length of hard palate from posterior of incisive fossa to posterior nasal spine, 12) NA = Nasal width, 13) NAS = Nasal width at the middle, 14) NL = Nasal bone length, 15) PBL = Length of premaxillar bone, 16) PL = Parietal bone length (sagittal border length of parietal bone), 17) UJI = Upper incisor length: 18) VAL = Length of incisive fossa, 19) VBL = Length between vomer and condyle before foramen magnum, 20) WI = Width of upper incisor and 21) ZYW = Width between outer margins of zygomatic arches.

Data Analyses

The twenty-one cranial facets were selected, and their measurements were subsequently subjected to R algorithm (R Core Team 2014). The R algorithm was used in the evaluation of the degree of normality of craniometrics (i.e. Shapiro Wilk was used to test for normality {W = 0.763, P < 0.05, n = 55}) and determination of standard descriptive statistics including mean and standard deviation. Generalized Linear Model (GLM) was used to evaluate ontogenetic variations and its extent between relative age classes and sexes, with Student-Newman-Keuls (SNK) used as a *post hoc* statistical test between relative age classes. Moreover, Principal Component Analysis (PCA) was employed to examine the nature and extent of variations of craniometrics between and within relative age classes and sexes (*sensu* Katandukila 2017). The level of significance for all statistical tests was α = 0.05.

Results

Each side of the cranium of adult individuals had a row of four cheek teeth comprising of one premolar tooth and three molar teeth which mark a dental formula of 1/1, 0/0, 1/1, 3/3 amounting to 20 teeth. Based on the degree of molar eruption and wear, eight relative age classes were revealed, in which age class I was characterized by one fully-grown molar, while age class II consisted of one fully-grown molar and erupting the second molar,

and age class III consisted of one fully grown and one half-grown molar. Relative age class IV consisted of two fully-grown molars, while age class V consisted of two fully-grown molars and erupting the third molar with age class VI consisted of two fully-grown and third half-grown molars. The relative age class VII consisted of three fully-grown molars featured with the uplifted and sharp crown, while age class VIII was characterized by three fully-grown molars equipped with a short and blunt crown as a result of teeth wear.

Craniometrics of *H. a. emini* showed small measurements in lower relative age classes with large measurements in higher relative age classes (Table 1). The orderly increase of craniometrics was observed in both sexes although in some cranial facets variations between age classes and sexes were minimal. Among the cranial facets, DOC and WI had small measurements when compared to other metrics of other facets. The ZWY, GLS, IW and ITC had larger metrics deviations within age classes (Table 1) than other cranial facets. The generalized linear model showed that craniometrics of all cranial facets varied significantly between relative age classes and sexes (Table 2). The extent of variation of craniometrics was expressed by mean of Sum of Squares (SSQ) in which relative age classes had 56.42% followed by variations contributed by sexes with SSQ of 19.49%. The variation contributed by measurement error was less than 10% which indicates that the craniometrics presented the actual measurements of the cranial facets of the species. Cranial facets that showed the highest variations with age classes included ZWY, GLS, BCW, ITC and PL, while the facets that showed lowest variations were VAL, UJI and WI (Table 2). The cranial facets which showed the highest significant variations between sexes were ZWY, NL and PL, while VAL and FW showed the lowest variations. Interaction between sexes and age classes showed significant variations in the number of facets, although it had insignificant variations on VAL and UJI facets.

Table 1: The descriptive statistics (mean ± standard deviation) of craniometrics (mm) of *Heliophobius argenteocinereus emini* within eight relative age classes (i.e. I-VIII). The sample size is indicated in parentheses. Cranial facets are defined and illustrated in Figure 1.

