

Variation and Distribution of the Sulawesi Giant Rat (*Paruromys dominator*) Based on Morphological Approaches

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ARTICLE INFO

Article history:

Received March 17, 2023

Received in revised form May 16, 2024

Accepted May 27, 2024

KEYWORDS:

Allometry,
Communication,
Mastication,
Muridae,
Skull

ABSTRACT

Correlations between natural geographic boundaries and variations in organisms' morphology have been well-documented in Sulawesi Island, which has a unique geological history and hundreds of endemic species. One of the widely distributed species of small mammals is Sulawesi giant rat (*Paruromys dominator*). Considering the geographic condition of Sulawesi, this species is a suitable model for studying geographic influences on morphological change. Moreover, there are no comprehensive studies on this species. Previous studies cannot fully explain the variability due to the lack of representative samples. Here, we measure 19 skull characteristics for 131 adult complete-skull specimens from six distribution areas in Sulawesi. We investigate the variation in skull characteristics using agglomeration nesting (AGNES) for cluster analysis and the standardized major axis (SMA) for allometry analysis. Our results show that *P. dominator* can be categorized into two groups, but distribution areas, elevation, or sex do not influence those. *P. dominator* in group 1 had a larger skull size than group 2. The two groups can be distinguished from four characteristics: breadth of mesopterygoid fossa (BMF), breadth of first upper molar (BM1), length of the auditory bulla (LB), and breadth of incisive foramina (BIF). The BMF and BM1 are related to mastication, and the LB and BIF are related to communication. We propose that the skull variation of this species is not correlated with geographical barriers but more clearly correlated with their feeding habits, mating behavior, and ability to escape predation. These findings were useful for future studies on the taxonomic status of *P. dominator*.

1. Introduction

The correlation between species' geographic range and morphological variation has been well-documented since Darwin's finding on finches' variations in Galapagos (Darwin 1859). Many previous studies across various species have shown such a correlation. For example, the cranial morphological variation of the water opossum (*Chironectes minimus*) along the neotropical region (from southern Mexico to northwestern Argentina; (Damasceno and Astúa 2016), morphometric measurements' variation for *Hydromantes shastae* complex (the Shasta salamander) divided into three groups based on its geographical distribution in the

southeastern Klamath Ranges, California (Bingham *et al.* 2018), and high variation of the skull shape in the short-tailed bat (*Carollia castanea*) between eastern and western Ecuador as a result of the barrier formed by the Andes mountain range (Jarrín-V and Menendez-Guerrero 2011).

Correlations between natural geographic boundaries and variations in organisms' morphology have also been found on Sulawesi Island (Reid *et al.* 2006; Lombogia *et al.* 2020). Sulawesi is the largest island of Wallacea, geologically formed from the collision of the Eurasian, Australian, and Pacific plates (Hall 2002; Nugraha and Hall 2018). Sulawesi is divided into three major tectonic subdivisions. The western part of Sulawesi (central to southwestern arm) originated from the Asian continental margin, the southeastern arm originated from the Australian continental margin, and the eastern and northern

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arms originated from orogeny due to geological processes during the Cenozoic era (Moss and Wilson 1998; Hall 2002). When this occurred, Asian and Australian fauna colonized Sulawesi Island (Stelbrink *et al.* 2012; Rowe *et al.* 2019). The morphological variation from several species in Sulawesi can be seen in the shape of ischial callosities of Sulawesi macaques (Juliandi *et al.* 2009), tarsiers' appearance (Shekelle and Leksono 2004), shape and coloration of the lined flying dragon (*Draco lineatus*) (McGuire *et al.* 2007), and also shape, size, and reproductive modes of the fanged frog (*Limnonectes*) (Setiadi *et al.* 2011).

Despite its origins in the distant past, most Sulawesi fauna is now considered endemic (Whitten *et al.* 2002). One of the widely distributed endemic species on Sulawesi is the Sulawesi giant rat (*Paruromys dominator*), which can be found in all Sulawesi mainland areas and on some southern satellite islands. This species can also be found in lowland evergreen forests and montane forests (Musser 2014). Based on the condition of Sulawesi, which has various geographical boundaries and a complex geological history, this species is a suitable model for studying geographical influences on morphology variation. Furthermore, there have been no comprehensive studies of this species. Although a previous study about this species has been done by

Handika *et al.* (2020), the study cannot fully explain the variation because it lacks a representative number of samples and distribution. Through this study, we aim to determine if there are any patterns to the morphological variations of the *Paruromys dominator* using more representative samples.

2. Materials and Methods

A total of 131 adult complete-skull specimens of *P. dominator* were studied. The samples were collected from the north (N), central (C), southeast (SE), and southwest (SW) of Sulawesi (Figure 1, Table 1). We used only adult specimens to remove the age effect, which marked that all teeth had fully erupted, sometimes several teeth were worn, and basicranial synchondroses in the cranium had advanced fusion (Musser and Heaney 1992; Musser 2014). All the specimens are part of a collection in the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB).

