COMPARISON BETWEEN *Trachypithecus auratus* AND *Trachypithecus cristatus* BRAIN SIZE IN INDONESIA

PERBANDINGAN VOLUME OTAK ANTARA *Trachypithecus auratus* DAN *Trachypithecus cristatus* DI INDONESIA

Endah Dwijayanti*, Anang Setiawan Achmadi, Maharadatunkamsi, Nanang Supriatna, Kurnianingsih, Apandi, Haerul
Museum Zoologicum Bogoriense, Pusat Penelitian Biologi LIPI
Gedung Widyasatwaloka, Jl. Jakarta-Bogor Km. 46, Cibinong 16911, Jawa Barat
E-mail: *endahdwijayanti1@gmail.com*

(received November 2019, revised April 2020, accepted June 2020)

ABSTRAK

Studi taksonomi spesies dari genus *Trachypithecus* di Indonesia menjelaskan bahwa terdapat dua spesies yaitu *Trachypithecus auratus* dan *Trachypithecus cristatus*. Studi ini untuk mengetahui perbedaan ukuran otak relatif antar spesies dari genus *Trachypithecus* di Indonesia. Studi ini menganalisis volume otak antara kedua spesies dan mengkaji hubungannya dengan pengukuran morfometri dan variabel seperti jenis kelamin, umur dan lokasi asal spesimen. Volume otak dihitung dari volume tempurung otak menggunakan silika gel 0,5 mm. Hasil penelitian menunjukkan bahwa terdapat perbedaan yang signifikan antara ukuran otak relatif antar spesies, jenis kelamin, dan interaksi antar variabel. Secara keseluruhan, *T. auratus* memiliki ukuran otak yang lebih besar dari pada *T. cristatus*, dan ukuran otak jantan lebih besar dari betina. Individu yang lebih tua cenderung memiliki ukuran otak yang sama dengan yang lebih muda. Ukuran tengkorak alometrik mempengaruhi ukuran otak secara langsung. Terdapat kecenderungan variasi klinal dalam ukuran otak relatif. Ukuran otak *Trachypithecus auratus* semakin meningkat dari Jawa bagian barat hingga Pulau Lombok. Diperlukan penelitian lebih lanjut untuk memahami pengaruh faktor eksternal seperti faktor ekologi dan sosial terhadap ukuran otak pada *Trachypithecus*.

Kata kunci: Volume otak, *Trachypithecus*, variasi klinal, Indonesia.

ABSTRACT

Taxonomic studies on genus *Trachypithecus* in Indonesia define that this genus separated into two species: *Trachypithecus auratus* and *Trachypithecus cristatus*. The aim of this study is to determine relative brain size differences between species of the genus *Trachypithecus* in Indonesia. This study analyzes the brain volume between both species and examines its relationship with morphometric measurement and variables such as sex, age, and specimen location. Brain volumes were calculated from braincase volumes using 0.5 mm silica gel as mini beads. This study reveals that there are significant differences in relative brain size inter-species, sex, and interaction among variable. Overall, *T. auratus* have a bigger brain size than *T. cristatus*, and the brain size of males are larger than females. The older individual tends to have similar brain size with younger ones. Allometric skull size affects the size of the brain directly. Also, there is a clinal trend in relative brain size. *Trachypithecus auratus* brain size is increasing from Western Java to Lombok Island. Further study is needed to understand the influence of external factor such as ecological and social factors on brain size in *Trachypithecus*.

Keywords: Brain size, *Trachypithecus*, clinal variation, Indonesia.

INTRODUCTION

Primates of the genus *Trachypithecus* are currently divided into 17 recognized species (Napier 1985; Groves 2001; Wilson & Reeder 2005). In Indonesia, there are two species based on Weitzel (1983), namely *T. auratus*, which has distribution in Java, Bali, and Lombok, and *T. cristatus*, which has distribution in Sumatra and Borneo. The two species have differences in their teeth. All the teeth of *T. auratus* are greater than *T. cristatus* and can be seen clearly from the ratio of body size allometrically. Maryanto *et al*. (1997) revealed that these two species could be distinguished from the main characters namely the distance between canines and third molars in the lower molars, the distance between the upper molars and the mastoid bone width. Study related to the dermatoglyphics of the palms shows the differences in the trait direction of palm fingerprint between the two species (Maryanto 1998).

