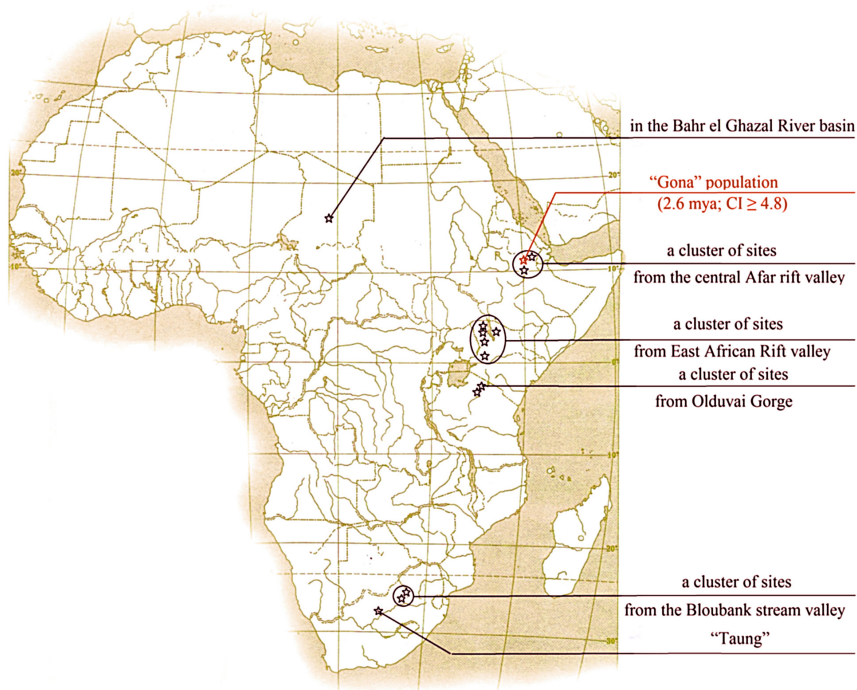


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The system of species of African bipedal primates from 6.2–0.9 mya



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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	<i>Orrorin tugenensis</i>	6.2–5.65
2	<i>Ardipithecus (ramidus) kadabba</i>	5.8–5.2
3	<i>Australopithecus (Ardipithecus) ramidus</i>	4.4
4	<i>Australopithecus anamensis</i>	4.2–3.9
5	<i>Australopithecus afarensis</i>	3.9–2.96
6	<i>Australopithecus</i> sp. indet. from Woranso-Mille	3.8–3.4
7	<i>Australopithecus deyiremeda</i>	3.5–3.3
8	<i>Kenyanthropus platyops</i>	3.5–3.2
9	<i>Australopithecus bahrelghazali</i>	3.4–3.0
10	<i>Australopithecus africanus</i>	3.3–2.3
11	<i>Homo</i> sp. indet. from Ledi-Geraru	2.8–2.75
12	<i>Australopithecus garhi</i>	2.5
13	<i>Australopithecus aethiopicus</i>	2.7–2.39
14	<i>Australopithecus sediba</i>	1.977
15	<i>Homo rudolfensis</i>	2.4–1.8
16	<i>Homo habilis</i>	2.3–1.5
17	<i>Australopithecus boisei</i>	2.3–1.2
18	<i>Australopithecus robustus</i>	2.0–1.5
19	<i>Homo erectus</i>	1.9–0.3
20	<i>Homo ergaster</i>	1.8–1.2
21	<i>Homo naledi</i>	>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 lower 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 amulium-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.

IV. Revision of the characters of the bipedal primate remains

4.1. *Orrorin tugenensis*

The specimen BAR 1002'00 (left femur) of *O. tugenensis* species (Senut et al. 2001) from 6.2–5.65 mya layers demonstrates the earliest time of bipedal locomotion of the primates in the African continent. Lingually inclined, wear facet, upper central incisors (BAR 1001'00) and the sharp tip of the upper right canine (BAR 1425'00) from this set of fossils also prove omnivorous specialization, which enabled us to include these samples in the omnivorous taxon.

It should be noted that the mesiodistal (MD) diameter of the upper right incisor I¹ (BAR 1001'00) is more than its labiolingual (LL) diameter, and the relation MD/LL amounts to $10\text{MD}/8.7\text{LL} = 1.15$ (Senut et al. 2001: Table II). Therefore, we added the characteristic $\text{MD}/\text{LL} > 1.1$ to the characters of the incisors of the remains, to identify them under the omnivorous taxon.

The head size of the left femur BAR 1002'00 is 31.9 mm, based on which the body weight of the individual *O. tugenensis* was calculated to 30.4–30.6 kg (Nakatsukasa et al. 2007: Table 3). According to our calculations, which we will offer later, the weight of the individual approximated 33.3 kg.

4.2. *Ardipithecus (ramidus) kadabba*

For *Ar. ramidus kadabba*, lately renamed as *Ar. kadabba*, a set of 17 fossil samples from 5.8–5.2 mya layers were discovered from sites in the Western margin of the Middle Awash, Ethiopia.

The humeral midshaft ALA-VP-2/101 was comparable to the smallest weighed individual of *A. afarensis*, weighing 26–27 kg. The corpus of right mandible of ALA-VP-2/10 with M3 molar is also comparable, in the absolute size, to the jaw of AL 288-1 individual of *A. afarensis* (Haile-Selassie 2001). Its M3 molar has MD = 13.3 mm, which is less than the MD (14.2 mm) of the M3 molar of the AL 288-1 individual (Kimbél et al. 2004). As the AL 288-1 individual has a body weight 27.6 kg (McHenry 1992a), we might conclude that the body weights of ALA-VP-2/10 and ALA-VP-2/101 individuals are approximately less than 30 kg.

In the set ALA-VP-2/10, besides the lower jaw with M3 molar, there are some other isolated teeth associated by spatial proximity. The form and

type of wear of the lower left canine Lc of this set and the canine height (CH) of more than 13.1 mm, showing protrusion through the occlusion (Haile-Selassie 2001: Table I), permitted us to identify this sample under the omnivorous taxon. The identical canine STD-VP-2/61 (5.8–5.2 mya) with CH = 14.3 mm and probably the canine ASK-VP-3/400 (5.8–5.6 mya) with CH > 15.5 mm, which protrudes above the occlusion level, might be identified under this taxon.

Unfortunately, among the studied species fossils there were no complete skeletons or related fossils that might represent both the diet and the size of the individual. Nevertheless, we might state that during the period 6.2–5.2 mya there was a phyletic line of omnivorous bipedal primates that weighed 30–33 kg.

However, in the set ALA-VP-2/10, some teeth had characters that were incompatible with the omnivorous diet type. The distal lower left incisor LI₂, with $6.3\text{MD}/8.3\text{LL} = 0.76$ (Haile-Selassie 2001), showed a character frequently designated as “MD-reduction,” which actually reflects the functional substitution of the cutting tip of the incisor on the working surface and the flatness of the occlusion. These are characteristic features of individuals with radicophagous diet. As the general increase of the crown surface is mainly due to the enlargement of the LL diameter, in the absence of a significant decrease in the MD diameter, here and further, we have used the term LL-expansion. Similarly, buccolingual expansion (BL-expansion) was observed in the postcanine teeth of radicophagous bipedal primates.

Considering that the increase of the occlusion surface reflects the adaptation to radicophagous diet, we included the incisor LI₂ of ALA-VP-2/10 set under the radicophagous taxon, and the relation MD/LL ≤ 0.76 for the incisors was considered as the accompanying character sufficient for including individuals in this taxon.

4.3. *Australopithecus (Ardipithecus) ramidus*

In the Aramis localities, Afar depression, Ethiopia, 17 fossils of *A. ramidus*, mostly teeth, from 4.4 mya were found (White et al. 1994).

The upper incisor from the ARA-VP-6/1 teeth set, with $9.6\text{MD}/7.5\text{LL} = 1.28$, lacked LL-expansion, and its height (12.5 mm) testified that the canines Rc (CH = 14.5 mm) and Lc (CH = 14.6 mm) of this set protrude above the occlusion plane. The canines from ARA-VP-6/1 and ARA-VP-1/28 and the lower premolar P₃ had very remarkable unworn tips at the occlusion plane and had thin enamel. The thickness of the buccal

enamel of the right upper canine R^C of ARA-VP-6/1 is about 1.0 mm and that of the caps of the crowns of three broken molars do not exceed 1.1–1.2 mm (White et al. 1994), which allowed us to identify these sets under the omnivorous taxon. Taking into account the fact that the crowns of the postcanine teeth of *A. ramidus* were significantly smaller than those of *A. afarensis*, which was interpreted as “species diagnostic” (White et al. 1994), and that the main comparison was conducted with the AL 228-1 species weighing 27.6 kg, we might consider that the individuals of these two sets also have body weights no more than 30 kg.

Analogically, we might include the samples ARA-VP-1/125 (left temporal) and ARA-VP-1/500 (right and left temporal and occipital) in the omnivorous taxon, because they demonstrate a size not exceeding the size of their counterpart bones of *A. afarensis* (White et al. 1994), weighing no more than 30 kg. However, there is some doubt in defining these samples as bipedal, as their founders pointed out some chimpanzee-like characters.

The height and width of the humeral head of the individual ARA-VP-7/2 (left humerus, radius, and ulna) are 36.5 mm and 34.6 mm, respectively, which are 30% more than those of AL 288-1 (*A. afarensis*) (White et al. 1994). On comparing these values with the values for the individuals whose forelimbs do not perform supporting function (McHenry 1992a: Table 4), we got the approximate individual body weight of 42 kg.

This remarkable difference between ARA-VP-7/2 body weight and the values relevant to the omnivorous taxon individuals enabled us to point out a new character—large-bodied, and correlate it with their radicophagous nature.

The partial skeleton ARA-VP-6/500 (Ardi) from 4.4 mya, with a cranial capacity of 300–350 cc, occupies a specific place among the fossils of *A. ramidus* (White et al. 2009). The fragmentation and the state of the skull and dentition prevented us from distinguishing the diet preference of the individual; however, the postcranium has many features useful for both vertical locomotion and climbing, implying that the individual spent a significant time on trees (White et al. 2009). This character mixture does not allow for identification of ARA-VP-6/500 specimen within the frameworks of the current work and demands a separate research.

4.4. *Australopithecus anamensis*

The holotype of *A. anamensis*, the mandible KNM-KP 29281 (4.17–4.12 mya), shows the wear of the front teeth in the occlusion plane, relative

and absolute enamel thickness of 1.5–2.0 mm of the molars, and robust relation between the front and cheek teeth sizes (Leakey et al. 1998) that corresponded to the radicophagous taxon. All incisors of this mandible, LI_1 , RI_1 , LI_2 , and RI_2 show LL-expansion with $MD/LL < 0.9$ (Leakey et al. 1995: Table 1b), thereby acquiring the characters necessary to include KNM-KP 29281 samples in this taxon.

The incisor I_1 of KNM-KP 34725 specimen (Leakey et al. 1998: Table 3) and some teeth of the maxilla fragments KNM-KP 29286 (Leakey et al. 1995) also showed LL-expansion, which without any other evidence gave us reasons to consider a radicophagous diet specialization.

The left maxilla ARA-VP-14/1 (4.2–4.1 mya) from the Aramis 14 site was also included in the radicophagous taxon, as it shows a high occlusal wear, including the incisor crown worn to the root and M3 to the dentine (White et al. 2006), similar to the occlusal wear observed in KNM-KP 29283.

Additionally, large sharp canines protrude from the occlusion of the samples ASI-VP-2/2 and ASI-VP-2/334 from 4.2–4.1 mya (White et al. 2006), and the blade-like morphology of the KNM-KP 47953 canine and premolars were functionally close to these canines. Moreover, formidable cusps of the molars (Manthi et al. 2012) provide evidence of the presence of individuals from the omnivorous taxon in the *A. anamensis* hypodigm.

Circumstantially, the lack of LL-expansion ($MD/LL > 1.1$) of the incisors RI^1 of KNM-ER 30202 (Leakey et al. 1995), LI^1 of KNM-KP 30498, and LI^1 of KNM-KP 35839 (Leakey et al. 1998: Table 3) proved the omnivorous nature of these specimens.

The postcrania represented by the tibia lacking diaphysis KNM-KP 29285 from 4.1 mya, with individual body weight 47–55 kg (Leakey et al. 1995), and the distal end of the left humerus KNM-KP 271 (Kanapoi Hominid 1) from 2.5 mya (Patterson and Howells 1967), individual weighing 57.9 kg (McHenry 1992a), were placed under the radicophagous taxon due to their large body weights.

4.5. *Australopithecus afarensis*

A. afarensis was represented by the largest number of fossils among all bipedal primate species, mainly from 4 sites: Laetoli (3.76–3.56 mya), Turwel (3.5 mya), Maka (3.4 mya), and Hadar (3.4–2.96 mya).

The most important specimen of *A. afarensis* was a 40% complete skeleton of AL 288-1 (Lucy) from 3.2–3.18 mya, excavated by D.C. Johanson and T. Gray in 1974. The craniodental morphology of the individual shows

its omnivorous nature (Johanson and Edey 1981). Its weight and height have been assessed to be approximately 27.6 kg and 105 cm, respectively (McHenry 1992a). The small body of this individual proved the small-bodied character of the omnivorous taxon, the diet preferences and morphotype of which have remained unchanged since 6.2 mya.

The complete form and well-preserved state of the specimen AL 288-1 allowed the author, with the help of morphometric relations of the skeleton, to create several equations for the possible reconstruction of the incomplete morphometric data of the other individual specimens.