Table 1. Area of origin and number of samples in this study

Area	Number of samples
North (N)	28
Central (C)	72
Southeast (SE)	19
Southwest (SW)	12

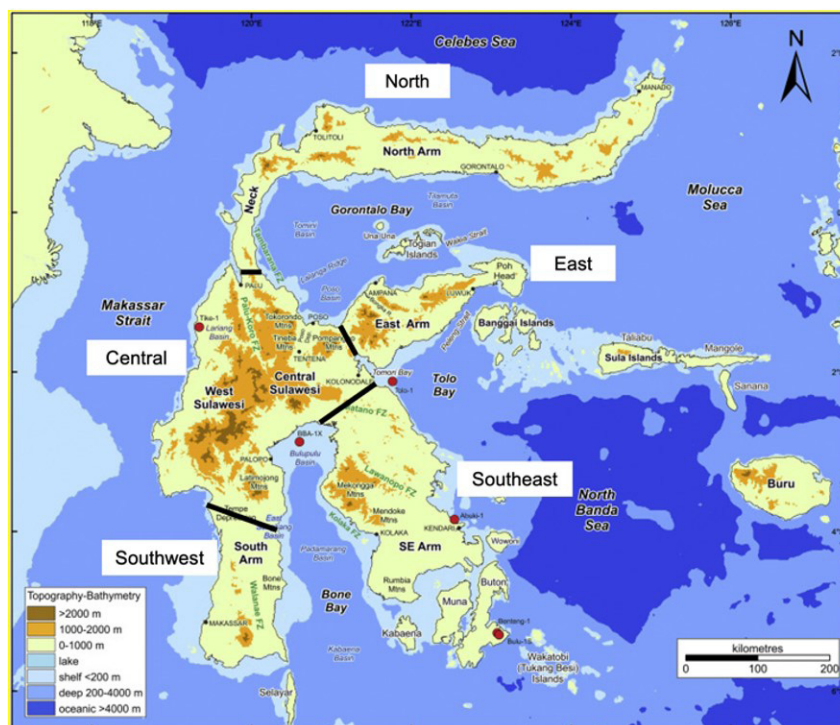


Figure 1. Division of area of distribution for *Paruromys dominator* on Sulawesi Island (modified from Nugraha and Hall 2018)

We measured 19 characteristics of a cleaned skull (millimeter) using a digital caliper (precise to 0.01 mm): the greatest length of the skull (GSL), zygomatic breadth (ZB), interorbital breadth (IB), length of rostrum (LR), breadth of rostrum (BR), breadth of the zygomatic plate (BZP), breadth of the braincase (BBC), the height of braincase (HBC), length of diastema (LD), post-palatal length (PPL), length of incisive foramina (LIF), breadth of incisive foramina (BIF), length of the bony palate (LBP), breadth of mesopterygoid fossa (BMF), length of the auditory bulla (LB), crown length of the maxillary molar row (CLMMR), alveolar breadth of first upper molar (BM1), mandibula length (ML), and ramus angular process (RAP). Measurements were taken following the processes set out by Musser and Newcomb (1983) and Musser *et al.* (2008) (Figure 2). Additionally, we conducted intraobserver tests by repeating each part measurement up to three times, ensuring consistent measurement points until achieving a consistent size. Subsequently, we analyzed the collected data using a box plot to detect any outliers. In case outlier data was identified, we carried out re-measurements until the data met the validity criteria. If outliers persisted, we investigated their cause or excluded them from further analysis.

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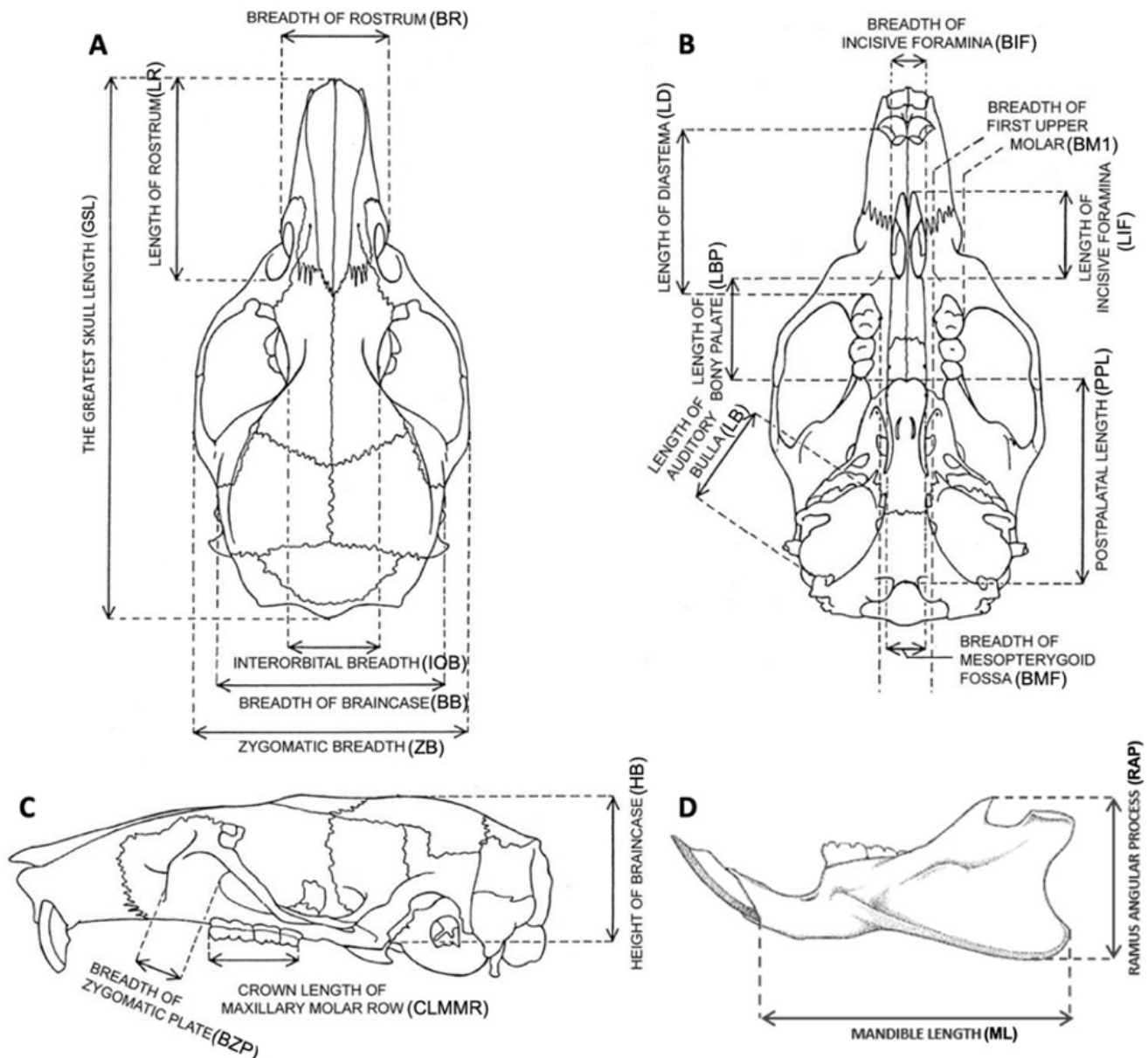


