The system of species of African bipedal primates from 6.2–0.9 mya

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Abstract

In the book it is reported about establishment of a family relation system between the species of African bipedal primates observed in deposits from 6.2 to 0.9 million years ago (mya).

For this purpose, the author presents a single method of assigning diagnostic "weight" when conducting character assessment of fossilized remains and has also formulated several equations and ratios that make use of morphometric measurements and can be used to predict the crucial parameters of paleontological individuals, such as body weight, endocranial volume, and cerebral index, and identify their diet.

Having simultaneously considered all the morphometric descriptions of the bone remains of bipedal primates and, by a single method of character evaluation, having established the degree of their affinity, the author reconstructed the phyletic lines, uniting almost all diagnostically significant samples and systematized paleoanthropological material of the 6.2–0.9 mya period.

The evaluation of the phyletic-associated fossils, in compliance with the Biological Species Concept (E. Mayr), revealed the existence of only two species of bipedal primates in the African continent at the beginning of the period under consideration. Later, a new, third, species emerged, the formation of which correlated with the exponential increase in the cerebral index and the advent of the first stone tools.

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Introduction

The current stage of study of bipedal primates is characterized by increases in site geography and the age of the remains discovered in deposits, improvements in the dating of the deposits, and the development of new instrumental methods for fossil analysis.

However, despite the considerable quantity and variety of the remains found, no commonly accepted treatment exists in the scientific community of the interrelation between all bipedal primate species. The majority of the existing phyletic schemes unite only a few species, which are usually closely located geographically and in geologic time, and a comparison of these schemes shows different types of relationships in many cases.

Moreover, with the nomenclatural assignment of paleontological taxa, various scientists use characterization methods based on different species concepts and employ different diagnostic "weight" assessments of the characters, leading to the lack of a single criterion for establishing the affinity of individuals widely scattered along the paleontological time scale.

This situation inspired the author to elaborate a single method of diagnostic "weight" for character assessment that allows for determination of the degree of affinity between any pair of individuals or character bearers, as "ancestor-descendant" or "siblings."

In addition, the author has formulated several equations and ratios that make use of morphometric measurements of fossilized remains and thus enable the reconstruction of the crucial parameters of paleontological individuals, such as body weight, endocranial volume, and cerebral index, and identification of their diet.

Having considered, in a single article, all the morphometric descriptions of the bone remains of bipedal primates and having established the degree of their affinity, the author reconstructed the phyletic lines, uniting almost all diagnostically significant samples and systematized paleoanthropological material of the 6.2-0.9 mya period.

The examination of the phyletic branches of the given system, in compliance with the Biological Species Concept (Mayr 1969) for the vertical dimension of deposit systematics (VDDS), allowed for reconstruction of the previously assigned species and helped reduce the superfluity in nomenclatural division.

I. Objects

The objectives of the current research were the morphometric characteristics of the remains of African bipedal primates and early *Homo* in the deposits from 6.2–0.9 mya. The source of the material used by the author was the descriptions of the fossils, published by their founders and subsequent researchers who had referred to them as being bipedal.

Bipedal locomotion can be assessed by means of the bone remains of the femur, foot, pelvic girdle, etc., which allows one to consider this feature as taxon-determining. This character can be used to unite all species of bipedal primates under a taxon for the purpose of the present work and can designate them as "bipedal primates," thus emphasizing their locomotion and behaving as a taxon-determining character.

Twelve species, classified by different authors under the genus *Australopithecus* in one case and under a subfamily of Australopithecinae in another case, show an aggregate chronological interval of spreading from 4.2–1.2 mya (Table 1). Undoubtedly, the most common feature inherent in all these species, separating them from all other paleontological apes, is the bipedal locomotion that allows us to include these species in a shaped taxon, "bipedal primates."

Kenyanthropus platyops (Leakey et al. 2001) must be included in this taxon, as it belongs to this interval and has been referred to as a bipedal type by early researchers. Two more species—*Orrorin tugenensis* (Senut et al. 2001) and *Ardipithecus* (*ramidus*) *kadabba* (Haile-Selassie 2001)—though they belong to a more recent time of spreading, are also thought to have bipedal locomotion and must belong to this taxon.

The chronologically earliest species *Sahelanthropus tchadensis* from 7.0–6.0 mya (Brunet et al. 2002) should also be noted, as it was regarded as a bipedal primate by some scientists. However, the craniodental description contains a mixture of characters, reflecting both arboreal and terrestrial diet and suggesting that this individual probably represents some primate population just shifting from arboreality to bipedal locomotion. We consider it more relevant to study this individual in another context.

