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An »Open Source« Perspective of Earliest Hominid Origins

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A B S T R A C T

The »Open Source« Perspective deals with the spatio-temporal distribution pattern of Miocene hominids and suggests a pan-African perspective on the evolution of bipedalism. The shrinking of the rainforest from the Middle Miocene resulted in a selection pressure that was similar along its wide-stretched margin. The earliest hominids might represent co-existing geographic variants.

Key words: *hominids, bipedalism, rainforest, Miocene*

Introduction

The time period between 10 and 5 Million years ago is crucial for our understanding of the origin of earliest hominids. Until recently this time period was almost void of hominid remains, and the hunt for the missing link was one of the major goals in paleoanthropology. Numerous debates and hypotheses had focused on the influence of the development of the East African rift valley on early human evolution[1,2]. The situation, however, has changed considerably with recent discoveries in the time frame of 7 to 5 Ma in Kenya, Ethiopia and Chad. Therefore, we propose to a new look at the pan-African biogeographic pattern emerging from these new discoveries and their significance for interpreting the earliest stages in hominid evolution.

Earliest hominids

For decades there have been only a few supposed hominid fossils, from sites older than 5 Ma, such as Lothagam 5.5 Ma[3], Lukeino 6.5 Ma[4] and Ngorora 12–9 Ma[5]. The recent discoveries of *Orrorin tugenensis*[6] in Kenya, *Ardipithecus kadabba*[7,8] in Ethiopia and *Sahelanthropus tchadensis*[9] in Chad, however, extended considerably the temporal and spatial knowledge of earliest hominid ancestors

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in Africa. The emerging picture makes the prophecy of P. V. Tobias[10] come true, that »the birth of the hominids was a pan-African phenomenon. The uncovering of those birth-stages requires a pan-African approach, free of regional or territorial preconceptions and predilections«.

Although the fossil record is fragmentary, the geographical position of fossil sites alone is sufficient information to start thinking about the bigger picture. It is often stated that the chronological order of fossils is an independent key factor in paleontological data, yet the geographical data are similarly valuable, at least on a large scale approach. Before elaborating on this point, we need to take a look at the morphological basis for reconstructing the earliest stages of hominid evolution. Morphological features which change significantly and early in this process, include mainly those of dentition and those associated with locomotion (both evident from recent discoveries).

Dentition

Haile-Selassie[8] used the functional canine-premolar (C/P3) honing complex present in modern and fossil apes to distinguish the older *Ardipithecus kadabba* from the younger *A. ramidus*. The honing and occlusal contacts between upper canine and lower canine/premolar complex are used to differentiate a more primitive from a derived stage of evolution. Since the age of *A. kadabba* is estimated to 5.6–5.8 Ma and *A. ramidus* around 4.4 Ma it seems that the earlier *Ardipithecus* shows more primitive features reflecting a stage closer to the common ancestor of apes and humans, probably more ape-like in morphological tooth characters. However, Haile-Selassie gives a comparison of all Miocene hominid canine/premolar complexes known so far in order to demonstrate the primitive conditions in *A. kadabba*. Only one partial upper canine of *Sahelanthropus tchadensis* and a complete tooth crown of *Orrorin tugenensis* are known. The single *Orrorin* molar is not worn enough to assess a possible honing condition[6] and the few elements of the C/P3 complex known from *S. tchadensis* are described as showing no sign of functional honing[9]. Furthermore, *Ardipithecus* teeth resembling a thin enamel condition[11,12] a typical ape-like feature of the dentition, not visible in other Late Miocene hominids[6,9]. The enamel of molars in *Sahelanthropus* is thinner than in most later hominid species and some Miocene hominoids[9].

Apart from differing functional interpretations, in this context it might well be argued, that these interspecific differences represent geographic variants independent of their exact phylogenetic relationships.

Locomotion

The evolution of the unique human-like bipedalism was considered to be closely linked to the development of the geological megastructure of the Great Graben System in Eastern Africa, therefore the rift valley seemed to be a playground for the evolution of hominids. During the complex rifting-uplifting processes appearing at about 8 Ma ago, the early hominids were supposed to have evolved in geographic isolation on an »island« with its own specific climatic conditions[2]. As a result of crustal uplifting and subsidence combined with common volcanic activity more and more savannah-like habitats occurred in Eastern Africa, whereas the rainforest was limited to the west of the western rift margin. Primate species with an erect posture, with less prognathic jaws and smaller canines were postulated to have evolved in a rain-shaded area in Eastern Africa, thus in dryer open woodland to savannah habitats, according to the »East Side Story« hypothesis of Coppens[1].

Today, the findings of late Miocene *Sahelanthropus* as well as Pliocene *Australopithecus bahrelghazali*[13] show that hominids lived far west of the East African rift valley during probably the last 7 Ma years. This suggests that the distribution pattern of hominids geographically and chronologically is much more complex than previously thought. Similarly, there is no comprehensive model to illustrate the complex morphological changes in locomotion, and particularly the mode of transitions from a basic stage, like knuckle walking, to the advanced form of habitual bipedalism.