Figure 2. Cranial (A, B, C) and mandibular (D) measurements used in the present study (Figure modified from Musser *et al.* 2006, 2008; measurements from Musser and Newcomb 1983; Musser *et al.* 2008)

To understand the variation in skull characteristics, we used hierarchical clustering analysis to group the samples based on their similarity. To do so, we applied agglomerative nesting (AGNES; (Kaufman and Rousseeuw 1990)), the Euclidean distance, and the unweighted pair group method with arithmetic mean (UPGMA) for agglomeration. In addition, we labeled samples based on their origin, elevation, and sex to determine whether the samples clustered into specific groups accordingly.

Subsequently, we used ANOVA to analyze the variation between groups formed from the clustering analysis. The ANOVA was conducted only on independent metric data, meaning we excluded data exhibiting multicollinearity. Collinearity is indicated when variables have a correlation coefficient (r) greater than 0.8 and a Variance Inflation Factor (VIF) greater than 5 to 10 (Kim 2019; Shrestha 2020).

To fulfill the ANOVA assumptions, we first conducted correlation analysis on the cranial metrics to determine the presence of correlations among variables. Spearman and Pearson correlation analyses were performed based on the data's distribution. The interpretation of the correlation results aligns with the guidelines provided by Evans (1996) and Papageorgiou (2022). Then, we conducted the VIF analysis following Kim (2019) and Shrestha (2020).

We also performed an allometric analysis to describe the patterns of characteristics' size variation between individuals (Abdala *et al.* 2001; Giannini *et al.* 2004, 2010; Kurihara and Oda 2009). The allometry coefficient was estimated using a standardized major axis (often called a reduced major axis) and with GSL as the linear estimator of the overall size (Warton *et al.* 2006). Allometry testing (whether α differs from 1.0) was conducted using the SMATR package (Warton and Ormerod 2007).

3. Results

Clustering analysis using AGNES showed that the samples from Sulawesi were clustered into two groups, not related to a specific area, elevation, or sex (agglomerative coefficient 0.73) (Figure 3).

As seen in Figure 4, many samples overlap in all areas of Sulawesi. Based on the sample distribution map between Group 1 and Group 2 does not show any group separation based on geographical distributions.

To address the differences between groups, we conducted an ANOVA analysis. Before performing the ANOVA, we conducted correlation and VIF analyses as assumption tests. The correlation analysis and identified several cranial metrics with correlation coefficients greater than 0.60 (Figure 5). Notably, correlation coefficients falling within the range of 0.60 to 0.79 indicate a strong correlation among cranial metrics, while coefficients exceeding 0.80 are classified as very strong correlations. In Group 1, strong positive correlations were observed between GSL with ZB, LR, LD, PPL, and ML; ML with ZB, BR, LD, PPL, and RAP; and ZB with PPL. In Group 2, GSL showed strong positive correlations with LR, LBP, and ML; RAP with ZB and ML; BZP with LBP; and LD with LIF. Furthermore, we noted that certain characteristics within Group 2 display a greater tendency for negative correlation among variables compared to Group 1, although these correlations remain below the threshold of 0.60.

Collinearity exists when variables have a correlation coefficient (r) value greater than 0.8. However, our correlation analysis found that none of our characters have a correlation coefficient (r) value exceeding 0.8. Additionally, to ensure the robustness of our findings, we conducted a Variance Inflation Factor (VIF) analysis to detect multicollinearity. The results of the VIF analysis are shown in Table 2. The greatest skull length (GSL) is used as the baseline for VIF analysis because GSL is the linear estimator of the overall size.

Based on the results above, we found multicollinearity on three variables in Group 2 (asterisk marks), which have VIF values between 5 and 10. Consequently, we removed LD, LIF, and LBP from the ANOVA analysis.

Based on ANOVA analysis, Groups 1 and 2 were distinguished by the size of each variable. Almost all variables differed significantly between groups 1 and 2, except for BM1. Overall, the variables in Group 1 were larger than those in Group 2, except for BM1 (Table 3).

The variation in skull size between groups was determined using allometric analysis. Group 1 showed positive allometry for almost all characteristics (ZB, IB, LR, BR, BZP, HBC, LD, PPL, LIF, BIF, LBP, BMF, LB, CLMMR, BM1, ML, and RAP), except for BBC, which showed isometry with GSL (isometry implies that a measurement grows in proportion with the skull