Besides the above-mentioned species belonging to the "bipedal primates" taxon during the interval 2.8–1.2 mya, six species of the genus *Homo* can also be considered: *Homo* sp. indet. from Ledi-Geraru (Villmoare et al. 2015), *Homo rudolfensis* (Leakey 1973), *Homo habilis* (Leakey et al. 1964), *Homo* (*Pithecanthropus*) *erectus* (Dubois 1894), *Homo ergaster*

(Groves and Mazak 1975), and *Homo naledi* (Berger et al. 2015). Taking into consideration the absence of a morphometric criterion characteristic of postcranial remains of bipedal primates and differing from the early *Homo* species and the necessity of establishing possible phyletic relations, we included the fossils of these species in the taxon.

Having arranged, in chronological order, the 15 species of bipedal primates and the 6 species of early *Homo* from the aggregate interval 6.2–0.9 mya (Table 1), we formed a “bipedal primates” taxon, the characters of whose individuals were the subject of the present study.

Table 1. – The list of original species included in the “bipedal primates” taxon

No.	Original species	Time (in mya)
1	*Orrorin tugenensis*	6.2–5.65
2	*Ardipithecus (ramidus) kadabba*	5.8–5.2
3	*Australopithecus (Ardipithecus) ramidus*	4.4
4	*Australopithecus anamensis*	4.2–3.9
5	*Australopithecus afarensis*	3.9–2.96
6	*Australopithecus* sp. indet. from Woranso-Mille	3.8–3.4
7	*Australopithecus deyiremeda*	3.5–3.3
8	*Kenyanthropus platyops*	3.5–3.2
9	*Australopithecus bahrelghazali*	3.4–3.0
10	*Australopithecus africanus*	3.3–2.3
11	*Homo* sp. indet. from Ledi-Geraru	2.8–2.75
12	*Australopithecus garhi*	2.5
13	*Australopithecus aethiopicus*	2.7–2.39
14	*Australopithecus sediba*	1.977
15	*Homo rudolfensis*	2.4–1.8
16	*Homo habilis*	2.3–1.5
17	*Australopithecus boisei*	2.3–1.2
18	*Australopithecus robustus*	2.0–1.5
19	*Homo erectus*	1.9–0.3
20	*Homo ergaster*	1.8–1.2
21	*Homo naledi*	>1.34

II. Methods

The research was conducted with a consequent chronological treatment of the study descriptions of the bone remains in terms of distinguishing characters with maximum diagnostic value, based on the method employing the reproductive differentiation of characters and by establishing the mutual relationship between their bearers.

Reproductive differentiation of characters method

The method involving the reproductive differentiation of characters should be elaborated owing to the need for objective, quantitative methods rather than empirical methods of diagnostic weight assessment.

It should be noted that different characters, inherent to zoological objects, have different times of emergence among their ancestors. This is why the basis of this method is a quantitative evaluation of the particular characters of the individual under study, which may be called "the weight" of the character and which is determined by the duration of the time interval during which the given character was registered in the paleontological record, i.e., it was reproduced by the ancestors.

It should also be noted that the reproduction of the character implies the reproduction of the individuals—the character bearers.

The consequence of these individuals reproducing a separated character is an allochronic taxon, the members of which show a vertical dimension in the deposits, a direct "ancestor-descendent" relationship, through that character. Consequently, the members spread across the time scale of this taxon represent a phyletic line, as they have the taxon-determining character.

The comparison of the phyletic lines of all significant characters of the individual under study, at the paleontological time scale, would reflect all the possible changes in the ancestor and would allow us to draw a conclusion about the level of its affinity with the other contemporary individuals.

The diagnostics of the species for the VDDS

As the definition of species suggested by different species concepts have significant differences, for further research we considered the Biological Species Concept and its relevant species definition—the members of the species level taxa must form a reproductive community, an ecological unit, and a genetic unit (Mayr 1969: 26).

However, this definition, stressing on the populational nature of the species and used for the horizontal dimension of systematics, needs improvement with respect to allochronic paleontological taxon.

We could suggest, within the frames of the current article, a species definition for the VDDS: the species is an allochronic taxon, the members of which are viewed for some time period, at each moment of which their characters meet the requirements of the Biological Species Concept for the horizontal dimension of systematics.

Besides, assuming that separate paleontological individuals were relevant representatives of the then existing population, we redefined the requirements of the species level population for the horizontal dimension of systematics under the species character triad of the VDDS for an allochronic taxon:

– A reproductive community becomes obvious as a sympatric coexistence of the taxon members with closely related species.

– An ecological unit represents a specific trophic basis for the taxon members.

– It is impossible to acquire genetic data of paleontological individuals; therefore, following the statement that the gene pool of the population is seen in the morphology of its individuals, we indirectly considered a gene pool of an allochronic taxon according to the changes in the morphometric characters of its members through time. In this case, the channel type of reproduction of the characters during some time period would prove that allochronic taxon during this interval represents a self-reproducing genetic unit.

