

Article

Evolutionary Insights from Dental Diversity in Afro-Asian Primates

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Abstract: The evolutionary development and phylogenetic division between Asian and African cercopithecoids (Cercopithecidae) have attracted significant attention in genetics, molecular biology, behavior, and morphology. However, less emphasis has been placed on how they have evolved morphologically after divergence, approximately 10 million years ago (mya) for Colobinae and 5–7 mya for Cercopithecinae, corresponding to the significant variation and diversity in landscape, climate, habitat, and ecologies between the two continents. This study examines whether such variation and diversity have been reflected in dental morphology. Our findings reveal substantial differences between Hylobatidae and Cercopithecidae, as well as between Colobinae and Cercopithecinae, indicating that size-adjusted dental variation mainly reveals the diversity associated with evolution and phylogenetic inertia. Interestingly, despite the earlier divergence of Afro-Asian colobines, their Euclidean Distance is comparable to that of Afro-Asian cercopithecines. This implies that latecomers (macaques) demonstrate equivalent diversity to colobines due to their extensive dispersion and broader adaptative radiation on the same continent. Colobinae exhibit more developed premolar and molar regions. However, when post-canine teeth are considered alone, Colobinae present a significantly larger molar size than Asian Cercopithecinae but not with the African Cercopithecinae. This contradicts the hypothesis that folivorous primates (Colobinae) have larger post-canine molars than frugivorous ones (Cercopithecinae). The considerable molar size in African Cercopithecinae must be associated with their more protrusive and larger facial structure rather than a specific dietary preference, being less diverse than their Asian counterparts—a trait that has evolved phylogenetically. This study also paves the way for further exploration of facial and cranial differences between the continental groups of Cercopithecinae and Colobinae, delving deeply into diversity variation due to geographical and climatic adaptations.

Keywords: Cercopithecidae; dental allometry analysis; environmental and climate changes; Africa and Asia primates; natural selection and environmental adaptation



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1. Introduction

The evolution of catarrhine primates (Old World monkeys, gibbons, great apes, and humans) in Asia experienced significant changes during the Neogene and Quaternary following the migrations from Africa to Asia via Europe [1–4]. Different groups of Asian Cercopithecidae (macaques and colobines) started their journey to varying timeframes from Africa. However, by the end of the Miocene and Early Pliocene, they settled in

a Convergence–Divergence Center (CDC) located in southeast Qinghai–Tibet Plateaus and Hengduan Mountains, a region linking East, South, and Southeast Asia [1]. Fossil hylobatids from India [5] and in the Center [6–8] also indicate that gibbons used the same paths entering the CDC, through which Asian catarrhines dispersed to various parts of Southeast and East Asia [1,9–11]. Unlike today, the region they colonized was relatively flat. However, it underwent significant changes during the Pliocene and Quaternary, showcasing remarkable diversity in many aspects due to the accelerated uplift of the Qinghai–Tibet Plateau and Himalayas, caused by the intense collision between the Indian and European plates [12,13]. This created significantly diverse geographic changes in Asia. Thus, similar to modern humans (*Homo erectus* and *H. sapiens*), Afro-Asian monkeys in Asia experienced a period of evolutionary radiation that was driven by the significant landscape diversity and the formation of land bridges among islands due to lowered sea levels of insular geography following the lowering sea level [1,14,15].

In contrast, similar changes in geography, climate, and habitats were relatively less noticeable in Africa [16–18], such as expanding savannas and grasslands in East Africa. Under humid global conditions, savannas spread northwards and eastwards over desert areas. Between 6.3 and 6.0 mya, a significant shift in vegetation was marked by a notable decrease in woodlands. Concurrently, West and East Africa experienced very arid conditions, evidenced by the sparse tree cover in the tropical regions. These changes were linked to global climate variations caused by the formation of the Arctic ice sheet, which induced intense tropical aridity. Finally, savannas expanded at the expense of rain forests in both West and East Africa [19].

These significant environmental changes and diversity would have affected the cercopithecoid primates' ecology in Africa and Asia. Dental diversity, linked to dietary selection and habits, represents a vital tool for exploring how dental structures have evolved phylogenetically and shaped biomechanically following the divergence in biology, climate, and geology between the two continents. Hence, exploring the magnitude of dental diversity related to environmental adaptations between the Cercopithecinae and Colobinae in Africa and Asia is essential. Previous studies have shown that frugivorous primates have a smaller post-canine dental size relative to body size than folivorous primates [20–23]. It is interesting to determine whether the African representatives, Colobinae or Cercopithecinae, exhibit larger molar size than their Asian counterparts or vice versa due to climatic, environmental, and dietary differences. This may raise the hypothesis that there may be significant continental differences in selective constraints and environmental adaptations among Cercopithecinae and Colobinae, particularly with their dental structures. A similar approach was developed by [24], but focusing only on Colobinae.

