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Morphometric analysis within populations of *Hylomyscus walterverheyeni* (Rodentia: Muridae) confirms complex relationships between small rodent populations of West Central African forests

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Abstract

Our recent morphometric study on the strictly forest-dwelling small rodent (*Praomys misonnei)* in West Central Africa revealed complex relationships between populations. The present study tests this hypothesis on another species of forest rodent (*Hylomyscus walterverheyeni*), and more precisely compares specimens from Kessala (Gabon) with specimens from southern Cameroon. Sixty-eight specimens were used for the morphometric analyses, and four standard external characters were measured: head + body length, tail length, hindfoot length, and ear length. Highly significant morphometric differences were observed between the *H. walterverheyeni* populations at the local and regional scales. A principal component analysis showed that the Gabonese *H. walterverheyeni* populations were morphometrically closer to one another than to the Cameroonian ones. Moreover, the body size of the Gabonese *H. walterverheyeni* populations was smaller than that of the Cameroonian populations.

Overall, *H. walterverheyeni* is characterized by a local morphometric structure pattern similar to that of *P. misonnei*. These new results further support the scenario of complex relationships between the forest populations of West Central African rodents. This suggests the existence of persistent local biogeographical barriers despite several forest expansion episodes in the upper Pleistocene, as documented by the landscape history of West Central Africa.

Keywords: Intraspecific variation; Multivariate analysis; Geographic variation; *Hylomyscus walterverheyeni*; Biometric measurements; Small African rodents; Central Africa

1 Introduction

Situated in the middle of the Guinean-Congolese region, the West Central African landscape is mostly characterized by an extensive forest cover and forest-savanna mosaics. It is a very heterogenous landscape with a high animal biodiversity. In view of these landscape differences, small rodent populations distributed across strong ecological gradients may be important reservoirs of morphological variation, since strong selection pressures imposed by environmentally heterogenous landscapes are likely to have driven morphometric variations.

The muroid family is one of the most diverse and abundant Mammalian clade [1] and inhabits nearly all habitat types [2]. Several species of this group have served as models for addressing questions about the consequences of climate change on the genetic structure of present-day faunas in various environments, such as tropical forests. Woodmice of the genus *Hylomyscus* (Thomas 1926) are small rodents belonging to the family Muridae. They are restricted to tropical

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Africa, where they are abundant in forests and dense vegetation. The present study is mainly focused on one of the most common Muridae species of West Central Africa – *Hylomyscus walterverheyeni* [3].

The central African rodent *H. walterverheyeni* is widely distributed across the Lower Guinean region and inhabits a broad range of forest and montane habitats, making it well suited landscape-level studies of morphometric variation. *H. walterverheyeni* is best known in the Republic of Congo, the Central African Republic, Gabon and South-East Cameroon. According to some authors, morphometric analyses have proved powerful to analyze skull and body variability among small rodents [3, 4, 5, 6]. Patterns of body external morphological characters have been particularly studied in central African populations of *Praomys misonnei* [6], revealing complex and unexpected relationships between and among Gabonese and Cameroonian populations, with two morphometrically distinct groups. Moreover, the authors observed similarities of the body measurements of individuals from the Batéké plateaux (south-eastern Gabon) with individuals from southern Cameroon: some populations of spatially neighboring forests in the Batéké Plateaux region – Kessala – showed a clear morphometric differentiation, while one of them – Mbaya, ~ 30 km from Kessala – was linked to very distant south Cameroonian populations. The authors suggested that these differences result from the history of the forest landscape rather than from events affecting a few populations of a single species.

If this morphometric structure pattern is correlated to local environmental factors [6] or reflects the general history of the West Central African forest, similar patterns should be discovered about other small rodent species with similar ecological constraints and a largely coextensive geographical range (sympatric species). Other small forest rodent species belonging to populations of neighboring forests of south Gabon (Kessala) and south Cameroon should show the same morphometric structure pattern. On the basis of these results, we studied morphometric data of *H. walterverheyeni* to check if the patterns of size distribution are similar to those of *P. misonnei* populations and confirm or not the relationships between south Gabonese and south Cameroonian populations at the local and regional scales. We expected to find the same pattern of exclusion of the Kessala populations from this association with the south Cameroonian populations.

