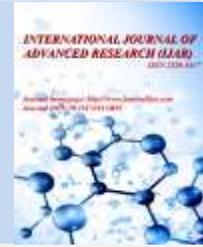




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RESEARCH ARTICLE

CRANIOMETRIC ANALYSIS OF ONTOGENETIC VARIATION AND SEXUAL DIMORPHISM IN THE EAST AFRICAN ROOT RAT, *TACHYORYCTES SPLENDENS* (RODENTIA: SPALACIDAE) FROM TANZANIA.

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Abstract

Ontogenetic variation and sexual dimorphism in the East African root rat, *Tachyoryctes splendens* (Rüppell 1835) from Tanzania, East Africa were examined using craniometric and body mass data. Ontogenetic variation was based on tooth eruption and wear in five relative age classes and revealed significant craniometric variation between them. Sexual dimorphism was evident in all three populations examined and revealed that males are larger in body size than females. The results of craniometric analysis of ontogenetic variation and sexual dimorphism in *T. splendens* are also reflected in the analysis of body mass data. These results suggest that male *T. splendens* invest energy into growth to facilitate male-male competition and sexual selection during the breeding season. Females however, show conservative growth with most energy being utilized for the excavation of complex burrow systems to increase foraging efficiency and allow for maternal care. Individuals of relative age classes 4 and 5 are reproductively mature and are thus capable of procreation.

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Introduction:-

Ontogenetic refers to growth and development of organism from embryo to adulthood (Alberch et al., 1979; Badyaev, 2000). As organism grows its body parts changes both on size and shape, and consequently results into ontogenetic variation from lower to higher age classes (Badyaev, 2000). The ontogenetic variation has been assessed between age classes as all individuals within age class assumed to have equal ontogenetic variation (Zelditch, 1988). Since it is difficult to examine growth rate from embryonic stage, most of ontogenetic studies were conducted from birth to adult-hood whereas growth ceases (Zelditch, 1988; Schultle-Hostedde et al., 2001; Schultle-Hostedde 2007; Chimimba et al., 2010).

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Ontogenetic variation between age groups has been however reported to be concealed by sexual dimorphism (Badyaev, 2002). The evidence of concealed ontogenetic variation as a result of sexual dimorphism was indicated by divergence of measurements between sexes within particular age class (Schultle-Hostedde et al., 2001). The nature and extent of sexual dimorphism reported be a result of different growth rate between sexes as a consequence of adaptation to reproductive or ecological roles (Badyaev, 2000; Schultle-Hostedde et al., 2001). The sex-specific adaptation to attain certain size or shape for mate selection and/or dominance over other individuals of the same sex has been attributed to sexual dimorphism however some genetic traits are shared between sexes within population (Andersson, 1994; Schultle-Hostedde et al., 2001; Badyaev, 2002). Example: In polygynous mating system, males are larger than females as consequences of male-male competition to acquire more adult female mates which is reproductive potential with females utilize their energy to overcome reproduction costs related to pup caring (Trives, 1972; Andersson, 1994; Schultle-Hostedde et al., 2001). Ontogenetic characteristics and sexual dimorphism have been studied in number of animals including rodents such as Giant mole-rats (*Fukomys mechowii*: Chimimba et al., 2010), Cape dune mole-rats (*Bathyergus suillus*: Hart et al., 2007), social Highveld mole-rats (*Cryptomys hottentotus pretoriae*: van Rensburg et al., 2004), Tete veld rats (*Aethomys ineptus*: Abdel-Rahman et al., 2009) and African Nile rat (*Arvicanthis niloticus* (Abdel-Rahman et al., 2009), Tuco-tuco (*Ctenomys* sp: Mora et al., 2003).

Studies of these rodents were based on analyses of craniometric data and body mass and reported the significant ontogenetic variation from sub-adult to adult-hood with presence of sexual dimorphism except but with absence of sexual dimorphism in *Cryptomys hottentotus pretoriae*. Despite ontogenetic variation and sexual dimorphism have been revealed on several species including subterranean rodent, none has been reported on spalacids including *Tachyoryctes splendens*. Although craniometrics have been analyses in *T. splendens* (Missone, 1974; Corbert and Hill, 1991; Beolchini and Corti, 2004), all studies were focused on investigation of taxonomy of the species rather than assessment of ontogenetic and sexual dimorphism. As a consequence of missing information on literature, the present study assessed ontogenetic variation, nature and extent of sexual dimorphism. This study analysed craniometrics and body mass data based on age classes.

Since chronological age classes were unknown in a population structure of *T. splendens*, the present study also estimated age classes within population based on degree of maxillary molar eruption and wear as the method was used successful on estimation of relative age classes on small mammals given the difficult to determine absolute age class (van Rensburg et al., 2004; Hart et al., 2007). The determination of chronological age classes is a key towards evaluation of ontogenetic variation and sexual dimorphism. The prediction for the present study was presence of ontogenetic variation between age classes from young age classes to adulthood. The study also hypothesized the presence of sexual dimorphism being prominent from sub-adult individuals (i.e. transitional age class to adulthood) as a consequence of sex-specific adaptation to behavioural roles.

Materials and Methods:-

A total of 215 *T. splendens* (103 males and 112 females) were sampled from three localities in the Kilimanjaro region, Tanzania, East Africa (Figure 1). These include: Marangu (03°16.54' S, 037°32.49' E; 1450 m above sea level (a.s.l.); $n = 75$), Keni-Aleni (03°13.53' S, 037°35.37' E; 1236 m a.s.l.; $n = 70$) and Uru-Shimbwe (03°25.32' S, 037°16.21' E; 1415 m a.s.l.; $n = 70$). All sampled sites are classified as agri-ecological zones with highly fertile volcanic soils supporting a variety of food and cash crops (Kilimanjaro Regional Profile (KRP), 1998). Animal capture and care procedures followed the guidelines of the Animal Ethics Committee of the University of Pretoria (Ethics clearance number ECO47-10) and sampling permits from the Commission of Sciences and Technology Tanzania (COSTECH; Permit number 2011-44-NA-2010-204). Voucher specimen preparation followed standard protocols as described by van Rensburg et al., (2004) and deposited in the reference collection of the Department of Zoology and Wildlife Conservation, University of Dar es Salaam, Tanzania.

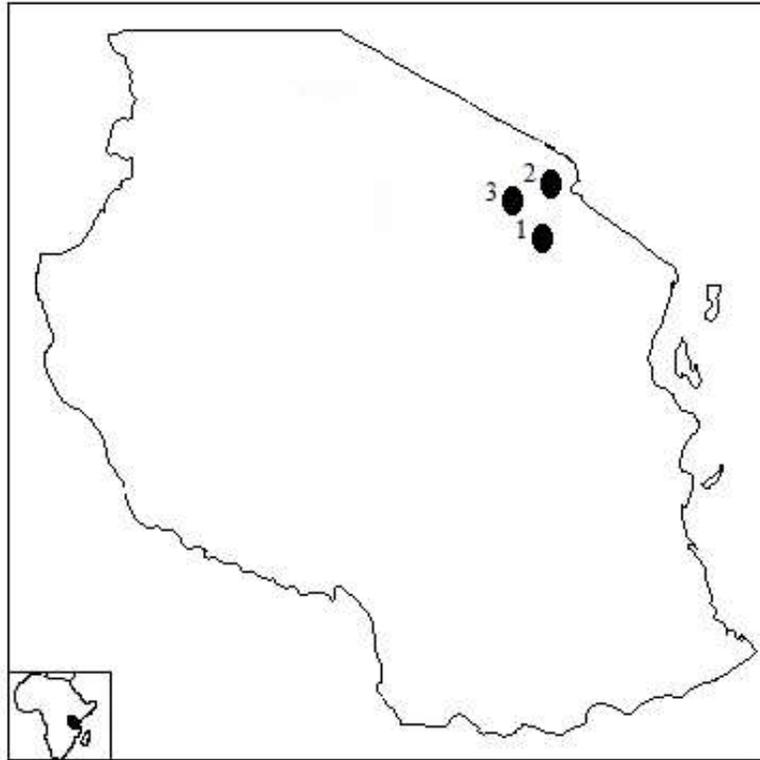


Figure 1:- Map of the study site in Tanzania (with an insert of Africa: 1 = Uru-Shimbwe; 2 = Keni-Aleni; 3 = Marangu).

Tachyoryctes splendens has highly trophied hypsodont dentition and the dental formula of adult individuals is 1/1, 0/0, 0/0, 3/3 = 16. Based on this dentition, estimation of relative age of classes was determined by the degree of maxillary molar eruption and wear based on one side of the maxillary row as described by van Rensburg et al. (2004) and Hart et al. (2007). Consequently, all individuals were allocated into the following five relative age classes (Figure 2): 1) Age class 1: two erupted anterior maxillary molars; 2) Age class 2: two erupted anterior maxillary molars with the 3rd molar beginning to erupt; 3) Age class 3: two erupted maxillary molars, with the 3rd molar half-grown; 4) Age class 4: three fully-grown maxillary molars, with worn crowns; and 5) Age class 5: three fully-grown maxillary molars, with extensively worn crowns.

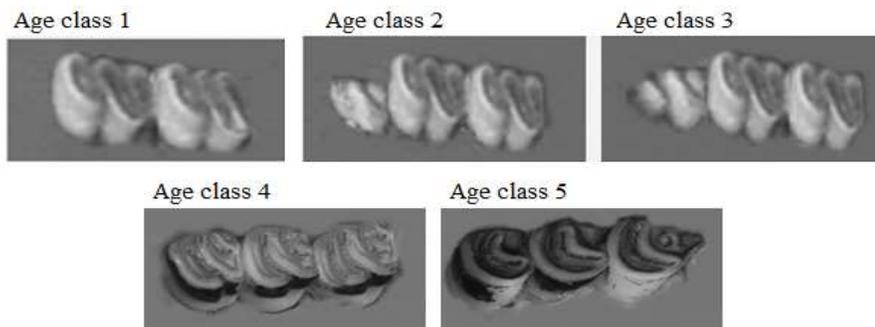


Figure 2:- Relative age classes based on maxillary molar eruption and wear in *Tachyoryctes splendens* from Tanzania.