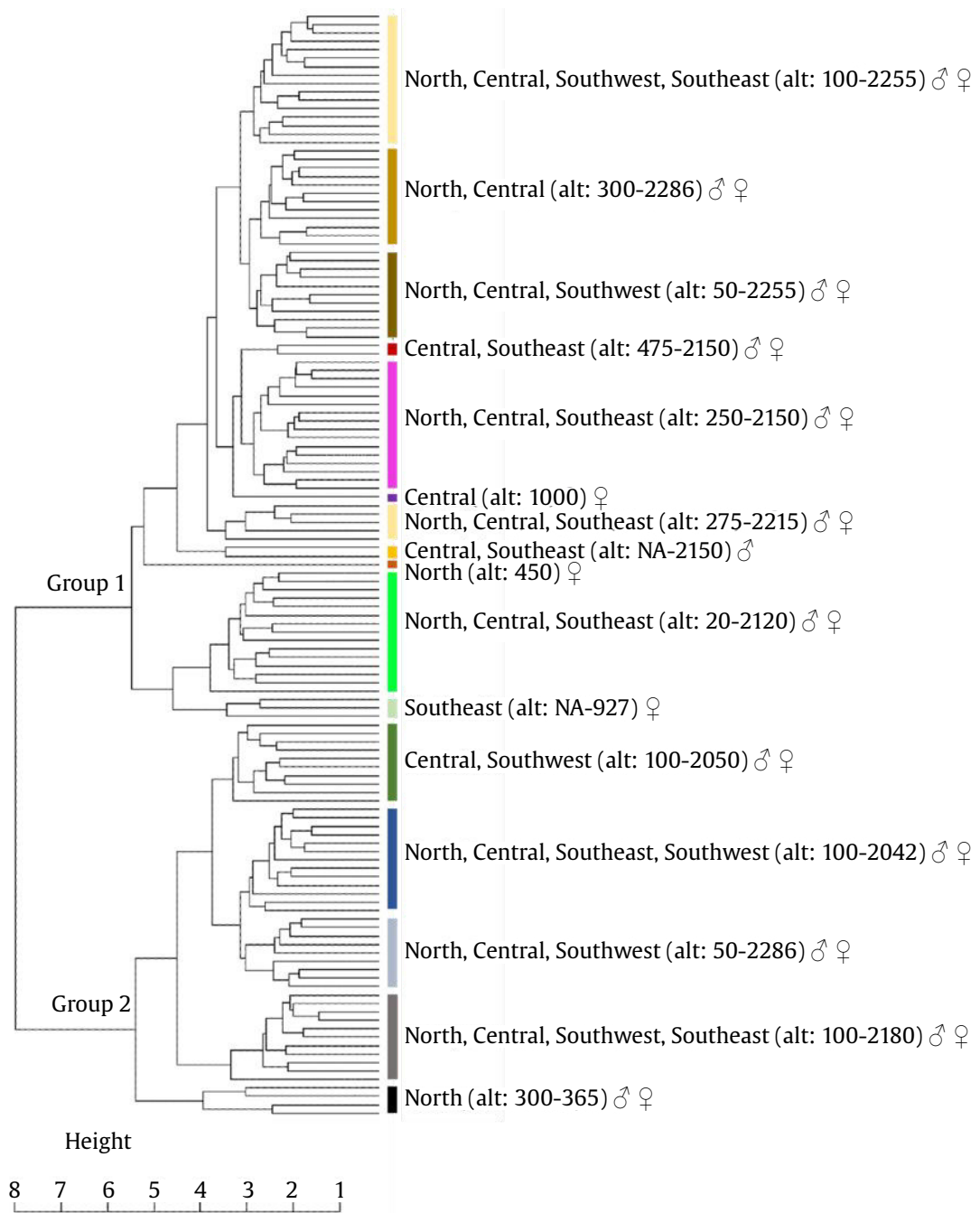


Figure 3. Clustering analysis using AGNES

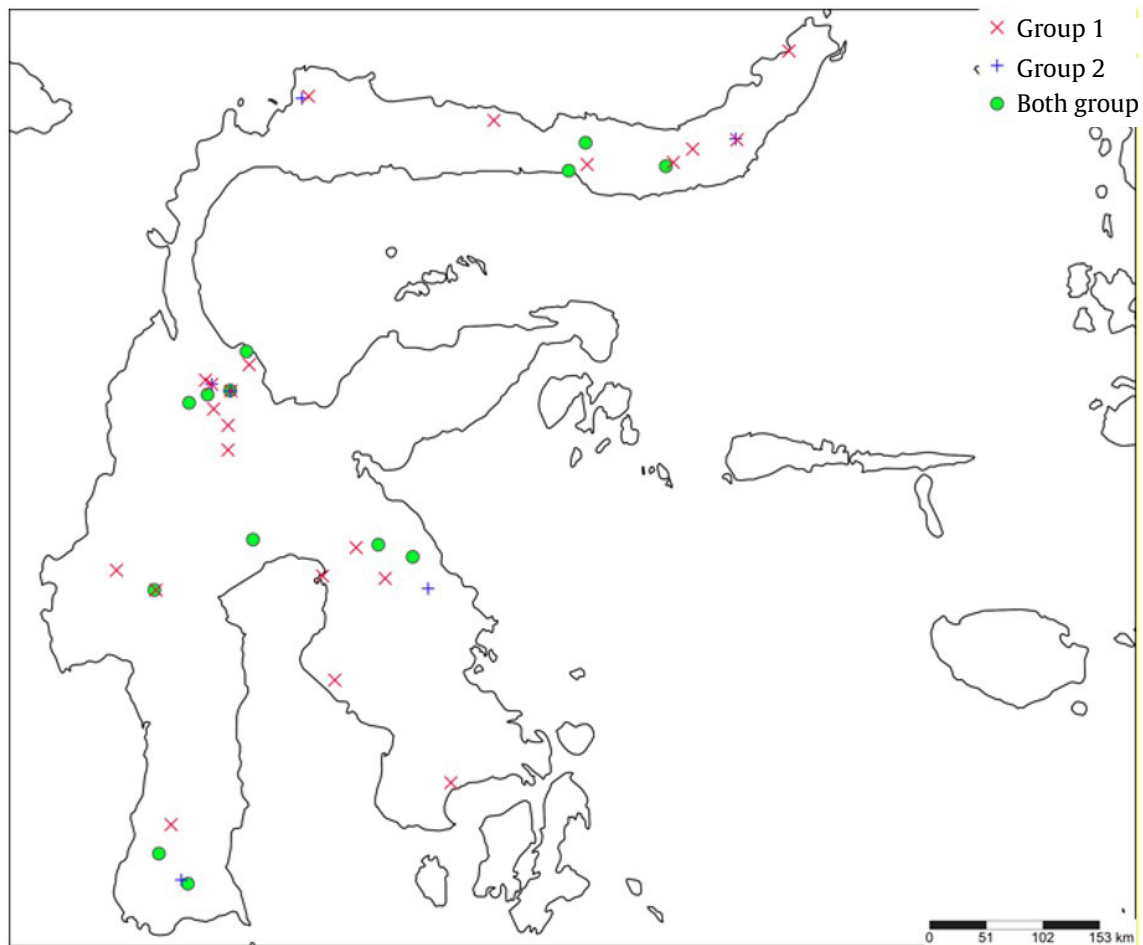


Figure 4. Samples distribution through Sulawesi

size). This means that almost all characteristics in group 1 increased more than expected with increasing skull size; only BBC's size increased on par with the skull size (Figure 6). Group 2 showed a different pattern from Group 1. Group 2 presented positive allometry for IB, LR, BR, BZP, LD, PPL, LIF, LBP, and RAP, isometry for ZB, BBC, HBC, CLMMR, and ML, and negative allometry (meaning the characteristics tend to be smaller or narrower than expected in larger skull sizes) for BIF, BMF, LB, and BM1 (Figure 6). Group 2 also had a broader slope range than Group 1, meaning that of the two groups, the slope values in Group 1 were more consistent across all characteristics, implying there was a low variance of skull sizes between samples in Group 1 compared to those in Group 2.

4. Discussion

4.1. Clustering Analysis