Prediction of the body weight function based on the femoral head diameter

One of the crucial parameters of the individual, necessary for the reconstruction of its morphotype, is the body weight. Note that, due to various reasons, the modern methods fail to establish real values for the weights of paleontological individuals. Therefore, to differentiate between individuals with the same weight and to find out the tendencies of changes in weights of taxon individuals, it was necessary to make calculations based on a single method, harmonizing all results this way.

H. McHenry (1992a) suggested that the range of the predicted body weights varies from 27.6 to 80 kg, with widest coverage of species being six, as assessed by a single method from among the current methods of weight assessment based on the bony remains. Without doubting these methods and results, we approximated, for more suitable usage, the table data obtained through mathematical functions and submitted by McHenry (1992a).

Thus, considering that the area of the bone support has a precise correlation with the body weight, we chose only the femoral heads among all the bone sets, which helped us to assess the body weight, and chose only those assessments that were based on the comparison of the objects with the support they provide, especially the hind limb.

In section "8. Femhead" Table 4 (McHenry 1992a), if we compare each value of the femoral head of the fossil with an average of the three predicted body weights (for supporting hind limb), then the dependency obtained could be described by the following mathematical polynomial of the second order:

$$P_b = (FHD + 5.3)^2/41.5 \quad (1),$$

where P_b is the body weight of the individual in kg and FHD is the femoral head diameter in mm.

Assuming that the mechanical characters of the bones were same for all bipedal primates, Eq. (1) could be used to predict the body weights of the individuals of any bipedal primate species.

Accordingly, without doubting the body weight of BAR 1002'00 *O. tugenensis* predicted by Nakatsukasa et al. (2007), we calculated its body weight according to Eq. (1), using $FHD = 31.9$ mm, as $P_b = (31.9 + 5.3)^2/41.5 = 33.3$ kg.

Formula for correlation between the dimensions of the maternal pelvic girdle and the maximum possible endocranial volume (ECV) of the fetus in its mature state

Note that the passing of the fetus through the birth canal is limited by the minimal conjugate (Con_{min}) of the maternal pelvis. The biparietal breadth (BPB) of the fetus head must be 5–8% lower than the Con_{min} (Wells et al. 2012), therefore the relation: $BPB \approx 0.95Con_{min}$.

We supposed that the neonate's head had a spheroid shape and the head-size proportions of a small-bodied bipedal individual from 3.2 mya deposit were equal to the head-size proportions of the neonate of the modern human being. If we take the cranial height as 65% of BPB (Wells et al. 2012) and the correlation between occipitofrontal-size and BPB as $11.5\text{ cm}/9.5\text{ cm} = 1.21$, then the ectocranial volume of the neonate's head (V_h), according to the formula of spheroid volume, could be expressed via BPB as:

$$V_h = (4/3 \times \pi \times BPB/2 \times 0.65BPB/2 \times 1.21BPB/2) = 0.412 \times BPB^3 \text{ cc}$$

On expressing the maximal V_h (V_{hmax}) through Con_{min} of the maternal pelvic:

$$V_{hmax} = 0.412 \times (0.95Con_{min})^3 = 0.353 \times (Con_{min})^3 \text{ cc}$$

Two reconstructions of the AL 288-1 pelvic bones, made by C.O. Lovejoy and P. Schmid, clearly showed a platypelloid type of individual (sagittal diameter (sd)/transverse diameter < 1), where Con_{min} is the outlet $sd = 7.1$ mm (Berge and Goularas 2010: Table 2). Based on the above-mentioned formula, we calculated that the female individual AL 288-1 could deliver, without any damage, a neonate with $V_{hmax} = 126$ cc.

The body weight of omnivorous taxon individuals, during the interval 6.2–3.2 mya, varied from 27.6 to 33.3 kg, and a gender weight dimorphism amounted to approximately 17%, within the limits of the body weight-

gender difference observed in modern human beings. Based on these, we could apply a modern approximate norm of brain volume difference of 10% between omnivorous males and females. Thus, the female individual AL 288-1, with its ECV = 387 cc, might deliver a male neonate with $V_{hmax} = 126$ cc and a maximal ECV ($ECV_{max} = 430$ cc in the adult stage.

Designating the ratio $ECV_{max}/V_{hmax} = 430/126 = 3.41$ as “Lucy neonatal index” and incorporating the Con_{min} value, we obtained the following formula for maximal possible ECV of the adult male:

$$ECV_{max} = 3.41 \times V_{hmax} = 3.41 \times 0.353 \times (Con_{min})^3 = 1.2 \times (Con_{min})^3 \quad (2),$$

where Con_{min} was measured in cm and ECV_{max} in cc.

Cerebral index

Uniting the bipedal primates and early *Homo* under a single “bipedal primates” taxon brings in the necessity of instrumental differentiation of the bone remains. The cephalic index is mostly used for this purpose and reflects the level of hominization. It is calculated as the ratio of the brain weight to the body weight. However, the author used the ratio of the square of the brain weight to the body weight (Roginsky 1977), which is more suitable for further analysis using the quadrangle system of coordinates:

$$\text{Cephalic index} = (P_{br})^2/P_b,$$

where P_{br} is the brain weight in g and P_b is the body weight in g.

We considered that the skull bones allowed the calculation of only the cranial cavity volume, which is 8–12% larger than the brain volume, as it includes meninges, cerebral fluid, cisternae, and cranial nerves. Therefore, to evaluate the level of hominization of paleontological individuals, it was necessary to shift from the brain weight to the ECV.

For this purpose, we introduced the index ratio $K = P_{br}/ECV \approx 0.91$ g/cc.

Eventually, the formula for cephalic index calculation could be used to calculate the following cerebral index (CI):

$$CI = (0.91 \times ECV)^2/P_b \quad (3),$$

where ECV was measured in cc and P_b in g.

Thus, for the AL 288-1 individual with $P_b = 27.6$ kg (McHenry 1992a) and $ECV = 387$ cc (Holloway et al. 2004), the CI was:

$$CI = (0.91 \times 387)^2/27600 = 4.5$$

Notice that we used the ECV value suggested by R.L. Holloway in one of his works, as there are a wide range of species and fossils, the volumes of which have been predicted by a single method (Holloway et al. 2004).

Referring again to the fossils of *A. afarensis*, we considered the partial skeleton AL 438-1 from the 3.0 mya deposit at Hadar, Ethiopia (Drapeau et al. 2005), which preserved some craniofacial and postcranial remains. The height and width of the right corpus, partial right ramus of the mandible corpus, at the M1 molar level were 41.3 and 24.7 mm, respectively, the thickness of the temporal squama being 10.8 mm.

The elbow had a physiological length of 252 mm, which considerably exceeded the 206 mm of the small-bodied omnivorous AL 288-1 individual, and it was slightly less than that of the more recent large-bodied individuals of *A. boisei*, OH 36 (277 mm) and L40-19 (295 mm).

A large body and large heavily worn postcanine teeth suggested the incorporation of AL 438-1 individual into the radicophagous taxon. Although some peculiarities of the elbow bone indicated the reduced manipulation capability of its hands with respect to that of the omnivorous AL 288-1, arboreality of this individual should be excluded in this case (Drapeau et al. 2005).

Two skulls, AL 333-45 (3.76–3.56 mya) and AL 444-2 (3 mya), have ECV of 485–500 cc and 550 cc (Holloway et al. 2004) and possessed a sagittal crest for the attachment of powerful masticatory muscles. Besides, AL 444-2 has the thickest temporal squama (10.5 mm) among all bipedal primates, a long massive zygomatic arch marked by wrinkles for attachment of the masticatory muscles, and corpus of the lower jaw—the deepest and widest in the species hypodigm.

The corpus width of the mandible at P_4-M_1 level is 23 mm, slightly less than that of AL 438-1. The front and cheek teeth are heavily worn, the molar cusps being worn to the dentine (Holloway et al. 2004). The entire combination of characters undoubtedly determined a radicophagous diet of the individual. The shape of the incisors' crown and the LL-expansion ($MD/LL \leq 1.1$) of the first upper incisor ($10.5MD/9.7LL = 1.08$) and the first lower incisor ($7.1MD/7LL = 0.99$) (Kimbell et al. 2004) also supported a radicophagous specialization character.

Unfortunately, due to the absence of the postcranial remains connected to AL 444-2, its body weight could not be predicted; however, taking into consideration its largest skull size among the *A. afarensis* hypodigm, we might assume it as the heaviest individual of this hypodigm. The five largest

A. afarensis individuals are likely to weigh between 60–71 kg (McHenry 1992a). If for the specimen AL 444-2, with ECV of 550 cc, we assume the maximum average weight of 65 kg, then we could obtain $CI = 3.9$ through Eq. (3), from the area of CI values for radicophagous individuals of *A. afarensis*.

Besides, the specimen AL 444-2 showed a high degree of subnasal prognathism, which together with a sagittal crest reflected the peculiarities of craniodental architecture functioning of the radicophagous individuals. The nasoalveolar clivus (angle between nasospinale-prosthion line and occlusion plane) of AL 444-2 is 36° (Kimbel et al. 2004). The absence of this measurement for omnivorous individuals did not permit us to study the character dichotomy, but considering the omnivorous nature of *Homo sapiens*, who have orthognathic snout contour with 82° angle (Kimbel et al. 2004), we marked this value as the maximal value for omnivorous diet.

As for the other fossils from Laetoli and Hadar deposits, they represented scattered bone remains showing separate characters unable to reconstruct the morphological type of the individuals; however, they still carried information about only two taxa based on diet type. For example, the incisors of AL 200-1a and L.H.-3 were characterized by the lack of LL-expansion, and the lower canines of AL 400-1a, AL 128-23, and L.H.-3 were large, pointed, and protruded slightly above the occlusion plane (Johanson and White 1979), implying omnivorous diet type.

The mandible MAK-VP-1/12 from the Maka deposit in Ethiopia from 3.4 mya has a corpus height of 31.2 mm and width of 18.47 mm, which was comparable to the sizes of AL 288-1 (height 30.0 mm, width 17.1 mm), has large canines and incisors, and expresses molar cusps and other characters (White et al. 1993), supporting the omnivorous diet of the individual. This jaw is morphologically and metrically comparable to the jaw of L.H.-4 *A. afarensis* (White et al. 1993: Fig. 2b, c), which also belonged to the omnivorous taxon.

In the small-bodied, and consequently the omnivorous taxon, we might also include a left proximal ulna MAK-VP-1/111, which is identical to AL 288-1 in size (White et al. 1993), allowing us to predict the weight of the individual as no more than 30 kg.

Among the other fossils of this deposit, we might distinguish a rather robust left humerus MAK-VP-1/3 with midshaft cortical thickness of up

to 8 mm (medial surface) (White et al. 1993). Reno et al. (2003) measured its FHD as 37.8 mm, and applying Eq. (1) we obtained its body weight as 44.8 kg. Similarly, for MAK-VP-1/1 with FHD value of 40.3 mm, the body weight was calculated to 50.1 kg.

Having considered the remarks concerning a possible big mistake in the chain of predictions, we, however, attributed these two specimens to a large-bodied radicophagous taxon, taking into account the range of the ultimate result value.

The skull and associated partial skeleton of a 3-year-old juvenile individual DIK-1-1 were found well preserved in a layer aged 3.35–3.31 mya, excavated from the Dikika site. The upper and lower incisors do not manifest LL-expansion and the canines are pointed and protrude above the occlusion plane (Alemseged et al. 2006), providing evidence of its omnivorous nature. The majority of the characters of bipedal locomotion observed in *A. afarensis* were also evident in the lower limbs and feet of DIK-1-1, but the gorilla-like scapula and long and curved manual phalanges (Alemseged et al. 2006) arouse some doubts.

In the set of fossils from DIK-1 deposit we could mark premolar LP3 (DIK-2-lb), heavily worn to the dentine. Its BL-expansion is accompanied by the strengthening of the teeth structure by a powerful mesially disposed transverse crest connecting protoconid and metaconid (Alemseged et al. 2005), which was missing among the omnivores.

The footprints in Laetoli, Tanzania

The footprint traces of bipedal primates, referred to as *A. afarensis*, were excavated by Leakey and Hay (1979) from partially lithified volcanic ash aged 3.6 mya in Laetoli, Tanzania. These are not the only footprints found in Africa, but the rest of them belong mainly to the Late Pleistocene–Early Holocene epochs, and the most recent footprints dated 1.5 mya were found at the site FwJj14E near the village Ileret in North Kenya.

The site G near Laetoli had two paths of traces: G1 with foot length of 180 ± 10 mm and step length ~ 92 cm and G2/3 were above these traces with foot length of 210 ± 10 mm and step length ~ 95 cm. Both chains of traces showed a well-developed medial longitudinal arch, adducted big toe, and some other peculiarities in the footprints, which were substantial evidences of bipedal locomotion. Applying the ratio between the skeleton segments of a modern human being and the foot length and pace length of the individuals from Laetoli, different sources suggest their approximate stature was 115–135 cm for G1 and 135–155 cm for G2/3.

Besides, the average depth of foot impression in the ash is three-fold deeper for G2/3 than for G1 (Deloison 2006). This proves a larger pressure per unit area of the surface, suggesting that G2/3 had a more massive body structure. Even under rather conditional predictions, we might assume that the individual G2/3 was large-bodied and must be attributed to the radicophagous taxon.

The different positions of the footprints belonging to G1 should be noted with respect to the positions of the impressions belonging to G2/3. The G2/3 feet were parallel to each other and even their direction of movement was slightly inside of tiptoes, whereas the traces of G1 form 20–30° angle toward the outer line of the direction of movement.

Studying the morphology of the femur and foot of the African bipedal primates, Deloison (2006) distinguished only two walking styles among the primates of that period—waddle mode of “*Australopithèques*” (as in the case G2/3) and stepping style of “*Prehomo*” (in the case G1).

