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Evolving Interpretations of *Homo*

The criteria for the inclusion of species within the genus *Homo* have changed over the years. The tendency has been for a stepwise relaxation of these criteria, yet it has been more than thirty years since the most recent, and most radical, revision of the boundaries of the genus. There is no widely accepted definition of a genus, but we suggest that genera should be both a clade and a grade. In other words a genus should be both a monophyletic group and a group of species that share a common adaptive regime. We have examined the available evidence relating to locomotion, diet, encephalization and body shape, and conclude that if *Homo habilis sensu stricto* and *Homo rudolfensis* are included in *Homo* that genus fails both the 'grade' and 'clade' tests. We suggest that *Homo* can only be defined both cladistically and adaptively if its membership, among the hominids of the late Pliocene/early Pleistocene, is limited to early African *Homo erectus/homo ergaster*. Even then, there are substantial differences in absolute and relative brain size between *H. ergaster* and temporally-later *Homo* species.

Introduction

When the genus *Homo* was introduced in 1758 by Carolus Linnaeus it embraced two extant species: One, *Homo troglodytes*, also known as *Homo sylvestris*, is now known to have been based partly on the orangutan, and partly on myth. The other was *Homo sapiens*, the species to which all modern human populations belong. In the course of the *c.* 250 years since its introduction, 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*. This paper traces this trend towards inclusivity, and sets out how it has affected the way *Homo* is defined. We will also demonstrate that some of the criteria that have been suggested are difficult, if not impossible, to determine from the fossil record. We conclude with a proposal for a revised definition of *Homo* that would result in the exclusion of two of the species, *Homo habilis* and *Homo rudolfensis*, that are presently included in the genus.

Relaxing the criteria - the major steps

It was the absorption of four fossil species, *Homo neanderthalensis, Homo heidelbergensis, Homo erectus* and *Homo habilis*, over the course of exactly a century, that brought about the most significant changes in our interpretation of the genus *Homo*. This section will explore in more detail the implications of each of these additions to the genus.

Homo neanderthalensis King, 1864

The type specimen of *H. neanderthalensis* consists of a single, adult, partial skeleton recovered from the Feldhofer Cave in the Neander Valley in Germany in 1856. With hindsight this was not the first evidence of Neanderthals to come to light, for a child's skull found in 1829, at a site in Belgium called Engis, and a cranium recovered in 1848, from Forbes' Quarry in Gibraltar, also display the distinctive

Neanderthal morphology. It was just less than thirty years after the recovery of the type specimen that the next Neanderthal discovery was made in Moravia (Sipka, 1880). Thereafter came discoveries from Belgium (Spy, 1886), Croatia (Krapina, 1899-1906), Germany (Ehringsdorf, 1908), France (Le Moustier, 1908 and 1914; La Chapelle-aux-Saints, 1908; La Ferrassie, 1909, 1910 and 1912, and La Quina, 1911) and in the adjacent Channel Islands (St. Brelade, 1911). Notwithstanding the range of taxa these remains were initially attributed to, all of them share the characteristic Neanderthal morphology. In 1924-26 the first Neanderthal was found outside of Europe at Kiik Koba in the Crimea. Thereafter came discoveries at Tabun Cave on Mt. Carmel (1929), and then in Asia, at Teshik Tash (1938). In the meantime, two more sites in Italy, Saccopastore (1929-35) and Guattari/Circeo (1939), had yielded the remains of Neanderthals. Further evidence was added after the 1939-45 war, first from Shanidar, Iraq (1953 and 1957-60), and then from Amud (1961, 1964 and thereafter) and Kebara (1964 and thereafter) in Israel, and more recently from sites in France and Spain (e.g. St. Cesaire, 1979 and Zafarraya, 1983 and 1992). Thus, Neanderthal remains have been found throughout Europe, with the exception of Scandinavia, as well as in the Near East, the Levant and Western Asia.

The inclusion of the Neanderthals within *Homo* resulted in modifications to the range of both the cranial and postcranial morphology within the genus. The Neanderthal cranium typically has discrete and rounded supraorbital ridges, a face which projects anteriorly in the midline, laterally-projecting and rounded parietal bones, a rounded, posteriorly-projecting occipital bone, large incisor teeth, and postcanine teeth with large root canals. The postcranial peculiarities include limb bones with stout shafts and relatively large joint surfaces, especially well-marked areas for the attachment of a muscle that helps to control the shoulder and an elongated pubic ramus of the pelvis. Despite the peculiarity of the pubis there is no indication that the Neanderthals were anything other than upright, obligate, long-range, bipeds. Estimates of their brain size suggest that their brains were as large as, if not larger than, the brains of living *Homo sapiens*.