Genetic studies conducted by Roos *et al.* (2008) reinforce Rosenblum *et al.* (1997) that *Trachypithecus* in Indonesia is divide into two species, namely *T. auratus* and *T. cristatus. T. cristatus* distributed in Sumatra and Borneo. *T. auratus* consists of two subspecies namely *T. a. mauritus* whose distribution area is in western Java and *T. a. auratus* whose distribution is in eastern Java. Maryanto *et al.* (1997) state that there are two species of *Trachypithecus* in Indonesia. Due to differences in environmental factors, the shape of the body and the skull increasingly enlarged to the east. The difference between *T. auratus* in Java is clinal. There is only one species namely *T. auratus*, with the population of Central Java, especially populations in the Mount Slamet region as intermediate populations. While the populations of Bali and Lombok is a subspecies from Java, *Trachypithecus auratus auratus*.

In terms of habitat, there are differences between *T. auratus* in Java and *T. cristatus* in Borneo and Sumatra. Most of *T. auratus* is spread in forests and mountains because *T. auratus* prefers natural habitats such as primary forests and secondary forests (Sulistyadi 2012). In comparison, *T. cristatus* prefers lowland forests, riverside forests, peat swamps, tidal areas, mangroves and, coastal areas. Sometimes *T. cristatus* can be found in rubber forests, primary forests, secondary forests up to a height of 600 meters above sea level (Supriatna & Wahyono 2000; Harrison et al. 2006; Harding 2010). According to Powel *et al.* (2017), home range in foraging shows the influence on brain size. The wider the field, the larger the volume of the brain. The size of a larger brain supports the ability to strategize in sustaining its life, as mention in Sol et al. (2008).

Based on to determine relative brain size differences between species of the genus *Trachypithecus* in Indonesia and to examine clinal variation, a study related to brain size and morphological characters that affect the size is carried out. This study analyzes brain size between the two species, sex, age, and location also examines its relationship with linear cranial measurements and other variables.

MATERIALS AND METHODS

The study was conducted at the Zoologicum Bogoriense Museum, Research Center For Biology LIPI from May to July 2018. Age determination of the specimen was seen from the sutures on the fused skull and the number of teeth. From each skull, We measured braincase volume (in ml) and collected eleven measurements (in mm) including Greatest Skull Length (GSL), Zygomatic Breadth (ZB), Braincase Breadth (BB), Post Orbital Width (POW), Least Interorbital Width (LIW), Mesopterygoid Fossa Width (MFW), Mastoid Breadth (MB), Cochlea Width (CW), Upper Canine Width (C1C1), Distance between Molar 3 to Canine on Mandible (C-M3), and Ramus Condylar Process (TH2). The parts measured followed the illustration of primate skull parts in Maryanto *et al*. (1997) (see figure 1). Mace *et al.* (1981) used 2 mm glass beads to measure volume, whereas, in this study, silica gel was used as mini beads measuring 0.5 mm. Glass beads have a density of 1.04 g / cm3 while silica gel has a density of 0.7 g / cm3, so it