Despite its smaller height, G1 had a higher speed of walking with “plantar” steps (but not running)—0.98 (1.15) m/sec, compared to that of G2/3—0.86 (1.02) m/sec (Raichlen et al. 2008). Researching the habitat of the species, a bit after the time of existence of *A. afarensis*, scientists concluded that the small-bodied species were more mobile and occupied a larger habitat compared to the large-bodied individuals (Copeland et al. 2011).

Considering the case that the traces of the smaller individual G1 might have belonged to a young one or a large-bodied female of the radicophagous taxon, we attributed the parallel, overstepping trace impressions to the radicophagous taxon and correlated the outside-looking tiptoes with the small-bodied individual of the omnivorous taxon.

4.6. *Australopithecus* sp. indeterminate from Woranso-Mille

Interestingly, unidentified species of individuals were found in 6 sites from 3.8–3.4 mya in the Woranso-Mille region of Afar in Ethiopia, which were attributed to the genus *Australopithecus* by scholars.

The size and shape of the corpus of the left mandible MSD-VP-5/16, with M1–2 molars aged 3.8–3.7 mya from Mesgid Dora, were identical to the size of the right mandible of AL 128-23 of *A. afarensis*. The height of MSD-VP-5/16 mandible decreases from C_1 (31.3 mm) to M_2 (24.7 mm), which is even less than that of AL 288-1 (Haile-Selassie et al. 2010a), and thus, we could predict the weight of MSD-VP-5/16 within the limits of

30 kg. Gracile jaws, shape and type of molar wear, and preservation of the occlusion cusps allowed us to categorize MSD-VP-5/16 under the omnivorous taxon.

The corpus height of the left mandible MSD-VP-5/50 from 3.8–3.7 mya at the crown level of M1 is 44.7 mm, which considerably exceeded the corpus heights observed among the largest fossils of the radicophagous, large-bodied type *A. afarensis* AL 444-2 and AL 438-1. Its fixed width is 20.7 mm, which was similar to that of the small-bodied specimens, being rather explicit based on the severe postmortal damage demonstrated by the P3 tooth body profile of the mandible (Haile-Selassie 2010: Fig. 3).

The craniodental robustness, type of postcanine teeth wear (with all cusps worn out), and presumably, canines not protruding above the postcanine teeth row (Haile-Selassie 2010)—all this evidence provided grounds to include MSD-VP-5/50 in the radicophagous taxon, and we predicted the individual's body weight as being 60–70 kg, which was close to the weights of the largest individuals of *A. afarensis*.

Many questions arose after the discovery of the partial hominin foot skeleton BRT-VP-2/73 from 3.4 mya at the Burtele 2 site. Along with the obligatory bipedalism, it shows the character of consistent arboreality—an abducent hallux, capability to grasp, lack of longitudinal pedal arch, etc. (Haile-Selassie et al. 2011). All these factors dramatically decrease the efficiency of locomotion and require additional study.

The main discovery in the Woranso-Mille region, Ethiopia, was the partial skeleton KSD-VP-1/1 (Kadanuumuu) from 3.6–3.58 mya, excavated from Korsi Dora (Haile-Selassie et al. 2010b). Using FHD of 41 mm obtained from the acetabular diameter (Haile-Selassie et al. 2010b), we predicted the individual's weight ($P_b = 51.7$ kg) through Eq. (1), which gave evidence of its large body, and categorized it under the radicophagous taxon.

The lack of the skull of KSD-VP-1/1 prevented us from identifying its cranial volume and the individual's diet. Moreover, the author had no idea about the reconstruction of its pelvic girdle and birth canal measurements.

It is of vital importance that neither the scapula nor the limbs of KSD-VP-1/1 show the characters of suspension or vertical climbing attributed to apes (Haile-Selassie et al. 2010b).

The rest of the fossils from Worsano-Mille region primarily represented separate teeth or parts of jaws, having characters appropriate to the studied taxa, some of them heavily worn from the occlusion to the dentine, whereas others had preserved sharp cusps.

4.7. *Australopithecus deyiremeda*

A. deyiremeda is represented in the deposits dating 3.5–3.3 mya from the Woranso-Mille region, Central part of Afar, Ethiopia from two sites—Burtele and Waytaleyta (Haile-Selassie et al. 2015).

The holotype of this species was the left half of the maxilla BRT-VP-3/1 with 6 teeth I^2 – M^2 . The premolars were not molarized, a tipped, protruding canine had a lingual wear, and the incisor I^2 did not show LL-expansion ($6.9MD/6.6LL = 1.05$), allowing us to categorize this sample under the omnivorous taxon.

The incisors of the other complete mandible BRT-VP-3/14 demonstrated the evident LL-expansion: $5.4MD/8.0LL = 0.68$ for LI_1 and $6.5MD/9.0LL = 0.72$ for LI_2 . Molars had a strongly flat occlusal wear. The width of the mandible corpus at M1 crown is 24.5 mm on the right and 23.6 mm on the left (Haile-Selassie et al. 2015: Extended Data Table 1), showing its robustness and allowing us to categorize this sample under the radicophagous taxon. However, the corpus jaw heights were 33.4 and 33.0 mm at M1 crown, more likely identifying an omnivorous diet. Note that for radicophagous individuals, with identical corpus width, the height at the M1 crown would be about 38 mm.

4.8. *Kenyanthropus platyops*

This species was represented by a set of more than 30 bone remains from the layers aged 3.5–3.3 mya from the deposits at Lomekwi and Kataboi, Kenya (Leakey et al. 2001). It was determined by the cranium KNM-WT 40000, the incompleteness and state of which prevented us from establishing its diet specialization and ECV. Statistical study of the sample, conducted after improved postmortal measuring of the maxilla KNM-WT 40000, also failed to show any similarity with species from the genus *Australopithecus* or *Paranthropus* (Sporer et al. 2010).

The rest of the samples mainly represented a bulk of scattered teeth, whose morphometrics definitely prompted us to identify some of them under the taxa being studied (Leakey et al. 2001: Table 1).

4.9. *Australopithecus bahrelghazali*

The mandible KT12/H1, originally of the species *A. bahrelghazali*, from 3.4–3.0 mya recorded the presence of bipedal primates in Central Africa. The forms of canine due to wear of the occlusion plane, resemblance to a premolar, and LL-expansion of the I_2 incisor with $5.5MD/7.6LL = 0.72$

(Brunet et al. 1995: Table 1), suggested a radicophagous diet specialization of the individual.

4.10. *Australopithecus africanus*

A. africanus is known from the hominid-bearing strata of South Africa, including fossils from Makapansgat: MLD 1–MLD 45 aged 2.5 mya; Sterkfontein: STS 5 (Mrs. Ples)–STS 71, STW 13–STW 513 aged 2.8–2.4 mya, TM 1511, and TM 1512; Taung: Taung Child; Gladysvale; and Drimolen.

Historically, it is quite natural to start with the Taung Child (Dart 1925). Note that the Taung endocast first showed the significant differences in the brain architecture compared to apes, including reduction in the primary visual striate cortex (Brodmann area 17) and relative increase in the posterior parietal cortex. This human-like brain structure allowed Dart (1925) to distinguish a new primate species, which later turned out to be bipedal.

An identical peculiarity, mainly based on the position of the lunate sulcus, was observed in the endocasts of AL 162-28, STW 505, and SK 1585 individuals, which some researchers connected with the emergence of stone tools. However, such brain structure was observed in the endocasts of both omnivorous and radicophagous bipedal primates, and therefore, it immediately reflected the shift of the primates to a terrestrial way of life.

Moreover, a recent fossil determined by the teeth age, close to the human metopic suture fusion, observed at Taung, reflects high early postnatal brain growth rates and expansion of the frontal neocortex (Falk et al. 2012).

Unfortunately, among the *A. africanus* fossils there were no skeletons or even associated bone remains that could help us to identify the diet and predict the weight and ECV of the individuals. However, supposing that an individual, among the *A. africanus* hypodigm, having the least weight and the least ECV could only be a small-bodied omnivore and an individual having maximal weight and maximal ECV could only be a large-bodied radicophagous type, we could obtain some quantitative data from the areas of the taxon CI values.

From the fossils allowing prediction of the ECV values, only the specimen STS 5 from 2.5 mya with ECV of 485 cc was identified as omnivorous or “gracile” (Robinson 1954). However, the smallest in volume were STS 60 (2.5 mya), with ECV of 400 cc, and STS 71 (2.5 mya), with

ECV of 428 cc, that had a non-identified diet (Holloway et al. 2004). We presumably categorized them under small-bodied.

STS 14 from 2.5 mya (McHenry 1992a) and the right hip bone of STS 65 from 2.2–2.0 mya (Wolpoff 1973) showed the smallest weight of 30 kg for *A. africanus*. Uniting the minimal recorded ECV of 400 cc (STS 60) with the minimal weight of 30 kg, we calculated the CI = 4.4 using Eq. (3), which corresponded the values for the omnivorous taxon.

The length of the femur STS 14 (2.5 mya) is ~285 mm (Geissmann 1986), which almost equaled the femur length of AL 288-1 (3.2 mya) of ~280 mm with stature of 105 cm (McHenry 1992b), but was slightly less than the height of the specimen BAR 1002'00 (108–116 cm) of *O. tugenensis* from 6.2 mya (Nakatsukasa et al. 2007). If we take into account that the weight of the omnivorous taxon individuals was within the interval of 27–33 kg during 6.2–2.5 mya, then we might conclude that the morphotype of the small-bodied omnivorous bipedal primates had undergone no changes.

The largest skull among *A. africanus* (STS 505; 2.6 mya) with ECV of 560 cc has a sagittal crest (Holloway et al. 2004), proving its radicophagous diet. The largest body weights observed were 62.3 kg of STW 431 (2.8–2.4 mya) and 54.6 kg of STS 7 (McHenry 1992a: Table 4). Combining the largest ECV (560 cc) of the radicophagous *A. africanus* individual STW 505 with the heaviest (62.3 kg) radicophagous individual STW 431, we get CI = 4.2, according to Eq. (3), which falls in the radicophagous taxon range.

Interestingly, D'Anastasio et al. (2009) discovered pathological lesions on the vertebral bodies of STW 431 individual, resulting from the initial stage of brucellosis, a disease commonly spread among then present pasturable domesticated cows, sheep, and goats. Instead of linking the repeated infection of STW 431 individual with the way modern human being is infected by eating meat and drinking milk of the sick animals, we considered brucellosis in STW 431 individual to prove its terrestrial radicophagous diet.

The original reconstructions of the sacroiliac of the partial postcranial skeleton STS 14 from 2.5 mya were compared with the earlier restored skeleton of AL 288-1, and it suggested identical platypelloid pelvis. The recent digital models created from computerized tomography scans of the bones and 3D assembly of the hip bone and sacrum showed that the proportions of the birth canal of STS 14 are very similar to those of humans, presupposing obstetrical mechanics characterized by ante-ischiatic birth

of the neonate and by way of rotation and flexion of the fetal skull in the pelvic cavity (Berge and Goularas 2010).

Compared to AL 288-1, the minimal pelvic conjugates of STS 14, mentioned in these reconstructions, were outlet sd = 8.5 cm and 3D-assembled midplane sd = 7.33 cm (Berge and Goularas 2010), which from Eq. (2) gave ECV of 663 and 425 cc, respectively, for a female with gender correction of -10%.

The body weight of 30 kg, predicted by the femoral head of STS 14 (McHenry 1992), categorized the individual under the small-bodied omnivorous taxon and enabled us to compute the CIs of the endocranes of both reconstructions: CI = 12.1 and 5.0. The value CI = 12.1 shows an extraordinarily high cerebral level for the first variant (AL 288-1) of the pelvic reconstruction, but, not denying this fact entirely, we followed CI = 5.0.

Unfortunately, the teeth remains attributed to *A. africanus* were in a bad state, hardly allowing the differentiation of the individuals' diet to a satisfactory level. We noted that the protostylid ridge of the enamel of the mandible molars of "gracile" *A. africanus* extends mesially around the base of the protoconid dentine horn, mesio-buccal corner of the crown (Skinner et al. 2009). Whereas in "*Paranthropus*" *robustus*, it connects the dentine horns of the protoconid and hypoconid, considerably strengthening the buccal face and virtually increasing its buccolingual width, which together with a thick enamel cap, prove odontological adjustment of the molars for a hard grinding of vegetable food (Skinner et al. 2009).

4.11. *Homo* sp. indeterminate from Ledi-Geraru

The left side of the mandible LD 350-1 and some teeth associated with it by spatial proximity, found in a deposit of layers aged 2.8–2.75 mya from the site Ledi-Geraru, Afar region, Ethiopia, have been assigned to *Homo* species indeterminate (Villmoare et al. 2015).

The height and breadth of the mandible body of M₁ were 31.7 and 19.3 mm, respectively, that were within the limits of the omnivorous taxon values and slightly exceeded those of AL 288-1 (30.0 and 17.1 mm, respectively). AL 288-1 weighed 27.6 kg, permitting us to predict the weight of LD 350-1 to about 30 kg.

The expressed occlusal relief of the molar cusps also showed omnivorous diet, but the premolars from this set showed a strong flat occlusal wear of the enamel to the dentine, implying a radicophagous diet type.

4.12 *Australopithecus garhi*

This species is represented by craniodental and postcranial remains aged 2.5 mya from Hatayae layers of Bouri formation in the middle current of the Awash River in Ethiopia.

The holotype of this species is a partial skull BOU-VP-12/130 with ECV of 450 cc (Holloway et al. 2004) that has parietal bones with a well-formed anteriorly-positioned sagittal crest (Asfaw et al. 1999), testifying a radicophagous diet specialization of the individual. It also provided evidence of the wearing out of the front teeth in the occlusion plane, molarization of premolars, and general megadontia of the cheek teeth, mainly because of BL-expansion of RP^3 (11.0MD/16.0BL) and RM^2 (14.4MD/17.7BL) (Asfaw et al. 1999).