Homo heidelbergensis Schoetensack, 1908

This species nomen was introduced for a hominin mandible found in 1907 during excavations to extract sand from a quarry at Mauer, near Heidelberg, Germany. The mandible has no chin and the corpus is a good deal larger than those of the mandibles of modern humans living in Europe today. The next evidence within Europe of fossil remains that showed equivalently archaic features came from Petralona (Greece), where in 1959 a cranium was recovered from a cave. Thereafter came evidence from Montmaurin (1949) and Arago (1964-9) in France, Vertesszöllös (1965) in Hungary, Bilzingsleben (1972-7, 1983 and thereafter) in Germany, and most recently from the Gran Dolina (1994-1996), at Atapuerca in Spain (but see Bermúdez de Castro *et al*., 1997, for an alternative classification).

The first African evidence for 'archaic' *H. sapiens* came in 1921 with the recovery of a cranium from a cave in the Broken Hill Mine at Kabwe, in what is now Zambia. Other morphologically comparable remains have been found from the same time range at Florisbad (1932), Eyasi (1935) and Rabat (1933), Jebel Irhoud (1961 and 1963) in southern, East and North Africa, respectively. The earliest evidence of this African 'archaic' group comes from Bodo (1976), which is dated at *c.* 600 Kyr, and specimens intermediate in age (*c.* 400 Kyr) include crania from Hopefield/Elandsfontein (1953), Ndutu (1973), Sale (1971), and Thomas Quarry (1969 and 1972). Asian evidence comes from Ngandong, (1931-33) in Indonesia, Dali (1978), Mapa (1958), and Yunxian (1989 and 1990) in China, and Hathnora (1982) in India.

If there is to be a single species name to cover the archaic material from Europe, Africa and Asia, then *H. heidelbergensis* Schoetensack, 1908 has priority. If there was compelling evidence that the latter two regions sampled equally good species, then the name for the African species would be *H. helmei* Dreyer, 1935, and if the Ngandong material is not to be included in *H. erectus* (see below), the appropriate species name for the Asian species would be *H. soloensis* Oppenoorth, 1932.

What sets this material apart from *H. sapiens* and *H. neanderthalensis* is the morphology of the cranium. The brain cases are often, but not always, smaller than those of modern humans and the Neanderthals. They are always more robustly built, with large ridges above the orbits and a thickened occipital region. They have some, but not all, of the features of *H. erectus* crania (see below), but they lack the derived features of Neanderthal crania. Postcranially the shapes of the limb bones are much like those of *H. sapiens*, except that the shafts of the long bones are generally more robust.

Homo erectus (Dubois, 1892) and *Homo ergaster* Groves and Mazák, 1975

In 1890 Eugene Dubois found a mandible fragment in Java at a site called Kedung Brubus. Less than a year later, in 1891, at excavations on the banks of the Solo river at Trinil, workers unearthed the skull cap that was to become the type specimen of a new, and significantly more primitive, species of fossil hominid. Initially Dubois placed the skull cap in the genus *Anthropopithecus*, but two years later he changed the generic designation to *Pithecanthropus*. The focus for the next phase of field research in Java was the Plio-Pleistocene sediments of what is called the Sangiran Dome. It was here that in 1937 a German palaeontologist, Ralph von Koenigswald, recovered a cranium, Sangiran 2, that resembled the distinctive shape of the Trinil skull cap, but which had a brain smaller (*c.*800 cm^3) than that of the Trinil calotte.

In the meantime the Swedish palaeontologist, Gunnar Andersson, together with a junior colleague from Austria, Otto Zdansky, had spent two seasons in 1921 and 1923 excavating a cave at Choukoutien (now Zhoukoudian), near Peking (Beijing), in China. Two teeth, an upper molar and a lower premolar, originally identified as being ape-like, were judged to be hominid. Together with a left permanent first molar (Ckn. A.1.1) found in 1927, the three specimens were referred to a new genus and species, *Sinanthropus pekinensis* Black, 1927. Cranial fragments were found at Locus B in 1928, the first calvaria at Locus D in 1929, and excavations continued at Zhoukoudian until their interruption by World War 2 (1939-45).

The morphology of the fossils recovered from Locality 1 at Zhoukoudian resembled that seen in the *Pithecanthropus erectus* remains from Java. Since then similar-looking material has been found at sites which include Lantian (1963-4), also in China, at Swartkrans (1949 and thereafter) in southern Africa, and at Olduvai, (1960 and thereafter), West and East Turkana (1970 and thereafter), Melka Kunturé (1973 and thereafter) and most recently at Buia (1995-1997) in Eritrea, in East Africa, and from Tighenif (1954-5) in North Africa. Many consider that the remains from Ngandong, Indonesia (see above), should be included in this hypodigm. Recent discoveries at Dmanisi, Georgia, have been referred to *Homo ergaster*.

