

Morphometric variation in the forest rodent *Malacomys edwardsi* (Rodentia: Muridae) in Côte d'Ivoire

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ABSTRACT

Objective: This study examined the intra-specific cranial morphometric variability between populations of *Malacomys edwardsi* from three distinct localities in Côte d'Ivoire.

Methodology and results: The data set focused on 23 cranial measurements recorded on 158 skulls of *M. edwardsi* from Adiopodoumé (n = 43), Bolo (n = 34) and Taï (n = 81). Sexual and geographical variations were investigated using univariate and multivariate statistics. No sexual dimorphism was recorded. However highly significant morphometric differences were observed between the three populations. This study observed a longitudinal clinal size variation for five measurements. Moreover, populations from the left bank of the Sassandra River are morphometrically closer to one another than to those found on the right bank.

Conclusions and application of findings: This study reveals that the three populations of *M.edwardsi* exhibited local morphological differentiation. Additional studies are needed to better explain the determinants of this variation (local adaptation, phylogenetic history). This is important for both the systematics and conservation of this endemic species of the West African forests.

Key words: Muridae, *Malacomys edwardsi*, Geographic variation, Traditional morphometric, Côte d'Ivoire.

INTRODUCTION

The genus *Malacomys* (Milne-Edwards, 1877) is composed of small rodent belonging to the family Muridae. This genus only occurs in tropical regions of Africa. The taxonomy at the species level of this genus has been highly debated for a long time (Hayman, 1935; Bellier & Gautun, 1968; Rosevear, 1969; Van Der Straeten & Verheyen, 1979; Musser

& Carleton, 1993, 2005). Indeed, nine species were described (*Malacomys longipes*, *M. centralis*, *M. wilsoni*, *M. edwardsi*, *M. australis*, *M. cansdalei*, *M. giganteus*, *M. verschureni* and *M. lukolelae*), but this number of species has been controversial. In their general taxonomic review of the Murids of the world, Musser & Carleton (2005) put many of

these species in synonymy and only retained 3 species: *M. longipes*, *M. edwardsi* and *M. cansdalei*. More recently, Elgoyen (2009) performed molecular phylogenetic analyses that confirm the existence of two distinct species in West Africa (*M. edwardsi* and *M. cansdalei*) and a third species in Central and East Africa (*M. longipes*). Very few studies investigated intra-specific morphometric variability within *Malacomys* species (Cole, 1972, Rautenbach & Schlitter 1978, Van der Straeten & Verheyen 1979). However, a good knowledge of intra-specific variability is an important pre-request before any systematic or taxonomic revision. Moreover, phenotypic traits are under selection; thus, the study of phenotypic variation is important to test the strength and impact of selection in differentiation processes. Concerning the species *M. edwardsi* (Figure 1) only three studies investigated morphometric differences within or between populations. Indeed, Rautenbach & Schlitter (1978) examined geographic variation in *M. edwardsi* from Côte d'Ivoire and Ghana, and concluded that geographic samples were generally homogeneous; and that little individual variation was noticed. Cole

(1972) and Van der Straeten & Verheyen (1979) did not show significant sexual dimorphism in *M. edwardsi* based on external or cranial measurements. However, these studies were conducted while the taxonomy of the genus *Malacomys* was still debated. In Côte d'Ivoire, the Sassandra River is an important geographic barrier between the Western and Eastern Guinean lowlands forests (Underwood *et al.*, 1998). Several studies have already shown that the Sassandra River is a barrier that has contributed to the speciation of numerous West African vertebrates, mainly primates (Kingdon, 1997; Koné, 2004; Gonedele Bi *et al.*, 2006). Moreover, distinct genetic clades were observed on both sides of the Sassandra River in several small mammal species (e.g. the rodent *Praomys rostratus*, Nicolas *et al.*, 2010; or shrews of the *Crociodura obscurior* species complex, Jacquet *et al.*, 2014). Morphometric differentiation between populations from both sides of this river was also recorded in the species *Praomys rostratus* (Akpatou, 2009). This study seeks to investigate sexual and geographic morphometric variation in *M. edwardsi* in Côte d'Ivoire.