Considering the importance of dental morphology for understanding phylogenetic and adaptive patterns, the present study aims to (a) comprehend the dental variation in African and Asian Cercopithecidae regarding the divergent evolutionary patterns and environmental changes specific to each continent; (b) examine whether Colobinae exhibit more significant dental variation due to the earlier continental separation, around 10.7 mya [25], compared to Cercopithecinae, which separated approximately 7.0–5.5 mya [26] or 5 mya [11]; and (c) determine whether there is a significant post-canine dental size variation between Cercopithecinae and Colobinae.

2. Material and Methods

2.1. Material

The studied material consists of the upper and lower teeth of African and Asian Cercopithecidae, representing different family clades with divergent ecologies (Table 1). For comparative purposes, we also included the teeth of Asian Hylobatidae as an out-group. Hylobatidae (i.e., gibbons or lesser apes) are quite different from great apes in terms of facial structure, showing the smallest facial size with insignificant sexual dimorphism [27]. They also exhibit significantly lower canine sexual dimorphism than great apes [28]. However, studies of gibbons' canine sexual dimorphism and comparison with

other catarrhines are still relatively uncommon (see [29–33]). Thus, they represent an excellent example for determining canine sexual dimorphism compared to that observed within the Cercopithecoidea.

Table 1. The Cercopithecoidea and Hylobatoidea studied *.

Continent	Family	Subfamily	Genus	Species (Sex)					
Africa	Cercopithecoidea	Colobinae	<i>Cercocebus</i>	<i>torquatus</i> (6F,10M)					
			<i>Colobus</i>	<i>guereza</i> (18F, 16M, 4U) <i>polykomos</i> (2F, 1M, 1U)					
			<i>Ptilocolobus</i>	<i>badius</i> (18F, 16M, 2U)					
			<i>Procolobus</i>	<i>verus</i> (21F, 14M, 7U)					
			Cercopithecoidea	<i>Cercopithecus</i>	<i>mona</i> (2F) <i>nictitans</i> (3M, 1U)				
		<i>Mandrillus</i>		<i>leucophaeus</i> (11F, 11M)					
		<i>Papio</i>		<i>hamadryas</i> (2F, 10M) <i>ursinus</i> (7F, 11M)					
		<i>Macaca</i>		<i>sylvanus</i> (10F, 11M)					
		Asia		Colobinae	<i>Nasalis</i>	<i>larvatus</i> (10F, 12M)			
<i>Presbytis</i>	<i>chrysomelas</i> (1F) <i>comata</i> (3F, 4M) <i>melalophos</i> (4F, 5M) <i>rubicunda</i> (7F, 5M)								
	<i>Pygathrix</i>				<i>nemaus</i> (11F, 16M)				
					<i>Rhinopithecus</i>	<i>avunculus</i> (3F, 3M) <i>bieti</i> (12F, 9M) <i>brelichi</i> (1F, 4M)			
						<i>roxellana</i> (34F, 32M, 9U)			
						<i>entellus</i> (5F, 5M)			
<i>Trachypithecus</i>	<i>cristatus</i> (19F, 15M) <i>francoisi</i> (8F, 10M) <i>obscurus</i> (10F, 10M) <i>phayrei</i> (26F, 10M) <i>vetulus</i> (5F, 5M)								
<i>Simias</i>	<i>concolor</i> (2F, 1M)								
Cercopithecoidea					Cercopithecoidea	<i>Macaca</i>	<i>arctoides</i> (3F, 3M) <i>assamensis</i> (3F, 3M) <i>fascicularis</i> (3F, 3M) <i>fuscata</i> (4F, 3M) <i>mulatta</i> (4F, 3M) <i>nemestrina</i> (3F, 3M) <i>nigra</i> (3F, 3M) <i>radiata</i> (3F, 3M) <i>silenus</i> (3F, 3M) <i>sinica</i> (4F, 4M) <i>thibetana</i> (2F, 4M)		
							Hylobatoidea	<i>Hylobates</i>	<i>agilis</i> (10F, 10M, 2U) <i>lar</i> (13F, 20M, 4U) <i>muelleri</i> (13U) <i>pileatus</i> (1F, 2M)
									<i>hoolock</i> (8F, 11M)

* Please see the Acknowledgments for data collection. F: female; M: male; and U: unknown sex.