Ontogenetic variation and sexual dimorphism were assessed using 34 linear cranial measurements (Figure 3) following van Rensburg et al. (2004), Hart et al. (2007) and Chimimba et al. (2010) with slight modification. All linear cranial measurements were recorded to the nearest 0.05 mm using a pair of Mitutoyo digital calipers (Mitutoyo American Corporation, Aurora, Illinois, U.S.A.), while body mass was recorded to the nearest 0.05 g using a Pesola spring balance (Pesola dynamometer-5 kg/10 lbs, Switzerland).

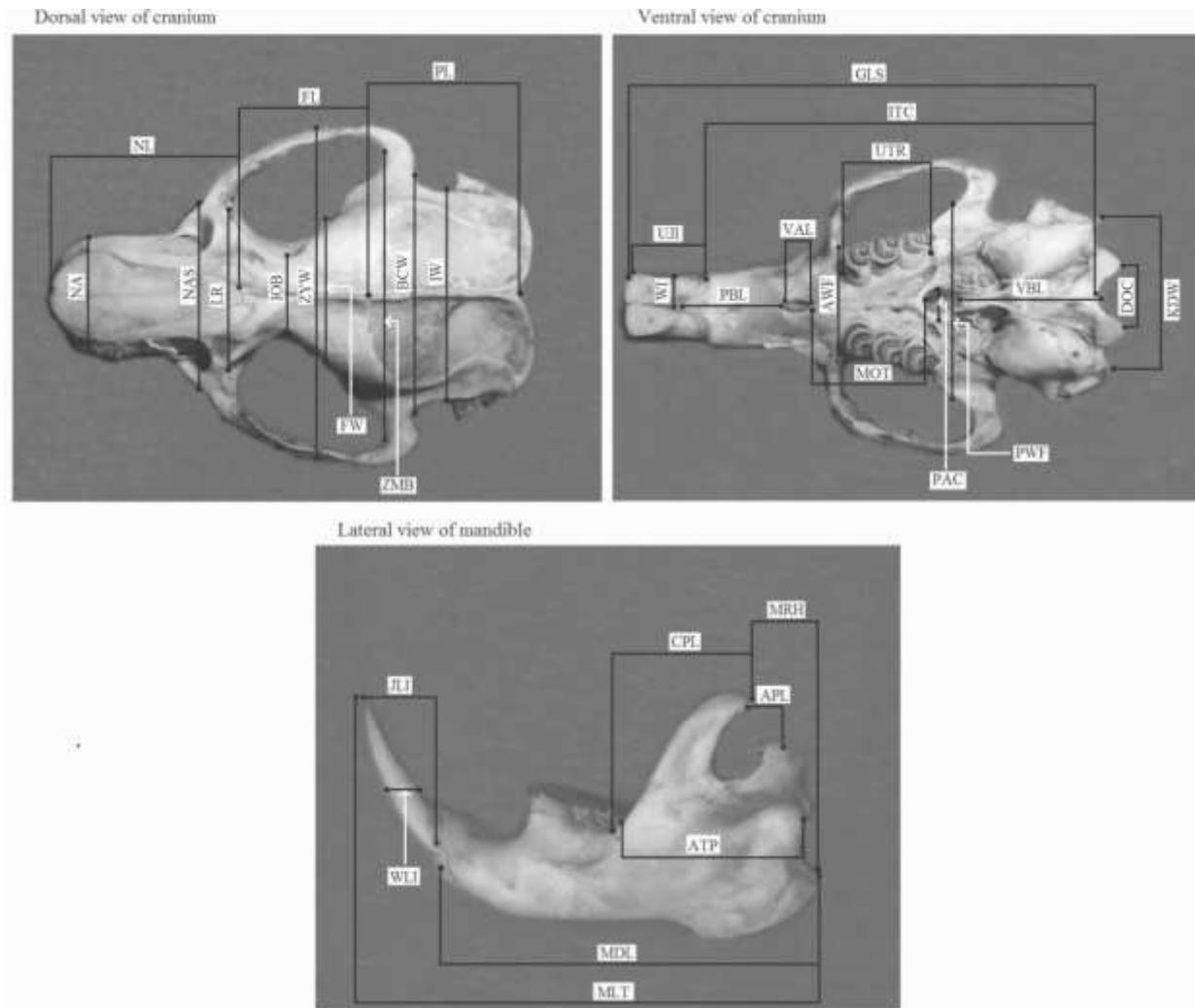


Figure 3: Linear cranial measurements used for craniometric analysis. Measurement abbreviations: 1) APL = Length of foramen articular facet; 2) ATP = Length of mandibular foramen-articular facet; 3) AWF = Ventral width from left to right of anterior frontal bone (at the anterior part of the 1st molar); 4) BCW = Brain case breadth; 5) CPL = Length of articular facet to edge of the 3rd molar; 6) DOC = Distance between right and left occipital condyle; 7) FL = Frontal bone length (sagittal border length of frontal bone); 8) FW = Frontal bone width; 9) GLS = Length from incisor to condyle (including incisor); 10) IOB = Least breadth of interorbital constriction; 11) ITC = Length from incisor to condyle (excluding incisor); 12) IW = Interparietal bone width; 13) JLI = Lower incisor length; 14) KDW = Distance between left and right paroccipital process; 15) LR = Distance between left and right anterolateral corner of frontal bone; 16) MDL = Length of mandible from anterior to posterior part (excluding incisor); 17) MLT = Length of mandible from anterior to posterior part (including incisor); 18) MOT = Length of hard palate from posterior of incisive fossa to posterior nasal spine; 19) MRH = Height of mandible-ramus; 20) NA = Nasal width; 21) NAS = Nasal width at the middle; 22) NL = Nasal bone length; 23) PAC = Width of hard palate at point of constriction; 24) PBL = Length of premaxillary bone; 25) PL = Parietal bone length (sagittal border length of parietal bone); 26) PWF = Ventral width of posterior part of frontal bone (after 3rd molar); 27) UJI = Upper incisor length; 28) UTR = Crown length of maxillary teeth row; 29) VAL = Length of incisive fossa; 30) VBL = Length between vomer and condyle before foramen magnum; 31) WI = Width of upper incisor; 32) WLI = Width of lower incisor; 33) ZMB = Breadth between zygomatic processes of squamosals; and 34) ZYW = Width between outer margins of zygomatic arches.

Data analyses:-

Craniometric and body mass data from all populations of *T. splendens* were initially tested for normality and homogeneity of variances and subsequently subjected to a two-way analysis of variance (ANOVA; Zar, 1999) to test

for ontogenetic variation, sexual dimorphism and the interaction between them. Where significant differences were detected, Student-Newman-Keuls (SNK) *post hoc* test of ranked means following ANOVA assumptions (Sokal and Rohlf, 1981) was used to partition non-significant subsets of relative age classes ($P > 0.05$). The sum of squares (SSQ) from the derived two-way ANOVA table were used to partition potential sources of variation (Wonnacort and Wonnacort, 1972) with reference to relative age, sex, the interaction between them and error (= residual). The %SSQ was computed by dividing the SSQ associated with each source of variation by the total SSQ. All univariate analyses were based on algorithms in the *Statistical Package for the Social Sciences (SPSS; Schneider, 1988)* version 20 (IBM® SPSS® Statistics 20; Chicago, Illinois, USA).

Given the equivocal results of *post hoc* analysis of the univariate analyses between age classes, multivariate analyses were used to further evaluate the source of equivocal results of ontogenetic variation since analysis of sexes does not fit assumptions of *post hoc*. Consequently, the craniometric data of all three populations of *T. splendens* were also subjected to multivariate analyses using principal components analysis (PCA) of standardized variables and Unweighted Pair-Group Method of Arithmetic Averages (UPGMA) cluster analysis. The PCA was based on correlation coefficients among variables and UPGMA cluster analysis was based on Euclidean distances and correlation coefficients among groups (Sneath and Sokal, 1973). The distinct groups of sexes within age classes and overlap of sexes between age classes revealed on multivariate analyses subsequently resulted into analyses of data with sexes separately. All multivariate analyses were based on algorithms in *STATISTICA* version 10 (<http://www.statsoft.com>).

Results:-

Univariate analyses:-

As exemplified by the Marangu population which had the largest representative sample size ($n = 75$) and all the five relative age classes, both sexes showed an orderly increase in cranial dimensions with increasing age and males were larger in body size than females (Table 1).

Table 1:- Standard descriptive statistics of cranial measurements (mm) of *Tachyoryctes splendens* from Marangu, Tanzania. SD = standard deviation; CV = coefficient of variation; f = female, m = male; sample size is indicated in parentheses. Cranial variables are defined and illustrated in Figure 3.

Age class	Statistics	Cranial measurements										
		APL	ATP	AWF	BCW	CPL	DOC	FL	FW	GLS	IOB	ITC
1f (2)	Mean	5.57	2.14	7.77	13.78	6.99	5.21	6.98	8.94	30.62	4.99	28.44
	SD	0.45	0.52	0.42	0.54	0.08	0.07	0.19	0.08	0.01	0.80	0.72
	CV	0.21	0.27	0.18	0.29	0.01	0.01	0.04	0.01	0.15	0.64	0.52
2f (8)	Mean	7.61	3.87	9.19	17.15	8.22	6.51	8.40	11.46	37.61	5.70	34.53
	SD	0.53	0.49	0.48	0.57	0.40	0.66	0.79	0.94	0.66	0.57	0.90
	CV	0.28	0.24	0.23	0.33	0.16	0.43	0.63	0.87	0.44	0.32	0.82
3f (8)	Mean	8.77	5.19	11.37	19.92	10.65	7.08	10.95	13.98	42.79	6.94	38.85
	SD	0.98	1.09	0.46	0.90	0.40	0.98	0.40	1.65	0.14	0.72	1.46
	CV	0.97	1.19	0.22	0.81	0.16	0.97	0.16	2.72	0.02	0.52	2.12
4f (18)	Mean	10.26	7.93	14.05	24.56	12.37	8.66	12.80	15.99	46.87	11.12	42.77
	SD	0.67	0.31	0.64	0.71	0.74	0.72	0.83	1.03	0.37	0.31	0.75
	CV	0.45	0.10	0.41	0.51	0.55	0.52	0.70	1.06	0.14	0.10	0.57
5f (2)	Mean	11.50	9.60	15.43	26.74	13.15	9.99	14.74	18.01	49.41	12.77	47.76
	SD	0.53	0.84	1.05	0.60	0.99	0.93	0.73	1.02	0.61	0.42	0.71
	CV	0.03	0.01	5.75	0.53	0.88	0.11	0.18	1.92	0.28	0.03	0.61