Figure 1 . Specimen of *Malacomys edwardsi*

MATERIAL AND METHODS

This study focus on *M. edwardsi* collected in 3 localities of Côte d'Ivoire (Figure 2). A total of 158 specimens from Adiopodoumé (n = 43), Bolo (n = 34) and Taï (n = 81) were included in our analyses (Appendix). All the skulls examined in this study are available at the 'Laboratoire de Zoologie et Biologie Animale (UFR Biosciences, Université Félix Houphouët-Boigny)', the

'Muséum National d'Histoire Naturelle de Paris (MNHN, Paris, France)' and the Royal Museum for Central Africa (RMCA, Tervuren, Belgium). Specimen identification at species level was confirmed through molecular analysis (DNA sequencing of 16S rRNA and/or Cytochrome b genes). Data from these molecular analyses are not shown here.

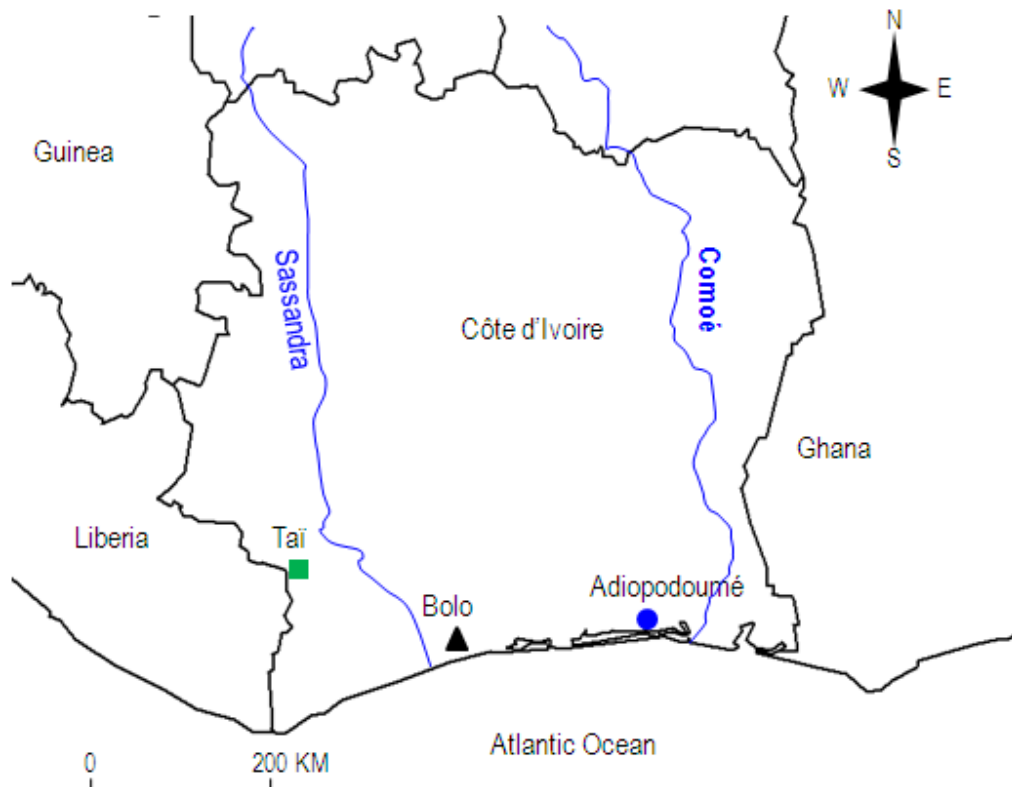


Figure 2: Map showing the geographical localities from which the specimens of *M. edwardsi* were collected in Côte d'Ivoire.

For each specimen, we recorded 23 craniodental measurements (in mm; Figure 3) that included greatest length of skull (GRLS), condylobasal length (PRCO), hensenion-basion length (HEBA), hensenion-palation length (HEPA), length of palatal foramen (PAFL), length of diastema (DIA1), distance between M1 alveolus and cutting edge of the upper incisor (DIA2), smallest interorbital breadth (INTE), zygomatic breadth on the zygomatic process of the squamosal (ZYGO), smallest palatal breadth between 1st upper molars (PALA), length of maxillary cheek tooth row (UPTE), breadth of upper dental arch (UPDA), greatest breadth of M1 (M1BR), smallest breadth of zygomatic plate (ZYPL), greatest breadth of nasals (BNAS), greatest length of nasals (LNAS), length of mandible tooth row (LOTE),