The materials used in this study are housed in various institutes, universities, and museums (see Acknowledgments for details). All specimens included are adults, identified by the full eruption of M3s.

2.2. Methods

A digital caliper (Mitutoyo Inc., Tokyo, Japan) with an accuracy of 0.01 mm was used to take the maximum mesiodistal (length) and buccolingual (width) measurements for each tooth on the maxilla and mandible. Tooth size (crown area) was multiplied by length with width. Cranial length from the tip of occipital protuberance to the alveolar between the right and left I¹ was also measured as a proxy for body size, e.g., [20,34].

Allometric analyses ($Y = aX^b$) have been widely used across various fields, such as biology, ecology, paleontology, and anthropology, to explore how an organism's structure or function changes relative to its size. These analyses provide valuable insights into growth patterns, physiological constraints, evolutionary adaptations, and ecological diversity [35]. When transformed using logarithms, this allometric formula becomes a linear regression, $\log Y = \log a + b \log X$, where Y (the dependent variable) represents the square root of the tooth crown area, and X (the independent variable) represents body size, approximated by its proxy, cranial length.

To delve into dental variation, we used the residual, a size-adjusted value, to indicate how far an individual deviates from the regression line of the allometric analysis. The following equation was used:

Residual = antilog (observed value-predicted value).

The observed values are those of the raw measurements, and the predicted values are those calculated from the allometric formula [24,36–38].

Ordinary least-square (OLS) regression analysis was used for allometric analysis (log-transformed data). OLS is considered more suitable for calculating residuals for size adjustment (e.g., [39,40]).

Three types of residuals were calculated:

- (1) Comparison between Cercopithecidae and Hylobatidae aims to explore the relationship between teeth and body size of catarrhines in Africa and Asia. As seen below, residuals were further analyzed using multivariate discriminant function analysis (DFA).
- (2) Comparison within the Cercopithecidae aims to decipher differences between the representatives of Colobinae and Cercopithecinae in Africa and Asia. Residuals of the four groups (African Colobinae, African Cercopithecinae, Asian Colobinae, and Asian Cercopithecinae) were also analyzed using DFA.
- (3) Comparing the post-canine teeth size within the Cercopithecidae aims to determine the magnitude of dental variation for Colobinae and Cercopithecinae in Africa and Asia.

DFA is a standard multivariate analysis for classification and dimensionality reduction, used to identify a linear combination of variables that best separates two or more groups or classes. Its main objective is to maximize the between-class and within-class variance ratio, finding a linear combination of variables that maximizes the differences between the means of the groups while minimizing the variation within each category [41]. We performed DFA to analyze residuals generated in comparisons (1) and (2).

Furthermore, Analysis of Variance (ANOVA) was employed to evaluate differences between the studied groups based on DFA scores (coordinates).

All the analyses were carried out by IBM SPSS Statistics v. 20.

3. Results

The results of the first two types of allometric analyses indicate that each tooth size (area) presents a significant positive relationship ($p < 0.001$) with body size, represented by cranial length. The primary purpose of this study is to explore the variation between the different groups of Cercopithecidae, correlation coefficients, and regression slopes, indicating that the allometric scale between teeth and body size is not reported here. Their corresponding residuals were further explored via DFAs. The results (eigenvalues, percentage of explained variance, coefficients of eigenvectors on the first two axes) of the three-group DFA (Colobinae, Cercopithecinae, Hylobatidae) and the four-group DFA

(African Colobinae, African Cercopithecinae, Asian Colobinae, Asian Cercopithecinae) are presented in Table 2.

Table 2. Eigenvalues, percentages of explained variance, and coefficients of eigenvectors of the first two DFA axes for the three-group DFA (Colobinae, Cercopithecinae, Hylobatidae) and the four-group DFA (African Colobinae, African Cercopithecinae, Asian Colobinae, Asian Cercopithecinae).

