Anthropogenesis in the light of the African discoveries of the last decade

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Anthropology, as every science, constructs hypotheses and theories on the basis of previously analysed material. One of the leading Polish anthropologists who undertook these tasks was Professor Andrzej Wierciński. His works show not only a wide range of research, but are clear evidence of great intellectual energy. The scope of his interest included also the problems of antropogenesis, which was reflected in such publications as The question of the occurrence of Homo sapiens forms in the Early and Middle Pleistocene (Wierciński, 1956a), On the antiquity of Homo sapiens (Wierciński, 1956b), or On the taxonomic distinctiveness, nature and species uniqueness of man (Wierciński, 1990). Professor Wierciński's intellectual acumen, his thorough analysis of the discoveries which he described in his works, as well as his intuition and way of reasoning have always called for unanimous admiration and respect. Such merits become specially valuable at a time when contemporary anthropology, having at its disposal the most recent technologies, must face the challenge of verifying and re-working old concepts. It appears that mere improvement of the methods of dating the remains (Valladas et al., 1987, 1988; Mercier et al., 1990), the possibility of the virtual reconstruction of damaged material (Zollikofer et al., 1995) or even the most advanced genetic analyses (Krings et al., 1997; Ovchinnikov et al., 2000; Knight, 2003) do not guarantee accuracy as far as conclusions are concerned, and consequently cannot warrant correctness of the constructed phylogenetic models. It therefore appears worthwhile, following the example of the Professor's admirable precision, to recall the most important discoveries of the last decade which largely influenced the perception of our history, i.e. the history of the family Hominidae.

1. Anthropogenesis in the context of excavations from East and Central Africa

Raymond Dart's discovery of an infant form of Australopithecus africanus in 1924 first refocused the paleoanthropologists' attention on the African continent, for up till then the scientists had focused their research mainly on Asian territories (Tomczyk, 2002). At present intensive explorations are being conducted in South, East and Central Africa. The East African excavations take place on the territories of present-day Kenya, Ethiopia and Tanzania. The wide variety of forms found there, as well as their spacial and temporal diversification, force us however to revise the traditional classification of the family Hominidae. In 1939 William Gregory and Milo Helman suggested that two sub-families should be distinguished within this family (Hominidae): namely the Australopithecinae and the Homininae. In the first group they allocated bone remains of early hominids found in South Africa, while the remains from Europe, Asia and Africa were subsumed into another group. In the early 1990s, the time span for the existence of the forms allocated to the sub-family Australopithecinae still embraced the period from Pliocene through early Pleistocene (Johanson and Shreeve, 1989). However, more recent excavations made it necessary to extend the time of occurrence of both the sub-family Australopithecinae and the whole family Hominidae onto Upper Miocene, reaching back in time to 7-6 million years ago. Moreover, the allocation of the new genera: Ardipithecus, Sahelanthropus and Orrorin has given rise to another vital question as to whether the family Hominidae should not be extended onto more than two sub-families (Leakey et al., 2001; Cameron and Groves, 2004; Schwartz and Tattersall, 2005).

In the mid-1990s a paleoantropological team led by Tim White, working in Aramis (10°28'N, 40°26'E), Middle Awash, Ethiopia, discovered fragmentary fossil remains of an Australopithecus, characterised by a mixture of features typical of early hominids and the Pongidae. White proposed to classify these fossils as Australopithecus ramidus. The teeth (ARA-VP-6/1, ARA-VP-1/128, ARA-VP-1/129) of the newly discovered form were characterised by thin enamel; large canines protruded above the line of occlusion. The molars were relatively narrow, which distinguished it from the other Australopithecinae. Moreover, the incisors were considerably smaller when compared with that of a chimpanzee or of the later Australopithecinae. The most distinctive hominid feature were the proportions of the upper molars; their labio-lingual width was much smaller than the length. The tooth arch, preserved in fragments, was U-shaped. Apart from the teeth, the findings in Aramis included fragments of the temporal bone and the occipital bone (ARA-VP-1/125, ARA-VP-1/500). The surface for the temporo-mandibular joint (facies articularis) was clearly flattened; there was no articular tuber. The occipital condyles were small. The location of the great foramen (foramen magnum) may be indicative of bipedality, although this guess cannot be corroborated since no remains of leg bones were found. The excavated fragments of the humerus, ulna and radius (ARA-VP-7/2) display a mixture of hominid and pongid features. The dating of the specimens excavated at the Awash locality indicates that the remains of A. ramidus come from 4.4 mln years ago (White et al., 1995a). In 1995 White, Suwa and Asfaw published in