Radicophagous diet specialization was observed in the cranial vault BOU-VP-12/87, which contained a cranial crest.

Among the *A. garhi* fossils, two humeri were described. First, BOU-VP-35/1 of length 310–325 mm (Asfaw et al. 1999) resembled STS 7 *A. africanus* of length 310 ± 15 mm (Wolpoff 1973) and weight 54.6 kg (McHenry 1992a), implying that its weight would be about 55 kg and categorizing it under the large-bodied radicophagous taxon. Second, BOU-VP-12/1A-G, nearly 236 mm long (Asfaw B. et al. 1999), equaled the length of AL 288-1 (235 mm) (McHenry 1992b), allowing us to consider its weight to be no more than 30 kg and including it in the omnivorous taxon.

Studying the place that might have been occupied by *A. garhi* among the bipedal primates of its time, Asfaw et al. (1999) pointed out two evidently adaptive specimens of bipedal primates during the period 2.7 mya. McHenry (1992b) also divides the early hominids, weighing 29 and 45 kg, into 2 groups or morphs according to their weights. Evaluating the body weights according to the four parameters, Steudel (1980) separated the bipedal primates into two groups based on average weight of 36 kg for gracile and 56 kg for robust. Actually, he had studied only *A. africanus* and *A. robustus* species of a recent period 3.3–1.5 mya, but all segregations were in compliance with the differentiation of the taxon individuals according to their weights. These were considered in the current research for the time period 6.2–2.5 mya, where the omnivorous species weight was within the range of 27.6–33.3 kg and that of the radicophagous species was about 38–70 kg.

This size dissimilarity between the omnivorous and herbivorous species can be predicted by the Jarman-Bell principle: dietary quality (i.e.,

energy and nutrient density of the diet) is inversely related to the body mass. The explanation for this is the cardinal difference in the functioning and size of the gastrointestinal tract adjusted for digesting raw starch (grain and bulbs) and protein flesh food (Chivers and Hladic 1980). For grass-consuming mammals, the ratio between the length of the tract and the stature is 15:1, for grain-eating mammals it is 8.7, for omnivores it is 6.8, and for human beings it is 5.0–6.3 (Nesturkh 1970).

4.13. *Australopithecus aethiopicus*

The most remarkable specimen of *A. aethiopicus* is the “Black Skull” KNM-WT 17000 from 2.5 mya (Walker et al. 1986). The cranial morphology of KNM-WT 17000, particularly the sagittal crest, implies the presence of the robust masticatory muscles, testifying the specialization of teeth-jaw apparatus in lengthy hard food processing, which is inherent in the radicophagous taxon. Previously, it was called *A. boisei* (Walker et al. 1986), but taking into consideration that holotype OH 5 and other fossils of *A. boisei* were discovered in recent layers, KNM-WT 17000 was united with an edentulous mandible of OMO 18 and a new species of *A. aethiopicus* was distinguished.

We would also like to draw attention to the fact that by this time the difference between the robust and gracile bipedal primates became so evident that the large-bodied specimens of *A. aethiopicus*, *A. robustus*, and *A. boisei* suffered similar reassignment and sometimes were even united under a separate genus, *Paranthropus*.

The ECV of KNM-WT 17000 was 410 cc. The premolar P³ of KNM-WT 17000 had the size ratio of 11.5MD/16.2BL, which was close to the maximum values among the large-bodied individuals from 3.0–2.5 mya. However, these values were slightly higher than those for RP³ of BOU-VP-12/130 of *A. garhi* (11.0MD/16.0BL).

Another specimen of the cranium, OMO L338y-6, from 2.39 mya has ECV of 427 cc (White and Falk 1999), with a sagittal crest, and is also attributed to the radicophagous taxon.

4.14. *Australopithecus sediba*

This species was represented by two partial skeletons, a young MH 1 and an adult MH 2, discovered from the Malapa site in the Gauteng province, South Africa (Berger et al. 2010) from deposits aged 1.977 mya (Pickering et al. 2011).

The weight of MH 1, predicted by Eq. (1) with FHD of 29.8 mm (Berger et al. 2010), equaled 29.7 kg, and this skeleton was attributed to the small-bodied type. The gracile architecture of the MH 1 skull indicated no possibility for robust muscle attachment for hard chewing. The corpus height and width of the mandible MH 1 at the M1 crown were 28 and 18 mm, respectively, which corresponded with the range of the omnivorous taxon. In addition, the crown shape and occlusal teeth wear (Berger et al. 2010) were not seen in the radicophagous taxon. ECV of 420 cc of MH 1 individual (Kibii et al. 2011) allowed us to predict $CI = 4.9$ using Eq. (3).

As for MH2, in spite of the lack of the cranial measurements, one can use pelvic measurements for calculating its ECV. The Con_{min} of its birth canal, inlet sd of 8.17 (Kibii et al. 2011), allowed us to compute the ECV of this individual to 589 cc, using Eq. (2), with a gender correction of -10% .

With body weight of 34.8 kg, predicted by Eq. (1), and taking FHD of 32.7 mm (Berger et al. 2010), the CI of MH 2 was calculated to 8.3 by Eq. (3). The CI value clearly pointed at the omnivorous diet of the individual, but we also observed an increase in the body weight of the omnivorous taxon members.

However, in the fossil set representing MH 2, the mandible UW 88-54 showed a large occlusal wear observed in radicophagous diet type, but which can be explained if the mandible belonged to another individual.

Besides, the fossils from the MH 2 set possessed some characters that poorly corresponded with the four million years of bipedal evolution. Thus, the peculiarities of the hand structure of MH 2 were connected with a regular arboreal locomotion (Kivell et al. 2011), and the foot, ankle, and distal part of the tibia morphology also suggested that exploitation of arboreal habitats was a crucial part of its behavioral ecology (Zipfel et al. 2011).

4.15. *Homo rudolfensis*

KNM-ER 1470, a typical specimen of this species, was a rather complete skull without any teeth, from 1.9 mya (Leakey 1973). A remarkable feature of this specimen was the lack of the sagittal crest and heavy muscle markings, which would have characterized the chewing and grinding specialization of the craniodental apparatus. A slight thickness (6 mm) of the temporal squama (Kimbel et al. 2004) attributed this specimen to the omnivorous taxon. The brain volume of 752 cc calculated for KNM-ER 1470 (Holloway et al. 2004) was later corrected to 700 cc (Bromage et al. 2008).

In addition, KNM-ER 1470 showed some new characters that were not observed earlier in bipedal primates—a rounded prefrontal lobe and triangle shape of the cerebellar lobe that indicated a shape similar to that of modern human beings. The endocast showed considerable asymmetry through the presence of a well-defined left occipital petalia, observable in both width and posterior projections. Additionally, a clear right frontal breadth petalia was also present, which indicated right-handedness of the bipedal primates of the omnivorous taxon, correlating with the fact that the production process of some stone tools point to right-handedness (Holloway et al. 2004). This increase in brain volume and changes in the brain structure of the omnivorous taxon members definitely proved the production and exploitation of stone tools by them.

The robust form of the mandible KNM-ER 60000 from 1.95–1.78 mya (Kremer and Sylvester 2009), with its height and width at M1 crown being 38 and 20 mm, respectively, small front teeth, and occlusal wear (Leakey et al. 2012), gave evidence of the radicophagous diet specialization of the individual and the lack of adaptations to meat food.

The right femur KNM-ER 1472 and the left femur KNM-ER 1481 from 1.9 mya (Kramer and Sylvester 2009) had FHD of 40.0 and 43.4 mm, respectively (McHenry 1992a), and according to Eq. (1) indicated large bodies of 49.4 and 57.1 kg, respectively, attributing both specimens to the radicophagous taxon.

4.16. *Homo habilis*

The holotype of *H. habilis* was a mandible with teeth from the set of associated remains OH 7 from 1.75 mya, including parts of the calvaria and various hand bones (Leakey et al. 1964). The lack of occlusal wear of the front teeth, projected canines, and absence of the molar megadontia categorized the individual under the omnivorous taxon. The brain volume of this individual is 687 cc (Holloway et al. 2004), which was close to the volume of the omnivore KNM-ER 1470 (700–752 cc) from 1.9 mya deposit and proved a gradual increase in the brain volume.

There is an opinion, that a rather complete foot OH 8, found not far from OH 7, belongs to the same individual. Additionally, the tibia proportions of the specimen OH 35 coincide with the proportions of the foot OH 8 to such a degree that one can admit they belong to the same individual (Häusler and McHenry 2004). The predicted body weights of OH 8 (31 kg) and OH 35 (31.9 kg) also considerably coincide (McHenry

1992a). With the ECV value of 687 cc of OH 7 and the weight of OH 8/OH 35 (31–31.9 kg), the CI of this compound omnivorous individual, according to Eq. (3), was calculated to 12.3–12.6.

With 5.2 mm thickness of the temporal squama (Kimbel et al. 2004) and a gracile mandible, the corpus height and thickness of which equaled 27 and 18 mm, respectively, OH 13 (Cindy) specimen from 1.66 mya (Leakey et al. 2012) with ECV of 650 cc (Holloway et al. 2004) could be included in the omnivorous taxon.

The partial skeleton OH 62 from 1.8 mya weighs 33 kg (McHenry 1992a), showing a small body type. Based on the gracile faciodental bones, it was identified as *H. habilis* (Johanson et al. 1987). The traditional reconstruction of the femur bone of OH 62, compared to AL 288-1, suggested an individual of 1.0 m stature with ape-like proportions of the limbs. However, we completely agree with Häusler and McHenry (2004), who pointed out the congruency of the femur of OH 62 with femur of OH 34 (*Homo* sp. indet.) from 1.15–0.8 mya that allowed the evaluation of the femur length of OH 62 as 354–404 mm. Importantly, it showed that humerofemoral proportions of gracile and robust individuals did not considerably differ from each other and together encompassed the range of the modern human being.

The calvaria ECV of the partial cranium KNM-ER 1805 (The Mystery Skull) from 1.85 mya was 582 cc, which was largest among the specimens of the *H. habilis* hypodigm, and it shows a sagittal crest (Holloway et al. 2004) that identified it under the radicophagous taxon. Due to the absence of associated postcranial remains, we considered the morphometrics of the heaviest individual of *H. habilis* for further analysis—the right humerus KNM-ER 739 from 1.6–1.5 mya with a predicted weight of 72.4 kg (McHenry 1992a). For this compound radicophagous type individual we obtained CI = 3.9, according to Eq. (3).

4.17. *Australopithecus boisei*

The *A. boisei* fossils were found mainly in East Africa in Ethiopia, Tanzania, and Kenya, in deposits aged 2.3–1.2 mya. The first specimen, which further determined the characters of the species, was a full skull without mandible OH 5 (Zinj) from 1.8 mya (Leakey 1959), with ECV of 520 cc (Holloway et al. 2004), and was found in Olduvai Gorge, Tanzania. The general occlusal wear, the heavy enamel, and megadontia of the cheek teeth of the maxilla: M¹, 18×15.5 mm; M², 21×17 mm; and M³,

21×16 mm (Leakey 1959), all allowed us to include this individual in the radicophagous taxon.

Further in time, the radicophagous line of the bipedal primates was continued by the robust cranium with sagittal crest KNM-ER 406 from 1.5 mya, with ECV of 500 cc (Holloway et al. 2004).

The cranium with mandible KGA10-525 from 1.4 mya, with cranial volume of 545 cc (Holloway et al. 2004), was recently discovered in Konso, Ethiopia. The sagittal crest, extensive dentine wear, megadontia of postcanine teeth (LM_2 : BL = 16.8 mm, LM_3 : 21MD/17.7BL, RM_2 : BL = 19.2 mm, RM_3 : BL = 19.1 mm), and massive mandible with corpus height and width of 41.5 and 29 mm, respectively, at M1 (Suwa et al. 1997) identified this individual as a member of the radicophagous taxon.

The calvaria of KNM-ER 407 from 1.85 mya, with ECV of 510 cc, and the partial cranium KNM-ER 732 from 1.7 mya, with ECV of 500 cc (Holloway et al. 2004), were extremely different in shape and size from the first three craniums, making their taxonomic classification difficult, such that earlier taxonomy referred to them as "...either a gracile species of *Australopithecus* or else early representative of *Homo*..." (Wood and Constantino 2007). Their cranial architecture did not suggest the attachment of massive muscles for hard chewing, and also a small thickness of the temporal squama of KNM-ER 407 (5.5 mm) and KNM-ER 732 (5 mm) (Kimbel et al. 2004) categorized these fossils under the omnivorous taxon. However, their cranial volumes, when compared with the contemporary omnivorous species OH 7 (687 cc; 1.75 mya) and OH 13 (650 cc; 1.66 mya), were too small, and the lack of teeth or associated postcranial remains failed to give a more precise diet diagnostic.

The fossil set OH 80, from 1.34 mya excavated from the fourth layer Bell's Korongo, Bed II, Olduvai Gorge, Tanzania, consisted of teeth and limb fragments (Dominguez-Rodrigo et al. 2013). The incisors OH 80-1, -5, -6, and -7 showing a "cutting" occlusion inherent in the omnivorous type and the postcanine teeth with occlusal wear to the plane testified the radicophagous diet specialization. Due to fragmentation and the state of the postcranial remains, we failed to determine the size of the individual.

The lack of associated remains, which would allow us to predict the diet, body weight, and ECV, of *A. boisei* led us to assume that radicophagous individual KGA 10-525 (1.4 mya) with the largest cranial volume of 545 cc had the largest weight of 61.5 kg among the *A. boisei* hypodigm, similar

to that registered for KNM-ER 993 (1.6–1.5 mya) (McHenry 1992a). The CI of the large-bodied individual KGA 10-525 of the radicophagous taxon was 4.0, according to Eq. (3).