Females (continued)

Age class	Statistics	Cranial measurements										
		IW	JLI	KDW	LR	MDL	MLT	MOT	MRH	NA	NAS	NL
1f (2)	Mean	10.64	10.09	7.84	7.91	20.19	30.35	5.99	9.98	5.69	7.32	5.74
	SD	0.06	0.17	0.14	0.06	0.04	0.11	0.28	0.23	0.59	0.07	1.01
	CV	0.03	0.03	0.02	0.04	0.01	0.01	0.08	0.05	0.35	0.01	1.02
2f (8)	Mean	15.43	11.56	10.76	9.43	23.72	33.35	8.57	13.06	7.63	8.71	8.78
	SD	0.64	0.48	0.93	0.60	0.95	0.68	0.60	0.60	0.63	0.58	0.98
	CV	0.40	0.23	0.86	0.36	0.89	0.46	0.35	0.36	0.40	0.34	0.97
3f (8)	Mean	23.20	14.22	14.94	11.68	27.72	37.23	10.19	14.42	9.63	11.01	12.91
	SD	0.94	0.58	0.65	1.01	1.37	1.40	1.18	0.76	1.16	0.93	0.80
	CV	0.88	0.34	0.42	1.02	1.87	1.95	1.39	0.58	1.34	0.87	0.64
4f (18)	Mean	25.59	16.91	18.10	14.57	30.64	40.79	12.86	16.00	11.94	12.52	16.03
	SD	0.57	0.86	0.33	0.55	1.36	1.10	0.97	0.83	0.68	0.78	0.79
	CV	0.32	0.73	0.11	0.30	1.86	1.20	0.94	0.69	0.47	0.61	0.63
5f (2)	Mean	27.52	18.76	19.04	16.12	38.37	51.94	13.98	17.25	13.11	14.79	18.92
	SD	0.68	0.77	0.15	1.06	0.99	1.47	0.91	1.23	0.70	0.45	0.48
	CV	1.28	1.11	0.30	0.25	1.22	3.56	0.20	0.30	0.57	0.01	0.91

Females (continued)

Age class	Statistics	Cranial measurements											
		PAC	PBL	PL	PWF	UJI	UTR	VAL	VBL	WI	WLI	ZMB	ZYW
1f (2)	Mean	1.64	5.56	8.54	8.92	5.84	5.08	2.03	6.66	1.97	1.61	19.04	24.07
	SD	0.07	0.04	0.56	0.20	0.11	0.07	0.01	0.25	0.03	0.32	1.29	0.72
	CV	0.01	0.20	0.31	0.50	0.01	0.01	0.40	0.07	0.30	0.10	1.66	0.52
2f (8)	Mean	2.27	8.18	11.15	12.17	6.75	7.25	2.58	9.80	2.28	2.12	22.26	28.06
	SD	0.47	0.84	0.60	0.51	0.54	0.68	0.28	1.35	0.11	0.09	0.94	1.27
	CV	0.22	0.70	0.36	0.26	0.29	0.46	0.08	1.83	0.01	0.01	0.88	1.61
3f (8)	Mean	3.33	11.15	15.10	14.72	10.58	9.08	3.17	13.43	3.08	2.34	26.23	32.64
	SD	0.42	0.70	0.59	0.51	0.84	0.41	0.49	0.86	0.15	0.17	0.49	0.86
	CV	0.17	0.49	0.35	0.26	0.70	0.16	0.24	0.75	0.02	0.03	0.24	0.73
4f (18)	Mean	4.73	13.22	17.55	16.45	12.08	10.09	4.23	16.06	4.04	3.07	29.32	36.76
	SD	0.26	0.64	1.28	0.93	0.41	0.57	0.64	0.79	0.15	0.21	0.64	1.27
	CV	0.07	0.41	1.63	0.86	0.17	0.33	0.42	0.62	0.02	0.04	0.41	1.62
5f (2)	Mean	4.95	14.18	19.09	17.62	13.93	11.04	5.05	18.67	4.13	3.23	31.98	39.12
	SD	0.58	1.18	0.84	0.80	0.98	0.84	0.61	1.36	0.10	0.23	1.44	0.61
	CV	0.01	2.08	0.11	0.14	0.11	0.25	0.05	4.96	0.30	0.04	1.14	0.86

Age class	Statistic s	Cranial measurements										
		APL	ATP	AWF	BCW	CPL	DOC	FL	FW	GLS	IOB	ITC
1m (3)	Mean	6.25	2.86	7.83	13.38	6.81	5.48	6.98	9.66	30.96	5.15	28.43
	SD	0.31	0.23	0.57	0.55	0.83	0.50	0.27	0.70	0.11	0.14	1.21
	CV	0.09	0.05	0.33	0.30	0.70	0.25	0.07	0.48	0.01	0.02	1.47
2m (4)	Mean	9.55	6.44	12.02	20.80	10.51	7.43	9.93	15.22	44.02	7.31	40.74
	SD	0.12	1.02	0.57	0.43	0.22	1.23	1.13	0.47	0.30	0.14	0.40
	CV	0.01	1.04	0.32	0.19	0.05	1.50	1.27	0.22	0.09	0.02	0.16
3m (15)	Mean	12.18	8.38	15.10	23.14	13.75	8.94	13.79	17.10	49.40	10.25	46.09
	SD	0.64	0.62	0.71	0.52	0.91	1.40	0.20	0.99	0.70	0.29	0.36
	CV	0.40	0.39	0.51	0.27	0.82	1.97	0.04	0.98	0.49	0.09	0.13
4m (14)	Mean	13.72	10.44	16.07	27.27	14.59	10.83	15.86	18.75	56.48	12.78	52.05
	SD	0.17	0.11	2.40	0.73	0.94	0.33	0.42	1.39	0.53	0.17	0.78
	CV	0.28	0.71	1.11	0.36	0.99	0.86	0.53	1.05	0.38	0.18	0.51
5m (1)	Mean	13.98	12.13	17.93	28.75	15.33	12.44	16.94	20.38	58.26	14.68	53.48

Males (continued)

Age class	Statistics	Cranial measurements										
		IW	JLI	KDW	LR	MDL	MLT	MOT	MRH	NA	NAS	NL
1m (3)	Mean	10.33	10.19	8.28	8.23	20.26	30.50	6.88	10.58	6.78	7.83	6.09
	SD	0.08	0.79	0.98	0.78	0.55	0.21	0.64	0.23	0.56	0.82	0.52
	CV	0.01	0.62	0.96	0.61	0.30	0.04	0.40	0.05	0.31	0.67	0.27
2m (4)	Mean	23.79	13.06	13.67	11.36	32.07	42.52	10.76	15.04	9.95	10.30	10.80
	SD	0.22	0.11	0.93	1.56	0.25	0.22	1.48	0.50	1.03	0.97	0.38
	CV	0.05	0.01	0.87	2.44	0.06	0.05	2.20	0.25	1.06	0.94	0.14
3m (15)	Mean	26.79	16.78	17.99	14.23	37.63	46.38	12.67	16.89	12.37	13.18	15.76
	SD	0.61	0.57	0.45	1.12	1.41	3.46	1.22	0.33	0.30	0.28	0.60
	CV	0.38	0.32	0.21	1.25	2.89	6.13	1.50	0.37	0.09	0.08	0.37
4m (14)	Mean	29.47	20.23	20.04	17.24	40.68	49.77	14.69	18.14	13.90	15.49	19.70
	SD	1.13	1.05	0.02	0.50	1.10	1.89	0.06	0.55	0.76	0.12	0.95
	CV	0.46	0.59	0.02	1.13	0.99	2.17	0.83	1.52	0.49	0.21	0.23
5m (1)	Mean	31.30	21.16	21.33	18.84	44.10	55.28	15.65	19.29	16.18	16.96	21.55

Males (continued)

Age class	Statistics	Cranial measurements											
		PAC	PBL	PL	PWF	UJI	UTR	VAL	VBL	WI	WLI	ZMB	ZYW
1m (3)	Mean	1.68	5.44	9.05	9.48	6.03	5.09	2.13	6.59	2.18	1.63	20.02	25.84
	SD	0.19	0.15	0.31	0.45	0.06	0.19	0.08	0.36	0.29	0.07	0.73	0.56
	CV	0.04	0.02	0.10	0.20	0.20	0.04	0.01	0.13	0.09	0.01	0.53	0.32
2m (4)	Mean	2.32	10.41	13.75	13.84	10.68	8.43	3.40	14.09	3.07	2.91	23.99	32.31
	SD	0.20	1.82	0.35	0.74	0.22	0.39	0.12	1.23	0.08	0.13	1.85	1.59
	CV	0.04	3.32	0.13	0.55	0.05	0.16	0.02	1.51	0.01	0.02	3.42	2.53
3m (15)	Mean	4.92	13.77	17.87	17.24	13.19	11.42	5.52	16.79	4.59	3.99	30.93	36.14
	SD	0.46	0.80	0.48	1.14	0.41	0.61	0.49	1.29	0.15	0.21	0.93	0.57
	CV	0.21	0.65	0.23	1.31	0.17	0.37	0.24	1.67	0.02	0.04	0.87	0.33
4m (14)	Mean	6.19	15.21	20.98	18.85	15.64	12.29	6.63	19.94	5.76	4.83	34.49	39.63
	SD	0.09	1.44	0.33	0.37	0.33	0.50	0.22	2.23	0.04	0.20	1.07	0.93
	CV	0.34	1.39	0.70	0.65	0.97	0.70	0.38	1.85	0.01	0.05	2.07	0.37
5m (1)	Mean	6.63	16.77	21.17	20.20	16.31	13.20	7.61	20.97	5.94	4.86	37.09	42.68

