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SYMPOSIUM

New findings – new problems in classification of hominids+

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ABSTRACT The criteria for the inclusion of species within the genus *Homo* have changed over the years. There has been a stepwise relaxation of these criteria, therefore the classification and the evolutionary place of hominid fossils have never been free of controversy. It is the main reason that the discoveries of new hominid fossils have not helped in solving the generally accepted classification of hominids. **Acta Biol Szeged 46(1-2):57-60 (2002)**

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"...neither the paleontological, nor the genetical, nor the archeological records as they now stand can tell us exactly when, where, or how..." (Howells 1967)

Although almost 35 years passed after Howells (1967) wrote the above cited statement concerning the evolution of the hominids, it remained as true as it was earlier.

The species of the hominids that have been recognised since the late Pliocene fossils in the continents of the Old World have always been in the center of a never ending debate: when, where and how they evolved into our species, the *Homo sapiens*.

One of the main reasons of this debate is the lack of consensus concerning the number of the taxa of the hominids and their hypodigms. However, the root of this controversy can be found in the different taxonomies of the order Primates.

The terms "hominoid", "hominid", and "hominin" are not interchangeable, but their classification criteria are variously in a state of flux. In general, the hominoids are a superfamily of Primates; the family *Hominidae* is currently considered to comprise both the great ape lineages and human lineages within the hominoid superfamily; the subfamily *Homininae* comprise both the human lineages and the African ape lineages within the hominids, and the tribe *Hominini* comprising only the human lineages. This current scheme is given in Table 1.

Classification: "...the ordering of (organisms) into groups (or sets) on the basis of their relationships..." (Simpson 1961).

Major changes in the classification of hominids

When the genus *Homo* was introduced in 1758 by Linné, it embraced two extant species. The first one, *Homo troglodytes*, also known as *Homo sylvestris*, is now known to have been based partly on the orangutan, and partly on myth. The second one was the *Homo sapiens*, the species to which all modern human populations belong. Since its introduction almost 250 years ago, our understanding of *Homo* has been changed by the addition of fossil species. This has resulted in the step-by-step relaxation of the criteria for the inclusion of species into the genus *Homo*.

Until the middle of the 1960s, all the classification of the primates were based on Simpson's classification (1945, 1961), which used only morphological characteristics, and a genus may be monopyletic or paraphyletic, too. These kind of classifications divided the superfamily *Hominoidea* into two families: *Pongidae* (for *Gorilla*, *Pan*, *Pongo* and *Hylobates*) and *Hominidae* for *Homo* alone. Among fossil taxa, *Australopithecus* was sometimes allocated to the *Pongidae* (Simpson 1945), sometimes to the *Hominidae* (Le Gros Clark 1959). In the 1960's an increasing trend appeared towards awarding the gibbons their own family, *Hylobatidae* (Napier and Napier 1967).

In 1963, Goodman's immunological study of serum proteins divided the superfamily *Hominoidea* into three branches: the gibbons, the orangutan, and an irreducible cluster of human, gorilla and chimpanzee. This can be recognised in taxonomy, with the families *Hylobatidae*, *Pongidae* (restricted to the orangutan) and *Hominidae* (for *Homo*, *Pan* and *Gorilla)*. Molecular evolutionary techniques have progressed from immunology through aminoacid sequencing, DNA-DNA hybridisation, RFLP to DNA sequencing, but all have confirmed the same basic groupings, merely refining the trifurcations, so it is now evident that the gibbon line did diverge before that of orangutan, and most studies have concluded that the gorilla diverged before the human and chimpanzee lines separated.

However, the contradiction between these two classifications is only apparent. Groves (1986) collected numerous morphological characteristics and found that, when analysed cladistically, the morphological analysis produced exactly the same phylogeny as the molecular ones (Table 2).

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Table 1. Current scheme of the primate superfamily.