2 Material and methods

2.1 Study area

The present research work was conducted in seven regions of Gabon. Gabon is known for its natural heterogenous habitats, with areas of savannas interspersed with strips of gallery forest and forest islands often in close proximity to continuous forest. We trapped mice across different habitats, including primary forests, secondary forests and periodically inundated secondary forests. We also sampled mice from two regions of Cameroon to a lesser extent. This small-scale project was also led along with an ongoing study by the Central African Biodiversity Alliance (CAB Alliance) program in Central Africa. It was carried out in the buffer zones of four national parks (NPs) in Gabon and two NPs in Cameroon (Figure 1). The sites included Gamba Forest (southwestern Gabon, 03°04.928' S, 10°25.981 E), Monts Birougou Forest (southwestern Gabon, 01° 38.177 S, 12° 21.997' E), Minkébé Forest NP (northwestern Gabon, 01°09.436' N, 12°41.849' E), Kessala Forest (southeastern Gabon, 01°51.907' S, 013°51.120'E), and Campo-Ma'an Forest NP (southwestern Cameroon, 02°20.52' N, 10°12.634' E) and Lobéké Lowland Forest (southeastern Cameroon, 02° 16' 59.8" N, 015° 40' 25.9" E). These sites encompass a range of lowland rainforest types [7].

In Gabon:

Gamba National Park (coastal forest) is located in southern Gabon [8]. In Gamba, the climate is tropical and rainfall is 1,850 mm on average. It is the largest protected area in the country [9] Lee et al. 2006). Habitats range from lowland rainforest with a closed canopy to more degraded, open secondary forest, a mosaic of forest patches within savanna, slightly hilly savanna terrain, and a variety of wetland types ranging from large lagoons to small stagnant marshes, seasonal pools, and small streams. Our study site was located in Setté Cama village. The average yearly temperature is 26 °C, with annual rainfall ranging from 2,200 to 2,400 mm, a short dry season in January, and a long dry season from June to August [9] or July to September. Our study was conducted in low-altitude forest (02°40’ S, 10°05’ E) within the coastal forest (less than 5 km from the Ocean) and the continental forest.

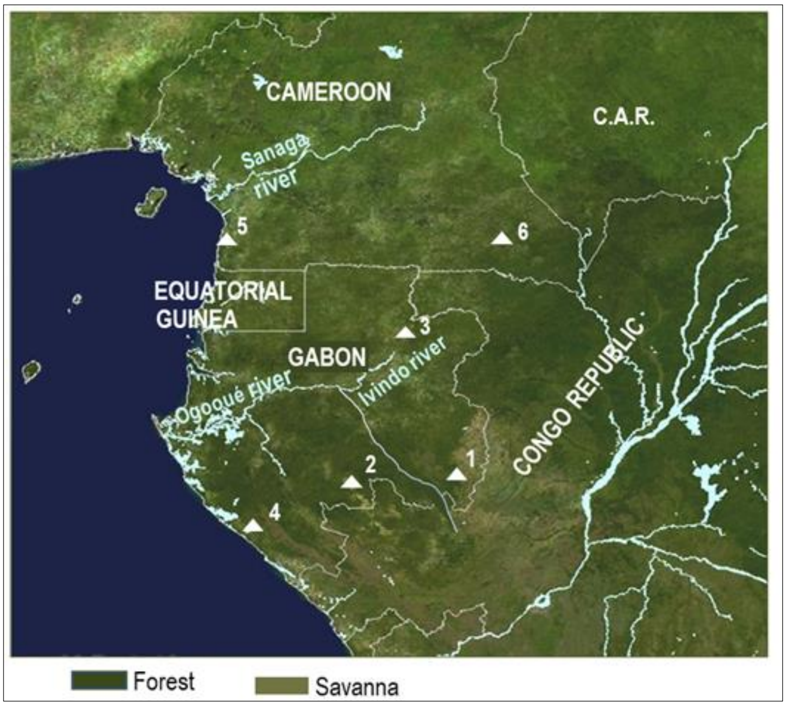

Figure 1 Map showing the geographical localities from which the *H. walterverheyeni* populations were collected in Cameroon and Gabon. 1, Kessala; 2, Monts Birougou; 3, Minkébé and 4, Gamba (Gabon); 5, Campo-Ma'an and 6, Lobéké (Cameroon)

Kessala (or Ossélé village) is located in the Batéké Plateaux region (southeastern Gabon) and located 2 km north of the northern border of the Batéké Plateaux National Park buffer zone [6]. It is crossed by Mpassa River. This natural barrier also marks the start of the transition from rainforest to savanna ecosystems that dominates Batéké Plateaux NP. This locality is characterized by lowland forest made up of a mosaic of forests and savannas. The mean annual rainfall is 1,800-2,000 mm minimum and 2,000-2,500 mm maximum, and the climate is a transition equatorial type.