4.18. *Australopithecus robustus*

The fossils attributed to *A. robustus* were recovered from six places in South Africa: Kromdraai, Swartkrans, Drimolen, Gondolin, Sterkfontein, and Coopers.

The type specimen of this species was the cranium TM 1517 with half a mandible (earlier *Paranthropus crassidens*) from the deposits of Kromdraai B from 2.0–1.5 mya (Broom 1938). The wear out and structure of the postcanine teeth of TM 1517a, b (Thackeray et al. 2001) allowed us to attribute this individual to the radicophagous taxon.

A rather small skull DNH 7 (Eurydice) was recovered from the deposits aged 2.3 mya in Drimolen. The front and lateral teeth in the upper and lower jaws showed a noticeable occlusal wear, molar cusps were worn, and the premolars were largely molarized. Although the sagittal crest was missing, we agree with Keyser (2000) that this was a female individual and attributed it to the radicophagous taxon. The common features of both specimens suggested the main morphological peculiarity of the species—a massive craniodental system designed for grinding hard and fragile vegetable food.

The skull SK 48 from 2.0–1.5 mya with ECV of 476 cc, a sagittal crest, and molar megadontia could also be attributed to the radicophagous specimens.

Note that among the fossils from the deposit site Kromdraai B, some specimens could be classified under the omnivorous taxon. Examples include the tipped canine Lc TM 1601c without occlusal wear and some incisors from Swartkrans, Gauteng province, that have span-like sharp shape, which allows for cutting function similar to scissors, but lack LL-expansion— LI^1 (SWT1/LB-13): $8.9MD/7.2LL = 1.24$; RI^1 (SWT1/LB-16): $7.0MD/6.3LL = 1.11$; I^1 (SWT/TC-4): $9.4MD/7.6LL = 1.24$; RI^1 (SK 3): $9.0MD/7.1LL = 1.27$; and I^1 (SK 40): $9.0MD/7.5LL = 1.2$. The canine Rc (SWT1/HR-1) has lingual wear (Pickering et al. 2012).

The omnivorous features were observable in the *A. robustus* specimens and in specimens from other sites. Thus, among the teeth found at the site Drimolen in Gauteng, South Africa, there were some samples that were not compatible with the radicophagous morphology (Keyser et al. 2000).

Despite the large quantity of the specimens (more than 500), *A. robustus* is not represented by any skeleton or associated fossils, which could have allowed for comparison of diet, body weight, and ECV.

Of great interest is a comparison of diaphyseal morphology of two samples from Swartkrans from 1.8–1.6 mya: the proximal femur SK 82 with FHD of 34.4 mm and the proximal femur SK 97 with FHD of 37.1 mm (Susman et al. 2001), which according to Eq. (1) have body weights of 38 and 43.3 kg, respectively.

The proximal femur shaft shows three main types of mechanical loading patterns based on the hip joint: axial loading, proportional to the body weight; loading of lateral bending on the femoral diaphysis, related to the biacetabular breadth of the pelvis and femoral neck length; and torsional loading, connected to the movement axis of the ankle joint with the axial movement of the “acetabulae-femoral head” pair, which extends 17–22° angle toward the mediolateral plane (Ruff et al. 1999). Some important points to consider are:

- The strength of the counteraction of the axial loading of body weight is proportional to the cross-section of the cortical area of the diaphysis.
- The counteraction of the lateral bend loading is mediolateral reinforcement of the proximal femur that makes the cross-section of the diaphysis oval-shaped.
- The adaptation of the femur bone to the torsional loading includes an increase in the periosteal diaphysis diameter of the femur, under which the diaphyseal cortex diminishes for a given weight and cortical area (CA), and a respective increase in the medullary canal diameter (Bleuze 2010).

Based on the configuration of the cross-section of the proximal femur, cluster analysis allowed Bleuze (2010) to divide the bipedal primates into two groups: the first group includes modern human and “early *Homo*” fossils and the second group includes “*Paranthropus*”.

Generally, the femur of “*Paranthropus*”, with a weight similar to that of the first group, is characterized by thicker diaphyseal cortex, but smaller periosteal diaphysis diameter. However, structural studies point out the elementary type of bipedalism among “*Paranthropus*” (Bleuze 2010).

We have arranged the values of cross-section dimensions of the femur, measured at the proximal part (80% of its length from the distal end) and the femur middle (50% of its length), for some of the fossils in Table 2.

Table 2. – The measurement data of the diaphysis cross-section dimensions

	Paleo-age (mya)	Cross-section dimensions of femur at 80% of its length				Cross-section dimensions of femur at 50% of its length			
		CA	MA	TA	%CA	CA	MA	TA	%CA
SK 82 ¹	1.8–1.6	490	87	577	84.9				
SK 97 ¹	1.8–1.6	457	135	593	77.1				
OH 80-12 ²	1.34	524	87	611	85.7	492	35	526	93.5
KNM-ER 1808 ²	1.69					478	73	551	86.8
Modern human ¹					44.5–78.7				71.48

CA, cortical area; MA, medullary area; TA, total periosteal area ($TA = CA + MA$); $\%CA = (CA/TA) \times 100$.

Sources of dates:

¹ (Ruff et al. 1999)

² (Dominguez-Rodrigo et al. 2013)

According to the magnitudes of the cross-sectional diaphyseal areas of SK 82 and SK 97 proximal femora (Table 2), although SK 82 had a CA (490 mm²) larger than that of SK 97 (457 mm²), its periosteal CA was generally lesser ($TA: 577 \text{ mm}^2 < 593 \text{ mm}^2$) and its medullary canal was almost half the size of that of SK 97 ($MA: 87 \text{ mm}^2 < 135 \text{ mm}^2$) (Ruff et al. 1999).

Besides, SK 97 had a more stretched, oval shape of the plane perpendicular to the axis of the acetabulae-femoral head pair, which proved the difference in cross-sectional geometries and vector directions of loadings on bones and muscles that emerged during the locomotion of these individuals. Mainly, there was a difference in the hip joint functions and different types of gaits of these individuals.

Considering the complex hip joint function of SK 97 and that the value of its %CA (77.1) was within the upper range for a modern human being (Ruff et al. 1999), we attributed SK 97 to the omnivorous taxon and SK 82 to the radicophagous taxon. Based on %CA values for the proximal femur, we took the following as taxon-determining characters: individuals with $\%CA < 77.1$ attributed to the omnivorous taxon, whereas individuals with $\%CA > 84.9$ attributed to the radicophagous taxon.

Another specimen from Table 2, the femur of OH 80-12 *A. boisei* from 1.34 mya, with cross-section of proximal femur similar to that of SK 82 and %CA of 85.7 (>84.9 of SK 82), could also be attributed to the radicophagous taxon.

Comparing the properties of the cross-section of the midshaft femur of OH 80-12 and KNM-ER 1808 (*A. robustus*), we observed the equal difference in their geometries from that of SK 82 and SK 97 (Table 2). Compared to OH 80-12, KNM-ER 1808 had smaller CA, larger TA, and two-fold larger area of medullary canal, which allowed us to attribute it to the omnivorous taxon. Therefore, for the midshaft femur, we took the following taxon-determining characters: for %CA < 86.8 we deal with the omnivorous taxon, whereas for %CA > 93.5 we deal with the radicophagous taxon.

Finally, it should be noted that the predicted weight of the radicophagous individual SK 82 (38 kg) was extremely small. Additionally, the basic section of its femur CA was larger than that of the omnivorous individual SK 97 (Table 2), which undoubtedly demands further research. In any case, the possibility of the superposition of the body weights of the taxa under study requires fossils from earlier than 2.0 mya to limit the alternative character “large-bodied/small-bodied” in the range of 38–43.3 kg.

The lightest individual of *A. robustus* was represented by the femoral head and neck SK 3121 from 1.8–1.0 mya, for which DeSilva et al. (2013) measured the FHD to 28.6 mm, and it had a predicted body weight of 27.7 kg according to Eq. (1), allowing us to consider it under the small-bodied omnivorous taxon. Unfortunately, among *A. robustus* fossils there were no skulls for predicting the value of ECV. However, obligatorily diagnosed as omnivorous, but found among the *A. boisei* fossils of a similar paleo-age, the partial skull KNM-ER 732 (1.7 mya) showed an ECV of 500 cc, small for individuals of this period, and was identified as omnivorous. Applying Eq. (3) to such a conditional compound individual, we obtained the CI value of 7.5 for the omnivorous taxon.

4.19. *Homo erectus*, *Homo ergaster*

Dating between 1.9–0.3 mya, the Eurasian species of *H. erectus* evolutionarily represents the one nearest to *H. sapiens*. The type specimen of *H. erectus* was the cranium Trinil 2 found in 1891 by Eugene Dubois at Trinil, Java, Indonesia. Some researchers consider *H. erectus* to be a European and Asian species, geographically positioning *H. ergaster* as its contemporary species in Africa. Others assume that some craniofacial

differences are species-specific and acknowledge the coexistence of these two species in the African continent.

Assuming that such morphometric differences have insignificant reproduction weight, that they fail to determine the ecology-diet of the individuals, and that their postcranial remains are indistinguishable, we considered a collective hypodigm of African fossils of both species.

The best-known, nearly complete skeleton KNM-WT 15000 was discovered in 1.6 mya deposits from Nariokotome III, west Lake Turkana, Kenya (Brown et al. 1985). The skull shape of KNM-WT 15000 did not indicate the possibility of muscle attachment necessary for hard chewing activity; the frontal teeth were without occlusal wear and supported a cutting function; the lateral teeth did not show megadontia; the ratio between the lateral and frontal teeth was not typical of radicophagous individuals; and the ECV of the skull was 900 cc (Holloway et al. 2004), all of which attributed it to the omnivorous taxon.

However, based on its FHD of 44 mm (Brown et al. 1985), the predicted body weight of 58.6 kg, according to Eq. (1), of the postcranial skeleton, categorized the postcranial part of KNM-WT 15000 to the large-bodied radicophagous taxon. The skull and postcranium belonged to different individuals, which was proved by the fact that there was a difference in their determined biological age at the moment of death: for the skull, according to the teeth, it was about 8 years and for the postcranial skeleton, based on the bone fusion, it was 13 years (Graves et al. 2010).

Walker and Ruff (1993) mentioned the restored sizes of the pelvic of KNM-WT 15000, but only for the inlet, where the Con_{min} was the maximal inlet sd = 8.8 cm, which allowed us to reconstruct the ECV and CI of the postcranial skeleton, separately from the cranium.

The existing reconstructions of the birth canal of both bipedal primates and a modern human show that the Con_{min} lies either in the midplane or in the outlet.

In platypelloid pelvic reconstruction of STS 14, the outlet sd is approximately 4.5% less than the inlet sd, whereas in the case of non-platypelloid pelvic, it is less by 10–11% (Berge and Goularas 2010). This required us to reduce the inlet sd (8.8 cm) (Walker and Ruff 1993) by at least 4.5% for KNM-WT 15000, giving the value of the Con_{min} of the birth canal outlet sd = 8.4 cm. According to Eq. (2), with gender correction of –10%, we calculated the ECV of the postcranial part of KNM-WT 15000 to 640 cc.

Moreover, the skull of the radicophagous individual has thicker bones and its ectocranial volume is the same as that of the omnivorous individual, resulting in a smaller ECV that was not taken into account while creating Eq. (2) for omnivores.

Taking into account the temporal squama, which is 5 mm thicker for radicophagous individuals than for omnivorous individuals (Table 3), and having recalculated ECV ($640 \text{ cc} = 4/3\pi R^3$, for $R = R - 5 \text{ mm}$), we obtained ECV of 560 cc for the postcranial skeleton of KNM-WT 15000, which was within the range of the radicophagous taxon and allowed us to calculate $CI = 4.4$, according to Eq. (3).

As for the skull of KNM-WT 15000, which had the largest registered ECV (900 cc) for bipedal primates from 1.6 mya, we assumed that the weight of the individual must correspond to the largest value of the omnivorous taxon individuals from 1.8–1.6 mya, which equals $P_b = 43.3 \text{ kg}$ (SK 97 *A. robustus*), and calculated its CI as 15.5 using Eq. (3).

The nearly complete pelvis BSN49/P27a-d from the deposits of the Busidima Formation aged 1.4–0.9 mya at Gona of Afar region, Ethiopia could provide us some important information. Small acetabulae of BSN49/P27 with 33.4–36.8 mm FHD (Simpson et al. 2008) suggested a body weight of 36.1–42.7 kg according to Eq. (1), which falls in the range of overlapping values of the individuals under study, but it failed to identify the diet.

Using the reconstructed dimensions of the birth canal, one can calculate ECV of the individual. For this, as in a previous case, it would be necessary to reduce the conjugate inlet sd of 9.8 cm (Kibii et al. 2011) by 4.5% to get the outlet sd as 9.4 cm, marking it closer to the Con_{min} of the birth canal. Furthermore, according to Eq. (2), with gender correction of –10%, we calculated the ECV as 897 cc, which almost coincided with the value 880 cc predicted for BSN49/P27 (Simpson et al. 2008). All these evidences allowed us to assume its omnivorous diet type, and using Eq. (3), we calculated its $CI = 15.6$ –18.5.

From the rest of the fossils, we could distinguish two crania of *H. ergaster*: KNM-ER 3733 with ECV of 848 cc from deposits aged 1.78 mya and OH 9 with ECV of 1,067 cc from deposits aged 1.2 mya (Holloway et al. 2004), which proved the increasing ECV of the omnivorous taxon individuals during 1.8–1.2 mya.