length of auditory bulla (BULL), greatest breadth of braincase (BRCA), depth of upper incisor (DINC), mediosagittal projection of rostrum height at anterior border of the first upper molars (ROHE), greatest rostrum breadth (ROBR), and distance between the extreme points of the coronoid and the angular processes of the mandibula (PCPA). All the measurements were recorded by H.K.B using hand-held calipers (precision of 0.01 mm) while viewing crania under a stereomicroscope. Body mass and external measurements (head and body length, tail length, hind-foot length, and ear length) were not included in this study, because these variables were collected by several field collectors, which could represent a bias in statistic analyses.

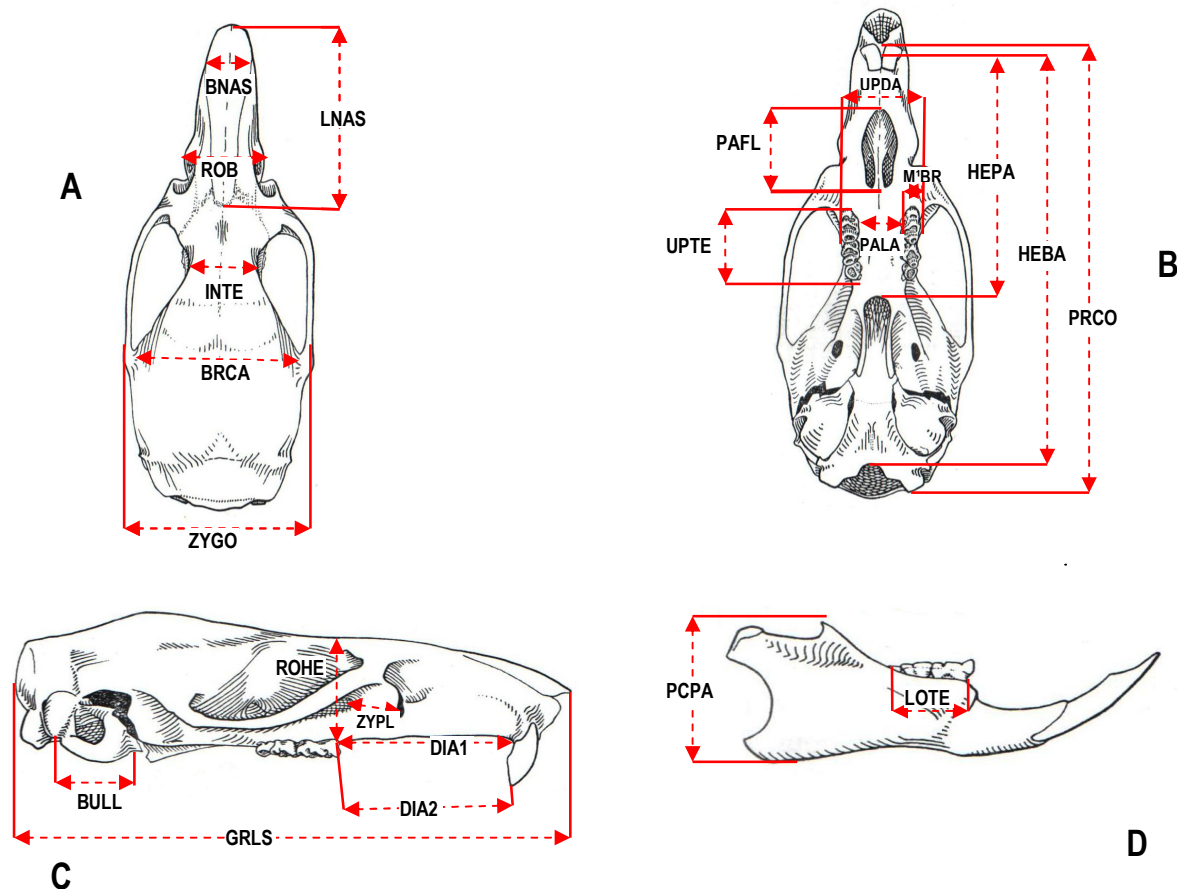


Figure 3: Localization of the 23-craniodental measurements recorded in this study. Abbreviations for variables are defined in material and methods. Dorsal = A; ventral = B; lateral = C; mandible = D.

