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MANDIBULAR MORPHOLOGICAL VARIATION IN HOMO GEORGICUS FROM DMANISI: IMPLICATIONS FOR EARLY HOMO EVOLUTION

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რუსუდან ვადაჭკორია, დიპაიონ ბჰატაჩარჯი

დმანისელი Homo Georgicus-ის ქვედა ყბის მორფოლოგიური ვარიაცია: ადრეული Homo-ს ევოლუციის შედეგები

საბუნებისმეტყველო მეცნიერებათა და ჯანდაცვის ფაკულტეტი,
ბათუმის შოთა რუსთაველის სახელმწიფო უნივერსიტეტი, საქართველო

რეზიუმე

წარდგენილი მიმოხილვითი სტატია განიხილავს საქართველოს დმანისის ტერიტორიაზე აღმოჩენილი ადრეული პლეიოსტოცენის პერიოდის Homo Georgicus-ის ქვედა ყბის ძვლის (ლათ. *mandibula*) ნაშთების სპეციფიურ მახასიათებლებს. დმანისის ქვედა ყბის ნაშთები წარმოადგენს დროითა და გეოგრაფიულად შეზღუდულ ნიმუშს, რომელიც უნიკალურ შესაძლებლობას იძლევა ადრეული Homo-ს წარმომადგენლების მორფოლოგიური ცვალებადობის შესაფასებლად. ქვედა ყბის სხეულის ზომების შედარებითი მორფომეტრიული ანალიზის გზით, შეფასებულია დმანისში აღმოჩენილი ნამარხი ძვლების ზომისა და ფორმის ცვალებადობა თანამედროვე ჰომინოიდებთან და სხვა ნამარხ ჰომინიდებთან შედარებით. მორფოანატომიური შედარებითი ანალიზის შედეგები აჩვენებს, რომ დმანისში აღმოჩენილი ქვედა ყბების ძვალს ახასიათებს მნიშვნელოვნად უფრო დიდი ზომა ვიდრე თანამედროვე ადამიანებში დაფიქსირებული და ქვედა ყბის სხეულის ფორმის ცვალებადობა, ვიდრე დიდი მაიმუნების ნებისმიერ არსებულ სახეობაში. აღმოჩენილ ნიმუშებს გააჩნია საერთო დიაგნოსტიკური მახასიათებლები, მათ შორის გამოკვეთილი ქვედა ყბის ტორუსი (*torus mandibularis)*, წინ გამოწეული მარგინალური ბორცვაკი (*tuberculum marginale anterius*), მენთალური ხვრელის (*foramina mentale*) თანმიმდევრული პოზიციონირება და კბილის რკალის დამახასიათებელი ფორმა. ეს სპეციფიკა ხელს უწყობს ადრეული Homo-ს მრავალფეროვნების გაგებას და მიუთითებს Homo-ს ადრეულ წარმომადგენლებში სქესობრივი დიმორფიზმის შესახებ ვარაუდების გადახედვის აუცილებლობაზე. ხაზსგასმით აღინიშნება დმანისის ნიმუშში ქვედა ყბის ვარიაციის ტაქსონომიური მნიშვნელობა და მისი გავლენა ჰომინიდების ევოლუციასა და აფრიკის მიღმა გავრცელებაზე. ყბის ძვლების თანმიმდევრული ევოლუციური ცვლილებების შესწავლა და ანალიზი აქტუალურია არა მხოლოდ ანთროპოლოგიის სფეროში, არამედ თანამედროვე სტომატოლოგიაშიც, რაც განპირობებულია ყბის ძვლის მნიშვნელოვანი მორფო-ანატომიური ცვლილებებით ძალიან მცირე ევოლუციური პერიოდის განმავლობაში.

Introduction

The discovery of hominin fossils at Dmanisi, Republic of Georgia, has revolutionized our understanding of early Homo evolution and the first dispersals of hominins beyond Africa. Dated to approximately 1.8 million years ago, the Dmanisi site represents one of the earliest securely dated hominin occupations outside the African continent. Among the skeletal elements recovered, the mandibular remains have attracted particular scientific interest due to their remarkable state of preservation and the unusual combination of primitive and derived features they display [4].

The Dmanisi Hominin sample includes four mandibular specimens that exhibit considerable morphological variation. These specimens are of exceptional significance, as they include one of the smallest Lower Pleistocene mandibles assigned to Homo, one of the largest, and the earliest known *edentulous hominin mandible*. The taxonomic status of these specimens has been the subject of ongoing debate, with some researchers arguing that the degree of variation exceeds that expected within a single species, while others contend that the variation represents intraspecific diversity [4].

The mandible, as the largest and strongest bone of the facial skeleton, plays a crucial role in mastication and serves as a receptacle for the lower dentition [6]. Its morphological characteristics have long been recognized as valuable indicators of taxonomic affiliation and evolutionary relationships in Hominin paleontology. The mandibular corpus, in particular, exhibits feature that can be quantitatively assessed and compared across different Hominin taxa.