As exemplified by the Marangu population, the ANOVA results of the three populations showed that although most measurements varied significantly with relative age classes, sex and the interaction between the two, the largest *F*-values were associated with age, followed by sex, the residual component and the interaction between relative age and sex (Table 2). Variance partitioning in the three populations using %SSQ showed that ontogenetic variation contributed more to the potential source of variation followed by sex, the residual component and the interaction between age and sex [Age: Marangu – Mean %SSQ = 53.22% (range = 33.96–73.97%); Keni-Aleni – Mean %SSQ = 53.23% (range = 34.04–74.04%); Uru-Shimbwe – Mean %SSQ = 53.19% (range = 33.98–73.99%); Sex: Marangu – Mean %SSQ = 18.34% (range = 2.84–38.41%); Keni-Aleni – Mean %SSQ = 18.37% (range = 2.87–38.39%); Uru-Shimbwe = 18.37% (range = 2.85–38.38%); Sex/Age interaction: Marangu – Mean %SSQ = 11.27% (range = 1.77–29.89%); Keni-Aleni – Mean %SSQ = 11.28% (range = 1.79–29.89%); Uru-Shimbwe = 11.30% (range = 1.80–29.92%); and Error component (= residual): Marangu – Mean %SSQ = 17.17% (range = 3.94–36.01%); Keni-Aleni – Mean %SSQ = 17.12% (range = 3.98–36.01%); Uru-Shimbwe = 17.13% (range = 3.95–35.99%). The %SSQ of the residual component in all three populations suggests that, apart from age variation, sexual dimorphism and the interaction between the two, there are also other factors that may be influencing the nature and extent of ontogenetic variation and sexual dimorphism in *T. splendens* from Tanzania.

Table 2:- Two-way analysis of variance (ANOVA) and percent sum of squares (%SSQ) of relative age classes (1-5) based on the degree of maxillary molar eruption and wear in male and female *Tachyoryctes splendens* from Marangu, Tanzania. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Cranial measurements are defined and illustrated in Fig. 3.

Cranial measurements	F-values			%SSQ			
	Age (A)	Sexes (S)	A x S	A	S	A x S	Error
APL	37.90***	16.06***	1.99	52.91	28.44	3.35	15.31
ATP	46.11***	9.41**	15.26***	50.97	15.94	20.59	12.50
AWF	75.01***	36.04***	6.09**	59.89	16.45	8.79	14.87
BCW	118.78***	60.13***	37.69***	52.45	20.03	15.74	11.79
CPL	39.97***	11.89**	15.95***	44.62	15.41	24.03	15.94
DOC	17.96***	7.29**	2.10	43.04	22.29	1.77	32.90
FL	91.14***	2.27	5.58**	60.56	7.99	19.85	11.60
FW	33.94***	11.34**	3.36*	58.52	10.55	5.92	25.01
GLS	130.85***	37.45***	19.14***	65.18	24.50	6.26	4.06
IOB	82.17***	22.99***	55.03***	33.96	21.51	29.89	14.64
ITC	171.95***	69.96***	11.90***	50.83	38.38	3.27	7.52
IW	121.02***	38.12***	22.17***	69.96	15.24	8.68	6.13
JLI	54.19***	19.89***	2.29	53.08	19.06	3.58	24.28
KDW	149.19***	48.06***	8.95***	73.97	14.28	5.23	6.52
LR	53.71***	10.06**	8.06***	49.11	12.60	10.50	27.80
MDL	97.85***	35.93***	11.48***	54.98	26.85	7.27	10.90
MLT	70.81***	26.24***	3.81*	51.58	34.89	9.51	4.02
MOT	42.58***	19.54***	0.97	48.94	13.81	7.31	29.94
MRH	21.85***	9.16**	5.06**	49.34	13.84	10.97	25.85
NA	86.13***	16.01***	6.31***	55.83	25.13	7.81	11.24
NAS	84.03***	42.96***	1.31	65.97	17.71	3.15	13.17
NL	90.95***	64.30***	10.27***	42.67	37.28	16.12	3.94
PAC	38.05***	14.25***	1.38	41.91	23.36	10.82	23.91
PBL	58.90***	13.02***	6.98***	61.12	10.91	8.34	19.63
PL	87.41***	10.93**	3.93*	71.69	4.35	2.44	21.52
PWF	139.16***	31.53***	4.13**	67.51	13.11	5.84	13.55
UJI	84.83***	7.37**	7.03***	66.26	9.50	8.56	15.69
UTR	49.11***	1.85	15.37***	47.03	6.86	26.40	19.71
VAL	42.94***	2.60	18.97***	42.99	2.86	27.79	26.37
VBL	56.59***	36.11***	5.01**	41.62	28.06	9.58	20.75
WI	20.13***	2.12	15.04***	39.99	3.12	20.88	36.01
WLI	87.14***	4.56*	5.13**	47.38	9.34	19.12	24.16
ZMB	118.04***	23.96***	12.04***	49.10	36.71	6.35	7.84
ZYW	88.12***	19.86***	6.07**	44.51	23.34	7.44	24.71
Mean				53.22	18.34	11.27	17.17

As exemplified by the Marangu population, the SNK tests are equivocal. These tests showed five major patterns (Table 3). The first pattern involved 33 out of 34 measurements that showed the separation of relative age class 1 from other relative age classes except for one measurement (IOB) which showed an overlap of relative age classes 1 and 2. The second pattern involved 16 out of the 34 measurements that grouped relative age classes 2 and 3 in the same non-significant subset. The third pattern involved 25 out of 34 measurements that grouped relative age classes 3 and 4 into the same non-significant subset. The fourth pattern involved 27 out of 34 measurements that showed

overlaps of relative age classes 4 and 5. The fifth pattern involved seven out of 34 measurements that showed all relative age classes to be significantly different from each other.

Table 3:- Student-Newman-Keuls (SNK) *post hoc* tests for cranial measurements (mm) of age classes 1-5 of *Tachyoryctes splendens* from Marangu, Tanzania. Results are presented as mean \pm 1 standard deviation. S = all means are significantly different; underlined = non-significant subsets of relative age classes ($P > 0.05$). The sample size is shown in parentheses. Cranial measurements are defined and illustrated in Figure 3.

Cranial measurements	Age classes				
	1 (5)	2 (12)	3 (23)	4 (32)	5 (3)
APL	4.63 \pm 0.32	<u>8.72 \pm 1.37</u>	<u>10.60 \pm 2.41</u>	<u>12.03 \pm 2.44</u>	12.74 \pm 1.68
ATP	1.97 \pm 0.27	5.30 \pm 1.82	<u>6.91 \pm 2.26</u>	<u>9.28 \pm 1.77</u>	10.88 \pm 1.78
AWF	6.76 \pm 0.38	10.75 \pm 2.00	<u>13.36 \pm 2.64</u>	<u>15.06 \pm 1.43</u>	16.69 \pm 1.76
BCW	12.68 \pm 0.28	19.12 \pm 2.58	21.66 \pm 2.28 S	25.94 \pm 1.91	27.76 \pm 1.42
CPL	4.74 \pm 0.38	<u>9.51 \pm 1.62</u>	<u>12.33 \pm 2.19</u>	<u>13.53 \pm 1.57</u>	14.26 \pm 1.54
DOC	4.30 \pm 0.26	7.11 \pm 0.65	<u>8.14 \pm 1.32</u>	<u>9.88 \pm 1.53</u>	11.23 \pm 1.73
FL	6.73 \pm 0.35	<u>9.31 \pm 1.08</u>	<u>12.50 \pm 2.01</u>	<u>14.46 \pm 2.16</u>	15.85 \pm 1.55
FW	8.60 \pm 0.08	<u>13.48 \pm 2.66</u>	<u>15.63 \pm 2.20</u>	<u>17.43 \pm 1.95</u>	19.21 \pm 1.67
GLS	30.29 \pm 0.24	40.84 \pm 4.53	45.15 \pm 4.68 S	49.15 \pm 4.59	52.16 \pm 4.23

Table 3 (continued)

Cranial measurements	Age classes				
	1 (5)	2 (12)	3 (23)	4 (32)	5 (3)
IOB	4.02 ± 0.19	6.65 ± 1.14	8.73 ± 2.34	11.96 ± 1.17	13.73 ± 1.35
ITC	26.83 ± 0.44	37.68 ± 4.39	42.51 ± 4.12 S	45.48 ± 5.56	49.95 ± 4.04
IW	10.89 ± 0.35	19.78 ± 3.86	25.13 ± 2.54	26.58 ± 2.74	29.41 ± 2.67
JLI	9.98 ± 0.44	12.48 ± 1.06	15.64 ± 1.81	18.67 ± 2.35	19.96 ± 1.69
KDW	7.41 ± 0.39	12.37 ± 2.06	16.60 ± 2.16	19.10 ± 1.37	20.19 ± 1.62
LR	7.27 ± 0.22	10.56 ± 1.36	13.06 ± 1.81	16.06 ± 1.89	17.48 ± 1.92
MDL	19.48 ± 0.40	27.94 ± 5.90	32.71 ± 6.01 S	35.73 ± 6.10	41.56 ± 4.15
MLT	30.28 ± 0.32	37.98 ± 6.48	41.85 ± 6.47 S	45.28 ± 5.35	49.91 ± 2.36
MOT	6.02 ± 0.37	9.83 ± 1.55	11.47 ± 1.76	13.82 ± 1.29	14.82 ± 1.18
MRH	9.89 ± 0.41	14.22 ± 1.40	15.79 ± 1.75	17.16 ± 1.51	18.28 ± 1.44
NA	4.99 ± 0.42	8.96 ± 1.64	11.14 ± 1.94	13.00 ± 1.38	14.65 ± 2.17
NAS	7.28 ± 0.36	9.66 ± 1.12	12.10 ± 1.54	14.02 ± 2.10	15.87 ± 1.53
NL	4.97 ± 0.32	9.96 ± 1.43	14.47 ± 2.02	17.96 ± 2.59	20.25 ± 1.86
PAC	1.36 ± 0.31	2.59 ± 0.39	3.17 ± 1.13	4.43 ± 1.03	5.01 ± 1.19
PBL	5.20 ± 0.34	9.46 ± 1.58	12.59 ± 1.85	14.20 ± 1.40	15.51 ± 1.83
PL	8.68 ± 0.47	12.59 ± 1.84	16.61 ± 1.96	19.42 ± 2.42	20.16 ± 1.47
PWF	8.72 ± 0.42	13.15 ± 1.18	16.11 ± 1.78	17.66 ± 1.70	18.94 ± 1.82
UJI	5.68 ± 0.47	8.86 ± 2.78	12.01 ± 1.85	14.00 ± 2.52	15.15 ± 1.68
UTR	5.21 ± 0.11	7.83 ± 0.83	9.27 ± 1.66	10.24 ± 1.55	10.49 ± 1.51
VAL	1.96 ± 0.25	2.99 ± 0.58	3.36 ± 1.66	4.41 ± 1.69	4.63 ± 1.81
VBL	5.93 ± 0.37	12.11 ± 3.03	15.24 ± 2.38	18.15 ± 2.74	19.85 ± 1.62
WI	2.08 ± 0.15	2.88 ± 0.77	3.34 ± 1.40	3.91 ± 1.21	4.15 ± 1.28
WLI	1.50 ± 0.13	2.57 ± 0.56	3.13 ± 1.17	3.44 ± 1.24	3.80 ± 1.15
ZMB	17.76 ± 0.37	23.27 ± 1.22	28.71 ± 3.33 S	32.03 ± 3.65	35.07 ± 3.61
ZYW	23.52 ± 0.32	30.33 ± 3.01	34.52 ± 2.48 S	38.40 ± 2.03	41.43 ± 2.51