Cranial facet	Age class I (5)	Age class II (6)	Age class III (10)	Age class IV (8)	Age class V (6)	Age class VI (9)	Age class VII (5)	Age class VIII (6)
BCW	9.00 ± 0.14	11.07 ± 0.63	13.82 ± 1.43	15.07 ± 1.76	17.37 ± 1.16	19.92 ± 1.39	22.30 ± 2.06	24.53 ± 2.27
DOC	2.18 ± 0.12	2.68 ± 0.15	3.54 ± 0.27	4.36 ± 0.33	4.50 ± 0.67	5.40 ± 0.80	7.13 ± 1.01	7.84 ± 1.11
FL	4.16 ± 0.20	5.12 ± 0.24	5.33 ± 0.46	6.56 ± 0.56	8.13 ± 1.24	9.76 ± 1.49	11.72 ± 1.64	12.89 ± 1.80
FW	5.68 ± 0.06	6.99 ± 0.07	8.72 ± 1.37	10.73 ± 1.68	10.78 ± 1.70	12.93 ± 2.04	14.76 ± 2.43	16.24 ± 2.67
GLS	15.32 ± 0.11	17.68 ± 0.13	22.07 ± 1.63	26.21 ± 2.01	29.23 ± 3.46	31.48 ± 4.15	34.06 ± 6.07	39.37 ± 6.68
IOB	1.95 ± 0.07	2.40 ± 0.08	3.17 ± 0.50	3.90 ± 0.62	4.98 ± 0.85	5.98 ± 1.02	9.34 ± 1.65	10.27 ± 1.82
ITC	14.00 ± 0.27	14.92 ± 0.33	17.48 ± 1.63	21.03 ± 2.01	26.22 ± 3.00	30.86 ± 3.60	34.30 ± 5.04	37.73 ± 5.54
IW	7.54 ± 0.19	9.27 ± 0.23	13.82 ± 0.83	17.00 ± 1.02	18.65 ± 2.83	22.38 ± 3.39	23.92 ± 4.22	26.31 ± 4.64
KDW	4.71 ± 0.23	5.79 ± 0.28	7.81 ± 0.44	9.61 ± 0.54	11.54 ± 1.54	13.85 ± 1.85	16.46 ± 2.64	18.11 ± 2.90
LR	4.59 ± 0.09	5.65 ± 0.11	7.15 ± 0.68	8.62 ± 0.84	8.79 ± 1.07	10.34 ± 1.28	13.29 ± 1.36	14.62 + 1.50
MOT	3.58 ± 0.21	4.40 ± 0.26	5.74 ± 0.84	7.06 ± 1.03	7.35 ± 1.03	8.82 ± 1.23	11.16 ± 1.77	12.28 ± 1.95
NA	2.74 ± 0.24	3.37 ± 0.30	5.02 ± 0.59	6.18 ± 0.72	6.99 ± 1.55	8.39 ± 1.86	10.31 ± 2.12	11.34 ± 2.33
NAS	4.60 ± 0.20	5.66 ± 0.25	5.73 ± 0.49	6.89 ± 0.60	7.90 ± 0.85	9.48 ± 1.02	11.39 ± 1.47	12.53 ± 1.62
NL	2.72 ± 0.17	3.35 ± 0.21	5.84 ± 0.74	7.18 ± 0.91	9.77 ± 1.25	11.72 ± 1.50	15.25 ± 2.07	16.78 ± 2.28
PBL	2.92 ± 0.19	3.59 ± 0.23	5.44 ± 0.86	6.69 ± 1.06	8.21 ± 1.11	9.85 ± 1.33	11.60 ± 1.88	12.76 ± 2.07
PL	5.74 ± 0.29	7.06 ± 0.36	9.84 ± 0.83	11.56 ± 1.02	13.87 ± 1.20	16.05 ± 1.44	17.99 ± 1.90	19.66 ± 2.09
UJI	3.30 ± 0.29	4.06 ± 0.36	4.97 ± 0.82	6.11 ± 1.01	7.73 ± 1.88	9.27 ± 2.26	11.25 ± 2.99	12.38 ± 3.29
VAL	0.28 ± 0.02	0.34 ± 0.03	1.93 ± 0.29	2.38 ± 0.36	3.11 ± 0.95	3.73 ± 1.14	4.82 ± 1.57	5.30 ± 1.73
VBL	3.50 ± 0.21	4.31 ± 0.26	7.59 ± 0.70	9.34 ± 0.86	10.42 ± 1.26	12.50 ± 1.51	15.39 ± 2.22	16.93 ± 2.44
WI	1.19 ± 0.03	1.46 ± 0.04	1.80 ± 0.20	2.22 ± 0.25	2.88 ± 0.48	3.46 ± 0.58	4.29 ± 0.69	4.72 ± 0.76
ZYW	13.80 ± 0.17	14.95 ± 0.21	16.61 ± 2.16	18.58 ± 2.66	22.58 ± 2.90	25.78 ± 3.48	31.58 ± 4.51	34.74 ± 4.96