Minkébé National Park buffer zone (northwestern Gabon) is an area of mixed heterogenous forest, Marantaceae forest, swampy flooded and inselberg forests [10, 11] with an equatorial climate. The average annual rainfall is 1,800-2,000 mm, and the mean annual temperature is 24 °C [12]. Minkébé is also the largest of all Gabonese NPs and is part of the Northwest Congolian Lowland Forest ecoregion. Our study site was located in Minkébé NP buffer zone [6].

Monts Birougou National Park buffer zone and its peripheral area have not experienced economic development based on the extraction of natural resources. It is located in south-central Gabon within the Chaillu Massif. Its environment has remained intact, with immense dense humid forests made up of huge very old plant populations with often very closed undergrowth. Several species present in Birougou Mountains are important internationally for conservation. Carbon isotope analysis of soil organic carbon indicates that Birougou Mountains have been continuously covered with rainforest vegetation since the Holocene climate optimum, serving as a refuge for Congo Basin flora and fauna [13]. It is subject to an equatorial transition climate, with a long dry season from July to September. Average annual rainfall is between 1,700 and 2,000 mm.

In Cameroon:

Campo-Ma'an (CM) National Park (NP) The sites were located in the coastal forests, in southwestern Cameroon. The Campo Ma'an rainforest [14] is unique at the species level, and its fauna and flora differ from those of Lobéké forest. The climate is equatorial with about 2,800 mm average annual rainfall, and the mean annual temperature is about 25 °C. Part of the area around the park acts as a buffer zone, making the forest contiguous with that of Equatorial Guinea and Gabon [14]. The sampling site was located at the southern periphery of CM NP (02°20.52' N; 10°12.634' E; [6]).

Lobéké National Park is located in the northwest of the Congolese basin slope [15], and characterized by the presence of clearings on hydromorphic soil. Its vegetation is very important for large- and medium-sized herbivores. The climate is typically equatorial, and rainfall occurs throughout the year. The maximum rainfall is approximately 1,500 mm/year.

Mean temperature is 25.4 °C, with a slight seasonal variation. From a phytogeographic viewpoint, Lobéké is a transitional forest between the evergreen forest of Dja and the semi-deciduous forest of Malvaceae and Ulmaceae. The site is located at the southern periphery of Lobéké NP (02° 16.940' N, 15° 40.428' E; [6]).

2.2 Sampling Method and Species Identification

We caught the animals alive using baited Sherman traps (7.5 × 9 × 23 cm) (see sampling protocol details in [7]). The specimens were collected by the authors during field studies in different localities of Gabon and Cameroon. The traps were checked twice a day in the early morning and late afternoon, and fresh bait was supplied when necessary. Most of the *H. walterverheyeni* specimens were determined using an identification key based on external morphological characteristics, morphometric measurements, and cranio-dental examinations [16]. Then, the individuals were sexed, weighed, and measured. All specimens were identified on the spot and released straight away.

2.3 Morphometric Analysis

The skeletal elements of mammals grow at different times depending on the species. This may further complicate the interpretation of correlations among traits. We avoided this potential problem by including only fully grown individuals in our analyses, with sufficient tooth wear and fully developed gonads. Therefore, only adult *H. walterverheyeni* specimens were used to compare several body parameters of different populations. This non-commensal species is a strictly forest-dwelling small rodent with a large geographical distribution in West Central Africa. We performed a classical morphometric analysis on external parameter distances focused on body size parameters. For each individual specimen, four standard biometric measurements (in mm) were made using calipers: head and body length (head included) (HBL; length from the tip of the nose to the root of the tail); tail length (TL; length from the root of the tail to the tip of the first caudal vertebra); hindfoot length (HFL; length of the hindfoot, claws included); and ear length (EL; length from the base of the auditory meatus to the farthest tip of the pinna, measured laterally). All these measurements were made by the same collectors. We excluded weight measurements because gravid females can cause a bias.