As exemplified by the Marangu population (Figure 4), a plot of the first two principal components of the PCA confirmed the unequivocal separation of the sexes within relative age classes and the partial separation of relative age classes. Similar to the SNK tests, the PCA revealed the separation of relative age class 1 from all other age classes with overlaps of age classes 2 and 3, 3 and 4 and 4 and 5. This suggests that although there are age class

differences within all three populations of *T. splendens*, the relative age groupings are confounded by sexual dimorphism.

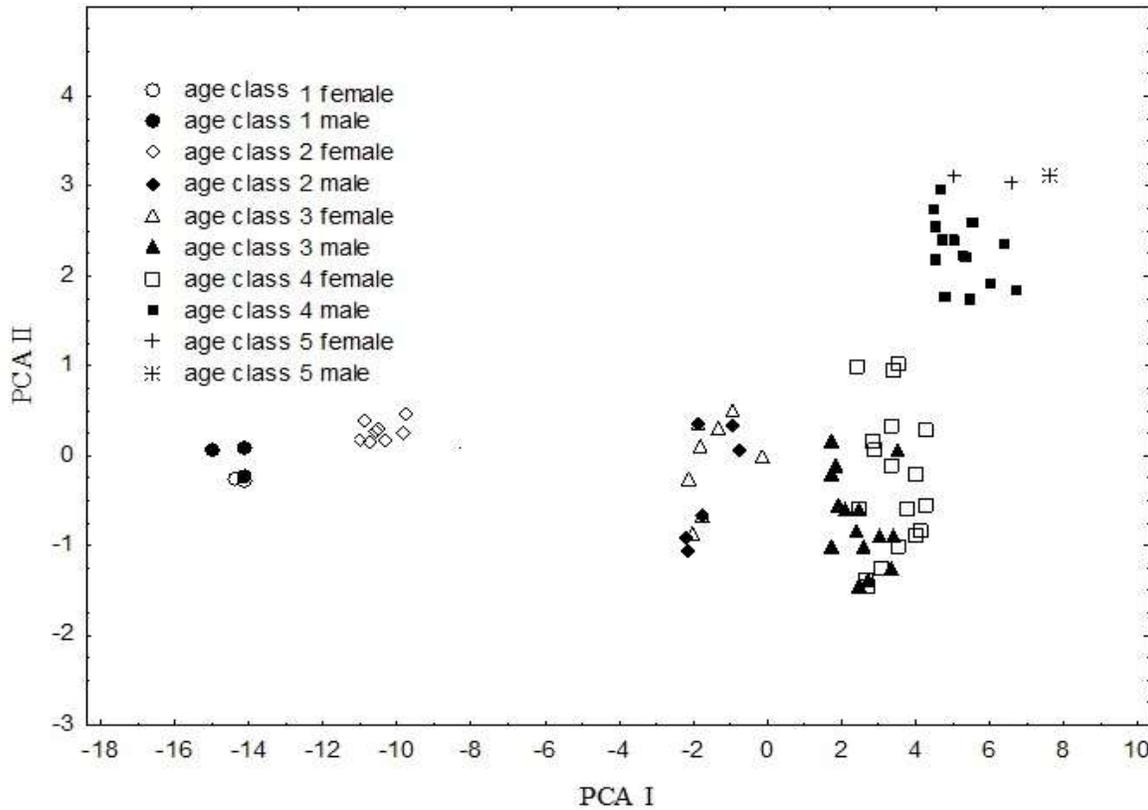
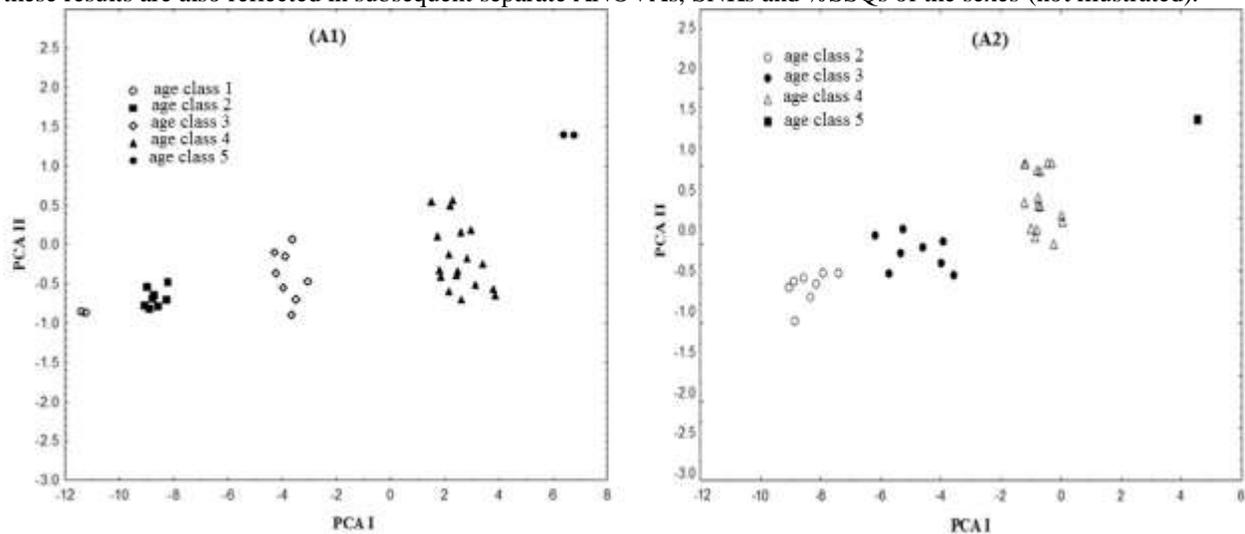


Figure 4:- The first two principal components from a principal components analysis (PCA) of cranial measurements from male and female *Tachyoryctes splendens* of age classes 1-5 from Marangu, Tanzania.

The equivocal placement of relative age class groupings in the PCA and UPGMA cluster analysis necessitated separate PCA and cluster analyses of the sexes from the three populations of *T. splendens*. Both the PCA (Figure 5) and cluster analysis (Figure 6) of the three populations of females (A1, A2 & A3) and males (B1, B2 & B3) revealed a separation of all the relative age classes 1–5 that reflect increasing body size from relative age classes 1–5. All these results are also reflected in subsequent separate ANOVAs, SNKs and %SSQs of the sexes (not illustrated).