Table 2: Analysis of variance of craniometrics and percentage of the sum of squares (%SSQ) of relative age classes (I-VIII) based on the degree of maxillary molar eruption and wear in male and female *Heliophobius argenteocinereus emini* from Mlali village, Tanzania. * $= P < 0.05$, ** $= P < 0.01$, ***$= P < 0.001$. Cranial facets are defined and illustrated in Figure 1.

| Cranial facets	Age classes (A)	Sexes (B)	AxB	% SSQ A	% SSQ B	% SSQ AxB	% error
BCW	90.31***	36.54***	22.37***	68.8	12.63	4.61	13.96
DOC	46.37***	23.36***	4.29*	68.01	11.99	17.97	2.02
FL	51.51***	7.3*	3.86*	60.07	9.74	11.84	18.34
FW	24.35***	4.32**	11.23**	58.19	11.71	24.75	5.35
GLS	90.96***	43.01***	31.45***	59.55	25.77	13.77	0.92
IOB	72.06***	17.41**	6.75**	64.66	20.09	10.72	4.52
ITC	89.46***	32.87***	4.90*	74.86	1.05	13.44	10.66
IW	28.29***	30.17***	17.73***	51.2	24.68	10.84	13.27
KDW	48.01***	33.14***	9.09***	72.54	17.97	6.79	2.7
LR	38.27***	15.08*	10.37***	54.07	7.22	26.45	12.26
MOT	44.65***	16.56***	10.29***	46.69	18.45	24.35	10.51
NA	74.91***	55.18***	31.83***	49.96	36.89	5.51	7.64
NAS	35.55***	20.52***	5.36**	62.94	18.87	13.57	4.63
NL	31.48***	97.67***	11.84***	64.6	24.94	5.56	4.89
PBL	58.78***	22.54***	7.96**	59.65	17.12	17.01	6.21
PL	75.05***	88.58***	5.68**	53.39	36.75	6.93	2.93
UJI	18.45***	10.21**	0.42	32.62	24.55	30.24	12.59
VAL	13.41***	4.83*	1.68	51.91	26.9	15.24	5.94
VBL	43.42***	38.32***	9.83***	40.74	36.08	17.45	5.73
WI	22.84***	5.36*	11.05***	45.68	3.37	33.55	17.39
ZYW	95.85***	106.16***	99.53***	44.62	22.52	6.91	25.95
Mean %				**56.42**	**19.49**	**15.12**	**8.97**

The *post hoc* analysis showed little variations in the mean values of fourteen craniometrics with seven cranial facets showed significant variations of their mean values. Cranial facets that showed a homogeneous mean of their craniometrics occupied the same subsets, while the cranial facets that had significant variations of their mean values occupied distinct subsets. The crania facets that showed little mean variations between relative age classes included DOC, MOT, WI and UJI. The cranial facets showed significance mean variations of craniometrics included BCW, GLS, ITC and ZYW. The trend of homogeneity of the mean values of craniometrics was across all the relative age classes although noticed more in relative age classes I and II than subsequent age classes.

Owing to the occupancy of different age classes in the same subsets, it prompted further analysis of craniometrics. The Principal Component Analysis (PCA) showed clustering of craniometrics of relative age classes I and II of both sexes, while subsequent relative age classes showed the sexual-separation clustering of craniometrics. The descriptive statistics showed smaller

measurements in females than males in their respective relative age classes except for relative age classes I and II that had a slight variation in craniometrics. Variations in craniometrics between sexes within age classes caused the clustering of males of lower age classes with females of higher relative age classes (Figure 2). When the sexes were analyzed separately, it showed an orderly occupancy of relative age classes on Principal Components Axes with the absence of overlap between relative age classes. The