Only adult specimens with approximately similar tooth wear were used for morphometric analyzes (i.e. tooth wear class 2 and 3 of Nicolas *et al.* (2008)). Sexual dimorphism was investigated in the population with greater sample size (i.e. Taï; 42 males and 39 females). We performed standard descriptive statistics (mean, range and standard deviation) for each group. Analysis of variance (ANOVA) and multiple analyses of variance (MANOVA) were used to test for statistically significant differences between sexes and localities. Where statistically significant differences were

detected, Scheffé post hoc tests were used to determine statistically non-significant subsets. Discriminant analysis was used to assess morphometric differences between localities. Statistically significant differences between geographic variables group centroids were evaluated by means of Mahalanobis distances and Wilks' lambda statistics (Klecka, 1980). All multivariate analyses were based on Log10-transformed cranial morphometric data. The statistical analyses were performed using statistica 7.1.

RESULTS

Sexual dimorphism: One way analysis of variance showed no statistically significant differences between sexes in craniodental (wilks' lambda = 0.730; P = 0.579) measurements. Consequently, males and females were treated jointly in all subsequent morphometric analyses.

Morphometric variation between localities: ANOVA indicated highly statistically significant differences between specimens from Adiopodoumé, Bolo and Taï localities (wilks' lambda = 0.201; p < 0.0001). Specimens from Adiopodoumé differ statistically significantly from those of Bolo and Taï by 6 and 11

measurements, respectively (Table 1 and 2). Eight out of the 23 craniodental measurements varied also significantly between Bolo and Taï specimens (Table 1 and 2). There is a size gradient between specimens from Taï, Bolo and Adiopodoumé for UPDA, PCPA, BULL, LOTE (largest values at Taï, lowest values at Adiopodoumé), UPTE (lowest values at Taï, largest values at Adiopodoumé) and M1BR (lowest values at

Bolo, largest values at Taï) measurements (Table 1). Specimens from Taï have significantly greater BRCA, ZYPL and PALA measurements, and lower INTE measurements than those from Adiopodoumé. Taï specimens also have a greater ZYGO than Bolo or Adiopodoumé specimens. Finally, Bolo specimens have a wider BNAS than specimens from Adiopodoumé and Taï.

Table1: Craniodental measurements (in millimeters) of *M.edwardsi* from Adiopodoumé, Bolo and Taï localities