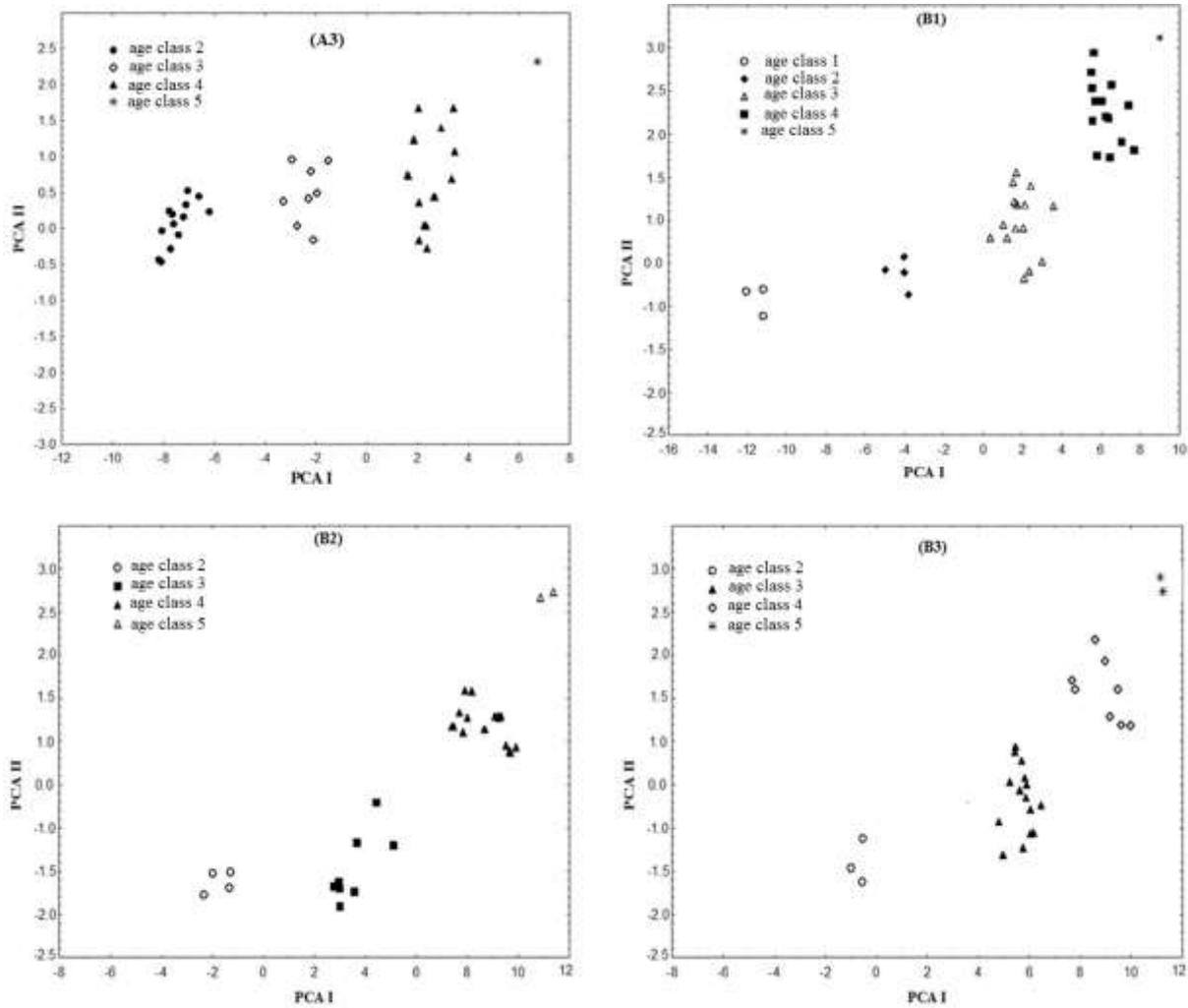
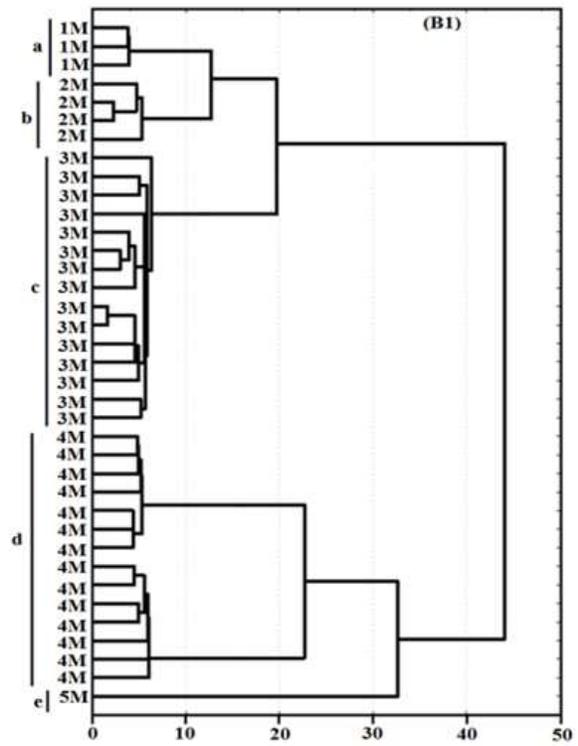
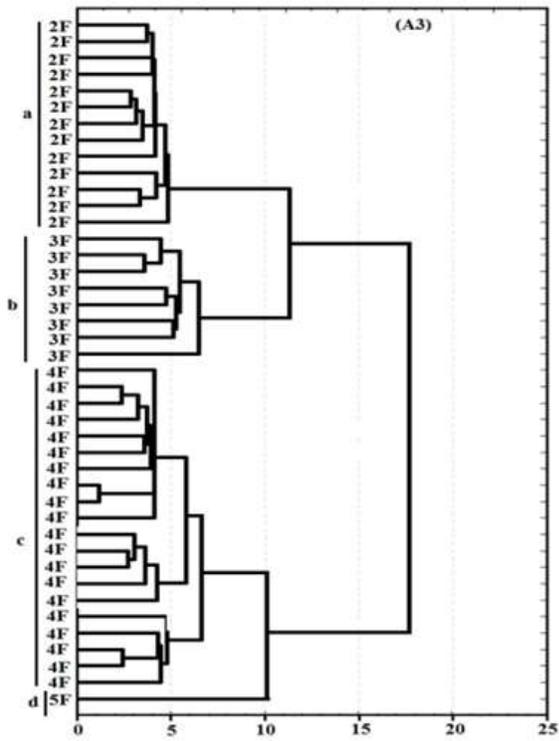
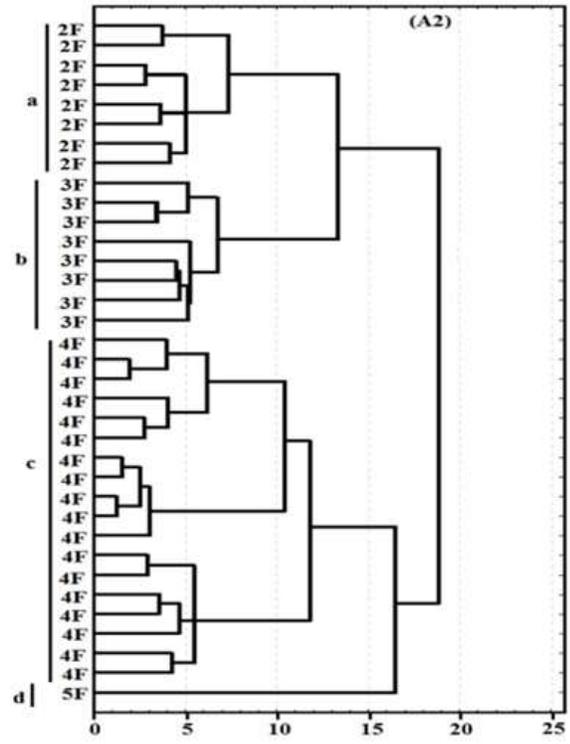
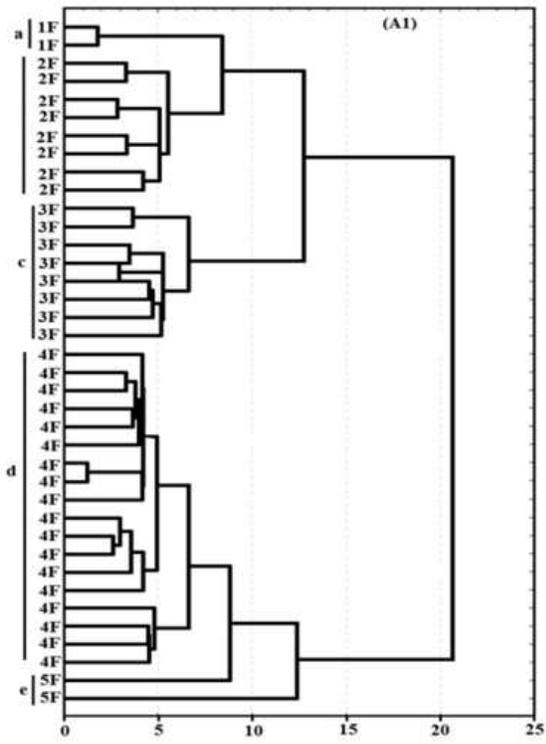


Figure 5:- The first two principal components from a principal components analysis (PCA) of cranial measurements of female (A1-3) and male (B1-3) *Tachyoryctes splendens* of age classes 1-5 from Marangu (A1: males & B1: females), Keni-Aleni (A2: males & B2: females) and Uru-Shimbwe (A3: males & B3: females), Tanzania.



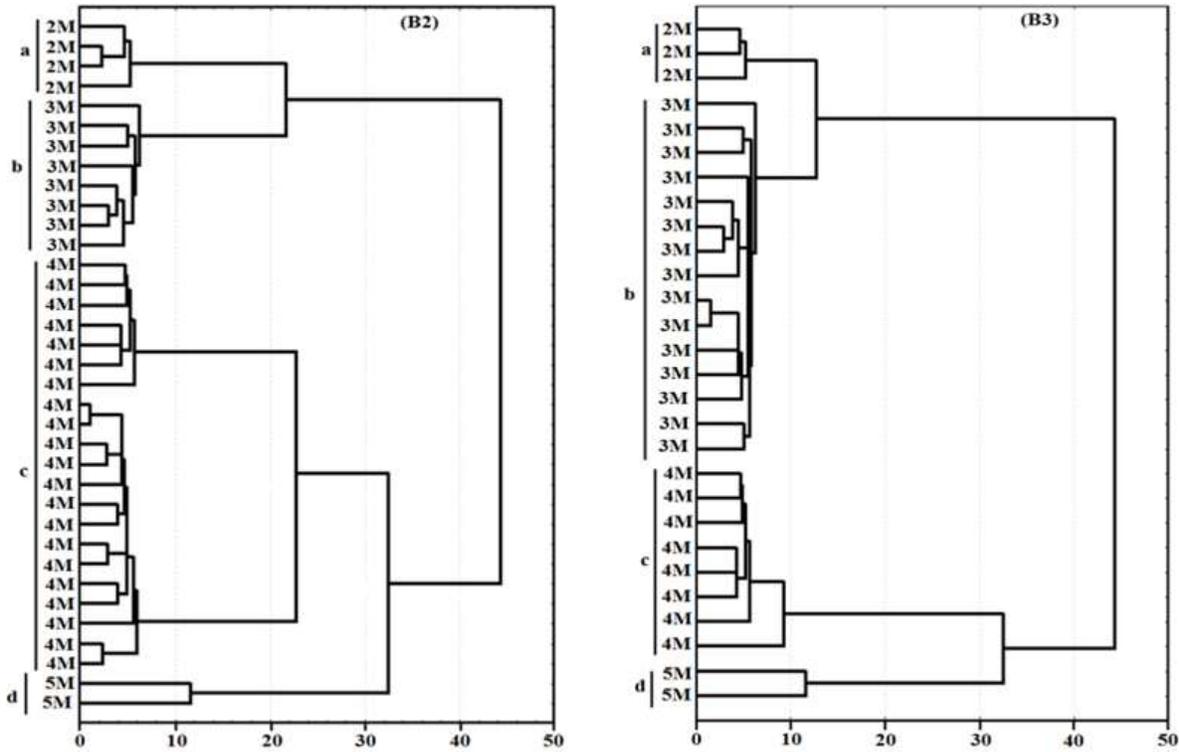


Figure 6:- A Euclidean distance phenogram from an Un-weighted Pair-group Method using Arithmetic Averages (UPGMA) cluster analysis of cranial measurements of male (M) and female (F) *Tachyoryctes splendens* of age classes 1-5 (Sub- clusters a-e) from Marangu (A1: females & B1: males), Keni-Aleni (A2: females & B2: males) and Uru-Shimbwe (A3: females & B3: males), Tanzania.