Nature magazine another article, where they suggested that the former generic name: Australopithecus should be replaced with another name: Ardipithecus, which means "terrestrial ape". They argued that the change was justified by the distinctly archaic morphology of the remains which they described. In effect, fossil remains from Awash have been allocated to a new genus, but what still needed to be decided was how to classify the fossils of Ardipithecus ramidus. The issue at stake was whether they belonged to the family Australopithecinae, or should they rather be classified within a new and distinct subfamily (White et al., 1995b)? The question became even more urgent with the discovery of other specimens of the Ardipithecus, announced in 2001 by Yohannes Haile-Salassie. The finding was allocated to a new subspecies, Ardipithecus ramidus kadabba (Haile-Selassie, 2001). The excavated material included right mandibular corpus with the third molar and some other teeth (ALA-VP-22/10), the left humerus and ulna (ALA-VP-2/101), as well as the hand phalanx (ALA-VP-2/11). The remains of the kaddaba were older than those discovered by White; their age was estimated for the Lower Pliocene: that is between 5.8–5.2 million years ago. In November 2002 another important discovery was made in Ethiopia at the Asa Koma location. The most interesting specimens discovered there were the right upper canine (ASK-VP-3/4), the right and left upper first molar (ASK-VP-3/400), the right upper first premolar (ASK-VP-3/405). The morphology of the teeth, especially the particular features of the canines and first premolars allows for assuming that the forms Ardipithecus kadabba and Ardipithecus ramidus must have constituted separate species rather than subspecies, as has been previously assumed (Haile-Selassie et al., 2004). It is beyond doubt, however, that the discussion concerning the taxonomic status of the remains from Middle Awash cannot be considered closed.

The catalogue of the oldest gracile hominids was further enriched by the remains excavated in 1995. Meave Leakey's team then discovered 21 hominidal bone fragments. The finding took place between the Kakurio and the Kalabata rivers, in Kanapoi (36°04'E, 2°19'N) and in Allia Bay on the east coast of Turkana Lake in North Kenya. The fossils included: a fragment of the mandible with teeth, a fragmentary piece of the left temporal bone (KNP-KP 29281), the maxilla (KNM-KP 29283) as well as the distal and proximal fragments of the tibia (KNM-KP 29285). The remains were allocated to a new species of Australopithecus: A. anamensis. They were dated to 4.17-4.12 million years ago (Leakey et al., 1998), thus they should be considered the oldest Australopithecinae remains found so far. On the one hand, the Australopithecus from Kanapoi and Allia Bay shared many features with A. afarensis, but the occurrence of numerous other, clearly distinctive characters called for establishing a new taxon. The excavated fragment of the temporal bone indicates that this part of the skull must have been massive and highly pneumatised. The canines are also robust; they have long and massive cusps and they are vertically settled. The first lower premolar is asymmetrical, its cusps are placed wide apart. The *trigon* of the upper molars, which is constituted by three tubers: the protoconid, the paraconid and the *metaconid*, is much wider than the *talon*, constituted by the *hypoconid*. The buccal surface of the molars is convex-shaped. The enamel is almost 1.3 mm thick. The morphology of the proximal and distal parts of the tibia indicates

a bipedal mode of locomotion. Thus the remains of *A. anamensis*, older than those found in Laetoli, move back in time the earliest records of bipedality. The size of the bone ends made it also possible to estimate the weight of this individual between 47–55 kg, which means that the presented species must have been bigger and heavier than *Australopithecus afarensis* (Collard, 2002).