2.4 Statistical Analyses

Morphometric characters were investigated to evidence potential geographic variability in the size of individuals among different regions of Gabon and Cameroon. Body variability within each population was first calculated using descriptive statistics, i.e., mean, minimum, maximum, and standard deviation. Standard univariate and multivariate statistics were calculated from the measurements. Sexual dimorphism was evaluated statistically by a one-way analysis of variance (ANOVA). An ANOVA was also used to assess differences between body parameters (see above). The normality of the data was checked beforehand using a Shapiro-Wilk test. In the absence of data normality, a non-parametric Kruskall-Wallis (KW) test was performed to compare the mean values of each morphometric parameter among populations. *Post-hoc* comparisons were carried out using Tukey's HSD test to identify significant differences. A principal component analysis (PCA, Hotelling, 1933) was performed to highlight the overall divergence between samples and visualize intra-species variability within each locality. The influence of growth on external measurements was analyzed. Males and females were pooled since preliminary analyses did not show any sexual dimorphism. One hundred and twenty-two individuals were used for the PCA. All analyses were performed with R software (version 4.1.2;[33], http://www.r-project.org).

3 Results

Data describing *H. walterverheyeni* body variation were generated from 68 individuals sampled from six localities (Table1).

3.1 Sexual Dimorphism

Student's t-test showed no morphological difference between sexes, regardless of the parameters tested for the variables 'body length' ($t = 0.72$, $P < 0.05$), 'tail length' ($t = 0.21$, $P < 0.05$), 'ear length' ($t = 0.79$, $P < 0.05$), and 'hindfoot length' ($t = 0.56$, $P < 0.05$). Therefore, there was no significant sexual dimorphism among the captured individuals. Consequently, males and females were pooled in all analyses.

3.2 Intra-population Morphometric Variation

Based on four characteristic body measurements of 68 individuals, Gabonese *H. walterverheyeni* individuals were slightly different from Cameroonian individuals (Table 1). However, the mean tail length varied depending on the locality, and so did the other parameters (HFL and EL; Table 1). Moreover, two morphological groups emerged based on the four criteria. Statistical univariate and multivariate analyses confirmed these observations.

Table 1 Standard body measurements (mm) (HBL, head and body length; TL, tail length; HFL, hindfoot length; EL, ear length) of *H. walterverheyeni* from Cameroon and Gabon localities. M, mean; s, standard deviation; min-max, minimum and maximum

Species	Country	Locality	Number	Head and Body (HBL)			Tail (TL)			Hind-foot (HFL)			Ear (EL)		
				m	s	min-max	m	s	min-max	m	s	min-max	m	s	min-max
Hylomyscus walterverheyeni (Nicolas et al. 2008)	Cameroon	Campo-Ma'an	13	104.6	9.23	90.9-111.9	130.1	5.02	124.9-139.3	20.1	0.86	18.3-20.6	15.9	1.15	14.2-18.6
		Lobéké	6	94.8	13.18	72.9-104.5	125.1	10.9	109.1-139.1	19.9	1.07	17.8-20.6	16.7	1.25	14,6-18,1
	Gabon	Gamba	20	88.6	9.73	66-102.5	114.5	7.31	92-128.5	18.2	1.11	13.7-20.4	14.5	1.48	12-17.7
		Minkébé	7	87.8	5.87	80-100	119.4	8.95	109.5-129.6	19.02	1.91	15.9-20.9	14.2	2.66	9-16.6
		Mt Birougou	13	75	5.62	61.2-84.5	115.4	11.99	94.8-137	17.5	1.33	15.8-18.7	13.9	0.75	13-16.2
		Kessala (Osselé)	9	86.7	8.31	74.8-130.6	121.5	6.31	107.9-130.6	18.3	1.47	15.7-19.7	14.9	1.47	10.9-16.9

3.3 Morphometric Data Comparisons

At the regional and local scales, a Kruskal-Wallis non-parametric test and a single-factor ANOVA were applied to all populations after verifying the normality and homogeneity of the data (Kruskal-Wallis test results for TL: $\chi^2 = 22.8$, df = 5, p-value < 0.001; for HFL: $\chi^2 = 25.2$, df = 5, p-value < 0.0001). At the sole regional scale, the one-way ANOVA results for HBL and EL measurements showed significant differences between different populations from Gabon and Cameroon (F = 10.53, p-value = 0 and F = 4.87, p-value = 0, respectively). However, pairwise comparisons of body length using Tukey's test showed that the *H. walterverheyeni* populations from the Gabonese localities were highly significantly different from those of the Cameroonian localities. By contrast, significant differences between specimens from Gabonese localities (Gamba *vs.* Mts Birougou; Table2) were found at the local scale.