The first principal components axis (PCA I) from the PCA explained > 88% of the total variance while PCA II explained < 5% of the total variance in all males and females of the three populations (Table 4). Most cranial measurements on PCA I in all males and females of the three populations loaded relatively highly than those on PCA II which collectively only has seven cranial measurements (APL, CPL, DOC, PAC, UTR, VAL & WI) loading relatively highly in all the analysis of males and females from the three populations. These relatively high loadings on PCA I suggest that cranial size rather than shape is an important component in age variation in *T. splendens* from Tanzania.

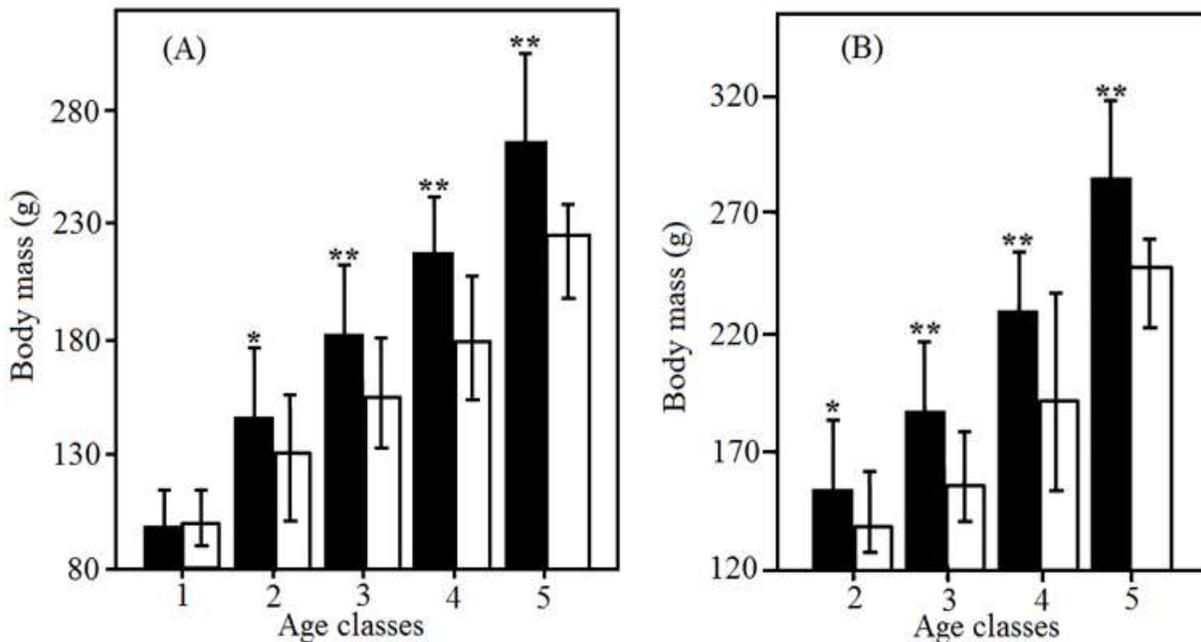
Table 4:- Relative loadings of cranial measurements of the first two principal components axes (I and II) from a principal components analysis (PCA) of *Tachyoryctes splendens* from Marangu (age classes 1-5), Keni-Aleni and Uru-Shimbwe (age classes 2-5), Tanzania. Marangu: A1 = males & B1 = females; Keni-Aleni: A2 = males & B2 = females; and Uru-Shimbwe: A3 = males & B3 = females. Cranial measurements are defined and illustrated in Figure 3.

Cranial measurements	Marangu				Keni-Aleni				Uru-Shimbwe			
	PC A I (A1)	PC A II (A1)	PC A I (B1)	PC A II (B1)	PC A I (A2)	PC A II (A2)	PC A I (B2)	PC A II (B2)	PC A I (A3)	PC A II (A3)	PC A I (B3)	PC A II (B3)
APL	0.8	0.1	0.8	0.2	0.8	0.1	0.9	0.2	0.8	-	0.9	0.2
	6	2	6	9	7	2	2	6	6	0.19	6	5
ATP	0.9	-	0.8	0.0	0.9	-	0.9	0.1	0.9	0.1	0.9	0.1
	3	0.20	4	3	4	0.20	2	5	6	4	7	0
AWF	0.9	0.1	0.9	0.0	0.9	0.1	0.9	-	0.9	0.0	0.9	-
	6	4	2	2	7	4	5	0.06	0	9	3	0.06
BCW	0.9	-	0.9	-	0.9	-	0.8	-	0.9	-	0.9	-
	2	0.13	6	0.07	3	0.13	6	0.05	9	0.02	7	0.13

CPL	0.9 5	- 0.06	0.8 1	0.3 2	0.9 6	- 0.06	0.8 7	0.3 1	0.8 6	0.0 2	0.9 4	- 0.34
DOC	0.7 7	0.2 8	0.7 8	0.1 1	0.7 8	0.2 8	0.9 6	- 0.05	0.8 7	- 0.29	0.9 6	0.1 1
FL	0.9 3	- 0.05	0.9 4	- 0.07	0.9 4	- 0.05	0.9 7	- 0.13	0.9 2	0.0 2	0.7 7	- 0.04
FW	0.8 9	0.0 8	0.8 8	- 0.09	0.9 0	0.0 8	0.9 4	0.1 2	0.9 7	0.0 4	0.9 6	0.0 7
GLS	0.9 8	- 0.02	0.9 6	0.1 2	0.9 9	- 0.02	0.8 6	- 0.01	0.9 6	0.0 2	0.9 3	- 0.02
IOB	0.9 1	- 0.13	0.7 7	- 0.13	0.9 2	- 0.13	0.7 8	0.0 9	0.9 3	- 0.15	0.9 6	0.0 1
ITC	0.9 7	- 0.03	0.9 8	- 0.10	0.9 8	0.0 3	0.9 2	- 0.02	0.9 6	0.0 1	0.9 1	0.1 2
IW	0.9 7	0.0 6	0.9 6	0.0 9	0.9 8	0.0 6	0.8 4	- 0.06	0.9 3	0.1 8	0.9 6	0.0 6
JLI	0.8 9	0.1 3	0.8 6	0.1 2	0.9 0	0.1 0	0.8 8	0.0 3	0.8 6	0.1 0	0.9 4	- 0.02
KDW	0.9 7	0.0 8	0.9 7	0.0 6	0.9 8	0.0 8	0.9 6	0.1 6	0.8 7	0.0 3	0.9 6	- 0.06
LR	0.9 5	0.0 8	0.8 2	- 0.02	0.9 6	0.0 8	0.8 6	- 0.07	0.9 0	0.0 1	0.9 6	0.1 4
MDL	0.9 0	0.1 0	0.9 5	- 0.14	0.9 1	- 0.13	0.8 6	0.1 2	0.8 5	0.0 1	0.8 7	0.0 3
MLT	0.8 4	0.1 4	0.9 4	- 0.10	0.8 5	0.1 1	0.9 2	0.1 4	0.7 8	0.1 2	0.9 7	- 0.06
MOT	0.9 0	- 0.06	0.8 5	0.1 7	0.9 1	- 0.05	0.9 2	- 0.02	0.9 3	0.1 6	0.8 8	0.1 2
MRH	0.9 2	0.1 4	0.8 3	0.0 8	0.9 3	0.1 4	0.8 5	0.1 6	0.9 3	- 0.06	0.9 1	0.1 8
NA	0.9 5	- 0.01	0.9 0	0.0 6	0.9 6	- 0.01	0.8 6	0.1 4	0.9 4	- 0.02	0.9 5	- 0.06
NAS	0.9 2	0.0 4	0.9 1	- 0.24	0.9 3	0.0 4	0.7 5	0.0 6	0.9 1	0.0 5	0.9 3	- 0.01
NL	0.9 6	- 0.04	0.9 6	0.0 6	0.9 7	0.0 0	0.8 7	- 0.01	0.9 5	0.0 3	0.8 2	0.0 8
PAC	0.8 5	0.1 9	0.7 7	- 0.33	0.8 6	0.0 2	0.9 6	- 0.35	0.8 6	0.1 8	0.9 9	0.3 3
PBL	0.9 6	- 0.02	0.9 2	0.0 7	0.9 7	- 0.02	0.9 2	0.0 7	0.9 3	- 0.02	0.9 2	- 0.10
PL	0.9 1	- 0.06	0.9 7	- 0.10	0.9 2	- 0.05	0.8 6	- 0.09	0.9 0	0.0 1	0.8 8	- 0.05
PWF	0.9 3	0.0 6	0.8 7	0.1 0	0.9 4	0.0 6	0.9 3	0.0 3	0.8 8	0.1 2	0.9 6	- 0.03
UJI	0.9 3	0.1 8	0.8 8	0.0 4	0.9 4	0.1 8	0.9 1	0.0 4	0.9 2	0.0 2	0.9 1	0.1 8
UTR	0.8 0	0.3 0	0.7 5	- 0.13	0.8 1	0.3 5	0.9 6	0.0 3	0.9 1	0.3 0	0.9 6	- 0.13
VAL	0.8 6	0.1 6	0.7 8	0.3 1	0.8 7	0.1 6	0.9 6	0.3 1	0.9 7	0.0 2	0.9 5	- 0.29
VBL	0.9 5	0.0 3	0.9 2	0.1 5	0.9 6	0.0 3	0.8 8	0.1 6	0.9 8	0.0 6	0.9 5	0.0 1
WI	0.8 7	- 0.34	0.8 2	0.0 1	0.8 8	- 0.33	0.8 9	0.0 1	0.9 0	- 0.34	0.9 5	0.1 8
WLI	0.9	0.2	0.7	0.1	0.9	0.0	0.8	0.1	0.9	0.1	0.8	0.1