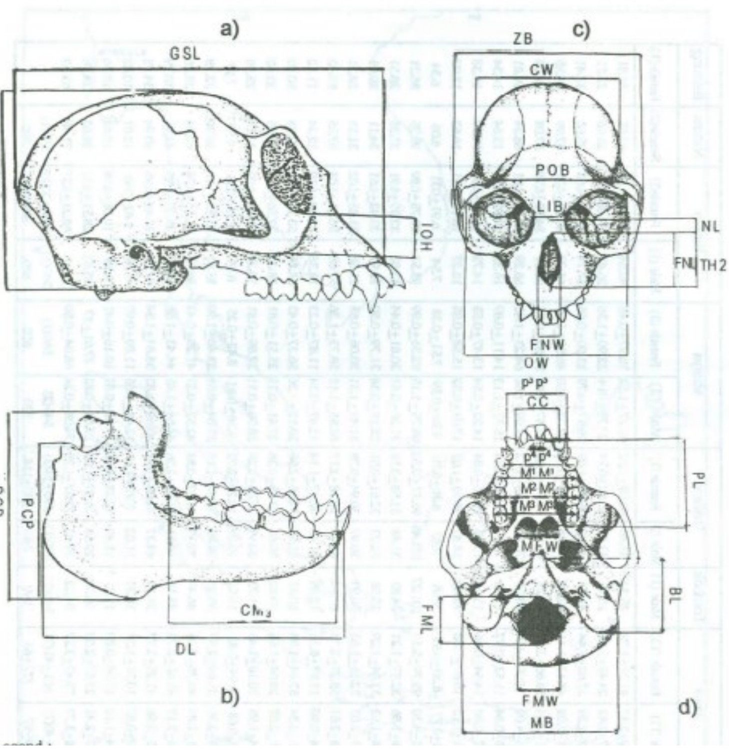

Figure 1. Measurement guideline of *Trachypithecus* (Maryanto *et al*. 1997).

will not change the skull structure of the specimen. Lineal measurements were collected using digital callipers with an accuracy of ±0.01 mm.

List of Specimens Used

Specimens analyzed included 50 individuals divided into 25 individuals *Trachypithecus auratus* and 25 individuals *Trachypithecus cristatus*. The specimens of *T. auratus* consisted of 13 adult individuals (Ad.), seven subadult individuals (S.Ad.), and four juvenile individuals (Jv.). The specimens of *T. cristatus* consisted of 12 adult individuals (Ad.), eight subadult individuals (S.Ad.), and five juvenile individuals (Jv.). Each specimen is compared by species, sex, age and location (coordinates defined by decimal degree). The location of specimen origin can be seen in Figure 2.

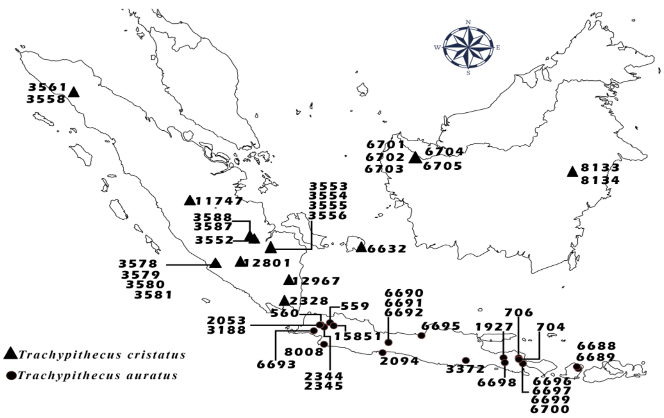

Figure 2. Specimen locations.

Trachypithecus auratus (É, Geoffroy, 1812)
Javan Lutung (Lutung Jawa)
Male Specimens (14). — Banten : MZB 6693 (Ad.), MZB 2053 (Ad.), MZB 2344 (Ad.); Sukabumi : MZB 8008 (Ad.); Gn. Slamet : MZB 6692 (Ad.), MZB 6691 (S.Ad.); Banyuwangi : MZB 6696 (Ad.), MZB 6699 (S.Ad.), MZB 6700 (Ad.); Jember : MZB 6698 (Ad.),; Blitar: MZB 3372 (Ad.); Semarang : MZB 6695 (S.Ad.); Lombok : MZB 6688 (Jv.), MZB 6689 (Ad.).
Female specimens (11). — Bogor : MZB 3188 (Jv.), MZB 15851 (S.Ad.), MZB 0559 (Jv.), MZB 2345 (Jv.), MZB 0560 (Ad.); Gn. Slamet : MZB 6690 (Ad.); Banyuwangi: MZB 0704 (S.Ad.), MZB 6697 (S.Ad.), MZB 0706 (Jv.), ; Gn. Ijang : MZB 1927 (Ad.); N. Kambangan : MZB 2094 (S.Ad.);