descriptive analysis of scores of axes (PCA I and II) showed higher explained variance of > 89% on Principal Component Axis 1 (PCAI) with PCAII showed < 5% (Table 3). The higher value of PCA I was observed in all relative age classes except relative age classes I and II. Males showed larger PCA scores than females which indicate variations in ontogenetic physiognomy between sexes and consequently avail the presence of sexual dimorphism.
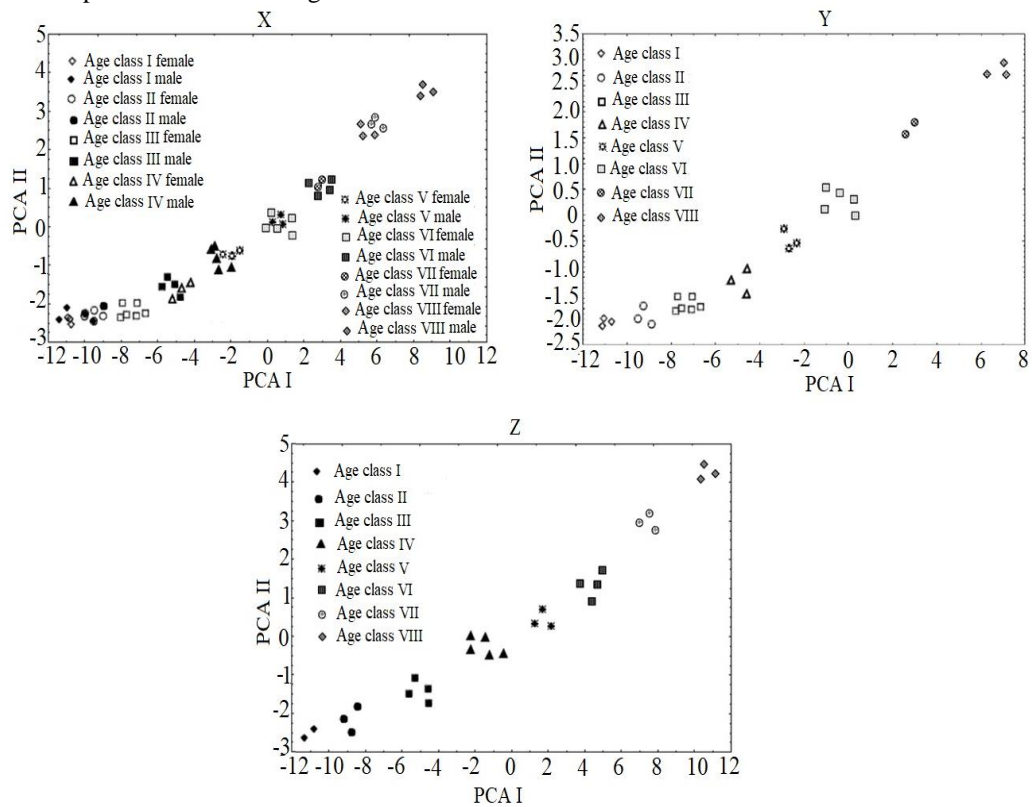
Figure 2: The Principal Components Axes (PCAI and PCAII) from a principal components analysis (PCA) of craniometrics of *Heliophobius argenteocinereus emini* between eight relative age classes (I-VIII). X = pooled sexes, Y = females, Z = males.

Table 3: Relative loadings of craniometrics of the first two Principal Components Axes (I and II) from a principal component analysis (PCA) of *Heliophobius argenteocinereus emini* from Mlali village, Tanzania (Relative age classes I–VIII): A = females: B = males: Cranial facets are defined and illustrated in Figure 1

Cranial facets	A		B	
	PCA I	PCA II	PCA I	PCA II
BCW	0.81	0.56	0.88	0.50
DOC	0.77	0.20	0.82	–0.08
FL	0.96	0.15	0.89	0.25
FW	0.80	–0.66	0.71	0.46
GLS	0.96	–0.22	0.96	–0.18
IOB	0.99	0.34	0.95	–0.34
ITC	0.94	–0.25	0.92	–0.29
IW	0.97	–0.02	0.96	–0.01
KDW	0.92	–0.04	0.94	–0.01
LR	0.91	0.24	0.82	0.35
MOT	0.77	0.37	0.90	–0.16
NA	0.84	0.30	0.89	0.43
NAS	0.86	–0.02	0.90	–0.24
NL	0.92	–0.34	0.90	–0.32
PBL	0.94	–0.04	0.93	0.06
PL	0.89	–0.07	0.89	–0.12
UJI	0.91	–0.30	0.94	–0.18
VAL	0.86	0.25	0.87	0.13
VBL	0.91	–0.10	0.90	0.19
WI	0.99	0.06	0.92	0.28
ZYW	0.95	0.28	0.82	0.22
% of explained variance	**89.89**	**3.29**	**89.10**	**4.48**