Essential evidence of existence of digestion physiology adapted to regular meat-eating among the members of the omnivorous taxon

was provided by the presence of the OH 81 specimen, recovered from deposits aged 1.5 mya at the SHK site, Olduvai Gorge, Tanzania. The parietal fragments of a two-year-old child exhibited a bone pathology (porotic hyperostosis) as a result of B12 (cobalamin) and B9 (folic acid) vitamin deficit, which is related to the deficiency in animal food products (Dominguez-Rodrigo et al. 2012).

4.20. *Homo naledi*

H. naledi was represented by a collection of 737 partial or complete anatomic remains found in a dolomitic horizon of unknown age in the Rising Star cave situated in the basin of Bloubaan River, Gauteng District, South Africa (Berger et al. 2015).

Rather homogeneously, the collection showed a trophic omnivorous diet specialization: the skulls lack sagittal crests and LL-expansion of incisors is missing (Berger et al. 2015: Table 2). The average height and width of the mandible body is 26 and 16 mm, respectively (Berger et al. 2015: Table 1), which also attributed the specimens to the omnivorous taxon.

Exceptionally, the M₃ molar of the lower jaw U.W. 101-361 had a flat occlusal wear that attributed its individual to the radicophagous taxon, and probably, the front teeth of the upper jaw U.W. 101-1277 had a heavy occlusal wear. In addition, nasoalveolar clivus of the upper jaw UW 101-1277 measured by us (Berger et al. 2015: Figure 2c), formed an angle of no more than 50°, indicating a prognathism more typical of the radicophagous taxon.

In any case, this collection lacked any specimens showing other trophic types, apart from the omnivorous and radicophagous types under study. The presence of radicophagous individuals in the deposit suggested the age of the deposit layers was not younger than 1.34 mya, allowing us to include this collection in the studied interval.

V. Results of the revision exercise

Diagnostic characters of radicophagous and omnivorous taxa

The revision of the characters of African bipedal primates from the 6.2–0.9 mya period confirmed the existence of the division of bipedal primates into two morphological types, two allochronic taxa corresponding to two diet types: omnivorous and radicophagous, throughout the whole study period.

At the same time, we distinguished the diagnostic characters of craniodental architecture (Table 3) and morphometrics of the femoral bones (Table 4), pointing out the basis of ecological niche for each taxon. It should be noted that dichotomy of these characters allows us to determine the trophic belonging of the individuals, based on separate scattered bone remains.

Table 3. – Diagnostic characters of the craniodental architecture of individuals of the radicophagous and omnivorous taxa

Diagnostic properties	Radicophagous taxon	Omnivorous taxon
LL-expansion of incisors	$MD/LL < 1.1$	$MD/LL > 1.1$
State of occlusion plane of the front teeth	Occlusal wearing	Cutting function
State of occlusion plane of the cheek teeth	Worn to the occlusion plane, sometimes to the dentine	Expressed cusps on the occlusion plane
Height of the mandible corpus at M1 crown	>38 mm	<32 mm
Width of the mandible corpus at M1 crown	>23 mm	<22 mm
Thickness of the temporal squama	8.5–11 mm	4.5–6 mm
Sagittal crest	Present in majority of the skulls	Excluded
Nasoalveolar clivus	$36\text{--}50^\circ$ (prognathism)	$\sim 82^\circ$ (orthognathism)

MD/LL, ratio of the mesiodistal diameter to the labiolingual diameter.

Table 4. – Diagnostic differences between the cross-sectional diaphyseal %CA of the radicophagous and omnivorous taxa

Femur part	%CA of the radicophagous taxon	%CA of the omnivorous taxon
Proximal part, at 80% of the bone length	>84.9	<77.1
Midline, at 50% of the bone length	>93.5	<86.8

CA, cortical area; %CA = $[CA/(CA + \text{medullary area})] \times 100$ (also see Table 2).

Analysis of the obtained data

In the course of revision of the total mass of the remains of the bipedal primates (Table 1), the specimens whose characters directly pointed out the diet type of the individuals, or which contained associated characters having a meaningful diagnostic weight, were distinguished. According to a trophic diagnostic, the distinguished samples, independent of their original species, were divided into two taxa: radicophagous (Table 5) and omnivorous (Table 6).

We arranged the samples in the chronological order of their deposits and added the morphometric characters, such as individual body weight, ECV, and CI, of the remains, which we managed to trace in the period under study. Some of the characters were taken from published descriptions, whereas others were calculated using methods mentioned above.

Table 5. – The list of radicophagous taxon specimens

International Registration Number of specimen	Original species	Age (mya)	Body weight (kg)	Endocranial volume (cc)	Cranial index
1	2	3	4	5	6
ALA-VP-2/10-LI2	<i>Ar. kadabba</i>	5.8–5.2			
ARA-VP-7/2	<i>A. ramidus</i>	4.4	42		
ARA-VP-14/1	<i>A. anamensis</i>	4.2–4.1			
KNM-KP 29281	<i>A. anamensis</i>	4.17–4.12			
KNM-KP 29283	<i>A. anamensis</i>	4.17–4.12			
KNM-KP 34725	<i>A. anamensis</i>	4.17–4.12			
KNM-KP 29286	<i>A. anamensis</i>	4.17–4.12			

1	2	3	4	5	6
KNM-KP 29285	<i>A. anamensis</i>	4.1–3.9	47–55		
MSD-VP-5/50	<i>Australopithecus</i> sp. indet. from Woranso-Mille	3.8–3.7	60–70		
AL 333-45	<i>A. afarensis</i>	3.76–3.56		485–500	
KSD-VP-1/1	<i>Australopithecus</i> sp. indet. from Woranso-Mille	3.58	51.7	494	
BRT-VP-3/14	<i>A. deyiremeda</i>	3.5–3.3			
MAK-VP-1/3	<i>A. afarensis</i>	3.4	44.8		
MAK-VP-1/1	<i>A. afarensis</i>	3.4	50.1		
KT12/H1	<i>A. bahrelghazali</i>	3.4–3.0			
AL 438-1	<i>A. afarensis</i>	3.0			
AL 444-2	<i>A. afarensis</i>	3.0	65	550	3.9
STW 505/STW 431	<i>A. africanus</i>	2.6	62.3	560	4.2
STS 7	<i>A. africanus</i>	2.58–2.0	54.6		
KNM-KP 271(K.H.-1)	<i>A. anamensis</i>	2.5	58		
BOU-VP-12/130	<i>A. garhi</i>	2.5		450	
BOU-VP-12/87	<i>A. garhi</i>	2.5			
BOU-VP-35/1	<i>A. garhi</i>	2.5	~55		
KNM-WT 17000	<i>A. aethiopicus</i>	2.5		410	
OMO L338y-6	<i>A. aethiopicus</i>	2.39		427	
DNH 7 “Eurydice”	<i>A. robustus</i>	2.3			
TM 1517	<i>A. robustus</i>	2.0–1.5			
SK 48	<i>A. robustus</i>	2.0–1.5		476	
KNM-ER 1472	<i>H. rudolfensis</i>	1.9	49.4		
KNM-ER 1481	<i>H. rudolfensis</i>	1.9	57.1		
KNM-ER 1805/ KNM-ER 739	<i>H. habilis</i>	1.85	72.4	582	3.9
SK 82	<i>A. robustus</i>	1.8–1.6	38		
OH 5 “Zinj”	<i>A. boisei</i>	1.8		520	
KNM-WT 15000 - Postcranium	<i>H. ergaster/</i> <i>erectus</i>	1.6	58.6	560	4.4
KNM-ER 406	<i>A. boisei</i>	1.5		500	
KGA10-525 (KNM-ER 993)	<i>A. boisei</i>	1.4	61.5	545	4.0
OH 80-12	<i>A. boisei</i>	1.34			

Table 6. The list of omnivorous taxon specimens:
(a) the area of CI values < 4.8; (b) the area of CI values > 4.8

(a) The specimens with the area of CI values < 4.8.					
International Registration Number of specimen	Original species	Age (mya)	Body weight (kg)	Endocra- nial vol- ume (cc)	Cra- nial index
1	2	3	4	5	6
BAR 1002'00	<i>O. tugenensis</i>	6.2–5.65	33.3		
BAR 1001'00	<i>O. tugenensis</i>	6.2–5.65			
BAR 1425'00	<i>O. tugenensis</i>	6.2–5.65			
ASK-VP-3/400 - Rc	<i>Ar. kadabba</i>	5.8–5.6			
ALA-VP-2/10 - Lc	<i>Ar. kadabba</i>	5.8–5.2			
ALA-VP-2/10 - Right mandible	<i>Ar. kadabba</i>	5.8–5.2	<30		
STD-VP-2/61	<i>Ar. kadabba</i>	5.8–5.2			
ALA-VP-2/101	<i>Ar. kadabba</i>	5.8–5.2	<30		
ARA-VP-6/1	<i>A. ramidus</i>	4.4	<30		
ARA-VP-1/128	<i>A. ramidus</i>	4.4	<30		
ARA-VP-1/125	<i>A. ramidus</i>	4.4	~30		
ARA-VP-1/500	<i>A. ramidus</i>	4.4	~30		
ASI-VP-2/2	<i>A. anamensis</i>	4.2–4.1			
ASI-VP-2/334	<i>A. anamensis</i>	4.2–4.1			
MSD-VP-5/16	<i>Australopithe- cus sp. indet. from Woranso- Mille</i>	3.8–3.7	~30		
L.H.-4	<i>A. afarensis</i>	3.8–3.6			
BRT-VP-3/1	<i>A. deyiremeda</i>	3.5–3.3			
MAK-VP-1/111	<i>A. afarensis</i>	3.4	<30		
MAK-VP-1/12	<i>A. afarensis</i>	3.4			
AL 288-1 “Lucy”	<i>A. afarensis</i>	3.2–3.18	27.6	387	4.5
LD 350-1	<i>Homo sp. indet. from Ledi-Geraru</i>	2.8–2.75	~30		
Taung Child	<i>A. africanus</i>	2.8–2.4			
STS 60	<i>A. africanus</i>	2.5	~30	400	4.4

1	2	3	4	5	6
(b) The specimens with the area of CI values > 4.8.					
STS 5	<i>A. africanus</i>	2.5		485	
STS 14	<i>A. africanus</i>	2.5	30	425–663	5.0
BOU-VP-12/1	<i>A. garhi</i>	2.5	<30		
MH 1	<i>A. sediba</i>	1.977	29.7	420	4.9
MH 2	<i>A. sediba</i>	1.977	34.8	589	8.3
KNM-ER 1470	<i>H. rudolfensis</i>	1.9		700–750	
KNM-ER 407	<i>A. boisei</i>	1.85		510	
OH 62	<i>H. habilis</i>	1.8	33		
SK 97	<i>A. robustus</i>	1.8–1.6	43.3		
KNM-ER 3733	<i>H. ergaster/erectus</i>	1.78		848	
OH 7/OH 8/OH 35	<i>H. habilis</i>	1.75	31.5	687	12.3–12.6
KNM-ER 732	<i>A. boisei</i>	1.7		500	
KNM-ER 1808	<i>A. robustus</i>	1.69			
SK 3121/ KNM-ER 732	<i>A. robustus</i>	1.7	27.7	500	7.5
OH 13 “Cindy”	<i>H. habilis</i>	1.66		650	
KNM-WT 15000 -Cranium	<i>H. ergaster/erectus</i>	1.6	43.3	900	15.5
OH 81	Sp. indet. from site SHK, Olduvai	1.5			
BSN49/P27	<i>H. ergaster/erectus</i>	1.4–0.9	36.1–42.7	897	15.6–18.5
OH 9	<i>H. ergaster/erectus</i>	1.2		1,067	

The preliminary consideration of Tables 5 and 6 showed certain changes in the morphometric characters with time. As the tabular representation of the data fails to demonstrate the nature of these changes, we have depicted this data through diagrams to compare the taxa.

The character “individual body weight”

We represented the changes in the body weight of individuals, belonging to the taxa under study, on a coordinate plane. For this purpose, we plotted the time scale in terms of mya on the x-axis and the values of the body weights in kg, taken from the Tables 5 and 6, on the y-axis.

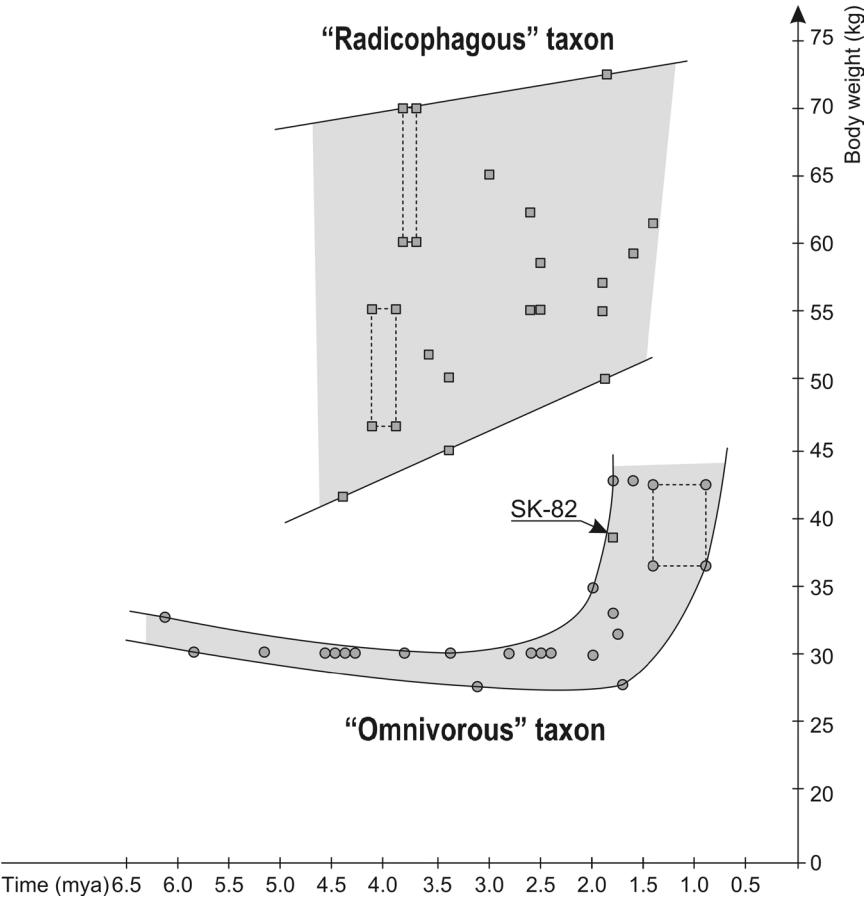


Fig. 1. Changes in the body weights of individuals belonging to the radicophagous and omnivorous taxa

In Figure 1, we can see two areas of different body weights corresponding to the two taxa, confirming the large body characteristic of the radicophagous and small body characteristic of the omnivorous individuals.