The fossil records of gracile forms from about 3-2 million years ago, excavated in East Africa, were poorly documented. Although in 1990 fragmentary hominid remains were found in Mataibaietu and Gamedeh in Ethiopia, their identification caused a lot of problems and became the reason for a long-running controversy. The fossils came from the Hata deposits that are known to be from 2.5 million years ago. The excavated material included: a small fragment of the parietal bone (GAM-VP-1/2), a fragment of the left mandible (GAM-VP-1/1) as well as the distal left humerus (MAT-VP-1/1). The explorations conducted in the years 1996–1998 by the Berhane Asfaw team in Bouri, at the area of Middle Awash in Ethiopia, yielded new, interesting material from the turn of Middle and Upper Pliocene. The findings included the proximal fragment of the ulna (BOU-VP-11/1), the proximal femur and associated forearm fragments (BOU-VP-12/1A-G), fragments of skulls (BOU-VP-12/130; BOU-VP-12/87), and an almost complete mandible with teeth (BOU-VP-17/1). Asfaw decided that these remains should be placed in a new species, Australopithecus garhi (in the language of the Afar people the word *garlii* means "surprise"). Their age was established by means of the Ar/Ar method at 2.49 million years. The remains should thus be considered as contemporary to Australopithecus africanus in the South and of the massive Australopithecus aethiopicus in the East of Africa. The skull of A. garhi is gracile and small. Holloway has estimated its size at 450cc. The parietal bone is well profiled. The skull viewed in the norma lateralis position displays strong prognathism of the lower part of the face. The incisors are inclined forward, instead of being set vertically. A. garhi was characterised by strong megadonty: the canines were relatively big and the molars were quite massive – 17.7 mm in cross-section. The mandible was U-shaped, and the palate was thin and long. One of the more intriguing characters of these specimens was the size of the forearm, which bore some resemblance to a pongid, rather than hominid, limb. On the other hand, the elongation of the femur was definitively a hominid-like feature and indicated bipedal locomotion. The differences in the size of the long bones were most probably caused by strong dimorphism, comparable with the dimorphism of A. afarensis. Asfaw has argued that A. garhi may have been, on the one hand, an ancestor to the gracile form A. afarensis and, on the other hand, ancestor to the early representatives of Homo (Asfaw et al., 1999). It could therefore be considered a link between the Australopithecinae and the Homininae. Close to the remains of A. garhi some animal bones were found, with clear marks of chopping and scratching which point to attempts at obtaining the nutritious marrow. Since no tools were discovered in the same place, it can only be inferred that the hominids from the Awash area must have made use of some primitive tools, though whether these were actually the work of the garhi form or any other hominid still remains problematic.

Presenting the excavations of hominidal fossils of the last decade one must not fail to mention the discovery of *Orrorin tugenensis*. The material was discovered in 2000 by Brigitte Senut and Martin Pickford on Tugen Hills in Kenya. The Lukeino Formation, where the discovery was made, is now dated to 6.2–5.6 Ma. The findings included two small mandibles, teeth (M, C, I); fragments of the femur, humerus and phalanges. The teeth are relatively small, characterised by thick enamel, like in the case of later hominids. Sentu and Pickford claim that *Orrorin* was a small, upright walking creature. The curved phalanges are generally similar to those of *Australopithecus afarensis*, which allows us to suppose that *Orrorin* did not its lose ape-like, arboreal features. This supposition is supported by the faunistic evidence that the habitat of *Orrorin* was covered with forest at the time when the species occurred there (Culotta, 1999; Aiello and Collard, 2001; Galik et al., 2004).

In 2001, Michel Brunet's paleoanthropological team, working in North Chad in Toros-Menalla (16°14'N, 17°28'E), discovered an almost complete skull with some teeth. The recovered items were classified as TM 266. The skull is long and narrow; its cranial capacity ranges between 328cc and 380cc. The face is high, characterised by reduced facial prognathism, a huge and massive supraorbital torus, and deep canine fossa (hollowed cheeks). The occipital condyles (*condulus occipitalis*) are small, the external acustic opening (*porus acusticus* externus) is rounded, the mastoid processes (processus mastoideus) are large and pneumatised. The back of the skull is characterised by flat but at the same time long nuchal line as well as a large external occipital crest (*crista occipitalis externa*). The incisors and canines are small, without diastema. The premolars are set on three and the molars on two cusps. The enamel is thicker than in contemporary representatives of the genus Pan, but much thinner than in the case of later *Australopithecinae*. The second molar is the largest of all, the first is the smallest (M2>M3>M1). The excavated material probably belonged to a male individual. The mixture of various features made Bruneta call the remains from Chad Sahelanthropus tchadensis (the name Sahel derives from the region of Africa south of the Sahara). The finding of the TM 266 skull is one more proof working against the "East Side Story" hypothesis. It allows us to assume that hominids inhabited South, East as well as Central Africa (Brunet et al., 2002). The geological age of the rocks where the TM 266 skull was found has been dated to Late Miocene, i.e. 7-6 Ma. Provided this dating is correct, the remains of Sahelanthropus would have been the oldest hominid remains discovered so far. It is extremely difficult to decide now whether Sahelanthropus tchadensis was a species which constituted an evolutionary blind end, or whether it actually did give rise to some phylogenetic line (Begun, 2004). It is beyond doubt, however, that the fossil records from Chad reach back further in time than the moment of separation of the chimpanzee and human lines as it has been established on the basis of the molecular data. The analysis of the similarities and differences in the DNA of a chimpanzee (*Pan paniscus*) and that of a contemporary human allowed for estimating that the divergence must have taken place about 5/6 Ma (Wood, 1994). But the dating of the specimens from Chad seems to indicate that the molecular data may be inaccurate, and that they should be revised. Some scientists refuse to recognise the hominid status of Sahelanthropus, claiming that it ought to be attributed to the *Pongidae*, and consequently postulating a change of the generic name to Sahelpithecus. Undoubtedly, the debate will remain open at least until another Miocene fossil is discovered in Chad (Wolpoff et al., 2002).