The two groups formed from the AGNES analysis with varied skull morphologies in the *Paruromys dominator* were not influenced by area distribution. Moreover, based on the specimen's collecting event data, several samples from both groups were collected at the same location (as shown in Figure 4) at the same time range. On the other hand, sex also did not influence the variation of skull morphology. This result agrees with those of Csanady and Mosansky (2018) and Musser (2014), who found that rodents have no sexual dimorphism in skull size or morphology. On the other hand, our findings reject

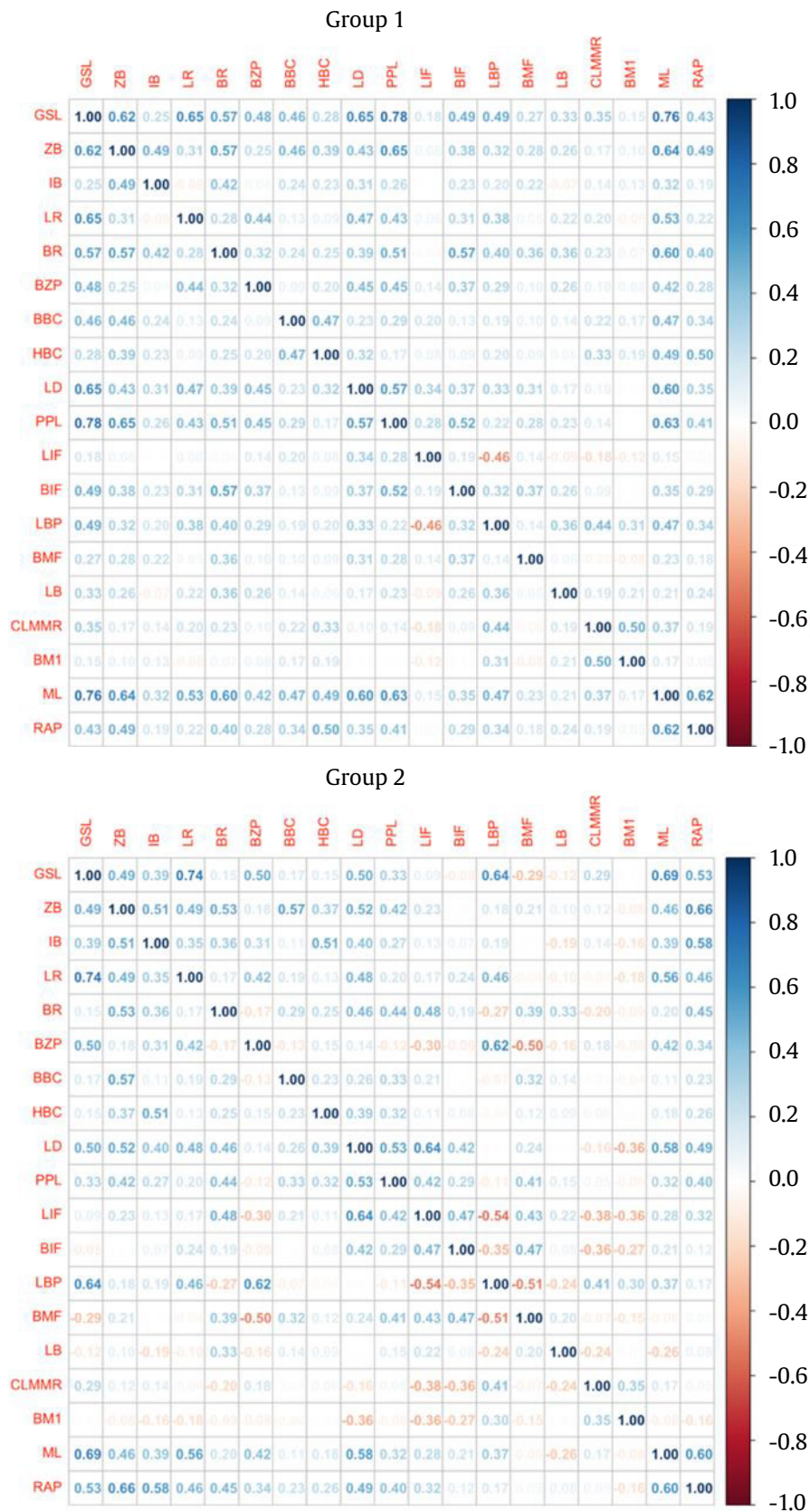


Figure 5. The coefficient correlation values between variables in Group 1 and Group 2. The interpretation of the coefficient is represented on the left scale, ranging from the deepest red, indicating a very strong negative correlation (-1), to the deepest blue, indicating a very strong positive correlation (1), with no correlation represented by white (0) in the middle