- Superfamilia *Hominoidea*
    - Familia *Hylobatidae*
    - Familia *Pongidae*
    - Familia *Hominidae*
        - Subfamilia *Homininae*
        - Tribe *Gorillini*
        - Tribe *Hominini*
            - Genus *Ardipithecus*
            - Genus *Australopithecus*
            - Genus *Paranthropus*
            - Genus *Kenyanthropus*
            - Genus *Homo*

The other classification is the cladistic one and in this interpretation of classification a genus must be monophyletic; it cannot be paraphyletic.

"...evidently, evolution at the structural gene level and at the morphological level do not obey the same rule." (Ney and Roychondhury 1982).

The cladistic taxonomy

Although the above cited statement is true, when the morphological characters and the molecular ones are analysed cladistically, they produce the same phylogeny (Groves 1986), as can be seen in Table 2.

Table 2. Phylogenetic classification of primates (modified after Goodman et al. 2001).

- Semiorder *Strepsirhini* (50 My)
    - Suborder *Lemuriformes* (45 My)
    - Suborder *Loriformes* (23 My)
- Semiorder *Haplorhini* (58 My)
    - Suborder *Tarsiiformes* (?)
    - Suborder *Anthropoidea* (40 My)
        - Infraorder *Platyrrhini* (26 My)
        - Infraorder *Catarrhini*
            - Superfamily *Cercopithecoidea* (25 My)
                - Family *Cercopithecidae*
                - Family *Hominidae*
                - Subfamily *Homininae* (18 My)
                    - Tribe *Hylobatini*
                    - Tribe *Hominini* (14 My)
                        - Subtribe *Pongina*
                            - *Pongo pygmaeus*
                        - Subtribe *Hominina* (7 My)
                            - *Gorilla gorilla*
                            - *Homo* (6 My)
                            - *H. (Pan)* (3 My)
                            - *H. (Pan) troglodytes*
                            - *H. (Pan) paniscus*
                            - *H. (Homo) sapiens*

The age (in million years) is shown in parentheses.

The founder of cladistic taxonomy was Hennig (1966), who observed that one of the more perplexing problems in taxonomy is the assigning of ranks to the groups in a hierarchical taxonomic classification. A partial solution to this problem is to have phylogenetic classifications in which all taxa represent monophyletic groupings, *i.e.* the names of the taxa can serve as the names of actual clades. Clearly, on so naming clades, a younger clade nested within an older clade, taxonomically must always have a rank at a lower hierarchical level than the older clade. For example, all taxa with the rank of family in a cladistic phylogenetic classification of primates should be of younger age than the order Primates, the older more inclusive taxon; similarly all orders of mammals should be of younger age than the class *Mammalia.* In as much as ranking solely by relative age does not ensure that taxa assigned the same rank represent clades that are equivalent to one another with respect, at least, to some key objective measure. Hennig (1966) reasoned that the optimal yardstick for measuring which clades are equivalent is the absolute age of origin of the clades, *i.e.* the taxa assigned the same rank should represent clades of about the same absolute age. Perhaps because such a temporal system of classification would be inordinately difficult to achieve across phyla, Hennig (1981) initiated a trend among cladists to abandon the use of ranks altogether. Nevertheless since long established rules in the practice of taxonomy require that taxonomic names with the endings *oidea*, *idae*, *inae*, *ini*, and *ina* designate the ranks of superfamily, family, subfamily, tribe, and subtribe, respectively, and since most systematists and taxonomists still use ranks in their classifications, Hennig's cogent reasons for a rank equals age system of phylogenetic classification still have merit. Moreover, molecular phylogenetic investigations have provided tools along with those of paleontological investigations for dating branch-points in phylogeny and thus for constructing phylogenetic classifications in which taxa at the same rank represent clades of equivalent age (Goodman et al. 2001).

Table 3. A genealogical classification of extant and extinct species within the genus *Homo* (Goodman et al. 2001).