This research aims to conduct a comprehensive comparative analysis of the mandibular features of Homo Georgicus, with specific focus on corpus dimensions, shape variations, and distinctive morphological traits. By comparing these features to those of extant hominoids and other fossil Hominins, we seek to evaluate the taxonomic significance of mandibular variation within the Dmanisi sample and its implications for understanding early Homo diversity. The objectives include: (1) documenting the distinctive *mandibular* features of *Homo Georgicus;* (2) quantifying the degree of variation within the Dmanisi sample; (3) comparing this variation to that observed in extant hominoids and other fossil *Hominins*; and (4) assessing the taxonomic and evolutionary implications of these findings.

Mandibular Anatomy and Variation in Modern Humans

General Mandibular Structure

The mandible consists of a horizontal body anteriorly and two *vertical rami* posterolaterally, which meet at the angle of the mandible. The mandibular body is curved in a horseshoe shape and features two main borders: the superior alveolar border containing sockets for the lower teeth, and the inferior base which serves as an attachment site for the digastric muscle. The *mandibular symphysis*, a small ridge of bone marking the midline fusion of the two halves during development, encloses the *mental protuberance* that forms the chin. Each *mandibular ramus* projects upward from the angle of the mandible and contains several important bony landmarks, including the head (which articulates with the temporal bone forming the temporomandibular joint), the neck (supporting the head and serving as an attachment site for the lateral pterygoid muscle), and the coronoid process (the attachment site for the temporalis muscle). The internal surface of each ramus features the mandibular foramen, which serves as a passageway for neurovascular structures [6].

Variation in Modern Human Populations

Studies of mandibular variation in modern human populations reveal substantial differences in dimensions and morphological features across geographical regions and chronological periods [4]. Research comparing modern and medieval mandibles has demonstrated significant differences in several parameters related to the mandibular canal position [4]. These findings suggest that mandibular morphology is influenced by both geographical and temporal factors, reflecting evolutionary changes and adaptations to different dietary patterns and environmental conditions. to different dietary patterns and environmental conditions.

Distinctive Mandibular Features of Homo Georgicus

Morphometric Characteristics

The Dmanisi mandibular sample exhibits remarkable variation in size and shape. Researchers have employed various measurements to quantify this variation, including height and breadth measurements of the mandibular corpus at the first molar and the symphysis. Shape analysis has been conducted using size-adjusted versions of these variables, typically employing a geometric mean to standardize the measurements [5]. Comparative analyses have revealed that the pattern of mandibular variation in the Dmanisi hominins differs significantly from that observed in any living species. The

Dmanisi specimens show significantly more size variation when compared to modern humans and exhibit greater corpus shape variation and size variation in corpus heights and overall mandible size than any extant ape species [5]. This exceptional degree of variation has important implications for understanding the evolutionary history and taxonomic status of early *Homo*.

Distinctive Morphological Traits

Beyond metric variations, the Dmanisi mandibles share several distinctive morphological traits that differentiate them from other hominin taxa. These include a characteristic torus mandibularis, which appears as a slight to moderate swelling on the lingual surface of the lateral corpus adjacent to the fourth premolar. While this feature is most prominently expressed on the specimen designated D2735, it is visibly and palpably present on all of the Dmanisi mandibles [4].

Another distinctive feature is the tuberculum marginale anterius, particularly in specimens D211 and D2600, which exists as an anteriorly projecting phalange inferior to the canine along the basal margin. Although this feature is present in many early Homo mandibles, only in these two Dmanisi specimens does it exhibit such an extreme anterior orientation, creating the impression of a groove along its medial edge [4].

The Dmanisi mandibles also share consistent patterns in the position and configuration of the foramina mentale, as well as in the orientation and shape of the foramen mandibulare. Additionally, they exhibit a distinctive dental arcade shape that appears to be characteristic of the Dmanisi sample [4].

Comparative Analysis

Comparison with Extant Hominoids

Comparisons between the Dmanisi mandibles and those of extant hominoids have been conducted at both the specific and subspecific taxonomic levels. These comparisons have typically involved calculating the ratio of measurements between specimens D2600 and D211 (representing the extremes of variation within the Dmanisi sample) and comparing this to ratios calculated for all possible pairs of individuals within each comparative taxon. Similarly, shape variation has been assessed using the average Euclidean distance (AED) between D2600 and D211 relative to the distribution of AEDs within comparative taxa [5].

The results of these analyses consistently indicate that the Dmanisi mandibles exhibit greater size and shape variation than would be expected if they represented a single species comparable to any extant hominoid taxon [5]. These finding challenges conventional expectations regarding levels of intraspecific variation in early Homo and raises important questions about the taxonomic unity of the Dmanisi sample.