3.4 Principal Component Analysis (PCA)

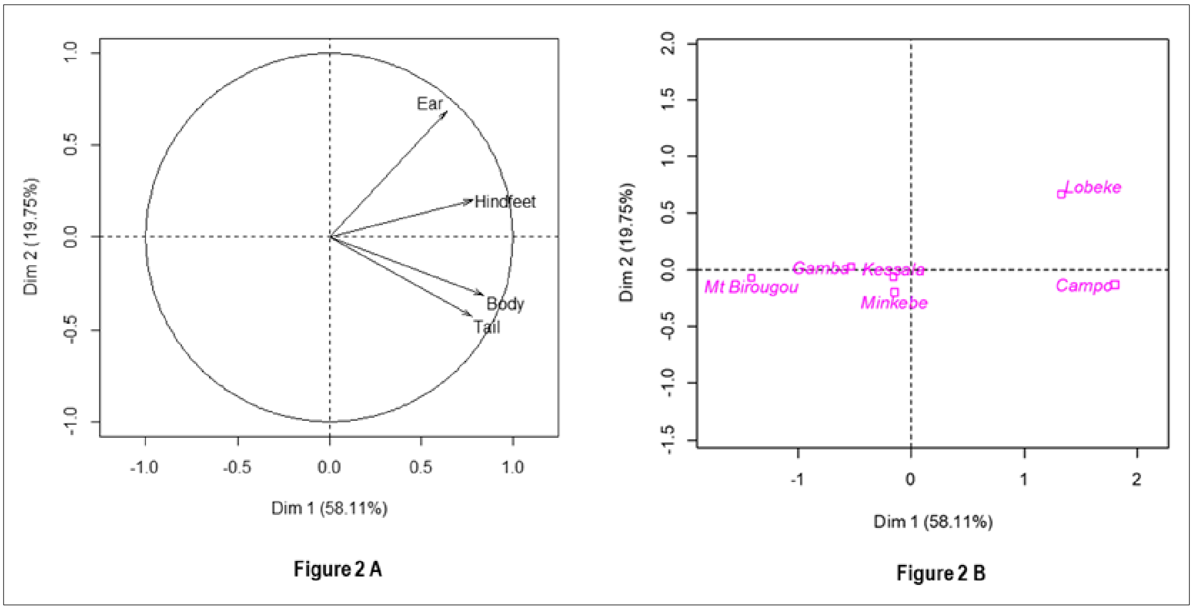

Figure 2 Principal component analysis (PCA) of external size variables from 68 *H. walterverheyeni* individuals. (A) Plot of the first (PC1) and second (PC2) principal components explaining 58.11% and 19.75% of total variation respectively. (B) Qualitative factor map **(**PCA), graph of the localities

Sixty-eight *H. walterverheyeni* individuals were used for these analyses. The first axis of the PCA (58.11%) showed a gradient of separation of the variables (Figure 2). The second axis (19.75% inertia) contrasted the tail and body values with the hind-foot and ear values (Figure 2A). Morphometric analysis of the *H. walterverheyeni* populations clearly differentiated two groups. Globally, the PCA showed a clear separation between the specimens from Cameroon on the right of the graph (Lobeké and Campo) and those from Gabon on the left of the graph (Figure 2B). The specimens from Cameroon shared high values for all four measured variables, while those from Gabon shared low values. Cameroonian populations were characterized by large-sized individuals as compared with Gabonese populations. In addition, we observed two sub-groups at the local scale in Cameroon: the first one included Lobeké specimens characterized by large ears and hindfeet (in contrast with the study of *P. misonnei* individuals, characterized by large body and tail sizes; [6]), while the second one included Campo individuals characterized by a long tail and a large body size. However, the individuals sampled in Campo presented the same body characteristics the *P. misonnei* individuals sampled in this same locality [6].

At the local scale, the PCA showed that the body variables of all the individuals from the Gabonese forests varied little, whatever the forest type. The individuals from Gamba and Monts Birougou shared low values for the 'tail', 'body' and 'hindfoot' variables (starting from the lowest).

4 Discussion

The analysis of sexual dimorphism data from the *H. walterverheyeni* populations did not reveal any discrimination based on sex-related variables. The only way males can be discriminated from females is by sex identification. The absence of sexual dimorphism implied that sex had no influence on the size of the individuals. This result is congruent with those of [17, 4, 18, 6].

