

Review of the *Homo naledi* Fossil Collection from South Africa Using the Biological Species Concept

Sergey V. Vyrskiy*

3-35, Dali Street Lok Volzhskie, Pristannoye Village, Saratov Region, Russia

Abstract

While analysing the description of *Homo naledi*, it was observed that the founders failed to specify any maternal or other species phylogenetically associated with *H. naledi*. Moreover, the direction of further evolution of the species was not determined, and it was concluded that the species is extinct. Furthermore, exclusively morphometric characteristics of the remains have been used for species diagnostics, which is typical of the methods of the morphological species concept. For a more precise definition of the position of *H. naledi* among other species of the genus *Homo* within the African bipedal primate system, this study attempted to identify the fossil characters that are diagnostically essential from the point of view of the biological species concept. This study helped reveal the age of the fossil collection deposit and concluded that *H. naledi* shares a common origin with other species of the genus *Homo*. In addition, it was shown that *H. naledi* had a hand structure that was progressive for its time and a high cerebral index, which raises doubts regarding the validity of its extinction.

Keywords: Biological species concept; *Homo naledi*; Bipedal primates; Omnivorous; Radicophagous

Introduction

The species *Homo naledi* is represented by a massive collection of fossils excavated within the period between 2013 and 2014 in two chambers of the Rising Star cave system located in the Bloubaan River valley, Gauteng Province, South Africa [1,2]. To date, the collection includes two sets of fossils (1,550 and 131 samples), containing several partial or complete anatomical elements, many of which consist of several refitted specimens.

The collection was attributed to the genus *Homo* by the founders, using the parameters set by Berger [1], who stated that, “all dental crowns (n=179) are hominin”, “these remains represent a minimum of 15 hominin individuals, ... as indicated by the repetition and presence of deciduous and adult dental elements,” and “the collection is a morphologically homogeneous sample that can be attributed to no previously known hominin species.” As far as the whole collection was concerned, it should “... include traits not found in any other hominin species yet described. These considerations strongly indicate that this material represents a single species, and not a commingled assemblage.”

Literature Review

While analysing the description of the *H. naledi* species, it should be emphasized that the researchers exclusively used the morphometric properties of the fossils for the phyletic weighting assessment of the fossil characters, which is necessary for species diagnostics. This method, although typical for the morphological species concept, is widely used in horizontal systematics to traditionally categorize all existing species.

However, a comparative analysis of the morphometric similarity (and differences) between the individuals widely scattered along the paleontological time scale does not establish their mutual affinity or restore their phyletic lines. Thus, the selection of the species concept and corresponding method for diagnostic “weight” assessment of the characters under such circumstances failed to determine the maternal or affiliated species for *H. naledi*. This inability in determining the trend for further evolutionary development led to the conclusion that the species became extinct.

Only the biological species concept (BSC) distinguishes the relationship between individuals and taxa in the vertical dimension of deposit systematics. This can be established with the help of a comparative analysis of fossil characters, with respect to the three characters recommended for establishing species in BSC: A reproductive community, an ecological unit, and a genetic unit [3]. By uniting the individuals in the family relation system, we have a real possibility of building phyletic lines and restoring phylogenesis. All the mentioned facts allow us to specifically follow the BSC while researching paleontological bone remains.

The overall characters of the African bipedal primate fossils

In this study, we seek to distinguish the bone remains characters of *H. naledi* corresponding to those of the species in the BSC, using the description of some diagnostically significant fossils from the collection. By comparing them with similar characters of other species, we could correctly determine the position of *H. naledi* within the African bipedal primate system. Thus, we must primarily consider the most common characters of the African bipedal primate fossils during the Australopithecus period (1–6 million years ago (mya)) that correspond to the characters of the species in the BSC.

While studying dentition and skull structures, Robinson [4] was among the first to distinguish the two types of craniodental architectures and link them to the type of diet. He divided all bipedal primates into two groups of species: *Paranthropus* (plant-based diet) and *Australopithecus* (omnivorous diet including a significant proportion of meat). The difference in these diets exists at the dichotomous level.

*Corresponding author: Sergey V. Vyrskiy, 3-35, Dali Street Lok Volzhskie, Pristannoye Village, Saratov Region, 410505, Russia, Tel: +7 9173224329, +7 9042408075; E-mail: sergey.vyrskiy@gmail.com

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The dentition of the *Paranthropus* group fails to process solid, elastic flesh food [5], and the lack of meat products causes a bone pathology (porotic hyperostosis) among the *Australopithecus* group [6].