	Three Groups		Four Groups	
	DF1	DF2	DF1	DF2
Eigenvalue	0.794	0.467	0.941	0.566
Percentage	63.0%	37.0%	53.0%	31.8%
Cum. Per	63.0%	100.0%	53.0%	84.8%
Eigenvector				
UI1	0.16	−0.45	0.14	−0.48
UI2	0.15	0.41	0.03	0.28
UC	0.32	0.29	−0.46	0.38
UP3	−0.56	0.43	0.01	0.47
UP4	0.50	−0.21	−0.70	−0.25
UM1	−0.08	0.89	0.84	0.61
UM2	−0.27	−1.12	0.23	−1.14
UM3	0.66	0.13	0.36	0.12
LI1	0.49	0.06	0.19	0.19
LI2	−0.14	0.18	−0.47	0.26
LC	−0.61	0.10	0.35	0.10
LP3	0.63	0.21	0.75	0.06
LP4	0.27	−0.68	0.30	−0.68
LM1	−0.51	−0.18	−0.82	−0.23
LM2	−0.39	0.36	0.03	0.47
LM3	0.35	0.50	−0.37	0.72

U: upper teeth areas; L: lower teeth areas.

Regarding the three-group analysis, the first and second DFs explain 63.0% and 37.0% of the total variance. On the positive side of DF1, the variables with the highest contribution are UM3 (0.66), LP3 (0.62), and UP4 (0.50), and on the negative side of DF1, UP3 (−0.56) and LC (−0.61). Figure 1 shows the dispersal pattern of the three groups along DF1 and DF2. The ANOVA results of the discriminant scores show that Hylobatidae, principally located on the negative side, are significantly distinct ($p < 0.001$) from both Colobinae and Cercopithecinae, both latter groups showing significant overlap along DF1.

Along DF2, the positive side of the axis is characterized by UM1 (0.89) and LM3 (0.50), whereas the negative side is characterized by UM2 (−1.12) and LP4 (−0.676). Along this axis, Hylobatidae shows substantial separation from Colobinae ($p = 0.002$) and Cercopithecinae ($p < 0.001$). Colobinae and Cercopithecinae are also significantly separated ($p < 0.001$). Our results indicate that Hylobatidae are distinct from Cercopithecinae in DF1 and DF2, whereas the monkey subfamilies are separated only along DF2.

Concerning the four-group analysis, the first and second axes account for 53.0% and 31.8%, respectively. UM1(0.84) and LP3 (0.75) contribute significantly to the positive side of DF1, whereas LM1 (−0.82) and UP4 (−0.70) are significant contributors to the negative side of the axis. The dispersal pattern of the four groups of Asian and African Cercopithecinae along DF1 and DF2 are illustrated in Figure 2. Along DF1, Cercopithecinae (African and Asian) appear significantly distinct ($p < 0.001$) from Colobinae (African and Asian). However, no significant separation between African and Asian Colobinae and African and Asian Cercopithecinae is observed.

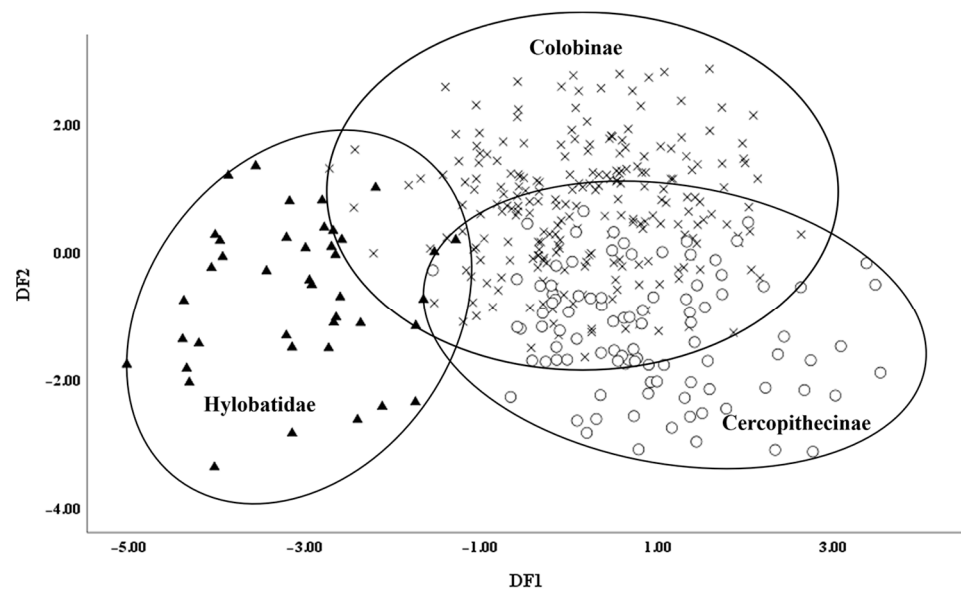


Figure 1. Individual scatter plots of the Hylobatidae, Colobinae, and Cercopitheciinae along DFA's first and second axes.