Table 2. Collinearity diagnostics using variance inflation factor (VIF)

Variable	Group 1	Group 2
ZB	3.15	3.93
IB	1.93	2.83
LR	2.22	3.01
BR	2.76	2.60
BZP	1.63	2.73
BBC	1.69	1.81
HBC	2.08	2.25
LD	2.80	5.77*
PPL	3.08	1.90
LIF	2.67	6.10*
BIF	2.20	2.57
LBP	3.41	7.62*
BMF	1.34	2.55
LBP	1.54	1.90
CLMMR	1.89	1.89
BM1	1.59	1.95
ML	4.80	3.30
RAP	2.05	3.12

Table 3. Descriptive statistics and analysis of variance between groups 1 and 2

Variable	Group 1 (n = 84)	Group 2 (n = 47)	P-value
GSL	58.96±1.49	54.43±1.40	< 2.2e-16 ***
ZB	27.63±0.86	25.80±0.70	<2e-16 ***
IB	7.95±0.42	7.54±0.39	1.77e-07 ***
LR	23.43±0.99	21.24±1.10	<2e-16 ***
BR	9.64±0.49	8.90±0.44	3.44e-14 ***
BZP	8.45±0.48	7.35±0.53	<2e-16 ***
BBC	20.74±0.58	20.25±0.50	3.24e-06 ***
HBC	14.95±0.49	14.39±0.40	8.39e-10 ***
PPL	19.52±0.76	17.70±0.65	< 2.2e-16 ***
BIF	2.96±0.22	2.70±0.23	1.3e-08 ***
BMF	3.26±0.21	3.09±0.31	0.000289 ***
LB	7.23±0.34	7.07±0.35	0.0123 *
CLMMR	9.76±0.34	9.33±0.31	5.7e-11 ***
BM1	2.70±0.15	2.71±0.15	0.532
ML	34.40±1.19	31.35±0.93	<2e-16 ***
RAP	18.89±0.66	16.87±0.61	2.2e-16 ***

*p<0.05, **p<0.01, ***p<0.001

All the abbreviations in the table above refer to paragraph two in Materials and Methods

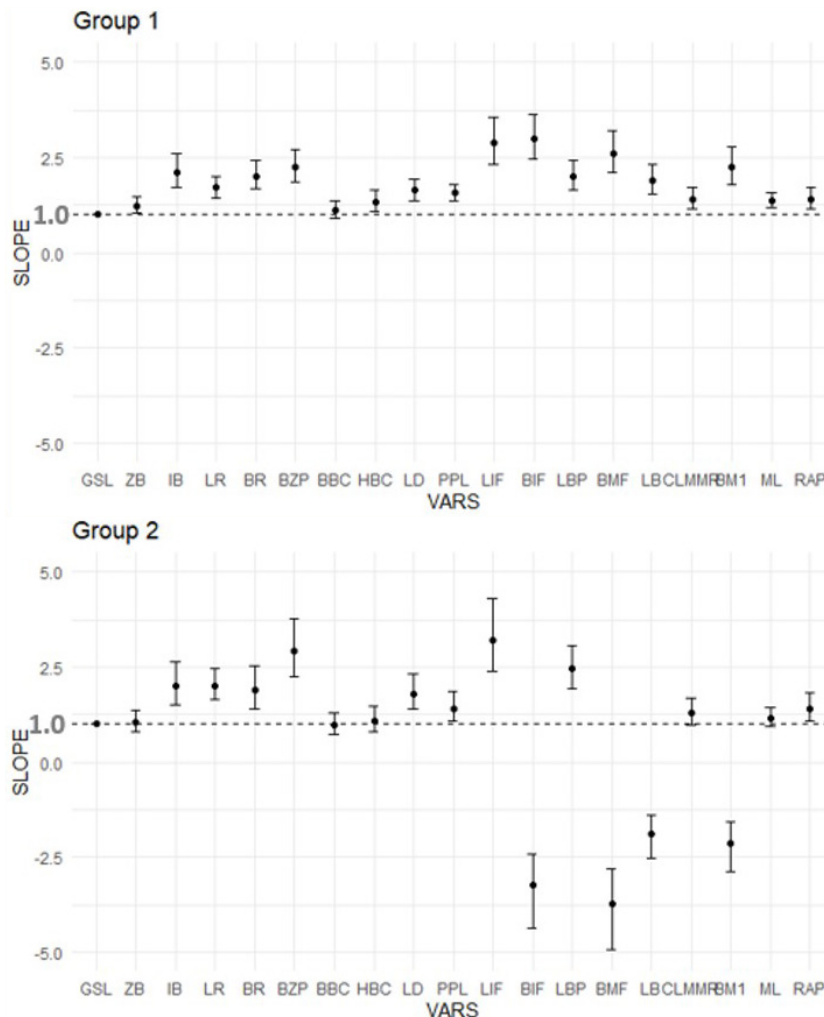


Figure 6. Standardized major axis analysis for groups 1 and 2 of *Paruromys dominator*. The dashed line at slope 1.0 represents isometry with GSL. A point above the dashed line shows positive allometry, and a point below the dashed line shows negative allometry

the effect of broad area distribution in Sulawesi. This result is in line with the findings of a previous study on *P. dominator* (Handika *et al.* 2020).