Despite the relatively large numbers of crania recovered from Java and China, relatively little was known about the postcranial morphology of this group of taxa, and it was discoveries from East African sites that provided the crucial evidence. This came in the form of a pelvis and femur from Olduvai Gorge (OH 28), two fragmentary partial skeletons from East Turkana (KNM-ER 803 and 1800), and the unusually well-preserved skeleton from West Turkana (KNM-WT 15000).

The crania of these remains all have a low vault, with the greatest width towards the base. There is a substantial, essentially continuous, torus above the orbits, behind which there is a sulcus. There is usually a sagittal torus, and an angular torus that runs towards the mastoid process. The occipital region is sharply angulated, with a well-marked supratoral sulcus. The inner and outer tables of the cranial vault are thickened and the cranial capacity is less than that seen in *H. heidelbergensis*. The roots of the premolar teeth tend to be more complex than in the latter taxon. The cortical bone of the postcranial skeleton is generally thick, the long bones are robust, and the shafts of the femur and the tibia are relatively flattened from front to back relative to those of other *Homo* species; this is referred to as platymeria and platycnemia, respectively.

Until the taxonomy was rationalized, the two main subsets of what is now the hypodigm of *H. erectus* were attributed to four genera, *Pithecanthropus* and *Meganthropus* in Java, *Sinanthropus* in China, with the fourth genus, *Atlanthropus*, being used for the North African material. In 1943 Franz

Weidenreich formally sank *Sinanthropus* into *Pithecanthropus*, and in 1964 Le Gros Clark supported the Mayr (1944) proposal that *Pithecanthropus* and *Atlanthropus* be sunk into *Homo*. This, of course, had the effect of changing the definition of *Homo* so that it could accommodate the relatively primitive remains that are included in the hypodigm of *H. erectus*. In particular this meant that the genus *Homo* now included a much wider range of cranial shape, brain size and mandible shape and size. It was the incorporation of this material into *Homo* that resulted in the change in diagnosis between the 1955 and 1964 editions of Le Gros Clark's *Fossil Evidence for Human Evolution*. The incorporation of the hypodigm of *H. ergaster* into this group extended the range of dental and mandibular morphology to include teeth with more complex crowns and roots and mandibles with robust corpora, and it confirmed the inclusion within *Homo* of individuals with endocranial volumes that barely exceed 800 cm^3.

Homo habilis Leakey, Tobias and Napier, 1964

A year after a new genus and species, *Zinjanthropus boisei* Leakey, 1959 (now referred to *Australopithecus* or *Paranthropus*) had been created for the OH 5 cranium, the Leakeys found more hominid fossil evidence in the form of substantial parts of both parietal bones, much of a mandible and at least 13 hand bones of a juvenile skeleton (OH 7). In the next year or so, further evidence of a 'non-robust' hominid was unearthed in Bed I of Olduvai Gorge (OH 4 and 6 - skull fragments and teeth; OH 8 - an adult foot; OH 14 - juvenile cranial fragments, and OH 16 - the fragmented cranial vault and maxillary dentition of a young adult) as well as in Bed II (OH 13 - the incomplete skull of an adolescent).

In 1964 Louis Leakey and two colleagues set out the case for recognizing a new species for the 'gracile' hominid remains from Olduvai, and they also proposed that the new species should be accommodated within the genus *Homo*, as *Homo habilis* Leakey, Tobias and Napier, 1964. The addition of *H. habilis* to the genus *Homo* meant that Le Gros Clark's 1955 diagnosis of the latter needed to be amended. This involved relaxing some criteria, such as brain size, so that the relatively small-brained (*c.* 600-700 cm^3) crania from Olduvai could be included. Leakey and his colleagues claimed that other criteria, such as dexterity, an erect posture and a bipedal gait, did not need to be changed because their interpretation of the capabilities of the *H. habilis* remains from Olduvai was consistent with these functional criteria.