Variables	Adiopodoumé (n = 43)		Bolo (n = 34)		Taï (n = 81)	
	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range
GRLS	37.81 ± 1.28	35.14 - 40.64	37.85 ± 0.93	34.86 - 39.63	38.22 ± 1.21	35 - 40.94
PRCO	33.58 ± 1.42	31.25 - 36.40	33.73 ± 0.94	30.70 - 35.32	34.07 ± 1.23	30.80 - 36.91
HEBA	29.64 ± 1.35	27.64 - 32.77	29.83 ± 0.79	27.06 - 31.31	30.14 ± 1.12	27.12 - 32.61
HEPA	16.42 ± 0.61	15.31 - 17.89	16.39 ± 0.53	14.97 - 17.34	16.58 ± 0.62	14.44 - 17.70
PAFL	7.023 ± 0.41	6.22 - 7.96	6.95 ± 0.33	6.10 - 7.63	7.01 ± 0.37	6.18 - 8.07
DIA1	11.26 ± 0.58	10.02 - 12.30	11.18 ± 0.41	9.98 - 11.98	11.33 ± 0.51	10.00 - 12.45
DIA2	11.77 ± 0.55	10.65 - 12.93	11.71 ± 0.46	10.12 - 12.48	11.74 ± 0.58	10.25 - 12.91
INTE	5.34 ± 0.23	5 - 6.08	5.31 ± 0.17	5.03 - 5.65	5.23 ± 0.25	4.95 - 5.80
ZYGO	15.02 ± 0.61	13.76 - 16.15	15.24 ± 0.42	14.21 - 15.85	15.51 ± 0.52	14.12 - 16.62
PALA	3.76 ± 0.22	3.15 - 4.20	3.84 ± 0.18	3.34 - 4.22	3.92 ± 0.24	3.45 - 4.06
UPTE	5.53 ± 0.22	5.17 - 5.89	5.36 ± 0.25	4.91 - 5.88	5.16 ± 0.20	4.94 - 5.61
UPDA	6.64 ± 0.26	6.16 - 7.28	6.77 ± 0.22	6.15 - 7.2	6.95 ± 0.20	6.23 - 7.29
M'BR	1.41 ± 0.05	1.30 - 1.52	1.39 ± 0.06	1.30 - 1.58	1.45 ± 0.04	1.34 - 1.54
ZYPL	3.39 ± 0.25	2.94 - 3.88	3.43 ± 0.27	2.95 - 3.87	3.50 ± 0.21	3.10 - 3.88
BNAS	3.61 ± 0.26	3.17 - 4.24	3.79 ± 0.21	3.24 - 4.29	3.62 ± 0.20	3.20 - 4.15
LNAS	14.91 ± 0.73	13.45 - 16.25	14.98 ± 0.47	14.05 - 15.70	15.06 ± 0.61	13.35 - 16.25
LOTE	4.91 ± 0.19	4.54 - 5.37	5.03 ± 0.16	4.66 - 5.30	5.19 ± 0.08	4.95 - 5.35
BULL	4.83 ± 0.18	4.40 - 5.20	4.93 ± 0.14	4.68 - 5.25	5.05 ± 0.12	4.77 - 5.20
BRCA	13.79 ± 0.42	12.86 - 14.69	13.90 ± 0.28	13.04 - 14.40	13.97 ± 0.38	13.00 - 14.98
DINC	1.68 ± 0.11	1.40 - 1.90	1.69 ± 0.06	1.52 - 1.85	1.713 ± 0.09	1.38 - 1.88
ROHE	7.79 ± 0.35	7.18 - 8.50	7.80 ± 0.24	7.14 - 8.26	7.86 ± 0.29	7.15 - 8.40
ROBR	6.10 ± 0.43	5.30 - 6.93	6.15 ± 0.23	5.53 - 6.60	6.22 ± 0.35	5.45 - 7
PCPA	8.78 ± 0.52	7.80 - 9.68	8.99 ± 0.32	8.03 - 9.52	9.21 ± 0.24	8.71 - 9.75

Standard univariate statistics (n = sample size, mean, SD = standard deviation, and range) are given for each locality.

Table 2: Results of the ANOVA analyses. The *a posteriori* Scheffé test was used to evaluate significant differences between *M. edwardsi* from Adiopodoumé, Bolo and Taï localities

Variables	Result of Scheffé test					
	Adiopodoumé & Bolo		Bolo & Taï		Taï & Adiopodoumé	
	p		p		p	
GRLS	0.988	NS	0.310	NS	0.185	NS
PRCO	0.871	NS	0.400	NS	0.112	NS
HEBA	0.776	NS	0.405	NS	0.069	NS
HEPA	0.992	NS	0.346	NS	0.361	NS
PAFL	0.668	NS	0.697	NS	0.984	NS
DIA1	0.802	NS	0.454	NS	0.856	NS

DIA2	0.903	NS	0.970	NS	0.960	NS
INTE	0.853	NS	0.245	NS	0.045	*
ZYGO	0.187	NS	0.046	*	0.000	***
PALA	0.296	NS	0.185	NS	0.000	***
UPTE	0.004	**	0.000	***	0.000	***
UPDA	0.035	*	0.000	***	0.000	***
M'BR	0.609	NS	0.000	***	0.000	***
ZYPL	0.771	NS	0.296	NS	0.039	*
BNAS	0.002	**	0.000	***	0.998	NS
LNAS	0.891	NS	0.796	NS	0.424	NS
LOTE	0.000	***	0.000	***	0.000	***
BULL	0.008	**	0.000	***	0.000	***
BRCA	0.440	NS	0.631	NS	0.038	*
DINC	0.719	NS	0.628	NS	0.130	NS
ROHE	0.971	NS	0.696	NS	0.479	NS
ROBR	0.794	NS	0.639	NS	0.183	NS
PCPA	0.036	*	0.010	**	0.000	***

(* p < 0.05; ** p < 0.01; *** p < 0.001; NS = no significant difference).