Note that if an allochronic taxon meets the requirements of the species character for the VDDS triad at any time interval, then the requirements of the species for the horizontal dimension of systematics would be met during that time interval, which would allow us to identify this taxon as the nomenclatural category — species, according to the International Code of Zoological Nomenclature (ICZN 1999).

Besides, we would have an objective chance to establish the emergence and extinction of the species.

III. Preliminary trophic taxonomy

Among all the characters of the remains described in the study on bipedal primates, two morphological complexes of the skull were observed throughout the period assessed, 6.2–0.9 mya, and thus, have the greatest diagnostic weight.

In the study of dentition and skull structures, Robinson (1954) was among the first to distinguish the two types of craniodental architectures, and linking them to the diet, he divided all bipedal primates into two groups of species: *Paranthropus* and *Australopithecus*. Being the trophic basis of the ecological niche, the diet is one of the main taxonomic properties for establishing population monophylia (Mayr and Ashlock 1991: 26) and is one of the species character in the character triad of the VDDS.

Among *Paranthropus*, the bony sagittal crest used for the attachment of powerful temporal muscles, robust mandible, and extraordinarily swollen cheek teeth with a thick enamel cap of up to 3 mm thickness proved that crushing and grinding were the main functions of their craniodental architecture. Naming such a structure of the skull as "robust", Robinson (1954) proposed that the most relevant diet of this species primarily consisted of plants, including shoots, leaves, berries, tough wild fruits, roots, and bulbs.

More slender and remarkably small in size, the skull of *Australopithecus*, with larger incisors and canines and smaller cheek teeth, compared to those of *Paranthropus*, showed the structure named as "gracile", implying an omnivorous diet, including a significant proportion of meat (Robinson 1954).

The convincing arguments for such a diet division were suggested by Zubov (1986) after studying the dentition structure of the bipedal primates.

However, considering the plant-based diet of the primates, we should be able to distinguish between its two types—arboreal diet consisting of leaves, fresh shoots, and fruits for arboreal primates and terrestrial amulum-full diet consisting of cereal grains, roots, bulbs of field herbs, and coastal plants (radicophagous diet) for bipedal primates.

The dentition system designed for the arboreal diet of arboreal species is well-represented by the dentition of the gorillas, with long canines for piercing and cleavage, molars with labial projections for cutting materials that are too long, and pestle and mortar type cusps for grinding.

The radicophagous amulum-full diet of the bipedal primates corresponds to the craniodental architecture of *Paranthropus* (Robinson 1954), with a robust skull structure and thick mandible: canines and incisors exclusively worn and adjusted to strip plant parts, such as seeds, roots, and rhizomes (Ryan and Johanson 1989) and molars having buccolingual megadontia with a plain occlusion surface used as millstone for grinding food. A significant molar enamel thickness is regarded as an adaptation to abrasion caused by grinding sand- or soil-polluted food (Teaford and Ungar 2000).

Dentition of the omnivorous bipedal *Australopithecus* (Robinson 1954) is dramatically different from the radicophagous *Paranthropus*. To make meat ready for digestion it is first necessary to cut an appropriate piece of it by piercing the flesh integument with the protruding canines and then cutting a portion of it with the scissor-like action of the upper and low incisors (Lucas and Peters 2000). After this, the flesh piece is ground using the postcanine teeth, whose occlusion area is significantly smaller with sharper cusps than that of the radicophagous teeth. Besides, one can see the lingual wear of the upper canines and labial wear of the lower canines.

Studying the diet features of the primates on the basis of the microwear of their teeth, Kaiser and Wolff (2005) classified the herbivorous dentition of the arboreal and terrestrial primates as extreme parameters, with the omnivorous primate dentition as an intermediate parameter. This division allows for amulum-containing terrestrial diet for radicophagous bipedal primates.

Comparing the radicophagous and omnivorous craniodental complexes of bipedal primates, we found their cardinal difference up to the dichotomy level, for instance, radicophagous dentition fails to process solid elastic flesh food (Lucas and Peters 2000).

The craniodental features of the bipedal individuals were observed throughout the time period under study, i.e., they have the highest index of the reproduction weight and demonstrate diagnostic dichotomy of feeding habit. Based on these features, we distinguished two taxa, radicophagous and omnivorous, at a lower level within the bipedal primates taxon, with their names reflecting the specific taxon-determining character and diet specialization of their members.

The revision of the bone remain characters of individuals of the bipedal primates taxon was required to establish morphometric characters indicating the diet type of the individuals, for their separation into newly assigned trophic taxa, and to establish characters accompanying the diet type and clarifying their reproduction weight.

Note that morphometric dichotomy of the diet complexes slightly simplifies the diagnostic practice, as it enables us to apply the alternative exclusion method when identifying the fossils.