In due course important additional specimens from Olduvai (e.g. OH 24 and OH 62) were added to the hypodigm. Fossils attributed to 'early *Homo*', or *H. habilis sensu lato,* had also been found at Koobi Fora, Members G and H of the Shungura Formation, Member 5 at Sterkfontein, and Member 1 at Swartkrans. This material displays a spectrum of cranial morphology, with endocranial volumes ranging from just less than 500 cm^3 to *c.* 850 cm^3. The mandibles also vary in size, the larger ones having robust bodies and premolar teeth with complex crowns and roots. Our knowledge of the postcranial skeleton has traditionally come from the remains from Bed I at Olduvai Gorge (e.g. OH 7, 8 and 35), but although these were allocated to *H. habilis*, it is by no means certain that one can exclude their allocation to *P. boisei*. The only postcranial evidence from Olduvai Gorge which can, with confidence, be allocated to *H. habilis* and not to *P. boisei*, is the associated skeleton OH 62. Unfortunately, very little useful morphology is preserved, but it is possible to determine the relative lengths of the segments of the upper and lower limbs, and these show that the skeleton had longer arms relative to leg length than is the case in any other species within *Homo*. If OH 62 does belong to *H. habilis*, then its inclusion in the genus would mean that the postcranial skeleton of at least one species of *Homo* cannot be distinguished from that of *Australopithecus* and *Paranthropus*.

Some researchers expressed the view that *H. habilis* was simply too variable to make a plausible single species. Views are polarized, with some researchers supporting the retention of a single taxon, *H. habilis sensu lato,* for this material, and others supporting a 'two-taxon' solution. This debate has been reviewed elsewhere (Wood, 1996).

Homo after *H. habilis*

Whatever the detailed morphological criteria for allocating individual fossils to species, in practice three of the four commonly used criteria for allocating those species to *Homo* are inferences about performance, or technical competence. The only one to be based directly on morphological evidence is absolute brain size, but even this has been shown to be of questionable biological significance (Martin, 1983).

The three inferred criteria related to performance are language competence (Tobias, 1991), the ability to manufacture stone tools, and the related possession of a modern human-like precision grip (Leakey *et al.* 1964; Tobias, 1991). There is 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.* For example, there is good evidence that language function cannot be reliably inferred from the gross appearance of endocasts, and that the language-related parts of the brain are not as well localized as earlier studies had implied (e.g. Galaburda & Pandya, 1982; Gannon *et al.*, 1998).

The connection between stone-tool manufacture and *Homo* is a long-standing one, which Kenneth Oakley made explicit in the content and the title of his book *Man the Tool-Maker* (Oakley, 1949). Although for five years *Zinjanthropus* was credited with being "the oldest yet discovered maker of stone tools" (Leakey, 1959, p.493), the mantle was soon passed to *H. habilis* (Leakey *et al.*, 1964). Thereafter, the link between stone-tools and *Homo* has been maintained (e.g. Hill *et al*., 1992; Kimbel *et al*., 1996). However, since there is now overwhelming evidence that for much of the Pliocene in East Africa hominid species were both synchronic and sympatric, the link between *Homo* and stone-tool manufacture is difficult to substantiate. For example, the earliest stone artifacts were almost certainly contemporaneous with both *Homo* and *Paranthropus* (Kibunjia *et al.*, 1992; Kibunjia, 1994; Wood *et al.*, 1994; Semaw *et al.*, 1997). There is also evidence that the type of dexterity needed for the manufacture of relatively crude stone artifacts is most likely not restricted to *Homo* (Susman, 1994; Marzke, 1997).

Defining *Homo*: an alternative proposal and its implications

There must first be agreement about the general criteria for defining a genus, then specific criteria for *Homo* need to be generated. We have proposed elsewhere that a genus should be both a clade and a grade and thus can be defined as "*a species, or monophylum, whose members occupy a single adaptive zone*" (Wood & Collard, 1999). Thus, in the case of *Homo* this means that the species within it should be more closely related to the type species, *H. sapiens*, than they are to australopithecine genera. Furthermore, their adaptive strategies should be more similar to those used by *H. sapiens* than to the strategies used by the various australopithecine genera. The first of these criteria can be investigated using cladistic analysis, the second by objective methods designed to generate reliable inferences about adaptation from the fossil record.

Investigations using both traditional qualitative characters and characters generated from quantitative data suggest that the only fossil species that form a robust clade with *H. sapiens* are *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus*, and *H. ergaster*. Likewise, when evidence about body size, body shape, and development is combined with inferences about locomotion and diet, it is clear that these are also the only *Homo* taxa whose adaptations are closer to those of *H. sapiens* than they are to the australopithecines*;* the relative brain size of *H. ergaster* does not align it so strongly with *H. sapiens.* Thus, according to cladistic and gradistic criteria, *H. habilis sensu lato*, or *H. habilis sensu stricto* and *H. rudolfensis*, are closer to australopithecines than they are to *Homo.* Consequently, they need either to be transferred to an existing australopithecine genus, or allocated to a new genus, or genera. We explored the taxonomic implications of the results of this analysis elsewhere (Wood and Collard, 1999).

Acknowledgments

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