As is the case in dental morphology, we therefore hypothesize, that differences also existed in the modes of bipedal locomotion between different geographic variants of earliest hominids. Environmental change, however, was at least one of the processes most likely linked to the origin of upright walking. Therefore, it is crucial to assess the evidence available for late Miocene African changing habitats.

The Miocene Gap

Paleoenvironmental reconstructions of Late Miocene to Early Pliocene localities in Eastern and Southern Africa are very diverse and range from savannah via mosaic habitats to woodland and forest. One of the underlying problems is, that an examined unit is often taken as being representative of the whole locality and the effect of time-averaging is being underestimated. White[14,15] underlined the very powerful taphonomic biases of habitat reconstructions, especially in the depositional context. Similarly, Behrensmeyer et al.[16], demonstrated the effects of the biases of sampling variability, stating, that high numbers of fossil localities per time unit and high FADs (First Appearance Datum) and most probably do not represent a classic biological signal. Therefore, our current knowledge might only stand for an approximation of the Miocene distribution of habitats.

According to Axelrod and Raven[17], Africa's modern flora was virtually extant by the border from Late Miocene to Early Pliocene. O'Brien and Peters[18] noted that Pliocene rainforests of the equatorial region – associated with the Guineo-Congolian phytochorion – could have extended uninterruptedly from West Africa to (what is today) the Eastern Rift Belt, at the same time also stretching further to the north and south. This humid area was sourrounded by broadleaved woodland and drier transition forests of the Sudanian and Zambezian phytochoria. Where the Western Rift Belt is situated today, no big mountain chains existed prior to the Late Pliocene. Not until the Late Pliocene to Early Pleistocene, tectonic and volcanic activity favored regional fragmentation, especially in Eastern Africa.

By the Middle Miocene, a global cooling had started[19] entailing reduced rainfalls in tropical Africa[20]. The scarcity of fossils between 10 Ma to 5 Ma is associated with the East and South African uplift[21]. The rise of the interior plateau led to a »rain-shadow« effect, that affected most of Eastern Africa[20] and resulted in a seasonality of precipitation.

In an analysis of the community structure of Miocene sites, Andrews and Humphrey[22] showed that Miocene apes likely occupied a variety of forested habitats, ranging from rainforests to woodland in the Early Miocene, and seasonal forest or woodland in the Middle Miocene. There is a marked increase in the proportion of terrestrial species from the early to the Middle Miocene, whereas semi-arboreal and arboreal species diminish. Fossil hominoid localities of the African Late Miocene are nearly absent (Figure 1).

Despite the biases and restrictions discussed, it is very plausible to infer that

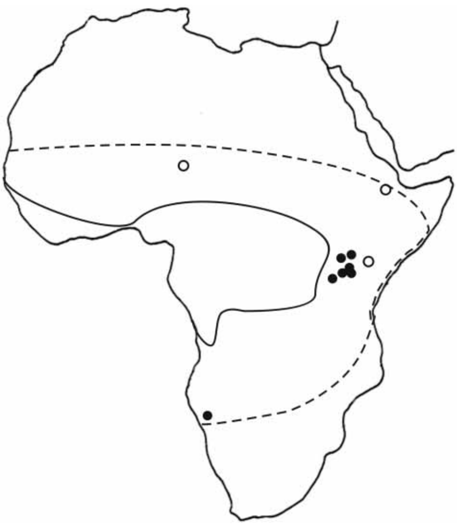

Fig. 1. Fossil localities in the African Miocene. Dashed line: likely Early Miocene rainforest boundary; solid line: present rainforest boundary; black circles: Early and Middle Miocene fossil localities; white circles: Late Miocene fossil localities.

one of the major habitat changes which occurred in Africa around the Mid/Late Miocene boundary, was the large scale reduction of the tropical rain forest. Its original range from the African West to East coast was dramatically reduced to its present distribution. This resulted in a broad peripheral zone of woodland and transitional forest in the Late Miocene, the potential source environment for the origin of bipedal locomotion.

Active faulting, erosion, and periods of non-deposition are biasing the geologic record. Thus, continuous records of African paleoclimatic change are rare from terrestrial sequences in Eastern Africa[23]. The records indicate that Eastern African climate changed from warmer, more humid conditions from the Late Miocene/Early Pliocene to a more seasonally contrasted, cooler and drier, perhaps also more variable climate during the Late Pliocene (after ca. 3 Ma)[23,24].

Habitat Changes and Evolution

Since Vrba[25,26] published the »turnover-pulse« hypothesis based on the analysis of faunal composition and global climatic datasets, other authors[15,16,27,28] used the obvious correlation between faunal (speciation and extinction) and global climatic changes (cooling and warming) to interpret processes of faunal and hominid evolution.