Asfaw [7] evidently pointed out two adaptive specimens of bipedal primates that existed 2.7 mya. McHenry [8] divided them into 2 groups or morphs according to their weights: one group weighing 29 kg and the other weighing 45 kg. Moreover, Steudel [9] distinguished two groups of bipedal primates based on the average weights of 36 kg for a gracile build and 56 kg for a robust build. Finally, Vyrskiy [10] distinguished bipedal primates into an omnivorous taxon (weighing 27.6–43 kg), and an herbivorous taxon consisting of an amyllum-based diet (43–73 kg). The Jarman-Bell principle states that dietary quality (i.e., energy and nutrient density of the diet) is inversely related to body mass, thereby correlating small-bodied individuals to an omnivorous diet and large-bodied individuals to a terrestrial amyllum-based diet. The morphology of the femur and its cross-sectional dimensions allowed Bleuze [11] to divide all bipedal primates into two taxa: The first group included contemporary people and early *Homo* individuals, whereas the second group embraced the *Paranthropus* individuals, which was characterized by a more elementary type of bipedalism.

The revision of the African bipedal primate fossil characters from 6.2–0.9 mya showed a large-bodied plant-eating taxon was present on paleontological records from 5.8–1.34 mya, after which it disappeared and supposedly became extinct [10]. For convenience, the term radicophagous was attributed to this taxon, which demonstrated its terrestrial amyllum-based diet, consisting of cereal grains, roots, bulbs of field herbs, and coastal plants. The conventional term omnivorous was attributed to the small-bodied omnivorous taxon observed in paleontological records since 6.2 mya, reflecting the significant proportion of meat in its diet. It should be noted that early individuals of the omnivorous taxon, such as the specimen BAR 1901'01 from the *O. tugenensis* hypodigm (6.0–5.7 mya) [12], possessed digital pulps on its fingertips to firmly grasp and manipulate objects by just pressing them to its palm with the help of its fingers. Moreover, the flexor pollicis longus muscle allowed objects to stay in place via the opposing pressure of the thumb, i.e., a “power grip” was established, as defined by J.R. Napier [13]. This showed that the use of bones and sticks as instruments (termed as “osteodontokeratic culture” by R. Dart) was common practice even among the earliest omnivorous taxon individuals.

The first proof of stones used to deflesh ungulate carcasses [14], and the first collection of stone tools appeared 3.3 mya; the sharp edges of these tools, which were necessary for defleshing, were made using the knapping method [15]. The most important indicator reflecting the level of hominization of the individuals is represented by the cephalic index, which is the ratio of the brain weight to body weight, or by the cerebral index (CI), which is the ratio of the endocranial volume (ECV) to the body weight. When calculating the CI as per Roginsky's method in 1977 with a certain correction using the following equation: $CI = (0.91 \times ECV)^2 / P_b$, a CI value <4.4 for the radicophagous taxon and a CI value >4.4 for the omnivorous taxon will be obtained [10].

A certain population of the omnivorous taxon inhabited the region near the current basin of the Kada Gona River in Ethiopia 2.6 mya and began to make the first “true” tools from the “Oldowan” industry [16]. This population began to expand its areal habitat while adaptively radiating outwards from this area, and substituted the maternal taxon from the paleontological records in the African continent within 2.0 mya [10]. Therefore, the individuals of the affiliated population exhibited an increase in body weight and ECV from 2.5 mya and a considerable

increase in CI (up to 18) by 0.9 mya [10]. Thus, researchers started to register the species associated with stone tools using the generic name, *Homo*.

The Review of *Homo naledi* Fossil Collection

While studying the collection of fossils from *H. naledi*, let us consider the descriptions of some fossils in the frames of correspondence of their characters to those of the BSC.

1. The maxillary and mandibular teeth of the LES1 cranium exhibited moderate occlusal wear on the second and third molars, near complete dentine exposure on the occlusal surfaces of the first molars, and substantial removal of the occlusal detail of the anterior dentition [2]. Extreme occlusive wear of the mandibular teeth in U.W. 101–361 from the DH3 paratype [1] also provided evidence to categorize these individuals to the large-bodied plant-eating taxon, radicophagous.

2. By approximately assessing the femoral head diameter (FHD) of the U.W. 102a-001 specimen shown [2] is expected to be ≈ 37 mm, we can obtain body weight $P_b = (FHD + 5.3)^2 / 41.5 = 43$ kg, using the formula Equation 1 [10], by generalizing the values [17]. The value obtained is typical for the large-bodied plant-eating taxon, radicophagous [10]. The inclusion of the sample to this taxon is explained by the cross-section of the round-shaped (not oval form) diaphysis at a distance of 12 mm from the greater trochanter or approximately 75% of its full length from the distal end [2] details the periosteal diaphysis diameter as 30 mm and the diameter of medullary canal as 10 mm. By calculating the total periosteal area, $TA \approx 707$ mm², and the medullary canal area, $MA \approx 79$ mm², we can calculate the cortical area index, $\%CA = [(TA - MA) / TA] \times 100 = 89$, using the formula established by Bleuze [11]. This value also corresponds to that of the plant-eating individual [10].