Trachypithecus cristatus (Raffles, 1821)
Silvered Leaf Monkeys (Lutung Budeng)
Male specimens (9). — Aceh : MZB 3558 (S.Ad.); Bengkulu : MZB 3578 (Ad.), MZB 3580 (Ad.); Kembang Janggut : MZB 8133 (Ad.); Landak : MZB 6703 (Jv.), MZB 6701 (Ad.); Palembang : MZB 3587 (Ad.); Lampung : MZB 2328 (S.Ad.); MZB 11747 (Ad.).
Female specimens (16). — Aceh : MZB 3561 (Ad.); Belitung : MZB 6632 (S.Ad.); Bengkulu : MZB 3579 (S.Ad.), MZB 3581 (Ad.), ; Kembang Janggut : MZB 8134 (Jv.), MZB ; Landak : MZB 6705 (Ad.), MZB 6704 (Ad.), MZB 6702 (S.Ad.); Palembang : MZB 3552 (Jv.), MZB 3588 (Jv.), MZB 3555 (S.Ad.), MZB 3556 (S.Ad.), MZB 3554 (Ad.), MZB 3553 (S.Ad.); Lahat : MZB 12801 (Jv.); Lampung : MZB 12967 (Ad.).

Statistical Analysis

Absolute brain size is rarely used as a correlate of biological significance based upon Jerison's arguments regarding brain-body allometry (Jerison 1979; Lesciotto & Richtsmeier 2019). To account the allometry, several measurements that can be used are body mass, vertebral bodies or cranial measurements (Ruff et al. 1997; Rightmire 2004; Lesciotto & Richtsmeier 2019). Because of the lack of body mass data, we use GSL to account the allometric scaling between brain volume and the skull size, and then we name it relative brain size. The analysis used to differentiate between species, sex, age and variations in brain size related to skull morphology was performed using regression analysis. Analysis of variance is used to determine differences between variables while regression analysis is performed to assess the correlation between variable also to reveal data trends. To understand the clinal variation, we use decimal degree coordinates from west to east in each species distribution. This clinal analysis using adult specimens because the specimens has reached maximum size. Statistical analysis using IBM SPSS Statistics version 25 and visualize in RStudio (RStudio Team 2016; IBM Corp. 2017).

RESULTS AND DISCUSSION

The results of the analysis of variance showed that there were significant differences in the brain volume relative to greatest skull length (volume/GSL) in each species, sex, and age, also a combination between sex and age. Coefficient of determination shows a low correlation (R Square = 0.370) (Table 2). Low R square indicated that although we found

Table 1. Summary of brain size measurements.

Species	Location	Age	Category	Male	Female
T. auratus	Java	Adult	A	68.72 ± 7.47 (n=9)	63.167 ± 2.25 (n=3)
			R	0.669 ± 0.054 (n=9)	0.669 ± 0.036 (n=3)
		Sub Adult	A	66.67 ± 12 (n=3)	63.625 ± 5.66 (n=4)
			R	0.726 ± 0.122 (n=3)	0.702 ± 0.093 (n=4)
		Juvenile	A	NA	54.75 ± 9.215 (n=4)
			R	NA	0.693 ± 0.106 (n=4)
	Lombok	Adult	A	92 (n=1)	NA
			R	0.91 (n=1)	NA
		Sub Adult	A	NA	NA
			R	NA	NA
		Juvenile	A	78.5 (n=1)	NA
			R	0.933 (n=1)	NA
	Java & Lombok	Adult	A	71.05 ± 10.186 (n=10)	63.167 ± 2.25 (n=3)
			R	0.693 ± 0.092 (n=10)	0.669 ± 0.036 (n=3)
		Sub Adult	A	66.67 ± 12 (n=3)	63.625 ± 5.66 (n=4)
			R	0.726 ± 0.122 (n=3)	0.702 ± 0.093 (n=4)
		Juvenile	A	78.5 (n=1)	54.75 ± 9.215 (n=4)
			R	0.933 (n=1)	0.693 ± 0.106 (n=4)
T. cristatus	Sumatra	Adult	A	62.87 ± 4.64 (n=4)	58.37 ± 4.62 (n=4)
			R	0.646 ± 0.044 (n=4)	0.62 ± 0.043 (n=4)
		Sub Adult	A	60.5 ± 6.36 (2)	56.1 ± 6.93 (n=5)
			R	0.647 ± 0.006 (n=2)	0.63 ± 0.075 (n=5)
		Juvenile	A	NA	57.67 ± 4.39 (n=3)
			R	NA	0.66 ± 0.015 (n=3)
	Borneo	Adult	A	63.75 ± 2.47 (n=2)	56 ± 2.83 (n=2)
			R	0.66 ± 0.021 (n=2)	0.632 ± 0.021 (n=2)
		Sub Adult	A	NA	66 (n=1)
			R	NA	0.708 (n=1)
		Juvenile	A	66 (n=1)	57 (n=1)
			R	0.796 (n= 1)	0.65 (n=1)
	Sumatra & Borneo	Adult	A	63.167 ± 3.79 (n=6)	57.58 ± 3.99 (n=6)
			R	0.651 ± 0.036 (n=6)	0.624 ± 0.035 (n=6)
		Sub Adult	A	60.5 ± 6.36 (2)	57.75 ± 7.4 (n=6)
			R	0.647 ± 0.006 (n=2)	0.646 ± 0.074 (n=6)
		Juvenile	A	66 (n=1)	57.5 ± 3.58 (n=4)
			R	0.796 (n= 1)	0.66 ± 0.013 (n=4)