In the discriminant analysis, 90 % and 10% of the total variation is explained by the first and second canonical variates axes, respectively (Figure 4; Table 3). Differences among specimens from separate areas are highly statistically significant (wilks' lambda = 0.201; P < 0.0001). Squared Mahalanobis distances between specimens are 4.28 between specimens from Adiopodoumé and Bolo, 6.97 between specimens from Bolo and Taï, and 14.58 between specimens from Adiopodoumé and Taï. The scattergram shows some differences between specimens from Taï and those

from Bolo and Adiopodoumé localities on the first canonical variates axis. However, there is no obvious separation between specimens from Bolo and Adiopodoumé localities on this axis. There is no good discrimination between specimens from the 3 localities on the 2nd canonical variates axis (Figure 4). The factor structure matrix indicates that LOTE, BULL, UPDA and PCPA are the most negatively correlated variables on the first canonical variates axis, whereas UPTE is the most positively correlated variable on this canonical variates axis (Table 3).

Table 3: Discriminant analysis performed on craniodental measurements of *M. edwardsi* from Adiopodoumé (n = 43), Bolo (n = 34) and Taï (n = 81) localities.

Variables	CV1	CV2
GRLS	-0.09	0.06
PRCO	-0.10	0.01
HEBA	-0.11	-0.00
HEPA	-0.07	0.09
PAFL	-0.00	0.13
DIA1	-0.04	0.13
DIA2	0.01	0.05
INTE	0.13	-0.04
ZYGO	-0.24	-0.06
PALA	-0.18	-0.07
UPTE	0.43	0.08
UPDA	-0.36	-0.05
M'BR	-0.25	0.40
ZYPL	-0.13	0.01
BNAS	0.04	-0.59

LNAS	-0.06	-0.02
LOTE	-0.53	-0.12
BULL	-0.39	-0.11
BRCA	-0.12	-0.08
DINC	-0.09	-0.04
ROHE	-0.06	0.01
ROBR	-0.09	-0.03
PCPA	-0.31	-0.11
Eigenvalue	2.81	0.30
% of variance	90	10

Correlation between selected variables and canonical variate axis. CV = canonical variate.