The cerebral index

The important difference between the taxa is the level of hominization of their individuals, determined by CI, calculated according to Eq. (3).

We mapped the phyletic lines of both taxa, according to their CI, on a coordinate plane. For this, we plotted the time scale in mya on the x-axis and CI values, from Tables 5 and 6, on the y-axis.

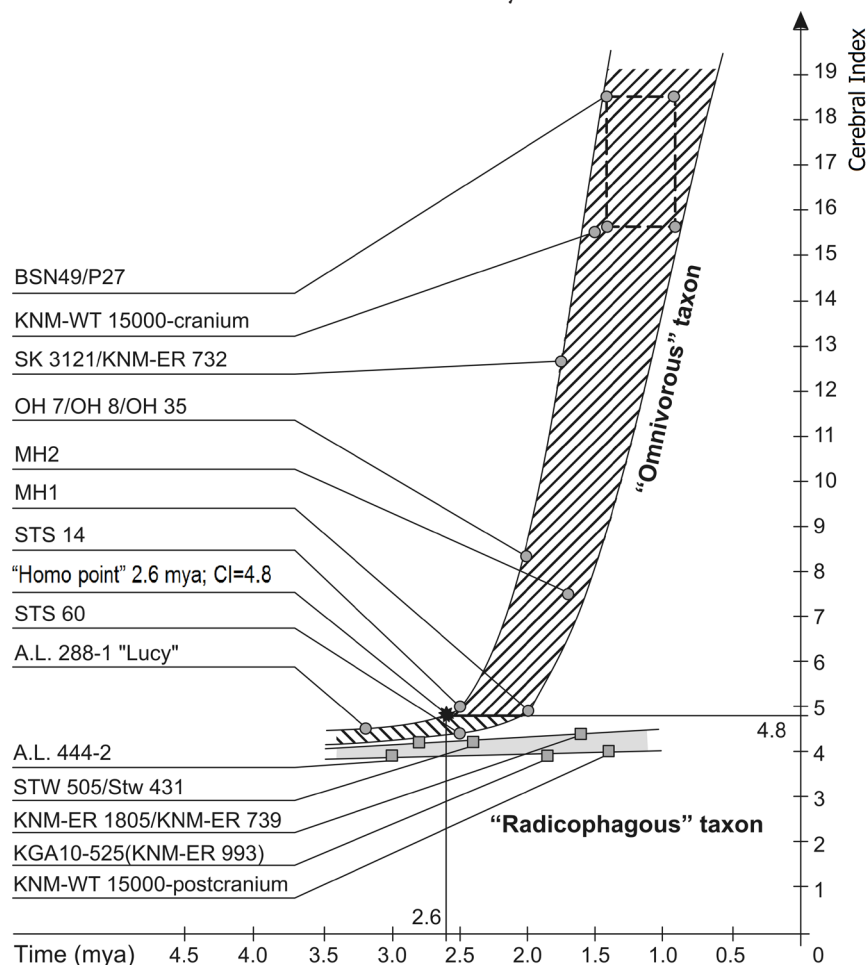


Fig. 2. Graphical representation of the cerebral index changes in the radicophagous and omnivorous taxa

Figure 2 shows that the taxa CI value areas form two phyletic branches, which lie close to each other in the 3.2–2.5 mya interval, almost in contact at CI = 4.4. Following this, the omnivorous taxon branch begins to grow exponentially, indicating a substantial increase in hominization.

The distinctive features of hand morphology and stone tools

Note that the characters with low reproduction weight were not considered.

We considered the peculiarities of hand morphology observed during the study period and the emergence of stone tools in the paleontological history of bipedal primates, which are directly connected to each other.

BAR 1901'01 *O. tugenensis* from 6.2–5.65 mya, the earliest member of the omnivorous taxon, displayed a dorsopalmar flatness of the thumb distal phalanx and mediolateral expansion of the apical tuft in its distal area, providing evidence of the presence of digital pulps on finger tips, which increases the surface of contact with objects being manipulated (Almecija et al. 2010).

Besides, the pollical distal phalanx (PDP) of BAR 1901'01 specimen showed the pronounced insertion of the musculus flexor pollicis longus, with a marked asymmetry toward the radial side (Almecija et al. 2010). When any object being manipulated is gripped by the hand and pressed into the palm by the fingers, this muscle allows additional grip on the object gripped, by means of the pressure from the thumb in the opposite direction (termed “power grip” by J.P. Napier). This showed that the use of bones and sticks as instruments (termed as “osteodontokeratic culture” by R. Dart) was a usual practice even among the earliest omnivorous taxon individuals.

In particular, a high level of robustness of the apex and diaphysis of the distal phalanges was observed in the thumb of the more recent OH 7 specimen of an omnivorous taxon individual from *H. habilis* hypodigm (1.75 mya). Its PDP robusticity index was $MLT/L = 0.611$ (Almecija et al. 2010), where MLT is the mediolateral width at the pollical tuft and L is the length of the PDP. This was considerably higher than that of BAR 1901'01 ($MLT/L = 0.43$), testifying to the increased role of the thumb in the daily activities of the omnivorous taxon individuals with the course of time. Such a feature of the thumb would provide a stable and powerful opposite pressure through the pad of its apical tuft, allowing a grip on objects of manipulation between the pad of the thumb and pads of the other fingers, termed as “precision grip” by J.R.J. Napier.

The evidence of the physiological abilities of the hands, and the ability to manipulate them, was found in the Sidi Hakoma layers aged 3.42–3.24 mya from Dikika site, Ethiopia, where the use of stones for defleshing ungulate carcasses was observed (McPherron et al. 2010).

The analysis of the cut-marks and percussion marks on the bones did not display any correlation between the shape of the stone edge used and the type of damage inflicted by it, which enabled McPherron et al. (2010) to suppose that stone tools had not previously been prepared. Yet, the coarse-grained stones used did not reflect the tool anisotropy necessarily observed in tools prepared with the chip-off method under the “Oldowan” industry.

The first collection of stone tools, found in Lomekwi Member (3.3 mya) of the Nochukui Formation, west of Lake Turkana, northern Kenya (Harmand et al. 2015), was also from this age. Total 149 artifacts made from stones of different rocks, of various shapes and sizes, from 1 cm plate to very big (15 kg) cobbles and cores were registered. The presence of anvils and precursors indicated the means by which the sharp edge of the core was accessed—splitting the stones by hitting them together (Harmand et al. 2015). The type of sharp edge and the average weight and rock of the stone tools correlated with the marks inflicted by tools on the bones of ungulates, found in the layers dated 3.42–3.24 mya at the Dikika site, Ethiopia (McPherron et al. 2010).

Technological and morphological differences between the knapping method and a later flaking-oriented technology led to it being named as “Lomekwian” (Harmand et al. 2015).

In our opinion, this technique of crushing stones, which did not assume manual formation of a sharp edge, illustrates the development of the final stage of the osteodontokeratic culture, a culture that used improvised objects, and precedes the manufacturing techniques of “true” tools from the “Oldowan” industry.

The first emergence of “true” instruments was registered from 15 sites in the Kada Gona basin of the Awash affluent, Ethiopia, where more than 3000 stone artefacts made according to the “Oldowan” technology were found in the layers aged 2.6–2.5 mya (Semaw 2000).

The processing of animal carcasses using instruments raised the question about which taxon could have been responsible for making the stone tools. Taking into account that terrestrial radicophagous type of teeth fail to process the elastic tough flesh food (Lucas and Peters 2000) and its digestion causes protein poisoning, we might exclude the radicophagous taxon members from the list of possible species involved in stone tool-making.

Thus, we might state that the first “true” tools emerged around 2.6 mya and correlated with the increasing cranial volume and evolution of the hand of the omnivorous taxon individuals.

The lack of morphometric data on the PDP of the “Gona” population individuals failed to indicate the marginal PDP robusticity index corresponding to $CI = 4.8$, which is why we consider it very important to further study PDP. Nevertheless, Table 7 shows the current PDP robusticity index for various areas of CI values.

Table 7. – Robusticity index pollical distal phalanx (PDP) for various areas of cranial index (CI) values of the omnivorous taxon

Areas of CI values	CI < 4.8 (maternal part)	CI > 4.8 (daughterly part)
PDP index of robusticity	$MLT/L \leq 0.43$	$MLT/L \geq 0.611$

MLT, mediolateral width at the pollical tuft; L, length of the PDP.

VI. Vertical dimension of the deposit system of the species of African bipedal primates

A-is bipedius incertae sp.

The similarity in the locomotor system with unique bipedalism as the mode of locomotion, the supposed closeness (almost touching) of the individual body weight areas (Fig. 1), and the asymptotic type of CI closeness (Fig. 2) of the two taxa under study allowed us to assume a common ancestor of the radicophagous and omnivorous taxa that already possessed bipedalism, establishing their mutual phyletic status as “siblings”.

At the beginning of the study interval (6.2 mya), the taxa were already divided morphologically and trophically, and therefore, their emergence and formation occurred before this time. Although the assignment of the ancestral species was hypothetical, we considered it important to denote it for theoretical systematization and further study.

We named this hypothetical common ancestor of the radicophagous and omnivorous taxa as *a-is bipedius incertae* sp.

The specific name *bipedius*, meaning “two-feet” in classic Latin, reflects the type of locomotion and the standing posture, based on only the feet of the lower limbs.

Note that neither the areal nor the horizons of the deposits of *a-is bipedius* were studied within the frames of this study. We could only assume that this species originated from some unknown arboreal species of the order Primates (Linnaeus 1758).

As the shift of species from arboreal to a bipedal one is connected with its entrance into a new adaptive zone, we could identify *a-is bipedius* species under a new genus, *Bipedius*, following Mayr (1969: 10.5.2).

It should be noted that the necessity for creation of the genus *Bipedius*, within the frames of this research, also had a system character and was designed, mostly, for the verification of the direction of further research.

Bipedius radicophagous sp. nov.

The first radicophagous taxon individuals in the African continent were registered from the deposits aged 5.8 mya and were observed till 1.34 mya, after which they disappeared from the paleontological record, supposedly becoming extinct (Table 5).

Sympatric coexistence of this taxon with its sibling omnivorous taxon during the more than four mya interval indicated that the allochronic radicophagous taxon meets the requirements of the first species character of the VDDS triad—reproductive community.

The radicophagous taxon diet specialization testified the isolated ecological niche as the second character of the VDDS triad.

Phyletic branches of the radicophagous taxon, based on body weights (Fig. 1) and CI (Fig. 2), pointed out their canal type of reproduction. Among all other morphometric characters of this taxon (Tables 3, 4), none appeared to have split and led to the emergence of a separate reproductive history. This proved the channel reproduction type of the taxon gene pool and its isolated character, which meets the requirements of the third character of the VDDS triad.

Thus, the allochronic radicophagous taxon, in the interval under observation, met all requirements of the VDDS species character triad, which could presently be assigned to the new species: *Bipedius radicophagous* **sp. nov.**

The word radicophagous means “root, rhizome, and bulb eater” in Latin, corresponding to the specialization of the feeding habit and verifying a terrestrial habitat type. The genus *Bipedius* presupposed the origin of a supposed ancestral genus-creating species, *a-is bipedius*, and its attribution to the *Bipedius* genus formed by this species.

The areal of this species was in the African continent, where it was present in the deposit horizons of 5.8–1.34 mya.

The diagnosis includes differential characters marked in Tables 3 and 4 for the radicophagous taxon, and the limit of CI was <4.4 (Fig. 2).

However, so far no individual has been found that would reflect simultaneous belonging to the species and genus, which is why it was impossible to identify any type specimen.

The *B. radicophagous* hypodigm comprises specimens enumerated in Table 5.

To include separate specimens of the various original species in a new *B. radicophagous* hypodigm, their nomenclature title should be changed, so that among the majority of the members of these original species there would also be specimens corresponding to the sibling omnivorous taxon.

Mayr (1969: 13.1.1) admitted the inevitable changes in the titles, even in cases where the original sibling species were described under one name.

To preserve the stability and universality of nomenclature and to avoid confusion, in case the name denotes more than one taxon, not affecting the availability of the name (ICZN 1999: Article 17), we suggest that the original status be lowered to subspecies level for all specimens included in the *B. radicophagous* hypodigm and establish a trinomen for them.

It is recommended to use parentheses around the author's name to indicate the changes in the combination of generic and specific names, preserve the authorship when changing the status, and mention the author's name in the original description of the specimen, if cited (ICZN 1999: 50.3.2.; 51.3.).

For example, for the incisor of ALA-VP-2/10, originally of *Ar. kadabba* Y. Haile-Selassie, included in the *B. radicophagous* hypodigm (Table 5), we should use the following name: *Bipedius radicophagous kadabba* (Y. Haile-Selassie) or *B. r. kadabba* (Y. Haile-Selassie).