A (Absolute brain size), R (Brain size relative to GSL / Relative brain size); NA (Not Available).

some differences, all variable less influenced the relative brain size to GSL.

Based on this result, we found that *T. auratus* have a larger brain size than *T. cristatus* (p-value < 0.05). In line with the previous study about morphology variation in *Trachypithecus* by Maryanto et al. (1997) that *T. auratus* has a larger skull size ratio than *T. cristatus*. Home range in foraging shows the influence on brain size (Clutton-Brock & Harvey 1980; Powel et al. 2017). The home range of *T. auratus* about 15-23 Ha and *T. cristatus* about 10-20 Ha. Daily travel distance on *T. auratus* about 500-1500 m,

Table 2. Analysis of Variance on Relative Brain Size .

Variable	Sig.	R Square all variable
Species	0.017*	0.370
Sex	0.007**	
Age	0.008**	
Species * Sex	0.439	
Species * Age	0.794	
Sex * Age	0.041*	
Species * Sex * Age	0.737	

farther than *T. cristatus* that only travel 300-600 m (Supriyatna & Wahyono 2000). The wider home range and daily travel distance on *T. auratus* influenced by a lot of degradation in forest habitat in Java Island. This factor is causing limited food source for *T. auratus*. Larger brain size on *T. auratus* helps to accommodate processing complex information about food distribution in their habitat.

The following result is about different brain size on sex. *Trachypithecus* species are smaller and less sexually dimorphic in size than most other colobine genera, but more dimorphic than *Presbytis* (Pan & Groves 2004; Harding 2010). *T. cristatus* females differ with the male from irregular white patches on the inside flanks. Also, females, only 89% of males body weight (Roonwal & Mohnot 1977), and males have larger canine-sectoral teeth (Groves 2001). *T. auratus* sexually dimorphic, females have yellowish-white pubic patches, and males are not (McCarthy 2019). The analysis showed that the relative brain size in the two sexes has a significant difference (p-value < 0.01). The measurement of absolute brain size in males is indeed greater (Table.1). This result is in line with studies on other primates such as Rhesus monkey (*Macaca mullata*) which states that adult male individuals have a larger brain size than adult female individuals by 10% or even less than 20% during juvenile age to adolescence (Franklin et al. 2000). Larger male body size will require a larger nervous system to coordinate his body (Deaner *et al*. 2007). The results of studies in humans show differences in the size of the brain size caused by sexual maturity in females faster than males, so that affects the cognitive abilities of females that mature faster than males, as mention in Lynn (1999).

The results also showed that the growth stage has a significant difference in relative brain size (p-value < 0.01). Based on measurement results, the relative brain size of juveniles is greater than adults, but the absolute brain size tends to be similar. The difference in GSL size is the cause of the difference in relative brain size. The GSL on adult reaches maximum size on the species. With the same brain size but a larger GSL in adults, it is causing a relatively larger brain size in juveniles. Brain development does not increase the size of the brain, and it's just that inability, the brain has increased. The brain experiences maturation as the species get older. This study indicated that cranial growth rate is higher than brain volume gain. According to Martin (1983), prenatal brain growth in primates, in general, will decrease after birth, except in humans which decreases after one year of birth. Walker et al. (2006) found that old world monkey brain size correlates with body size and diet; however, new world monkey brain size is influenced by body size and life span. *Trachypithecus* belongs to the old world monkey group, so the brain size is influenced by body size and diet.