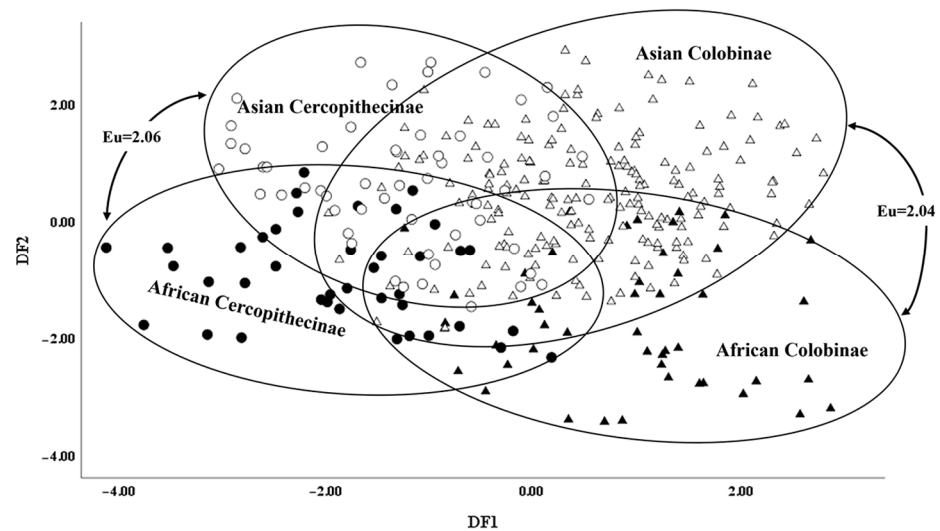


Figure 2. DFA among Asian Colobinae, African Colobinae, Asian Cercopitheciinae, and African Cercopitheciinae. The Euclidean Distance (Eu) between Asian and African Colobinae is 2.04, and between Asian and African Cercopitheciinae, it is 2.06.

Along DF2, LM3 (0.72) and UM1 (0.61) are major contributors on the positive side of the axis, whereas UM2 (−1.14), LP4 (−0.68), and UI1 (−0.58) show noticeable negative contributions. Asian Colobinae and Cercopitheciinae show significant separation from their African counterparts (Colobinae: $p < 0.001$; Cercopitheciinae: $p < 0.05$). The Euclidean Distances reflecting the magnitude of separation between the African and Asian representatives of the two subfamilies on the first two DFA axes are comparable: Colobinae = 2.04; Cercopitheciinae = 2.06. Our results indicate that DF1 separates between the two subfamilies, whereas DF2 separates the Asian and African representatives.

Figure 3 illustrates the residual differences between Cercopitheciidae groups from different continents, derived from an allometric analysis of both post-canine teeth and body size. The slope for both upper and lower molars exceeds 0.80 against body size, with a correlation coefficient of 0.86, indicating a strong correlation ($p < 0.001$). The ANOVA results indicate that African Cercopitheciinae have significantly higher values than the other

groups. Both African and Asian Colobinae show substantially higher values than Asian Cercopithecinae, which display the lowest variation compared to the different groups. Finally, the difference between Asian and African Colobinae is not statistically significant.

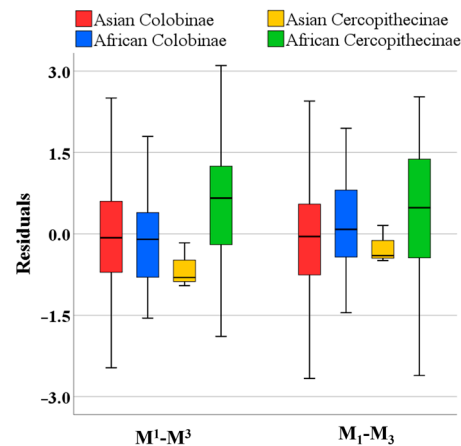


Figure 3. Comparison of residuals among the Cercopithecinae groups derived from the allometric analysis between post-canine teeth and body size (proxied by cranial length).

Regarding canine sexual dimorphism, we calculated the degree of lower canines among the three studied groups. Hylobatidae are characterized by the lowest degree of sexual dimorphism ($SD = 0.0596$), whereas Cercopithecinae show the highest degree ($SD = 0.6062$) (Figure 4). Colobinae show moderate lower canine sexual dimorphism ($SD = 0.3185$).