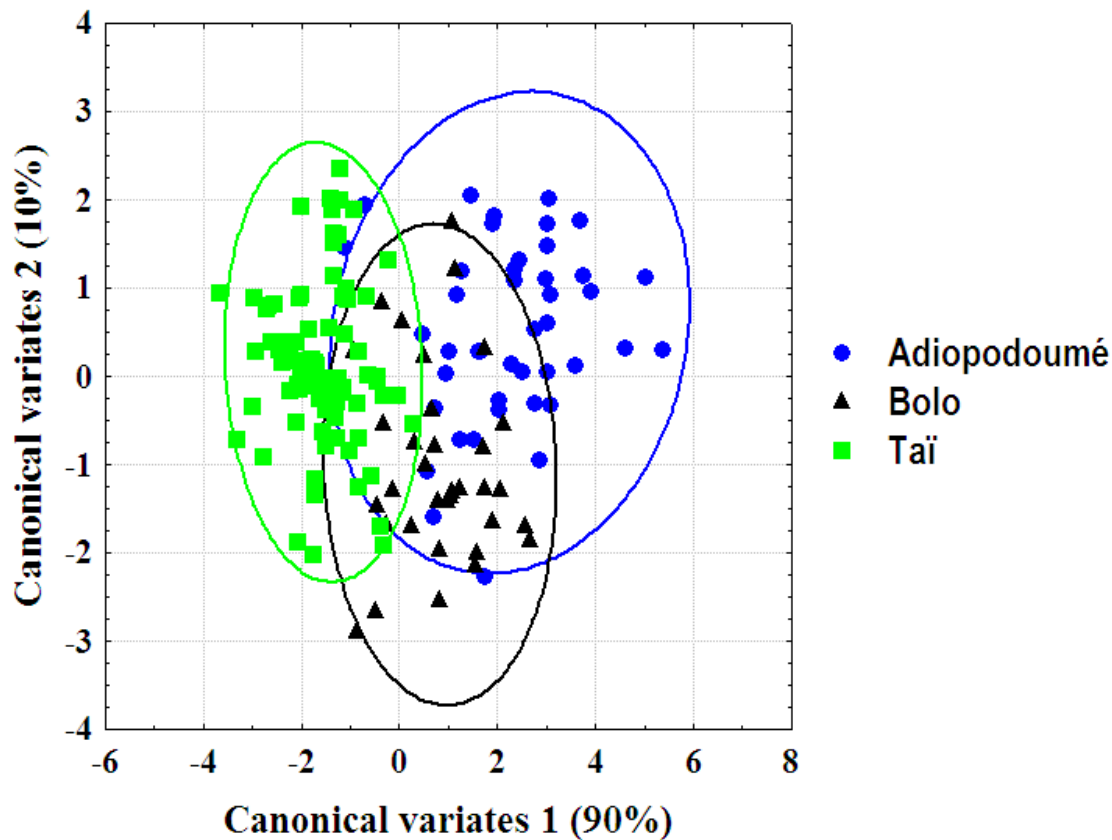


Figure 4: Discriminant analysis performed on craniodental measurements of *M. edwardsi* from Adiopodoumé (n = 43), Bolo (n = 34) and Taï (n = 81) localities.

DISCUSSION

This study results confirm the lack of sexual morphometric dimorphism in *M. edwardsi*, already noted by Cole (1972) in Ghana and by Van Der Straeten & Vereyen (1979) in Adiopodoumé (Côte d'Ivoire). The multivariate analyses demonstrate that the three populations of *M. edwardsi* exhibit important differences in craniodental measurements. This result is not congruent with those of Rautenbach & Schlitter (1978) who find little variation between populations of

M. edwardsi from different localities in Côte d'Ivoire. Discrepancies between our results and those of Rautenbach & Schlitter (1978) could be explained by differences in sample size (very few specimens in their study, with 6 to 8 specimens per operational taxonomic units) and the number of craniodental measurements involved. In this study, we used 23 craniodental measurements against only 8 (GRLS, PAFL, INTE, ZYGO, UPDA, LOTE, BRCA and LOB (not included in

this study)) in the study of Rautenbach & Schlitter (1978). Our results show that these measurements do not differ significantly (GRLS and PAFL) or weakly (INTE and BRCA) between populations. This study reveals that *M. edwardsi* exhibits geographical morphological differentiation, which may be explained by local adaptation. Indeed, several studies have shown the presence of local population level differentiation in the size and shape variation of skull, molars and mandibles in mammals (Cardini *et al.*, 2007; Polly, 2007; Caceres *et al.*, 2014). These structures covary with many environmental factors, such as latitude, longitude, altitude, temperature, vegetation and precipitation (Cardini *et al.*, 2007; Faleh *et al.*, 2013; Caceres *et al.*, 2014). A longitudinal clinal size variation was observed between our three localities for 5 out of the 23 morphometrical variables. Longitudinal clinal size variation was also observed in other African mammal species (e.g. Cardini & Elton, 2009, Cardini *et al.*, 2007), but on a larger geographical scale, and was partly explained by differences in rainfall. Determinants of the longitudinal size variation observed in *M. edwardsi* should be further explored. Additionally to this clinal variation, our data show that the two populations from the left bank of the Sassandra River (Bolo and Adiopodoumé) are more similar to one another than to the one found on the right bank (Taï). A similar pattern of morphometric and/or genetic variation

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between populations from both sides of this river was observed in other small mammal species (Nicolas *et al.*, 2008; Akpatou, 2009, Jacquet *et al.*, 2014). However, this result is surprising for *Malacomys* since this rodent is known to be a very good swimmer (Nicolas & Colyn, 2006) and to be commonest near streams or swampy areas (Happold, 2013). It is important to note that it is possible that the patterns observed in this study today not only reflect adaptations to the environment in the present or in the recent past but also events that took place earlier in the evolutionary history of *M. edwardsi*. For a better understanding of the morphometric intra-specific variation in *M. edwardsi* from Côte d'Ivoire, it would be very interesting to include more populations and to compare our morphometric results with additional markers, such as molecular markers, in order to infer its evolutionary history. *Malacomys edwardsi* is one of the remaining representatives of endemic West African forest small mammal species. This species is one of the most abundant rodent species in forest habitats (Decher *et al.*, 2005). Its conservation and survival is closely related to the challenge of African tropical forests, which are disappearing at an alarming rate. A better understanding of intra-specific variation and evolutionary history of this ecologically important species is important not only for systematics, but also for its conservation.