- *Homo*
    - *H. (Pan)*
        - *H. (P.) paniscus*
        - *H. (P.) troglodytes*
    - *H. (Homo)*
        - *H. (H.) ramidus*
(*Ardipithecus ramidus*, 4.4 My)[a]
            - *H. (H.) anamensis*
(*Australopithecus anamensis*, 4.2-3.9 My)[a]
        - *H. (H.) afarensis*
(*Australopithecus afarensis*, 3.6-2.8 My)[a]
            - *H. (H.) africanus*
(*Australopithecus africanus*, 2.8-2.4 My)[a]
                - *H. (H.) boisei*
(*Australopithecus boisei*, 2.4-1.3 My)[a]
                - *H. (H.) robustus*
(*Australopithecus robustus*, 2.0-1.6 My)[a]
            - *H. (H.) habilis*
(*Homo habilis*, 1.9-1.8 My)[a]
                - *H. (H.) erectus*
(*Homo erectus*, 1.8-0.9 My)[a]
                    - *H. (H.) sapiens neanderthalensis*
(*Homo neanderthalensis*, 0.5-0.1 My)[a]
                    - *H. (H.) sapiens sapiens*
(*Homo sapiens*, 0.5-0.0 My)[a]

[a] Shown in parenthesis is the species' name and age from Yoon (1995) for each species that are treated as a member of subgenus *Homo (Homo)*.

Molecular phylogenetic investigations utilize the knowledge that each present-day genome contains a range of DNA sequences from rapidly to extremely slowly evolving. This makes it possible to discover the phylogenetic relationships that exist among living species at all levels of the taxonomic hierarchy from the most recently to the most anciently separated. The advances in doing so are bringing about a twofold shift in paradigms, one in systematics and the other in how we humans should view our place in nature. The new paradigm in systematics is essentially that first envisioned by Charles Darwin and further developed in a rigorous scientific way by Willig Hennig. It calls for disbanding the use of so-called grade taxa, such as the traditional primate taxa *Prosimii* and *Pongidae* with their paraphyletic groupings and instead calls, as sketched out above, for strictly genealogical (*i.e.* cladistic) classifications that depict sister-group relationships and, ideally, denote by rank level the clades of equivalent age. The other new paradigm rejects the traditional anthropological view that humans are greatly different from all other animal species. Instead, the molecular view emphasizes how much humans hold in common with other species, especially with our sister-group the common and bonobo chimpanzees. Table 3. presents, in terms of the DNA and paleontological evidence on primate phylogeny, the phylogenetic classsification of hominids based on the work of Goodman et al. (2001).

“Human evolution is like a bush, not a ladder” (Gould 1977).

New findings of hominid fossils – new problems of taxonomy of hominids

One of the main reasons of the different interpretations of the evolutionary way of the hominids is that the classification and the evolutionary place of hominid fossils has been under constant debate. It is caused partly because hominid fossils are not plentiful – inspite of the growing number of the fossils – and perhaps partly because there are a number of rival discovery teams, and the importance of a new hominid fossil discovery is enhanced if the discovery apparently requires new classifications and/or new interpretations.

The criteria for the inclusion of species within the genus Homo have changed over the years. The tendency has been for stepwise relaxation of these criteria, moreover, the last revision of the boundaries of the genus *Homo* happened several years ago.

In practice, there are four commonly used criteria for allocating individual fossils to species of *Homo*, and three of

Table 4. List of the current species of hominids.