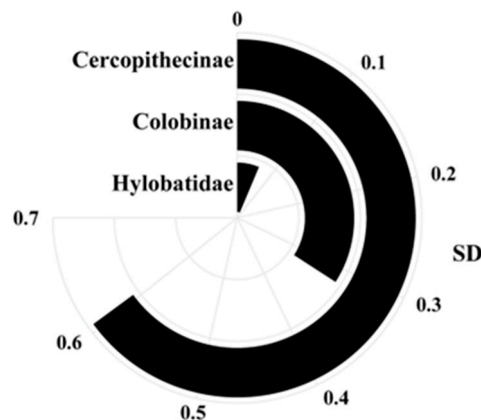


Figure 4. Sexual dimorphism ($SD = 1 - \text{Female/Male}$) of mandibular canines in Cercopithecinae, Colobinae, and Hylobatidae.

4. Discussion

Dental morphology, combined with the osteo-muscular morphology of the skull and mandible, strongly correlates with body size [42] and is tightly linked to food items' selection, acquisition, and process. Therefore, it provides insightful and diverse information on the dietary ecology of organisms and, ultimately, on the climate, geography, and environment where they dwell. Moreover, teeth are the most available fossil elements frequently used to explore evolutionary patterns, phylogenetic relationships, and dietary diversity selection. In this study, we used basic metrics (tooth length and width) to analyze the dental variation in African and Asian Cercopithecinae concerning the divergent evolutionary patterns and environmental changes specific to each continent to determine whether Colobinae exhibit more significant dental variation compared to Cercopithecinae and to identify

whether there is a significant post-canine dental size variation between Cercopithecinae and Colobinae.

4.1. Evolutionary and Phylogenetic Diversity

Regarding dental morphology, the two studied primate catarrhine families appeared well separated. Our analyses showed that mandibular canines (LCs), premolars (LP3 and LP4), and maxillary molars (UM2 and UM3) are responsible for the differences between Cercopithecidae and Hylobatidae (Figure 1, Table 1). Fossil evidence indicates that hominoids (Hylobatidae + Hominidae) and Cercopithecoids (Victoriapithecidae + Cercopithecidae) most likely diverged around 23.0 mya in the Early Miocene [43]. During this differentiation, there was an evolutionary reduction in prognathism and tooth size, with gibbons exhibiting smaller teeth relative to body size, especially the mandibular canines, and very low canine sexual dimorphism (Figure 4), most likely related to their monogamous mating system [44,45]. These differences may reflect maxillary, mandibular, and dental morphological selections that can trace the divergent evolutionary histories of the two groups, which have adopted distinct behavioral and ecological selections in Africa and Asia.

Even though Cercopithecidae appeared relatively homogeneous compared to Hylobatidae, our within-family analysis demonstrated two exciting findings. First, there was a clear distinction between the two subfamilies, Colobinae and Cercopithecinae (Figure 2, DF1), most likely reflecting evolutionary and phylogenetic disparities between the two groups. Secondly, we identified geographic separation (Africa vs. Asia) within each subfamily (Figure 2, DF2), probably related to the climatic, vegetational, and environmental differences and diversities between the two continents during the Neogene and Quaternary. The evolutionary history of Asian and African cercopithecids, after their divergence during the Neogene, has been significantly influenced by climatic and geographic diversity [46,47], followed by remarkable environmental shifts during their dispersal from Africa to Asia [1,25,26].

As addressed above, the ancestors of Asian cercopithecids left Africa and moved eastwards via Europe following the collision of the Afro-Arabian plate with Eurasia during the early Miocene (23.8–18 mya). These events allowed different groups of cercopithecids to disperse towards Asia in various periods. Colobinae most likely migrated first in the Middle Miocene, around 10.9 mya (9.6–12.3) [43], whereas *Macaca* probably migrated much later in the Late Miocene (7.0–6.7 mya) [26]. Ultimately, they reached a Convergence–Divergence Center (CDC) linking South, East, and Southeast Asia at the southeast corner of the Qinghai–Tibet Plateau and Hengduan Mountains during the Miocene–Pliocene [1]. Colobinae spread and diverged in South, East, and Southeast Asia [48]. On the other hand, the cercopithecine genus *Macaca* (except *M. sylvanus* in North Africa) was widely spread in East and South Asia through alternative dispersal paths [1,49].