AGNES clustering showed that elevation also failed to correlate with the skull morphology in *P. dominator*. This result did not follow Bergman's rule, which states that the body size will increase in response to a colder environment in a higher-altitude habitat (Bergmann 1847; Mayr 1956). However, the result is consistent with Holmes (2015), who found no correlation between elevation and size in the eastern deer mouse (*Peromyscus maniculatus*).

We propose that geography is not a dispersal barrier for *Paruromys dominator*. This species has good locomotion on vertical, steeply sloping, horizontal, and discontinuous surfaces above ground level (Musser 2014). The good locomotion of *P. dominator* helps this species to disperse in all geographic areas of Sulawesi. Moreover, their characteristics, such as general frugivores, make them easy to adapt to various environments (Zhou *et al.* 2011; Musser 2014).

4.2. ANOVA and Correlation Analysis

The result of the ANOVA analysis of all variables shows that Group 1 has a larger skull size than Group 2, which indicates a larger body size in Group 1. In most cases, intraspecific variations in skull and body size are very common in rodents, related to different food availability in different geographical areas or influenced by climate change (Yom-Tov *et al.* 2003; Yom-Tov and Yom-Tov 2004; Zhang *et al.* 2012). However, this is not in line with this study. Some samples from both groups came from the same location and at the same collection time. We need further study on the ecological aspect to find environmental factors correlated with size variation on *Paruromys dominator*.

The correlation analysis indicates that several cranial metrics display significant correlations, suggesting that alterations in specific areas of the skull may influence changes in size in other areas. This result is consistent with findings from previous studies on rodents and mammals in general (Cheverud *et al.* 1979; Biswas and Motokawa 2019; Ikbali *et al.* 2019; Noftz and Calede 2022). The observed pattern in Group 2, characterized by a greater number of negative correlations among cranial metrics compared to Group 1, correlates with the subsequent findings in the allometry analysis.

4.3. Allometry

Groups 1 and 2 had different patterns in the allometry analysis, particularly for four characteristics: breadth of incisive foramina (BIF), breadth of mesopterygoid fossa (BMF), length of the auditory bulla (LB), and breadth of first upper molar (BM1). The four characteristics in Group 1 had positive allometry, but they had negative allometry in Group 2. Two characteristics (BMF and BM1) are related to mastication, and the other two (BIF and LB) are associated with communication.

Differences in the breadth of mesopterygoid fossa (BMF) allometry patterns could reflect different processes for biting food between the two groups. The size of the mesopterygoid fossa is related to the size of the pterygoid fossae and the internal pterygoid muscles (Rinker and Hooper 1950). The pterygoid muscles in mammals play a significant role in generating lateral movement of the jaw (Hiemae and Houston 1971). Consequently, the size of the internal pterygoid muscles is responsible for bite power (Weijs and Dantuma 1975; Tuncer 2020). Group 1 has larger internal pterygoid muscles than Group 2, inferred from BMF size, which means Group 1 has a more powerful bite than Group 2. This difference may be related to adaptations within each group, as suggested by Weijs and Dantuma (1975), who stated that the arrangement of the pterygoids and other related masticatory apparatus indicates an adaptation for optimal force transmission from muscles to teeth, facilitating effective food grinding and gnawing.

The first upper molar (BM1) is the largest tooth in the maxillary molar row, meaning it plays an important role in mastication. Our descriptive statistical analysis (Table 3) showed that the first upper molar did not significantly differ between the groups, but the allometry analysis showed a negative pattern. Tomé *et al.* (2020) found that the first upper molar length strongly correlated with the body size in *Neotoma* (Rodentia), and dietary specializations influenced its shape in the local geographic area. Based on our results, we predict that BM1 may reflect local dietary adaptation, such as in previous research. Further study is needed to explore the difference in food preference and availability among area distributions.

The breadth of the incisive foramina (BIF) is associated with the vomeronasal organ (VNO; Zagrodniuk 2021). This breadth plays a role in

chemical sensation and communication, particularly in the perception of pheromones and the formation of mating behavior (Wysocki and Lepri 1991). In our findings, the allometry pattern of BIF between the groups was different from the allometry pattern of feeding-related characteristics, probably caused by variation in the VNO. The variation of the VNO potentially affects the limitations of chemical communication between these two sets of individuals. Furthermore, there is a possibility that VNO affects food preference, as found in the gray short-tailed opossum (*Monodelphis domestica*) (Halpern *et al.* 2005)—however, the expression of food preference results from the interaction of multiple sensory systems.

The smaller skulls in Group 2 tended to have shorter auditory bullae (LB) compared to the larger skulls in Group 1. The size of the auditory bullae is related to the hearing ability in mammals. Small mammals with smaller skulls, such as rodents, have small vocal organs, which create high-pitched vocalization (Heffner *et al.* 2001). Smaller skull size in Group 2 is expected to result in higher frequency vocalizations, reducing the necessity for larger auditory bullae compared to Group 1.

In contrast, due to their larger bullae size, Group 1 is able to hear low-frequency vocalizations better than Group 2. This condition may be related to several reasons. Firstly, Group 1 has a lower population density, which subsequently requires long-distance vocalization between individuals. This finding aligns with previous studies by Petter (1953), Holman (1980), Dempster & Perrin (1991), Dempster *et al.* (1991), and Mason (2016). Secondly, the larger skulls in Group 1 are indicative of a bigger body size, which carries a higher risk of being seen by predators. The benefit of having a larger bullae size may offset this risk, as suggested by many previous studies by Lay (1974), Kotler (1984), Longland & Price (1991). These studies indicate that larger bullae in certain rodent species, enabling them to hear low-frequency sounds, could enhance their ability to detect potential predators.