3. To reconstruct the conjoined femoral bone of the U.W. 102a-003 and U.W. 102-004 having a total length of 375 mm, [2] used a similar sized sample from KNM-ER 1481 that had a length of 396 mm [18] and weighed approximately 57 kg [17]. Thus, the weight of such a compound individual with conjoined bones, U.W. 102a-003 and U.W. 102a-004, was assumed to be similar to that of the sample; it is suggestive of the fact that it was large-bodied. The cross-sectional morphology of the sample, U.W. 102a-004, observed in [2] was identical to that of the sample, U.W. 102a-001, of the plant-eating individual, and refers the conjoined femoral bones, U.W. 102a-003 and U.W. 102a-004, to the taxon radicophagous.

4. The occlusive characteristic of the mandibular fragment U.W. 101-377 demonstrates a good morphology of the omnivorous diet type. The height and width of the mandibular corpus at the M1 crown was assessed to be ≈ 25 mm and ≈ 19.5 mm, respectively [1]. This result also demonstrated the omnivorous diet type [10]. This morphology is also confirmed by the sharp canines in the occlusive U.W. 101-985, U.W. 101-1126, and U.W. 102b-511 samples [2].

5. The medio-lateral width at the pollical tuft (MLT) reflects the specimen's ability to hold and manipulate objects by pressing them between the pad of the thumb and pads of the other fingers, also termed as “precision grip” by J.R. Napier. The robusticity index of the pollical distal phalanx (PDP) was observed to be $MLT/L = 0.43$ from the sample BAR 1901'01 (6.0–5.7 mya) of the *O. tugenensis* hypodigm, which corresponded to the “osteodontokeratic culture”, as elucidated by R. Dart. The sample OH 7 (1.75 mya) of the *H. habilis* species [19] exhibited an index of $MLT/L = 0.611$ [13], which corresponded to the Oldowan industry. Therefore, the robusticity index of the PDP for the Dinaledi hand 1 (H1) found from [1] was calculated to be $MLT/L \approx$

10 mm/15 mm=0.67, which possibly corresponds to the Acheulean industry (L, the length of PDP).

6. The approximate FHD of U.W. 101-1391 measured [1] was estimated to be 29 mm. Using the formula in Equation 1, the body weight of the individual was calculated to be no more than 30 kg, which suggested that these individuals were small-bodied; the oval-shaped cross-section of the diaphysis also corresponded to the omnivorous taxon. Not excluding the body weight value of 40.8–45.3 kg, which was obtained by comparing the FSTpr (femoral sub-trochanteric m-l and a-p breadths) of this individual against the FSTpr of contemporary humans [1], we consider the size of the femoral head to be the most appropriate for calculating body weight [17].

7. An 85 mm proximal shaft fragment of a U.W. 102a-002 right humerus comprises approximately 50–60% of its total length [2]. Thus, the full length of the humerus is \approx 180 mm, appropriate for a small-bodied omnivorous individual such as A.L. 288-1 “Lucy” [20], which assumes the same height (105 cm) and weight (27.6 kg). If we presume that the omnivorous small-bodied individuals, U.W. 101-1391 and U.W. 102a-002, weighed near 30 kg and corresponded to the smallest volume of 465 cm³ as seen in composite craniums DH3 and DH4, then the cerebral index of this complex individual will be $CI=(0.91 \times 465 \text{ cc})^2/30000 \text{ gr}=5.97$. This proves the earlier appearance of these characters within the phyletic line of the omnivorous taxon i.e., \sim 2.3 mya [10].

Discussion and Conclusion

The following conclusions can be drawn from the above data:

1. We observed the fossils of the bipedal individuals categorized under the omnivorous and radicophagous taxon within the *H. naledi* species hypodigm. They were found to belong to different ecological niches and are believed to have coexisted sympatrically over the African continent 5.2–1.34 mya. This fact classifies them as different species according to the BSC and prompts the exclusion of the radicophagous taxon samples from the *H. naledi* hypodigm.

2. The omnivorous taxon individuals demonstrated a cerebral index of 5.97, obtained by the bipedal individuals not earlier than 2.3 mya, and a robust index of the distal phalanx $MLT/L \approx 0.67$, acquired about 1.75 mya. This determines the lowest limit of the *H. naledi* from the collection of fossils. The radicophagous taxon individuals became extinct about 1.3 mya on the continent, and their presence in the collection determines the highest limit of the interval deposit.

3. It should be noted that there are fossils in this collection that were deposited over succeeding time periods i.e., 0.41–0.24 mya [21], which need to be researched separately.

4. There is not enough evidence to believe that *H. naledi* became extinct because their functioning hands were more progressive than those of specimens like the OH 7 *H. habilis* species (1.75 mya), which allowed them to make tools in Acheulean industries.

5. Comparing the morphometric differences between the *H. naledi* species and the other bipedal primates of the genus *Homo*, we see that the differentiating characters in previously mentioned works [1,2] exhibit no significant value, but truly correspond to the polytypic species concept, as elucidated by Mayr [3]. Thus, we can conclude that

the species represent a polytypic taxon of a single bipedal species in the genus *Homo*, which occupied the African continent from 2.6–1.0 mya.

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