Subsequently, environmental and climatic changes in Africa and Asia during the Pliocene and Quaternary further shaped the divergent evolution of these groups. Over the last 3 mya, East Africa has experienced a long-term drying trend related to the formation of the East African Rift Valley [50]. Throughout the Pliocene and later during the Pleistocene, tectonic changes and glaciation in the northern hemisphere increased climate variability, reduced the rainfall, and caused shifts from woodlands to grasslands and even more open areas [51,52], leading to the formation of modern African environments [53]. Consequently, about 90% of Africa has a tropical climate with higher temperatures than the other continents, characterized by high seasonal and diurnal temperature variation and wet seasons [54].

In Asia, changes were more drastic. The collision between the Indian and the Eurasian plates generated the accelerated uplift of the Qinghai–Tibet Plateau (with an average altitude of 4500 m), linking it to the Himalayas and the Hengduan Mountains [55–57], profoundly influencing Asian climate and environmental and biodiversity evolution [58–61]. These changes were especially evident in areas such as South, East, and Southeast Asia, where the ancestors of extant Asian Cercopithecids dispersed and radiated [11,26,62].

In South Asia, the environment of the Indian subcontinent experienced a shift from forests and shrubs to grasslands during the Miocene and Pliocene [63–65] with intense monsoonal rains, especially during the Early and Middle Pleistocene [66]. Its position is pivotal for animal migrations and the only path for Asian macaques and humans toward East and Southeast Asia [11,26,67].

During the Quaternary, in East Asia, the environmental and geographic diversity was higher than in other continents, providing suitable ecological and environmental conditions for the dispersal of Cercopithecids [4]. The eastern coastal plains were humid, with moist tropical and subtropical forests covering southern regions and deserts with meadows and alpine and subalpine woodland habitats [61,68]. That created a tremendous convergence–divergence faunal and floral center [1,69]. Finally, Southeast Asia was dominated by a mix of savanna, open woodlands, and evergreen forests throughout the Pleistocene. These conditions were ideal for early hominin and nonhuman primate survival [70]. Moreover, during the Last Glacial Period (LGP; 125–10 kya) and particularly in the Last Glacial Maximum (LGM; 23–19 kya), a north–south savanna land bridge connecting the Malaysian Peninsula to the major Indonesian islands established shelter for “rain forest” refugia [71,72]. These were most likely nurtured by the double monsoon system, southwest between May and August, transforming moisture from the Indian Ocean, and northeast between September and April, conveying water from the South China Sea [15].

Considering the geological, climatic, and environmental differences between the two continents, it is unsurprising that both Cercopithecinae and Colobinae exhibit the observed intrinsic dental diversity between African and Asian representatives. These differences are also evident in their similarly high Euclidean Distances (Figure 2), even though the divergence time of the Colobinae is much older than that of the Cercopithecinae [11,26,43]. This may be related to the broader past and present Asian distribution of the cercopithecine genus *Macaca* (Figure 5), currently found in 20 Asian countries, covering more than 5×10^6 km² in primary, secondary, deciduous, coniferous, riverine, and mangrove forests [73] and displaying a significant phylogenetic diversity [49].

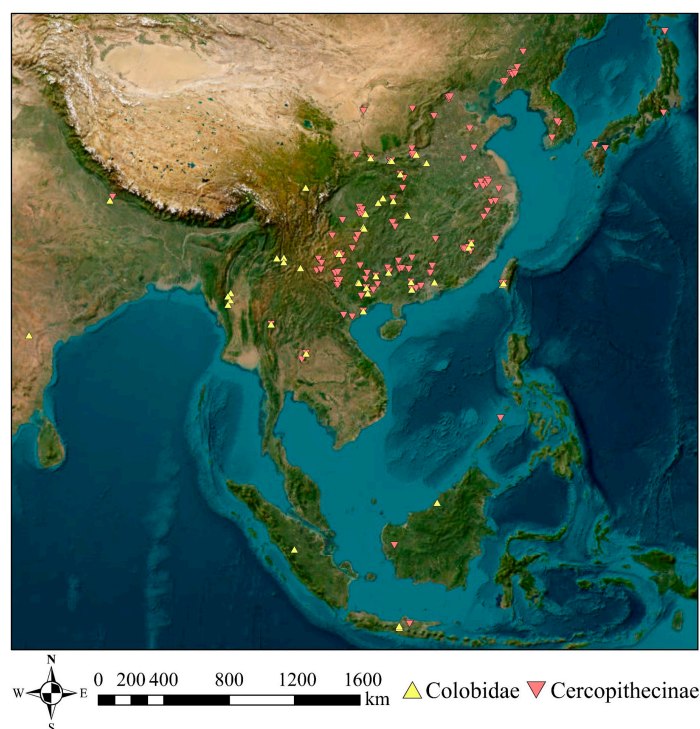


Figure 5. Fossil distribution of Colobinae and Cercopithecinae in Asia [3,7,8,11,74–100].