Species	Type specimen	Named by
Orrorin tugenensis	BAR 1000’00	Senut et al. 2001
Australopithecus ramidus		
Ardipithecus ramidus	ARA-VP 6/1	White et al. 1994
Australopithecus anamensis	KP 29281	M. Leakey et al. 1995
Australopithecus afarensis	KT 12/H1	Johanson et al. 1978
Homo antiquus	AL 288-1	Ferguson 1984
Australopithecus bahrelghazali	KT 12/H1	Brunet et al. 1996
Kenyanthropus platyops	KNM-WT 40000	M. Leakey et al. 2001
Australopithecus africanus	Taung	Dart 1925
Australopithecus garhi	BOU-VP-12/130	Asfaw et al. 1999
Paraustralopithecus aethiopicus		
Australopithecus aethiopicus	Omo18	Arambourg & Coppens 1968
Paranthropus robustus		
Australopithecus robustus	TM 1517	Broom 1938
Australopithecus walkeri	KNM-WT 17000	Ferguson 1989
Zinjanthropus boisei		
Australopithecus boisei	OH 5L.	Leakey 1959
Paranthropus crassidens		
Australopithecus crassidens	SK 6	Broom 1949
Homo antiquus praegens		
Australopithecus praegens	KNM-T1 13150	Ferguson 1989
Homo habilis	OH 7	L. Leakey et al. 1964
Homo louisleakeyi	OH 9	Kretzoi 1984
Pithecanthropus rudolfensis		
Homo rudolfensis	KNM-ER 1470	Alexeev 1986
Homo microcranous	KNM-ER 1813	Ferguson 1995
Homo ergaster	KNM-ER 992	Groves & Mazak 1975
Pithecanthropus erectus		
Homo erectus	Trinil 2	Dubois 1894
Homo antecessor	ATD6-5	Bermudez de Castro et al. 1997
Homo heidelbergensis	Mauer 1	Schoetensack 1908
Homo rhodesiensis	Kabwe	Woodward 1921
Homo helmei	Florisbad	Dreyer 1935
Homo neanderthalensis	Neandertal 1	King 1864
Homo sapiens	–	Linnaeus 1758

them are connected with performance or technical competence. These are 1) the ability to manufacture stone tools, 2) the related possession of modern human-like precision grip (Leakey et al. 1964; Tobias 1991), and 3) the language competence (Tobias 1991). However, there is good evidence that these criteria are either impossible to operate within the constraints of the hominid fossil record, or that the competencies they refer to can no longer be confidently restricted to *Homo* (Gannon et al. 1998). The fourth one, 4) the absolute brain size, is only to be based directly on morphological evidence, but even this has been shown to be of questionable biological significance (Martin 1983).

The chaotic state of the species of genus *Homo* can be recognised in Table 4. Among the several species listed here there are only a few whose taxonomic place or given name are not under debate.

"If taxonomy (above species level) is ever to become more than mere stamp collecting, it must define its spheres of usefulness and examine its philosophical basis. It will be an objective science if it can reflect some part of the real world and if it can be made testable against some other standard..." (Groves 1986).

Conclusions or solutions?

The first step on the long way to reach an agreement should be the determination of the criteria of a genus, then specific criteria for *Homo* have to be generated. Wood and Collard (1999) proposed that a genus should be both a clade and a grade and can be defined as "a species, or monophylum, whose members occupy a single adaptive zone". That means, in case of genus *Homo,* the species within it should be more closely related to the type species, *Homo sapiens*, than they are to australopithecine genera.

Wood and Collard (1999) also suggested based on investigations using both traditional qualitative characters and characters generated from quantitative data that the only fossil species that form a clade with *Homo sapiens* are *Homo neanderthalensis*, *Homo heidelbergensis*, *Homo erectus*, and *Homo ergaster*. This opinion is supported by their body size, body shape, locomotion and diet. The only uncertainty can be seen in the case of *Homo ergaster*, whose relative brain size does not align it so strongly with *Homo sapiens*. On the other hand, according to cladistic and gradistic criteria, *Homo habilis sensu lato*, or *Homo habilis sensu stricto* and *Homo rudolfensis*, are closer to australopithecines than they are to *Homo*. That means that these two species need either to be transferred to an existing australopithecine genus or to be placed to a newly created genus (Wood and Collard 1999).

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