Discussion

Using a dental formula of the adult *Heliophobius agenteocinereus emini*, eight relative age classes were revealed. The dental formula of the species is reported for the first time by the present study. The *Heliophobius argenteocinereus emini* possesses premolar teeth that are absent in other African subterranean rodents. Studies reported that the premolar teeth of *H. a. emini* grow during the embryonic stage (Rodrigues and Šumbera 2015), which justifies the use of molar teeth for aging as they grow immediately after birth. In contrary to Rodrigues et al. (2011) who reported the continuous dental replacement in *Heliophobius* species, the present study did not observe any indication of the eruption of new molar(s) teeth in adult age classes. Adults were characterized by fully-grown molars with old individuals possessing short cusps which indicate the presence of molar wear during adulthood rather than a molar eruption. The conspicuous eruption of molar teeth in young individuals and wear of molar teeth in adult-hood is typical in rodents (Hench et al. 1984, Taylor et al. 1985, Chimimba and Dippenaar 1994, Van Rensburg et al. 2004, Abdel-Rahman et al. 2009, Chimimba et al. 2010, Katandukila 2017).

The pattern of craniometrics of *H. a. emini* indicates that growth is slow in

juveniles (i.e. relative age classes I and II) but increases significantly in sub-adults (i.e. relative age classes III) and more conspicuous in adults. The slow growth in juveniles is apparent since acquired bioenergy is utilised for the full development of body structures, while in sub-adults acquired bioenergy is utilised to attain the acceptable body structures for adulthood. The higher craniometrics variations in relative age classes III to VI indicate an evolutionary investment of energy for growth to attain competitive adult-hood characters that are advantageous to survival as reported in other studies of rodents (Taylor et al. 1985, Bennett et al. 1990, Schulte-Hostedde et al. 2001). Similar to other studies, *H. a. emini* has a little increase in craniometrics from relative age class VII to VIII which indicates cessation of growth during adulthood (Van Rensburg et al. 2004, Hart et al. 2007, Abdel-rahman et al. 2009, Katandukila 2017).

The rapid growth of individuals of relative age class III (i.e. sub-adults) compared to relative age class II (i.e. juveniles) may perhaps be the evolutionary strategy for sub-adults to attain specific sizes before dispersal (Thomas et al. 2009, Katandukila et al. 2014). Sub-adults of solitary rodents species have been reported to leave their maternal burrows after weaning in a sense that they have grown to sizes capable of withstanding the dispersal costs including individually foraging, burrow excavation and self-defense against enemies such as predators and invaders (Rado et al. 1992, Herbst and Bennett 2006, Katandukila et al. 2014). The dispersal age class at sub-adulthood in solitary subterranean rodents has been reported in pocket gophers, *Thomomys talpoide*s (Andersen 1978), blind mole-rats, *Spalax enhrenbergi* (Rado et al. 1992), tucotuco *Ctenomys* sp. (Malizia et al. 1995) and root-rats, *Tachyoryctes splendens* (Katandukila et al. 2014). The dispersal of Emin's silvery mole-rats at relative age class III is also a reproductive behavioural strategy of most solitary subterranean rodents to

influence hormonal regulation in lactating females before forthcoming reproductive cycle as suggested in other species (Šumbera et al. 2003, Isaac 2005, Katandukila et al. 2013, Katandukila and Bennett 2016, Katandukila et al. 2017, Ngalameno et al. 2017).

The significant variations of sizes of zygomatic arch (ZYW), braincase breath (BCW), interparietal width (IW) and length of the skull from the incisor to condyle (GLS and ITC) between relative age classes indicate that when *H. a. emini* grows into higher age classes there is a distinctively increase in size. The present study corroborates Dechow and Wang (2016) observation that individuals grow to increase the size for more muscle attachment and enhancement of jaw movements (i.e. ZYW) to increase biting force and food grinding capability.