The recovered remains of the oldest, East African hominids, have certainly blurred our picture of the past. In a gloss included in the Polish translation of Roger Lewin's seminal study, the editor explains that: "the excavations of early hominids from 5–7 Ma indicate that the group was larger, more widespread and more varied than it has been realised so far. Probably some of these earlier forms constitute evolutionary blind ends, i.e. forms extinct without progeny. It is therefore extremely difficult nowadays to point out which parts of the early hominids' evolutionary mosaic are closest to our genealogical line" (Lewin, 2002).

2. Anthropogenesis in the context of South African excavations

Large scale excavations in southern territories were initiated by Robert Broom who in 1936–1938 obtained some interesting specimens in the Sterkfontein limestone caves (Broom, 1951). The latest series of research was undertaken by Phillip V. Tobias in 1966, and has continued till now. Its aim has been not only the discovery of new fossil material, but also a detailed definition and description of the geological strata and chronology of the Sterkfontein locality. In 1980, in the layer defined as Member 2, bone fossil of various animals were found. Initially, the material was deposited in university storage; in the mid–90s, however, it turned out by chance to have included four bones of a hominid left foot: the talus (talus), the navicular bone (os naviculare), the cuneiform medial bone (os cuneiforme mediale) as well the first metatarsus bone. Later, other fragments of the same skeleton were discovered. Since the bone material was set in pieces of limestone, its recovery has taken a long time; so far only foot bones have been fully recovered. The material was classified as Stw 573, and in university jargon it was called "Little Foot". It displays an amazing mixture of pongid and hominid features. The latter include the shape of the talus and the tuberculation of the navicular bone (tuberositas ossis navicularis) which are indicative of bipedality. On the other hand, the shape of the joint surface of the navicular bone as well as the morphology of the cuneiform bone suggest that the big toe was set apart from other toes, which is a typical pongid condition. It should thus be inferred that the ability of upright walking did not develop at the expense of a prehensile foot suited for climbing trees. The remains were allocated to the species Australopithecus africanus, and they were initially dated at 3.5-3.0 Ma, now even at 4 Ma (Partridge et al., 2003; Pickering et al., 2004). Thus they ought to be considered the oldest Australopithecinae remains from South Africa, contemporary to Australopithecus anamensis from East Africa.

The fact that new methods call for a revision of the formerly affirmed views is best evidenced by the debate about the skull from Sterkfontein – Sts 5. Ever since 1947 it has been considered a female individual, which was reflected in