Table 3. Regression analysis between brain volume and cranial parts.

Variable	Sig.
Great Skull Length (GSL)	0.034*
Zigomatic Breadth (ZB)	0.761
Least Interorbital Width (LIW)	0.462
Post Orbital Width (POW)	0.009***
Cochlea Width (CW)	0.236
Mesopterygoid Fossa Width (MFW)	0.824
Mastoid Breadth (MB)	0.600
Braincase Breadth (BB)	0.064
Upper Canine Width (C^1C^1)	0.424
Distance between Molar 3 to Canine on Mandible ($C\text{-}M_3$)	0.297
Ramus Condylar Process (TH2)	0.630
p-value	< 0.000***
Adjusted R Squared = 0.7109	

The results of linear regression analysis on parts of the skull that affect the size of the brain size can be seen in Table 3. Based on these results, there is a significant correlation between the size of the brain with parts of the skull (R square = 0.797, p-value < 0.001). The parts of the skull with the most significant correlation are GSL and POW, with the regression equation are as follows:

Volume = -85.76 + 0.64 GSL + 0.11 ZB – 0.72 LIW +1.21 POW + 0.43 CW – 0.19 MFW – 0.23 MB +1.08 BB – 0.36 C1C1 – 0.52 C-M3 – 0.18 TH2

The difference in brain size in *Trachypithecus* causes different sizes in GSL and POW. The greater the size of the brain, the greater the size of GSL and POW in this genus. POW is the distance between the curve behind the orbital bone called postorbital constriction. Increased brain size causing the widening of the gap in postorbital constriction. It is causing postorbital constriction will be shallower. Another study in human skull reveals that postorbital constriction was confirmed a strong relative correlation with the upper facial breadth and maximum cranial breadth (Asfaw *et al.* 2008; Bruner & Holloway 2010; Kubo *et al.* 2012).

Regression analysis on the adults relative brain size and coordinates shows that *T. auratus* has a significant data trend, increasing from west to east (Multiple R-squared = 0.37; p-value < 0.05). Contrast with *T. cristatus* that does not show any correlation and significance between relative brain size and coordinates (Multiple R-squared = 0.0117; p-value = 0.74) (see Fig.3).

Based on the results of the analysis, the data shows that the relative brain size of

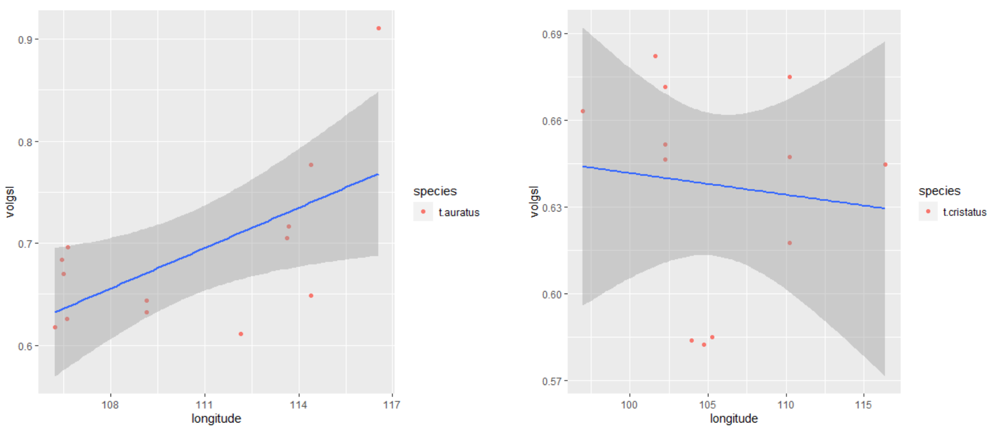

Figure 3. Relationship between relative brain size and longitude: *T. auratus* (left) and *T. cristatus* (right)

T. auratus is getting bigger eastward from Western Java to Lombok (Multiple R-squared = 0.37; p-value < 0.05). This result in line with Maryanto *et al*. (1997) which states that there are clinal variations in the type of *T. auratus* from western Java to the east in terms of the size of the skull, teeth, and dental characteristics. Lombok specimens have a distinct and the largest relative brain size (Table 1.), this result supporting Maryanto *et al*. (1997) that state *T. auratus* from Lombok Island is subspecies from Java. This case is not found in *T. cristatus*. This result means home range or habitat of *T. cristatus* in Sumatra and Borneo does not influence the brain size.