4.1 Intra-population morphometric variation

The results of the Kruskal-Wallis test and the one-way ANOVA showed significant differences between the morphological parameters of the different *H. walterverheyeni* populations from Gabon and Cameroon. The morphometric study results revealed significant morphological variability among the *H. walterverheyeni* populations from these two countries. Two distinct groups of populations were identified at the regional scale and showed a difference in the body sizes of the Gabonese and Cameroonian populations, in line with [6]. This suggests some influence of local environmental parameters in each forest and a role of regional biogeographic barriers.

However, the comparative analysis of the *H. walterverheyeni* populations showed high similarities between the specimens from Lobeké (Cameroon) and those from Gamba (southwest), Minkébé (northeastern) and Kessala (southeastern Gabon) at the regional scale. Differences were also observed at the local scale on parameters such as a HBL between *H. walterverheyeni* populations from different sites of a same country (Gamba *vs*. Monts Birougou or Kessala). This last result suggests a role of persistent local biogeographical barriers, despite several forest expansion episodes upper Pleistocene [19]. This first analysis was supplemented by an analysis of Principal component analysis

4.2 Principal component analysis (PCA)

The PCA showed great variability in the morphology of individuals within the same forest. Otherwise, the analysis of body parameters revealed a clear separation at the regional scale between the *H. walterverheyeni* populations from Gabon and Cameroon. The specimens from Cameroon were characterized by larger sizes than those from Gabon, probably explained by climate and the nature of their diet. No similarity between the north Gabonese and south Cameroonian populations was observed, despite their geographical proximity. This result is in agreement with [6]. The *H. walterverheyeni* specimens from Gabon clustered together and differed morphologically from the specimens from Cameroon. This pattern is very similar to that of *P. misonnei* [6].

Once again, no grouping of the locality of Kessala (southeastern Gabon) was observed with the localities of southern Cameroon. This finding is not surprising and confirms a pattern already observed in *P. misonnei* populations. This result is in accordance with [6], who showed with *P. misonnei* that population of Kessala is no grouping with southern Cameroon populations. This result shows that the local ecological factors have an influence on the development of *H. walterverheyeni* populations. But also, this morphometric structuring could be explained by the wide distribution of this species in West Central Africa and the vast landscape and environmental diversity of the region; Or this morphological pattern obtained in the strict forest *H. walterverheyeni* populations of Kessala suggests long-lasting divisions of the forest landscape of southeastern Gabon. An ancient and lasting division would explain the large-scale difference between the Kessala and south Cameroonian populations. It also confirms that the peripheral forests of the southeastern Gabon were affected by savanna transgression. This hypothesis is in agreement with [20]. The similarity of the *H. walterverheyeni* and *P. misonnei* patterns shows the specificity of the Batéké Plateaux NP buffer zone (Kessala) and confirms the complex relationships between the forest populations of southern Gabon and southern Cameroon.

At the local geographical scale, the present study shows no similarity between the two groups from Cameroon (Lobéké and Campo Ma'an). This result disagrees with [6], who observed that *P. misonnei* individuals from these two localities were all characterized by a large body size and a long tail.

The morphometric analysis of the present study shows that the specimens from Lobéké were characterized by larger ears and hindfeet, while those from Campo-Ma'an were characterized by a large body size and a long tail, although these two localities are both located in the south of Cameroon. This scenario reveals strong ecological differences between two forest localities: Campo Ma'an (coastal forest and rainforest; southwestern Cameroon) *versus* Lobeké (transitional forest; eastern Cameroon), in addition to a biogeographical barrier that probably persisted durably in south Cameroon and isolated these local populations. These results also suggest an influence of local ecological factors on the external morphological characters of small mammals (Muridae). The evolutionary history of *H. walterverheyeni* is expected to be closely tied to that of the forest landscape in West Central Africa.

5 Conclusion

The results showed an identical scenario: the populations of the Kessala forest (or all the Gabonese populations) differ from the populations of the southern Cameroonian. We can conclude that *H. walterverheyeni* populations from Gabon can be characterized as a rather homogenous entity in terms of body morphology despite the presence of deeply distinct localities that differ by their vegetation, micro-climate and degree of geographical isolation. This suggests a low sensitivity of these populations to environmental constraints in these different types of forests, unlike in Cameroonian populations. The analyse also revealed some redundant morphometric relationships: notably Kessala populations are highly distinctive and very original. The results also suggest that local environmental factors probably best explain such morphological differences between small rodent populations.

Compliance with ethical standards

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