the popular name attributed to this specimen: "Mrs Ples". More recent analyses, however, speak in favour of another hypothesis, namely that the individual was rather a representative of the male population of *Australopithecus africanus*. Such an argument has been put forward, for instance by Yoel Rak, who has analysed the shape and size of the anterior pillars, extending from the edges of the nasal aperture to the side parts of the dental curve. His view has been further confirmed by the exposure of glabella, the shape of supraorbital toruses and the morphology of zygomatic processes (processus zygomaticus) (Thackeray et al., 2002). Moreover, the team led by Francis Thackeray claims that the Sts 5 skull belonged to the same individual as the material recovered from the site defined as Member 4 (Thackeray et al., 2002). On the one hand, their conclusions are based on the analysis of the sacrum bone (Sts 14q) and pelvis (Sts 14r), and, on the other hand, on the tomography scan of the Sts 5 skull. The unfused sacrum bone and underdeveloped upper anterior iliac spine (spina iliaca anterior superior) indicate that the specimens represent an adolescent individual. A tomography scan has displayed the presence of an underdeveloped root of the third molar (M³) which allowed for further conclusions that Sts 5 belonged to a juvenile male individual. The skull and other bones were deposited close to each other and are dated to the same geological period (2.8-2.3 Ma). Had Thackeray's guess been definitively confirmed, the material from Sterkfontein would have become the second most complete Australopithecinae skeleton after "Lucy" from Hadar.

The most recently discovered habitats of South African hominids include also the caves in Drimolen, located about 7 km north-east of Sterkfontein. The age of the caves has been estimated at 2.0-1.5 Ma (Keyser et al., 2000). In 1992 it was there that André W. Keyser found not only specimens attributed to baboons and elephants, but also hominid fossils allocated to the species Australopithecus robustus and the genus Homo. First explorations have yielded some milk-teeth, forearm bones and fragments of mandibles. This catalogue of bone remains was supplemented in 1994 with the discovery of an almost complete skull (DNH 7) and a mandible (DNH 8). The skull is massive but without strong prognathism, the glabella is very prominent, the zygomatic arches are set widely apart, and the front teeth are clearly reduced. The face is flat, and the anterior pillars are hardly visible, which may be due to the small size of the canine fossa. The overall size of the skull is small: it is 75 mm high (*po-b*); 163 mm long (*pr-op*); its mastoidal breadth is 119 mm (*nus-nus*), and the porion breadth is 105 mm (po-po). Worth notice is the absence of bone crests which in massive forms occur on the sagittal suture (sutura sagittalis). It should therefore be concluded that the DNH 7 represented a female form of A. robustus (Keyser, 2000). The mandible DNH 8 is markedly bigger and more massive than that of DNH 7. The morphological differences are most probably caused by strong sex dimorphism, which characterised robust Australopithecinae from South Africa (Schwartz and Tattersall, 2005).

The most recent discoveries carried out at the above mentioned locations make us question the previously accepted opinions concerning the South African *Australopithecinae*. According to the current state of knowledge, the hominidal stratum of Sterkfontein, dated to almost 4 Ma, should be considered the

oldest known fossil record of this kind. It is earlier than the specimens from the Makapansgat location (3 Ma), the Kromdraai and Drimolen location (2.0–1.5 Ma), and the Swartkrans cave (1.5 Ma).

The excavations conducted in Africa allow us to propose a hypothesis, according to which the first hominids from the taxonomic circle of *Australopithecinae* first appeared about 5 Ma in East Africa. The most recent discoveries in the Kanapoi Formation and Allia Bay in Kenya prove that the oldest *Australopithecinae* did not belong – as it has been thought on the basis of the earlier excavations in Lothagam, Kanapoi, Laetolil, Hadar and Omo – to the species *Australopithecus afarensis*, but should rather be classified as *Australopithecus ananuensis*. The most rapid development of Plio/Pleistocene African hominids took place between 3.5–1.5 Ma: it was then that they reached South Africa and at the same time their population and biological diversification reached its peak in East Africa. *Australopithecus* became extinct 1.5–0.5 million years ago: first, it disappeared from East Africa and then from the south of the continent (Clarke and Tobias, 1995; Lewin, 2002; Cameron and Groves, 2004).

Conclusion

Anthropology, which is concerned with the history of humankind, is by no means a static discipline. New excavations and the development of research methods subject our knowledge to continuos verification. The affirmed models of anthropogenesis are more and more often questioned, and the new scenarios which replace them frequently proceed on completely different assumptions. The unceasing necessity to confront the models of human phylogenesis with currently available data poses great challenge for anthropologists. All scientists like to base their hypotheses on firmly established axioms, widely acknowledged patterns and stable statements. Many contemporary disciplines, including anthropology, are deprived of such a privilege. It is worth remembering, however, that it is precisely this restless search and continuous reconstruction of our picture of the world that make science such a fascinating occupation. Professor Andrzej Wierciński, to whose memory the present paper is dedicated, was well aware of this simple truth.

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