CONCLUSION

This study shows that there are differences of relative brain size inter-species, sex, age either some interaction among variable caused by home range, body size and the size of the skull. Brain volume has a significant positive-correlation with Greatest Skull Length and Post Orbital Width. Greatest Skull Length can substitute body mass as allometric scaling in case the lack of body mass data. However, we use the skull-based method for age determination. Further research is needed to determine the maturity of brain growth in this species related to the adult age. Clinal found in *T. auratus* relative to brain size supporting statement of the previous study about cranial measurements on this species, also supporting the idea of *T. auratus* subspecies that found in Lombok Island.

ACKNOWLEDGEMENT

Thanks to Eko Sulistiyadi M.Si and Dr. Ulfah Mardhiah, for their assistance in statistical analysis, Alamsyah Elang N.H., S.Si for his assistance in using Rstudio as a statistic tool, Dr. Achmad Dinoto and Prof. Ibnu Maryanto for their guidance in writing KTI, also the colleagues of PNS Zoologi 2018 who support authors during the study.

AUTHORSHIP AND DECLARATION OF CONFLICTING INTERESTS

Endah Dwijayanti is the principal author of this paper. The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

REFERENCES

Asfaw, B., Gilbert, W. H. & Richards, G.D. (2008). *Homo erectus* cranial anatomy. In: W.H. Gilbert & B. Asfaw (Eds.), *Homo erectus*: *Pleistocene Evidence from the Middle Awash, Ethiopia* (pp. 265–327). Berkeley and Los Angeles: University of California Press.

Bruner, E. & Holloway, R. L. (2010). A bivariate approach to the widening of the frontal lobes in the genus *Homo*. *Journal of Human Evolution*, *58*, 138–146.

Clutton-Brock, T. H. & Harvey, P. H. (1980). Primates, brains and ecology. *Journal of Zoology*, *190*, 309-323. doi:10.1111/ j.1469-7998.1980.tb01430.x

Deaner, R. O., Isler, K., Burkart, J. & Van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, behavior and evolution, 70*(2), 115-124.

Franklin, M. S., Kraemer, G. W., Shelton, S. E., Baker, E., Kalin, N. H. & Uno, H.

(2000). Gender differences in brain volume and size of corpus callosum and amygdala of rhesus monkey measured from MRI images. *Brain research, 852* (2), 263-267.

Groves, C.P. (2001). *Primate Taxonomy*. Washington: Smithsonian Institution Press.

Harrison T., Krigbaum J. & Manser, J. (2006). Primate biogeography and ecology on the Sunda Shelf Islands: A paleontological and zooarchaeological perspective. In Shawn M. L. & John G. F. (Eds.), *Primate Biogeography: Developments in Primatology Progress and Prospects* (pp 331-372). Boston, MA: Springer. https://doi.org/10.1007/0-387-31710-4_12

IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp.

Jerison, H. J. (1979). Brain, body and encephalization in early primates. *Journal of Human Evolution*, *8,* 615–635.

Kubo, D., Kono, R.T. & Suwa, G. (2012). Endocranial proportions and postorbital morphology of the Minatogawa I and IV Late Pleistocene Homo sapiens crania from Okinawa Island, Japan. *Anthropological Science, 120* (2), 179-194.

Harding, L.E. (2010). *Trachypithecus cristatus* (Primates: Cercopithecidae). *Mammalian Species, 42*(1), 149-165. https://doi.org/10.1644/862.1

Lesciotto, K. M. & Richtsmeier, J. T. (2019). Craniofacial skeletal response to encephalization: How do we know what we think we know?. *American journal of physical anthropology, 168* (Suppl 67), 27–46. https://doi.org/10.1002/ajpa.23766

Lynn, R. (1999). Sex differences in intelligence and brain size: a developmental theory. *Intelligence, 27* (1), 1–12.