Bipedius manusciensis **sp. nov.**

The omnivorous taxon was studied in the 6.2–0.9 mya interval, but its phyletic branches, based on body weight and CI, were compound.

Figure 1 shows the consistency of the individual body weight in the 6.2–2.5 mya interval. Figure 2 conditionally shows the consistency of the CI values in the 3.2–2.5 mya interval, but bearing in mind that the area of CI values during this period was asymptotically near the area of *B. radicophagous* values, we might claim that the CI had constant values during the whole period of 6.2–2.5 mya.

However, starting from 2.5 mya, the omnivorous taxon indicated an increase in the body weight, ECV, and especially, considerable increase in the CI (Fig. 2). It should be remembered that 2.6 mya some population of the omnivorous taxon inhabited the region of current basin of Kada Gona River, Ethiopia ("Gona" population) and produced the first stone tools (Semaw 2000).

If on the time scale of phyletic branch of the omnivorous taxon (Fig. 2), based on CI data, we plot the point of abscissa $t = 2.6$ mya, then the upper border of this branch would show the ordinate value as $CI = 4.8$ and a horizontal line through it would divide the phyletic branch into two areas of values. The taxon members involved in stone tool-making would be included in the area $CI > 4.8$, whereas those who failed to do it would be included in the area $CI < 4.8$ (Fig. 2). Actually, the omnivorous taxon, at the

time point 2.6 mya, underwent a split with respect to the morphometric character complex: weight, cranium, and hand morphology, and especially, more evident—the CI.

Thus, the allochronic omnivorous taxon that existed from 6.2 mya without any changes in the morphotype $CI < 4.8$ (maternal) gave rise to a new morphotype with $CI > 4.8$ (daughterly), which developed its own history of reproductive evolution (Fig. 2).

Investigating the maternal part of the omnivorous taxon, in compliance with the nomenclature category, we might claim that its morphological character complex in the 6.2–2.6 mya interval meets all requirements of the species character triad of the VDDS. Its reproductive isolation from sympatrically coexisting sibling species *B. radicophagous*, specific omnivorous diet and ecological niche, and consistency between all diagnostic characters (Tables 3, 4), such as unramified area of the individual body weight and CI (Figs. 1, 2), all proved a channel reproduction type of maternal gene pool of the taxon.

Note that from 2.6 mya, the coexistence of the maternal morphotype bearers, STS 60 (2.5 mya) with $CI = 4.4$, and the daughter bearers, STS 14 (2.5 mya) with $CI = 5.0$, was observed on the phyletic line for some time period, but the maternal morphotype completely disappeared from the paleontological record by 2.0 mya, supposedly becoming extinct (Fig. 2).

All this evidence enabled us to assign the maternal part of the allochronic omnivorous taxon, observed between 6.2–2.0 mya and restricted by $CI < 4.8$ (Table 6a), to the new species: *Bipedius manuscirens* **sp. nov.**

The genus *Bipedius*, which was formed by *a-is bipedius*, now includes this species together with its sibling species *B. radicophagous*.

The specific name *manuscirens*, meaning “manipulating hands” in Latin, reflects the use of objects at hand—sticks, bones, and stones—using hand morphology (Almecija et al. 2010), stone tool-inflicted marks on the bones of ungulates (McPherron et al. 2010), and stone artifact collection (Harmand et al. 2015).

The entire African continent was the areal habitat of *B. manuscirens* from 6.2–2.6 mya, but with the emergence of the “Gona” population in 2.6 mya, the species started to reduce and by 2.0 mya the species disappeared from paleontological record.

The diagnosis of species includes differential characters presented in Tables 3 and 4 for the omnivorous taxon, restricted according to $4.4 < CI < 4.8$ and PDP robusticity index close to $MLT/L \leq 0.43$ (Table 7).

The species specimen type was appointed a partial skeleton of AL 288-1 (Lucy), recovered by D.C. Johanson and T. Gray from the Afar site, Ethiopia, in 1974. The AL 288-1 individual possessed both a generic character—bipedalism and a specific trophic character—omnivorous diet and served as a model for morphometric measurements, enabling us to identify it as the incomplete remains of its species.

The *B. manuscirens* hypodigm comprises specimens enumerated in Table 6a.

The uniting of the *B. manuscirens* hypodigm with separate specimens of various original species exactly repeats the situation with its sibling species, *B. radicophagous*, when the original names were found to denote more than one taxon, requiring alteration of its nomenclature. Therefore, to preserve the availability of the name (ICZN 1999: Article 17), we suggest to establish a trinomen for all specimens included in the *B. manuscirens* hypodigm. However, to indicate the change in the generic and specific name combination and preserve the authorship when altering the range, one should use parentheses around the author's name (ICZN 1999: 50.3.2.; 51.3.).

For example, for the lower right jaw of ALA-VP-2/10, originally of *Ar. kadabba* Y. Haile-Selassie incorporated in the *B. manuscirens* hypodigm (Table 6a), one should apply the following name: *Bipedius manuscirens kadabba* (Y. Haile-Selassie) or *B. m. kadabba* (Y. Haile-Selassie).

Homo communitas **sp. nov.**

Around 2.6 mya, the “Gona” population of *B. manuscirens* of the omnivorous taxon inhabited the region in the modern basin of Kada Gona River of the Awash affluent, Ethiopia and began making the first stone tools using the “Oldowan” technology (Semaw 2000). Here, we did not study the shift in the mechanism, from tuning the improvised objects at hand to making the tools themselves. However, the divergence of the “Gona” population showed a high speed of morphometric changes in the skeleton, particularly the CI (Fig. 2).

Having more adaptive advantage than the maternal species, the “Gona” population, during the process of radiation, began to expand its areal habitat, and by 2.0 mya (Fig. 2) had substituted the maternal species in the African continent, which allowed us to consider a nomenclature status for this part of the omnivorous taxon.

First, the degree of the morphological divergence, for example, the brain architecture demonstrated by KNM-ER 1470 (Holloway et al. 2004), undoubtedly reflected a genetic and reproductive isolation of the “Gona” population from the maternal species *B. manuscirens*, fulfilling the first character of the VDDS triad.

Second, the stone tool-making ability was an extension of the trophic base and led to the formation of a new, dramatically different ecological niche.

Third, the phyletic branch of the “Gona” population, separated from the maternal species, did not display any characters that would have provided evidence of a further split of the morphotype. Moreover, the expressed exponential nature of the phyletic branch depicted a channel character of the reproduction of morphotype and gene pool.

Within the studied time interval, the daughter part of the omnivorous taxon did not reach the stabilization of its characters, described as “evolutionary intermediacy,” and was not reflected in the nomenclature anyhow (Mayr 1969). However, it met all the requirements of the species character triad of the VDDS, which allows us to reflect on its nomenclature level and assign it to a new species: *Homo communitas* **sp. nov.**, for a rather long period (not less than 1.7 mya) of its isolated reproductive existence.

It should be noted that the stone tool-making and the shift in the character from the bipedal gatherer-scavenger to the active explorer of the environment meant that it had entered a new adaptive zone. Based on the work by Mayr (1969: 10.5.2), we could identify a new genus-creating species, when creating a new genus. Besides, starting from the deposits of 2.4 mya, when registering bipedal primate species with increased brain size or associated with stone tools, the researchers begin to refer them to the *Homo* genus (Table 1). From the results of the current study, it was discovered that the emergence of both these characters correlated with $CI > 4.8$ for a newly assigned species; therefore, we leave the generic name *Homo* to be used in the context of a modern, generally accepted meaning.

Additionally, on the phyletic CI branch of the omnivorous taxon (Fig. 2), we marked the time (2.6 mya) of the making of the first stone tools by the “Gona” population as “Homo point”, which we correlated with $CI = 4.8$.

The specific name *communitas*, from Latin meaning “life on the communal basis,” reflects the rather complicated process of making, storing, and using stone tools, implying a collective mode of activity.

Having emerged 2.6 mya in the region of the basin of the Kada Gona River in Ethiopia, *H. communitas* occupied the entire African continent by 2.0 mya, where it was recorded in the deposits of up to 0.9 mya, which was restricted by the time frame of this research.

The diagnosis of *H. communitas* was a relative brain increase determined by $CI > 4.8$, established using Eq. (3), and tool-making ability determined by the “Oldowan” technology, correlating with the PDP robusticity index of $MLT/L \geq 0.611$ (Table 7).

Unfortunately, during the 2.6–0.9 mya interval, no single, or rather complete fossil, reflecting the determining characters of *H. communitas* was found, which is why we could not designate any type specimen to this species.

The *H. communitas* hypodigm comprises specimens enumerated in Table 6b.

The inclusion of separate specimens of various original species in the *H. communitas* hypodigm presented the same situation as mentioned above, requiring alteration of its nomenclature. Hence, so as not to affect the availability of the original name (ICZN 1999: 17.1), the use of trinomen is suggested for all specimens within the *H. communitas* hypodigm.

In addition, to indicate the change in the generic and specific name combination and preserve the authorship when altering the range, one should mention the author’s name in parentheses (ICZN 1999: 50.3.2.; 51.3.).

For example, to include STS 5, originally from *A. africanus* R. Broom, in the *H. communitas* hypodigm (Table 6b), one should apply the name: *Homo communitas africanus* (R. Broom) or *H. c. africanus* (R. Broom).

VII. Results

Revision of the characters of the fossilized remains of African bipedal primates showed that the bipedal primates appeared in the paleontological record of the continent from 6.2–5.8 mya, in the form of two morphologically accomplished and trophically and ecologically isolated species: *Bipedius radicophagus* sp. nov. and *Bipedius manuscirens* sp. nov., who supposedly originated from some hypothetical *a-is bipedius* incertae sp. already possessing bipedalism.

The species *B. radicophagus*, with its specialized diet, had existed without any remarkable changes for up to 1.34 mya, maybe a bit longer, and then supposedly became extinct.

The omnivorous species *B. manuscirens* had also existed for a long time with an unchanged morphotype, but 2.6 mya one of its populations began to make stone tools, which involved the alteration of its morphotype, till the appearance of a new species *Homo communitas*. Having adaptive advantage, *H. communitas* spread through the whole continent for the next 0.6 million years, substituting the maternal species *B. manuscirens*, which after 2.0 mya disappeared from the paleontological record.

H. communitas was observed in the deposits till 0.9 mya, which was restricted by the time frame of the present work.

Figure 3 shows the phyletic relation system of species of African bipedal primates, built on a paleontological time scale.

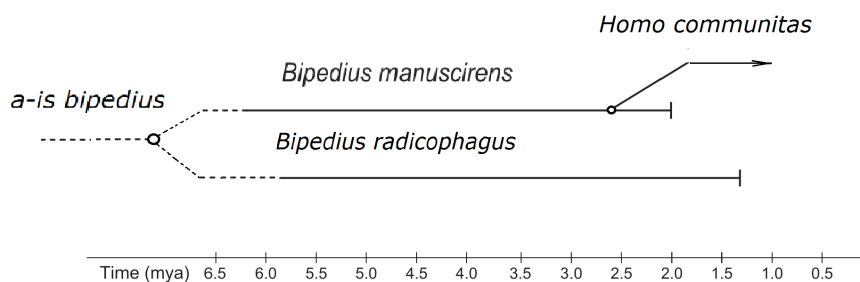


Fig. 3. Vertical dimension of the deposit system of the species of African bipedal primates

VIII. Discussion

8.1 In the course of character revision, four sets of associated fossils were found, which showed a mixed terrestrial-arboreal locomotion type:

- The partial skeleton of ARA-VP-6/500 “Ardi” (4.4 mya) had peculiarities incompatible with bipedalism—the feet were relatively flat and lacked arches and the first toe had a grasping abducted feature.
- The juvenile individual DIK-1-1 (3.35–3.31 mya), together with bipedalism, had gorilla-like scapula and long and curved manual phalanges used for grasping.
- The partial set of bones of the foot of BRT-VP-2/73 (3.4 mya), together with the obligatory bipedalism, showed stable arboreality—the lack of longitudinal pedal arch and abducent hallux capable of grasping.
- The peculiarities of the hand structure of MH 2 (1.977 mya) were connected with a regular arboreal locomotion, and the pedal foot, ankle, and distal tibia morphology suggested that exploitation of the arboreal habitats was an important part of the behavioral ecology.

Taking into consideration that the paleoperiod 4.4–2.0 mya in the African continent was characterized by the emergence of open C4-grasslands and considerable reduction in forests, the emergence of mixed type of locomotion, probably, might be explained by the later forced shift of particular populations of arboreal primates toward terrestrial type. In any case, all the specimens mentioned above require additional investigation.

8.2 Some objections can be expected concerning the ungrounded nomenclatural acts conducted without relying upon the existing classification, especially when assigning species to the genus *Bipedius*.

In the present work, only the African continent was analyzed, and obviously during a rather insufficient time interval, to cover the moment of emergence of the bipedal primates. Therefore, the scientific names were assigned to focus on revealing the most important characters that would be useful to researchers for further studies involving expanded geography and time interval.

In any case, only the ultimate establishment of the phylogenies of bipedal primates will allow for the final nomenclature assignments.

Conclusion

The importance of the current research, in the author's opinion, is the revision of the characters of the remains of African bipedal primates, which allowed us to systematize almost all the African paleoanthropological material of the 6.2–0.9 mya period.

The main directions for further research to establish the phylogenies of the bipedal primates were determined.

The practical value of the application of some of the methods, borrowed or designed by the author, was confirmed and they were useful for the reconstruction of separate morphometric bone remain characters.

We would like to express the awareness that new researches and fossil finds will provide a predictive value for the conducted work.

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S.V. Vyrskiy

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