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APPENDIX

List of specimens of *M.edwardsi* included in the cranial morphometric analyses with reference to sampling localities.

Adiopodoumé (05°19'53"N, 04°08'02"O): RMCA 77-54-M-456, RMCA 77-54-M-458, RMCA 77-54-M-459, RMCA 77-54-M-463, RMCA 77-54-M-464, RMCA 77-54-M-465, RMCA 77-54-M-467, RMCA 77-54-M-469, RMCA 77-54-M-471, RMCA 77-54-M-472, RMCA 77-54-M-473, RMCA 77-54-M-474, RMCA 77-54-M-476, RMCA 77-54-M-477, RMCA 77-54-M-478, RMCA 77-54-M-479, RMCA 77-54-M-480, RMCA 77-54-M-481, RMCA 77-54-M-482, RMCA 77-54-M-483, RMCA 77-54-M-484, RMCA 77-54-M-485, RMCA 77-54-M-487, RMCA 77-54-M-490, RMCA 77-54-M-493, RMCA 77-54-M-494, RMCA 77-54-M-499, RMCA 77-54-M-500, RMCA 77-54-M-501, RMCA 77-54-M-518, RMCA 78-36-M-1, RMCA 78-36-M-4, RMCA 78-36-M-7, RMCA 78-36-M-12, RMCA 78-36-M-13, RMCA 78-36-M-14, RMCA 78-36-M-16, RMCA 78-36-M-17, RMCA 78-36-M-19, RMCA 78-36-M-20, RMCA 78-36-M-21, RMCA 78-36-M-22, RMCA 78-36-M-23.

Bolo (05°20'29"N, 05°59'07"O): MNHN-ZM-MO 1997-2256, MNHN-ZM-MO 1997-2262, MNHN-ZM-MO 1997-2266, MNHN-ZM-MO 1997-2269, MNHN-ZM-MO 1997-2270, MNHN-ZM-MO 1997-2271, MNHN-ZM-MO 1997-2272, MNHN-ZM-MO 1997-2299, MNHN-ZM-MO 1997-2300, MNHN-ZM-MO 1997-2303, MNHN-ZM-MO 1997-2314, MNHN-ZM-MO 1997-2328, MNHN-ZM-MO 1997-2367, MNHN-ZM-MO 1997-2368, MNHN-ZM-MO 1997-2382, MNHN-ZM-MO 1997-2403, MNHN-ZM-MO 1997-2404, MNHN-ZM-MO 1997-2405, MNHN-ZM-MO 1997-2428, MNHN-ZM-MO 1997-2432, MNHN-ZM-MO 1997-2436, MNHN-ZM-MO 1997-2442, MNHN-ZM-MO 1997-2443, MNHN-ZM-MO 1998-50, MNHN-ZM-MO 1998-59, MNHN-ZM-MO 1998-62, MNHN-ZM-MO 1998-66, MNHN-ZM-MO 1998-69, MNHN-ZM-MO 1998-73, MNHN-ZM-MO 1998-80, MNHN-ZM-MO 1998-81, MNHN-ZM-MO 1998-83, MNHN-ZM-MO 1998-92. MNHN-ZM-MO 1998-99.

Taï (05°51'39"N, 07°19'14"O): BHT 03, BHT 07, BHT 08, BHT 12, BHT 15, BHT 16, BHT 27, BHT 28, BHT 29, BHT 33, BHT 34, BHT 38, BHT 45, BHT 46, BHT 48, BHT 49, BHT 51, BHT 52, BHT 64, BHT 69, BHT 78, BHT 79, BHT 80, BHT 82, BHT 87, BHT 88, BHT 93, BHT 94, BHT 107, BHT 124, BHT 134, BHT 141, BHT144, BHT145, BHT152, BHT 157, BHT158, BHT161, BHT 181, BHT 215, BHT 224, BHT 242, BHT 251, BHT 256, BHT 257, BHT 261, BHT 267, BHT269, BHT 271, BHT 299, BHT 300, BHT 303, BHT 309, C2, C6, C17, R24587, R24610, R24662, R24683, R24689, R24707, R24708, R24763, R24778, R24794, R24795, R24833, R24834, R24844, R24852, R24887, R24892, R24894, R24897, R24900, R24938, R24950, R24953, R24954, R24960.