Mace, G. M., Harvey, P. H., & Clutton-Brock, T. H. (1981). Brain size and ecology in small mammals. *Journal of Zoology, 193*(3), 333–354. https://doi.org/10.1111/j.1469-7998.1981.tb03449.x

Martin. (1983). *Human brain evolution in an ecological context*. New York: American Museum of Natural History.

Maryanto, I., Mansjoer, I., Sajuthi, I. & Supriatna. (1997). Morphological variation in the Ebony and Silver leaf monkeys [*Trachypithecus auratus* (E. Geoffrey, 1812) and *Trachypithecus cristatus* (Raffles, 1821)] from South-east Asia. *Treubia, 31,* 113-131.

Maryanto, I. (1998). Silver and ebony leaf monkey dermatograph marker. *Indonesian Journal of Primatology, 3* (1), 17–24.

McCarthy, B. (2019, July). Javan Langur *Trachypithecus auratus*. Retrieved from https://www.neprimateconservancy.org/javan-langur.html

Napier, P. H. (1985). *Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part III: Family cercopithecidae, subfamily colobinae.* London: British Museum (Natural History).

Pan, R. L., & Groves, C. P. (2004). Cranial variation among Asian colobines. In F. C. Anapol, R. Z. German, & N. G.

Jablonski (Eds.) *Shaping primate evolution: form, function, and behavior* (Pp. 45–65). Cambridge, United Kingdom: Cambridge University Press.

Powell, L. E., Isler, K. & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proc. R. Soc. B. 28420171765* http://doi.org/10.1098/rspb.2017.1765

Reader, S. M. (2003). Relative brain size and the distribution of innovation and social learning across the non-human primates. In D. Fragaszy & S. Perry (Eds.) *The biology of traditions: models and evidence* (Pp. 56–93). Cambridge: Cambridge University Press.

Rightmire, G. P. (2004). Brain size and encephalization in early to mid-Pleistocene Homo. *American Journal of Physical Anthropology, 124*, 109–123. https://doi.org/10.1002/ajpa.10346

Roonwal, M. & Mohnot, S. M. (1977). *Primates of South Asia: ecology, sociobiology, and behavior*. Harvard University Press, Cambridge, Massachusetts.

Roos, C., Nadler, T., & Walter, L. (2008). Mitochondrial phylogeny, taxonomy and biogeography of the silvered langur species group (*Trachypithecus cristatus*). *Molecular Phylogenetics and Evolution, 47*(2), 629-636.

Rosenblum, L.L., Supriatna, J., Hasan, M.N., & Melnick, D.J. (1997). High mitochondrial DNA diversity with little structure within and among leaf monkey populations (*Trachypithecus cristatus* and *Trachypithecus auratus*). *Int. J. Primatol, 18*, 1005– 1028.

RStudio Team. (2016). *RStudio: Integrated Development for R*. Boston, MA: RStudio, Inc.

Ruff, C. B., Trinkaus, E., & Holliday, T. W. (1997). Body mass and encepha-lization in Pleistocene Homo. *Nature, 387*, 173–176. https://doi.org/10.1038/387173a0

Sol, D., Bacher, S., Reader, S. M, & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *Am Nat., 172*, Suppl 1, S63-S71. doi:10.1086/588304

Sulistyadi E. (2012). Komunitas Mamalia Besar Gunung Slamet. In: I. Maryanto, M. Noerdjito, & T. Partomihardjo. *Ekologi Gunung Slamet*. Jakarta: LIPI Press. ISBN: 978-979-799-700-7.

Supriatna, J. & Wahyono. (2000). *Panduan Lapangan Primata Indonesia.* Jakarta: Yayasan Obor Indonesia.

Walker, R., Burger, O., Wagner, J. & Von Rueden, C. R. (2006). Evolution of brain size and juvenile periods in primates. *Journal of Human Evolution, 51*(5), 480-489.

Weitzel, V. 1983. Preliminary Study of the Dental and Cranial Morphology of *Presbytis* and *Trachypithecus* in Relation to Diet, unpublished M.A. thesis, Australian National University, Canberra.

Wilson, D.E, & Reeder, D.M. (Editors). (2005). *Mammal Species of the World. A Taxonomic and Geographic Reference* (3rd ed). Baltimore, US: Johns Hopkins University Press, 2,142 pp.