4.2. Dental Structure and Dietary Selection

Our multivariate analyses showed that the separation between Colobinae and Cercopithecinae (Figure 2) was mainly due to the contribution of several dental variables, such as UM1 (0.84), LP3 (0.75), LM1 (−0.82), and UP4 (−0.70) along DF1, as well as LM3 (0.72), UM1 (0.61), UM2 (−1.14), and LP4 (−0.68) along DF2. These variables represent the size of the post-canine teeth, premolars, and molars, suggesting that Colobinae have larger premolars and molars than Cercopithecinae. This difference may be related to the overall folivorous diet of Colobinae. Compared to frugivorous and insectivorous primates, folivorous monkeys have larger premolars. This increase may result from premolar molarization [101] or accommodate considerable loading while taking leaves and biting stiff leaf fibers during mastication [102]. This post-canine morphology is closely related to this dietary specialization. As leaves have low nutritional quality, folivorous primates must ingest large quantities to meet their metabolic demands [e.g., [103]], implying the frequent use of premolars and molars to leverage food loading, leading to repetitive crushing, chewing, and grinding [104]. On the other hand, Cercopithecinae are mainly frugivorous [105–107] or omnivorous with a flexible dietary strategy [108]. They tend to display great ecological flexibility and adjust their diet, group size, habitat use, and home range size according to environmental shifts [109].

Additionally, our residual analysis of molars (Figure 3) showed that Colobinae have larger molars, as suggested by previous studies [20–23], when compared to Asian Cercopithecinae, but not when compared to African Cercopithecinae. The latter possess massive molars, most likely linked to their more pronounced and prognathic facial structure, particularly in *Mandrillus* and *Papio*. This observation aligns with previous studies [23], indicating a derived phylogenetic trait. Thus, the hypothesis regarding post-canine tooth differentiation seems applicable between Colobinae and Asian Cercopithecinae but not their African counterparts, primarily known for consuming fruits and seeds [110,111]. Plio-Pleistocene papionin fossil evidence, particularly for *Papio* and *Theropithecus*, suggests that their diet closely resembled that of contemporary species, mainly comprising the herbaceous layer and mostly monocotyledons [112]. Thus, the well-developed post-canine molars in African Cercopithecinae may be advantageous for accommodating hard-object foods and may be linked to evolutionary and phylogenetic factors.

Finally, another interesting finding of this study is the lack of significant dental variation between African and Asian Colobinae (Figure 2; DF1), exhibiting very similar post-canine molar size (Figure 4). This contrasts with results from studies based on absolute dental size [24]. These findings imply that, despite the significant diversity in dietary habits among African and Asian Colobinae related to different environmental adaptations [113–115], they display very similar molar patterns relative to body size, supporting their classification as folivorous primates [103,116–118].

5. Conclusions

Based on an extensive morphometric database and references, the present study explored the variations in size-adjusted dental diversity between Hylobatidae and Cercopithecidae and between African and Asian Colobinae and Cercopithecinae. The findings primarily highlight differences associated with evolutionary history, phylogeny, geographic separation, and environmental adaptation. Notably, although Colobinae split earlier than Cercopithecinae, they exhibit less diversity variation. This is likely due to their more restrained geographic distribution and less varied environments. The previously suggested hypothesis that folivorous primates show more prominent post-canine teeth appears valid only when comparing Colobinae to Asian Cercopithecinae. In contrast, African Cercopithecinae, such as *Mandrillus* and *Papio*, exhibit significantly larger post-canine teeth than the other Cercopithecidae, probably linked to their more pronounced and prognathic facial structure. Cercopithecinae are also characterized by a high degree of canine sexual dimorphism, implying different physiological, ecological, and behavioral adaptations between sexes within the same social systems [119,120]. Thus, further studies on dental variation

and its relationship with body size across sexes are needed to better understand their evolutionary and adaptive interplay [121–123]. Additionally, further studies on the differences in facial and cranial structure between Cercopithecinae and Colobinae, as well as the continental groups within each subfamily, are vital for clarifying the patterns of post-canine differentiation observed in this study.

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