The increase of sizes of BCW and IW facets suggest that as *H. a. emini* grows, the braincase also increases in size to accommodate the enlarging brain as explained in studies of cranial anatomy (Patel et al. 2014). The length of crania from incisor to condyle was a consequence of increases in the length of associated cranial facets, including frontal bone (FL), parietal bone (PL) and nasal bone (NL). Increases of lengths in FL, PL and NL reported increasing surface area for muscle attachment which contributes to the efficiency of activities performed by cranium (Thomason 1991, Wilson and Sánchez-Villagra 2009).

The silvery mole-rats use incisors for digging the earth during burrow excavations, therefore, the ontogenetic physiognomy of *H. a. emini* may mirror the evolutionary strategy to their subterranean lifestyles (Bennett and Faulkes 2000, Faulkes et al. 2011). Consistently to other solitary subterranean rodents (Katandukila et al. 2013, 2017, Katandukila and Bennett 2016), *H. a. emini* are very aggressive towards their counterparts. Males use the fights to secure more female mates and or defend from

invaders before the onset of reproductive activities and hence fighting signifies an evolutionary behaviour towards courtship display and or defense. Multidisciplinary analyses of craniometrics signify distinctive growth patterns between females and males *H. a. emini* from relative age class III within their respective age classes, indicating the presence of sexual dimorphism. Sexual dimorphism was more conspicuous in adults (i.e. relative age classes IV to VIII), although it started to manifest in the sub-adult stage (i.e. relative age class III). These findings denote that sexual dimorphism starts from sub-adult and becomes more pronounced in adults. The larger size in males of *H. a. emini* has advantages in mate selection like in other solitary subterranean mole-rats as larger sized males can secure more mates as a reflection of their genetic fitness (Schulte-Hostedde 2007, Katandukila et al. 2013, 2014, 2017). Females' smaller sizes are thought to be a consequence of conservative growth as increases of size is not an evolutionary advantage as in males. Most of the bioenergy in females *H. a. emini* is invested in overcoming reproduction costs including lactation and excavation of complex tunnels to accommodate youngs and increasing foraging efficiency of burrow occupants as reported in other studies of African solitary subterranean rodents (Sichilima et al. 2008, Thomas et al. 2009, Katandukila et al. 2013, 2014).

The trend of increasing lengths of cranial facets from lower to higher age classes and sexes indicates that sexual dimorphism in *H. a. emini* is attributed by size rather than shape. The deviations of shapes between sexes within relative age classes are not apparent to cause significant shape-sexual dimorphisms. This scenario was verified by a scatterplot visualisation which showed the most substantial variation of PCA I, which is a function of size, while PCA II was relatively small, suggesting a low variation in the cranial shape. The analyses of craniometrics of all sexually dimorphic species of African subterranean rodents studied to-date show similar patterns in which size has been verified to cause sexual dimorphism than shape variations (see Daly and Patton 1986, Van Rensburg et al. 2004, Hart et al. 2007, Chimimba et al. 2010, Katandukila 2017).

Conclusion
The results of this study align with the hypotheses of the study that ontogenetic characteristics of *H. a. emini* vary significantly between age classes. The ontogenetic physiognomy varied also between sexes, in which higher relative age classes presented conspicuous sexual dimorphism. The results from PCA have coincided with the predicted hypothesis of the presence of sexual dimorphism, which is speculated to be attributed by maternal pup(s) caring. The pattern of visualisation of scatterplots of PCA suggests that sexual dimorphism in *H. a. emini* is attributed by size rather than shape. Sexual dimorphism in *H. a. emini* starts from age class III intimating that distinctive investment of acquired bioenergy starts from sub-adult and becomes more conspicuous in adults. Moreover, this study presented the dental formula of the species for the first time, thus, a presented formula may be worthwhile in the taxonomy of the species among bathyergids. The molecular study between sexes from relative age class III to VIII is highly recommended to reveal the actual time for changes of genes and nature of their diversity which are perhaps attributed to the craniometrics trends reported in the present study.

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