	0	3	8	5	1	6	6	0	2	4	8	6
ZMB	0.9 6	- 0.02	0.9 3	0.0 6	0.9 7	- 0.02	0.8 3	- 0.04	0.9 8	0.0 6	0.8 2	- 0.02
ZYW	0.9 2	0.1 7	0.9 5	0.1 4	0.9 3	0.1 7	0.9 5	- 0.03	0.9 3	- 0.13	0.8 8	0.1 7
% of variance explained	91. 43	4.5 2	88. 23	3.0 8	92. 42	3.1 9	89. 52	4.4 4	91. 47	2.1 5	92. 57	2.6 3

The general trend of age variation and sexual dimorphism in populations of *T. splendens* shown by the preceding analyses was also evident in the analysis of body mass (Figure 7). The ANOVA of body mass showed significant variation in all three populations of *T. splendens* [Age: Marangu – $F_{(4,65)} = 31.21$; $n = 75$; $P < 0.001$; Keni-Aleni – $F_{(3,62)} = 26.44$; $n = 70$; $P < 0.001$; Uru-Shimbwe – $F_{(3,62)} = 25.91$; $n = 70$; $P < 0.001$; Sex: Marangu – $F_{(1,65)} = 15.14$; $n = 75$; $P < 0.001$; Keni-Aleni – $F_{(1,62)} = 15.08$; $n = 70$; $P < 0.001$; Uru-Shimbwe – $F_{(1,62)} = 14.91$; $n = 70$; $P < 0.001$]. The SNK tests of the pooled data and sexes separately of the relative age classes with reference to body mass revealed the same results reflected by the analysis of craniometric ontogenetic variation and sexual dimorphism.



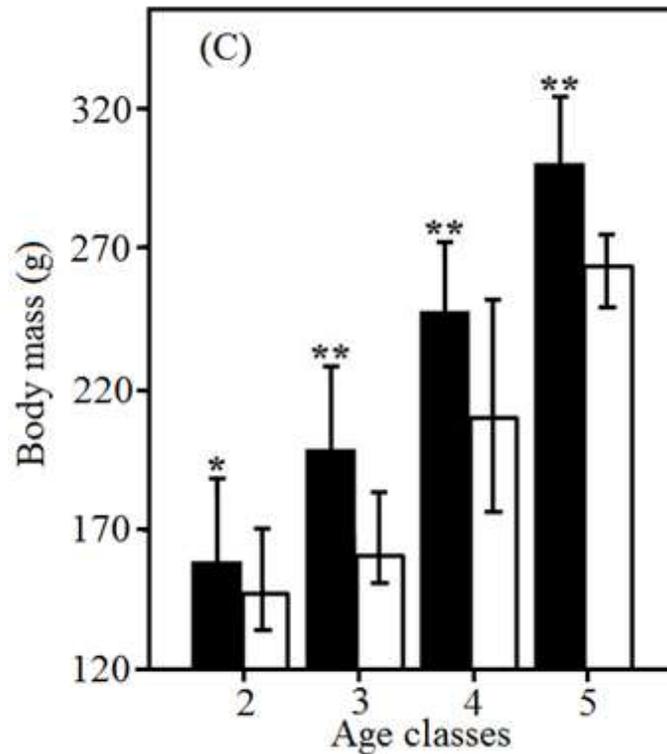


Figure 7:- Body mass (mean \pm SD) between males (black bars) and females (white bars) of *Tachyoryctes splendens* of age classes 1-5 from Marangu (A), Keni-Aleni (B) and Uru-Shimbwe (C), Tanzania. Statistical significance: * = $P < 0.05$; ** = $P < 0.01$.

Discussion:-

Based on the dental formula of adult *T. splendens*, the present study revealed five relative age classes in populations from Tanzania. Individuals of relative age classes 1 and 2 were sampled from maternal burrows suggesting that they are juveniles since the species is solitary except during pup caring, whereas of relative age class 3 were sampled from simple independent burrows adjacent to maternal burrows indicating that they are sub-adults. Individuals of relative age classes 4 and 5 were sampled from complex independent burrow systems suggesting that they are adults as they possess fully-developed reproductive organs (Katandukila et al., 2013). Univariate analyses of craniometric data in the present study revealed craniometrics ontogenetic variation with age classes however it was difficult to determine trend of variation across age classes as a result of overlap between age classes except age class 1.

The multivariate analyses were however shown that sexual dimorphism was a source of concealed ontogenetic variation. Upon analyses of sexes separately, the clear ontogenetic variation between age classes was noted with measurements increasing on orderly pattern from lower to higher age classes indicate that growth increases with increasing age. The increased ontogenetic variation from age class 2 in *T. splendens* indicate that growth pattern which favours adult-hood ecological selection and survival is prominent from young age before dispersal with age class 2 being the preparatory to dispersal. The *T. splendens* disperse at age class 3 when individual starts to carry on adult-hood tasks including burrow construction, independent foraging and defense (Katandukila et al., 2014). The significant ontogenetic variation at age class 3 and 4 than age class 5 imply that mean growth variation is more obvious on mid age classes than the oldest and youngest age classes as reported on other rodents (Zelditch, 1988; Hart et al., 2007; Chimimba et al., 2010).

The craniometric ontogenetic variation was also reported in Damaraland mole rats (*Cryptomys damarensis*; Bennett et al., 1990), Namaqua dune mole rats (*Bathyergus jannetta*; Jarvis and Bennett, 1991), Pocket gophers (*Geomys* sp.; Mauk et al., 1999), Talarum tuco tuco (*Ctenomys talarum*; Zenuto, 1999), Highveld mole-rats (*Cryptomys hottentotus pretoriae*; van Rensburg et al., 2004), Cape dune mole rats (*Bathyergus suillus*; Hart et al., 2007) and giant mole-rats (*Fukomys mechowii*; Chimimba et al., 2010). Similar to the present study, ontogenetic variation the

mentioned subterranean rodents was reported between age classes with higher age classes possess the greatest measurements.

The cranial size of male *T. splendens* implies more utilization of energy for growth to attain large skeletal to support more muscles as adaptation to reproductive and ecological roles. As the species is solitary, males have to fight for adult female mates to foster reproductive success. The successful adaptation of large body size in males *T. splendens* intimate that the species has polygynandry mating strategy as this mating system has been reported to be characterized by larger males and smaller females as a consequence of both sexual selection and intense male-male competition (Bennett and Faulkes, 2000; Schutle-Hostedde et al., 2001; Schutle-Hostedde, 2007). *Tachyoryctes splendens* is aggressive and xenophobic to con-specifics of both sexes but the intense fights between adult males was observed prior to reproduction season. The increased male-male fights before onset of breeding seasons has been also reported in bathyergids whereas more aggressive interactions noted to occur before and during the reproductive phase (Bennett and Faulkes, 2000). Male-male aggression in *T. splendens* was evident in the wild where some males were found with wounds inflicted around their necks prior to becoming reproductively active. The larger-sized males rather than small body-sized males were observed to have their burrows in close proximity to those of adult females. Sampling of fewer small-sized males in the present study suggests that smaller-sized males were forced to live far from adult females and large-sized males to avoid injury from male-male aggressive interactions. Male *T. splendens* possesses more fatty deposits around the neck region than females, suggesting that these fatty deposits may act as a cushion to avoid extensive injuries during male-male aggressive interactions as suggested by studies of Cape dune mole rats (*Bathyergus suillus*; Hart et al., 2007). Although all mature individuals of solitary species have an equal opportunity to mate, the body size of adult male *T. splendens* may have a reproductive advantage such that males strive to attain a larger body size in order to be competent in searching for and guarding female mates.

The smaller body size of female *T. splendens* imply limited growth as adaptation to conserve energy to overcome reproduction related costs including construction of burrow system which explores the earth thorough for nutrients acquisition for maintenance of burrow to accommodate lactating female and pups for space and foraging; burrow maintenance is also energy demanding activity. The investment of energy for reproduction was evidenced on burrow architecture of *T. splendens* whereas female constructs more complex and reticulated burrow systems with more long foraging tunnels than males (Katandukila et al., 2014). The foraging efficiency of females *T. splendens* would expect to have large sizes than males but in contrast they are smaller-sized than males intimate that reproduction selectivity among females is less based on large size rather other criteria which is still unknown. The lower female-female fight than male-male was noted prior to reproduction seasons indicate the absence of female-female combat to attain more male mates rather normal fight as *T. splendens* is generally aggressive and xenophobic.

As revealed on craniometric results, males are heavier than females except perhaps for individuals of age class 1 where there was no significant difference in the body mass in both sexes, although this may not be conclusive given the few individuals of this age class available for study and only from the Marangu population. The presence of sexual dimorphism in body mass and craniometric data in all populations studied suggests that body mass may also be an appropriate indicator of sexual dimorphism in *T. splendens* from Tanzania. The suitability of body mass as an indicator of sexual dimorphism has also been demonstrated in Talarum tuco tuco (*Ctenomys talarum*; Zenuto, 1999), Damaraland mole-rats (*Fukomys damarensis*; Bennett and Faulkes, 2000), deer mice (*Peromyscus maniculatus*; Shuttle-Hostedde et al., 2001), bushy-tailed wood rats (*Neotoma cinerea*; Shuttle-Hostedde et al., 2001), southern red-backed voles (*Myodes gapperi*; Shuttle-Hostedde et al., 2001), Cape dune mole rats (*B. suillus*; Hart et al., 2007) and giant mole-rats (*F. mechowii*; Chimimba et al., 2010). Analyses of craniometrics and body mass is therefore signify that size attributed to nature and extent of sexual dimorphism rather than shape implying that sexual-size dimorphism is apparent in *T. splendens* as adaptation to ecological role. Sexual-size dimorphism was also documented on blind mole-rats (*Spalax*; Corti et al., 1996) reported to have sexual-size dimorphism on mandibular metrics.

Analyses of craniometrics and body mass within and between relative age classes (1-5) support our prediction of presence of ontogenetic variation between age classes. The sexual dimorphism was apparent as predicted with nature of dimorphism be attributed by size rather than shape. In contrast to other subterranean rodent showing sexual dimorphism at sub-adult (transitional age to adulthood), *T. splendens* shows sexual dimorphism from young age class (relative age class 2).

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