The *Turnover Pulse Hypothesis*[25,26] refers to speciation and extinction events over a short time period due to climate change. Vrba[25,26] underlined her studies by evolutionary traits of bovids, rodents and hominids. The spread of open savannah between 2.8–2.5 Ma due to global cooling should have resulted in faunal turnovers. Indeed many (especially bovid) FADs and LADs (Last Appearance Date) are found around 2.5 Ma. Behrensmeyer et al.[16] studied the faunal remains and localities of the Omo Group, probably East Africa's best documented strata, and did not find a turnover pulse between 2.8–2.5 Ma or at 2.5 Ma, but turnovers between 2.5–1.8 Ma. In addition the authors note, that several woodland to forest species even persisted between 3–2 Ma. An aridification trend in the Turkana basin is marked by peaks at 3.58–3.35 Ma, 2.52–2 Ma and 1.81–1.58 Ma[29]. Nevertheless, the ones at 2.5 Ma and 1.81 Ma seem to support the turnover hypothesis. Difficulties arise in the general definition of a turnover and its assumed duration.

The *Variability Selection Hypothesis*[27] refers to important adaptive change in response to environmental variation. Whereas short-term variability takes into acount habitat variations (especially seasonality), the (long-term) variability selection hypothesis states, that certain adaptations have evolved as a result of large, environmentally caused inconsistencies in the selective conditions, independent of a given habitat. This hypothesis seems to be the most comprehensive way of trying to interpret human origins. It is independent of distinct faunal data and does not refer to certain regions and time periods.

An »Open Source« Perspective

From habitat reconstructions as outlined above we may thus infer that the spatio-temporal distribution pattern of earliest hominids suggests a pan-African rather than an Eastern African perspective on evolution of bipedalism. The periphery of tropical rain forest provided all necessary environmental features for development of bipedalism, and was distributed from the eastern edge of the original rainforest boundary to its northwestern and southwestern margins all across tropical Africa. Reviewing the fossil record, it seems probable that different Miocene taxa might represent geographical variants existing simultaneously.

Based on these assumptions we can hypothesize that the earliest stages of hominid evolution might have followed a different evolutionary pattern than was previously thought. Therefore, we propose four elements which are important in an alternative hypothesis to explain this evolutionary process:

1. Similar selection pressures occurred along the entire margin of the shrinking tropical rain forest (an edge of roughly 8,000 km in length) in the Middle to Late Miocene;
2. Evolutionary changes resulted in different geographical variants of earliest bipedal hominoids along this area;
3. Different evolutionary solutions were adopted in order to face similar problem;
4. Instead of a single taxon, geographical variants of biological forms existed in an open source setting, which all represent earliest stages of hominid evolution.

Some of the major questions resulting from these conclusions are those on modes of parallel evolution of bipedal locomotion and modes of isolation and interaction of resulting geographic variants as well as on potential multiple origins of later hominids. Probably, these questions can only be answered with the discovery of new Miocene hominid and related faunal material. However, this alternative view might provide a hint to the geographic regions, in which the search for new fossil sites should be concentrated: in a pan-African sense it encompass the entire biogeographic region of the peripheral Miocene rain forest. It extends from Chad all the way to Mali and Mauritania in North-Western and from Kenya and Uganda to Angola in South Western Africa.

Conclusion

The »open source« view on earliest stages of hominid evolution derives mainly from expectations about early hominid evolution in the context of environmental change. The spatio-temporal distribution pattern of Miocene hominids suggests, that earliest hominids might represent co-existing geographic variants in an early »experimental« evolutionary stage prior to the establishment of fully developed early hominid characteristics. This situation might be comparable to the early evolutionary stages of other faunal groups such as the Cambrian Burgess Shale organisms[30], birds[31,32] and even of mammals[33]. It becomes increasingly evident, that their first appearance was usually preceded by parallel »experimental« phases. Some of their typical morphological characters or functional features in different combinations were established long before the onset of these groups.

In addition, the accumulation of more fossil material strengthened the view that neither birds nor mammals can be traced back to one »missing link« only. The growing number of remains of morphologically and functionally diverse earliest hominids will probably make such an »experimental« evolutionary phase increasingly visible in hominid evolution as well.

Even if some of the implications are as yet unsubstantiated by traditional analyses of character states, we hope this view will incite focused research in new hypotheses based on a more holistic accounting of morphology, biogeography, and ecological change on a larger, pan-African, scale.

Dedication

This contribution, intended to throw new light on old problems, is dedicated to Horst Seidler, whose open mind and courage to break new ground in paleoanthropology are remarkable and an inspiration to his friends and colleagues.

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PERSPEKTIVA »OTVORENOG IZVORA« U RAZVOJU NAJRANIJIH VRSTA HOMINIDA

S A Ž E T A K

Perspektiva »otvorenog izvora« bavi se rasprostranjenošću miocenskih hominida u prostoru i vremenu te je suglasna s pan-afričkom teorijom evolucije dvonožnosti. Povlačenje kišnih šuma od vremena srednjeg Miocena rezultiralo je u selektivnim pritiscima koji su bili slični u čitavom prostoru rasprostranjenosti. Najraniji hominidi tako su mogli predstavljati istodobne zemljopisne varijante.