A study by Scarpitti and Calede (2021) reveals another association between auditory bullae shape and locomotion in broad rodent species. Locomotion type of rodents divides into arboreal, fossorial, semi-fossorial, and terrestrial. These types of locomotion are associated with auditory bullae shape, size, and variation in particular apparatus to support them

in particular habitats. However, this study does not explain our finding because both Group 1 and Group 2 are arboreal-terrestrial, so they will probably cluster in the same group.

Other physical characteristics related to feeding, such as the rostrum, diastema, palate, and mandible, had similar positive allometric patterns for the two groups and provided unique benefits to each group. Group 1, with the longer size of the rostrum, has more elongated snouts. This characteristic is also found in shrew species such as *Crocidura foxi* and *Crocidura grandiceps* (Voet *et al.* 2022). The benefit of a longer snout in Group 1 is to have the same access as with a smaller skull in Group 2 to reach resources in narrow spaces (Samuels 2009). Conversely, Group 2, with smaller skulls, gains an advantage from having a short diastema, which increases the bite force of the incisors (Álvarez *et al.* 2021).

Variation in the size of skull characteristics related to mastication in *P. dominator* implies that this species might be adapted to eat many kinds of fruit in its habitat. *Paruromys dominator* is generally considered a frugivorous rat species (Musser 2014), but Pangau-Adam *et al.* (2006) reported that this species is a common visitor to birds' nests, claiming that *P. dominator* is an egg predator. There are no ecological studies on the food preferences of *P. dominator*. However, from Musser's (2014) field notes, we can surmise that this species is often seen around fig trees, decaying trunks, dense and tall shrubs, tall gingers, rattan, trunk bridges above streams, the understory's woody vines and trees, wanga palm (*Pigaffetta filaris*), *Lithocarpus havilandii*, *Dacrycarpus imbricatus*, walnut (*Engelhardtia serrata*), *Pandanus* sp., *Eugenia* sp., *Podocarpus neriifolius*, *Areca vestiaria*, and *Planchonia valida*. A more comprehensive study of the food availability in each of its habitats is needed for us to understand the correlation between *P. dominator* skull variation and its dietary habits. High variation in feeding-related skull characteristics has also been found in Callosciurinae (Sciuridae) in the tropical and subtropical forests of Southeastern Asia, probably related to the exploitation of its previously diverse and continuously available food resources (Casanovas-Vilar and van Dam 2013). Another finding by Cui *et al.* (2022) reveals that food availability and inter- and intraspecific competition have an impact on variation in rodent morphology.

Additionally, the variation in skull size probably results from the range of expansion in the past. Although we do not have any evidence yet of the history of this species occurrence in Sulawesi (or the ancestral species from *P. dominator*), the study by Louys *et al.* (2020) reveals that the direction of expansion in the past by several *Rattus* species in Nusa Tenggara Indonesia associated with craniometric changes especially in the skull size. In the case of *P. dominator*, we did not find any pattern of enlargement of the skull size in a specific direction through Sulawesi. Further study is needed to test whether the variation in skull size is associated with any expansion scenario in the past.

Communication in *Paruromys dominator* has also never been studied before. Nevertheless, this study has found variations in two parts of the skull related to the auditory organs and the VNO, respectively. A previous study on rats showed that the vomeronasal organ can detect alarm pheromones (Kiyokawa *et al.* 2013) and predators' kairomones (McGregor *et al.* 2004). We propose that variations in the auditory and vomeronasal organs in *P. dominator* are related to antipredator behavior. The antipredator behavior would be useful to avoid potential predators in Sulawesi, such as the Sulawesi Civet (*Macrogalidia musschenbroekii*) and Reticulated python (*Malayopython reticulatus*).

The vomeronasal organ is also useful in mating behavior (Wysocki *et al.* 1983). The differences in results between groups in the same area distribution probably influence mating partner preferences. More evidence is needed to determine whether there is no cross-breed between groups caused by their ability to recognize pheromones. We predict there is a reproductive barrier between groups. Although further study is needed, these two groups might be different species.

In conclusion, the variation of the skull is not influenced by age because we only use adult specimens. Furthermore, area distributions, elevation, and sex do not influence variations in the skull characteristics of *Paruromys dominator*, nor does geography represent a dispersal barrier because this species has good locomotion to help it survive in various geographic conditions. However, two groups formed in the AGNES analysis, with Group 1 having bigger-sized skull characteristics than Group 2. Allometry analysis then highlighted four characteristics for which the patterns differed

between groups 1 and 2. Two (BMF and BM1) were related to mastication, and the other two (BIF and LB) were associated with communication. Allometry analysis also showed that other characteristics related to mastication in bigger skulls had positive allometry patterns in both groups. The variation in mastication between groups 1 and 2 could be reflected in the different dietary habits of the rats, influenced by local environmental factors, food availability, and inter and intraspecies competition.

Furthermore, the variation in size could result from the historical direction of the species' expansion. Meanwhile, the variation in communication is probably related to antipredator and mating behavior. All of this variation reflects that the two groups of *P. dominator* underwent different evolutionary processes, which could ultimately lead to their divergence into separate species given favorable environmental conditions. We suggest that further studies should be conducted on the feeding, antipredator, and mating behavior of this species in relation to local ecological factors. Additionally, subsequent future research should explore internal factors that contribute to skull variation, such as molecular analysis. Furthermore, these additional studies may potentially lead to a taxonomic revision, splitting *P. dominator* into two distinct species.

Acknowledgements

I gratefully acknowledge financial support from the Indonesian Endowment Fund for Education/ Lembaga Pengelola Dana Pendidikan (LPDP). I also would like to express my gratitude to Museum Zoologicum Bogoriense BRIN for providing research materials.

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