Comparison with Other Fossil Hominins

Comparisons with other fossil *hominins* have yielded more complex results, partly due to the different taxonomic hypotheses that have been applied to the *hominin* fossil record. When compared to fossil hominins, the Dmanisi specimens appear more dimorphic in size, although this result is influenced by the taxonomic framework adopted for the analysis [5].

The distinctive combination of primitive and derived features in the Dmanisi mandibles has made them difficult to classify within existing taxonomic schemes. Some researchers have suggested that they represent an early form of Homo Erectus, while others have proposed that they constitute a separate species, Homo Georgicus. Still others have argued that they represent an early form of Homo Habilis that dispersed out of Africa [4].

Implications for Taxonomy and Human Evolution

Taxonomic Considerations

The exceptional degree of mandibular variation observed in the Dmanisi sample has significant implications for hominin taxonomy. If all specimens are considered to represent a single species, as many researchers have argued, then this suggests that early Homo taxa exhibited levels of intraspecific variation far exceeding those observed in extant hominoids [4]. This would necessitate a reevaluation of the criteria used to distinguish between hominin species based on morphological differences.

Alternatively, if the variation is interpreted as evidence for multiple species at Dmanisi, this would have profound implications for understanding the pattern of *hominin* dispersals out of Africa. It would suggest that multiple Homo lineages coexisted at this early date and successfully expanded their range beyond the African continent [4].

Evolutionary Implications

The Dmanisi mandibular remains provide important insights into the early evolution of the genus Homo. Their combination of primitive and derived features suggests a transitional position in Hominin evolution, potentially representing an early stage in the emergence of the Homo Erectus lineage [4]. The significant size dimorphism observed in the Dmanisi sample may reflect evolutionary processes operating at this critical juncture in human evolution. Some researchers have suggested that the pronounced variation could be indicative of sexual dimorphism, with males being substantially larger than females. This would contrast with the reduced sexual dimorphism characteristic of later Homo species, including Homo Sapiens, and may reflect different social and ecological adaptations in these early Hominins.

Conclusion

This research has examined the comparative anatomical aspects of mandibular bone features in Homo Georgicus, focusing on the remarkable fossil assemblage from Dmanisi, Republic of Georgia. The analysis has revealed that the Dmanisi mandibles exhibit levels of size and shape variation exceeding those observed in any extant hominoid species, while also sharing distinctive morphological traits that set them apart from other hominin taxa.

The findings of this study highlight the need to reevaluate expectations regarding levels of sexual dimorphism and intraspecific variation in early members of the genus Homo. The unique combination of primitive and derived features in the Dmanisi mandibles provides valuable insights into the evolutionary processes operating during the early dispersal of Hominins beyond Africa.

Several limitations must be acknowledged in interpreting these results. The fossil sample from Dmanisi, while exceptionally well-preserved, is still limited in size, and additional discoveries may alter our understanding of the range of variation present at this site. Furthermore, the comparative samples used for analysis may not fully capture the range of variation that existed in past Hominin populations.

Future research should focus on expanding the comparative framework to include additional fossil specimens as they are discovered, employing advanced three-dimensional imaging techniques to capture more subtle aspects of mandibular morphology, and integrating mandibular data with evidence from other skeletal elements to develop a more comprehensive understanding of early Homo diversity and evolution.

Ethics Statement

This review was based exclusively on previously published fossil data. No new human or animal subjects were involved.

Conflict of Interest

The authors declare no conflict of interest.

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SUMMARY

This review article examines the distinctive characteristics of the mandible (Lat. *mandibula*) of Homo Georgicus specimens discovered at the Early Pleistocene site of Dmanisi, Georgia. The Dmanisi mandibular remains represent a temporally and geographically restricted sample that provides a unique opportunity to assess morphological variability in early Homo. Through comparative morphometric analysis of mandibular body dimensions, the variability in size and shape of the Dmanisi fossils is evaluated relative to modern hominoids and other fossil hominins. The results show that the Dmanisi mandibles display significantly greater size variability than that observed in modern humans and greater shape variability of the mandibular body than in any extant species of great apes. The specimens share several diagnostic features, including a prominent *torus mandibularis*, a forward-projecting *tuberculum marginale anterius*, consistent patterns of *foramina mentale* positioning, and a characteristic dental arch shape. These findings contribute to our understanding of early Homo diversity and suggest a need to reconsider assumptions about sexual dimorphism in early members of our genus. The study underscores the taxonomic significance of mandibular variation in the Dmanisi sample and its implications for Hominin evolution and dispersal beyond Africa. Additionally, examination of evolutionary changes in jaw morphology has relevance not only in anthropology but also in modern dentistry, due to significant morpho-anatomical transformations over a relatively short evolutionary timespan.

Keywords: Homo Georgicus, Mandibular Morphology, Dmanisi Hominins, Early Pleistocene