

THE MEANING OF HOMO

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ABSTRACT. The taxonomic history of the genus *Homo*, up to the inclusion of *Homo habilis* and *Homo rudolfensis*, is reviewed. The two main contemporary interpretations of the genus concept, that differ according to whether information about grade is used, and in the way a clade is interpreted, are presented. It is suggested that neither of these definitions is satisfactory, and a new definition, that a genus should be 'a species, or monophylum whose members occupy a single adaptive zone', is offered. For a newly discovered, or newly recognized, taxon to be included within an existing genus two criteria are suggested. First, the candidate species should belong to the same monophyletic group as the type species of the proposed genus. Second, the adaptive strategy of the candidate species should be closer to the adaptive strategy of the type species of the proposed genus than it is to the type species of any other genus. When applied to the taxa presently subsumed within *Homo* two taxa, *H. habilis* and *H. rudolfensis*, fail the tests. It is suggested that at least one new genus, and probably two new genera, are needed to accommodate the taxa excluded from *Homo*.

KEY WORDS. Genus, *Homo*, grade, clade, *Homo habilis*, *Homo rudolfensis*, phylogenetic analysis, language, tool-making.

INTRODUCTION

This paper interprets 'meaning' simply as what authors intend their readers to infer when an extinct hominid species is referred to the genus *Homo*. What are the features or properties of the species that justify its allocation to *Homo*? What do the species assigned to *Homo* have in common and what distinguishes them from non-*Homo* taxa? The paper begins by reviewing the different interpretations that have been placed upon the *Homo* genus by evolutionary biologists. It considers the ways influential systematists have interpreted the genus category, and explains and clarifies a recent proposal by the authors for interpreting the genus category.

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The proposal recommends using criteria that can be assessed directly with fossil material. The paper concludes by applying those criteria to the extinct species presently allocated to *Homo*.

EVOLVING INTERPRETATIONS OF HOMO

The genus *Homo* was established by Carolus Linnaeus in the tenth revision of his monumental *Systema Naturae* (Linnaeus, 1758). Linnaeus' genus *Homo* subsumed two species. One, *Homo sylvestris*, or *Homo troglodytes*, was described as 'nocturnal' with its distribution confined to Java. We now know that this taxon was part orang-utan and part myth. Linnaeus described the second species, *Homo sapiens*, as 'diurnal' and he divided it into six groups. Two groups, described as 'wild' and the 'monstrous', are of historical rather than biological interest. The four remaining groups are geographical variants drawn from the four major geographical regions, Africa, America, Asia and Europe, known to Linnaeus.

The first fossil evidence to be included within the genus *Homo* comprised the remains recovered from the Feldhofer cave in the Neander Valley in Germany, and which were referred to *Homo neanderthalensis* by King (1864). The next addition to the genus was the male skeleton, Cro-Magnon 1, which was made the type specimen of a novel species, *Homo spelaeus*, Lapouge, 1899. Schoetensack's (1908) decision to refer the Mauer mandible to *Homo heidelbergensis* altered the interpretation of *Homo* in that it added a taxon with a mandible more primitive than those of either *H. spelaeus* (now a junior synonym of *H. sapiens*) or *H. neanderthalensis*. Thereafter, the addition of *Homo rhodesiensis*, Woodward, 1921, and *Homo soloensis*, Oppenoorth, 1932 to *Homo* meant that the genus now included species with more heavily built crania.

In the ensuing decade, major changes were proposed for the *Homo* genus. Weidenreich (1940) suggested that two existing taxa, *Pithecanthropus erectus*, Dubois, 1892 and *Sinanthropus pekinensis*, Black, 1927, should be incorporated into *Homo* as subspecies of *Homo erectus*. Mayr (1944) broadened the proposal by suggesting that *Meganthropus* and *Telanthropus* be added to the list of taxa to be transferred to *Homo*. Robinson (1961) added his support to the proposal to transfer *Telanthropus capensis*, Broom and Robinson, 1949 to *Homo*, and subsequently Le Gros Clark (1964) suggested that *Atlanthropus mauritanicus*, Arambourg, 1954 and *Meganthropus palaeojavanicus*, von Koenigswald, 1950 should be transferred to *Homo erectus*. The transfer of these taxa into *Homo* resulted in that genus subsuming a substantially wider range of morphological variation than it had done prior to their assimilation (Le Gros Clark, 1964). However, the lower limit of cranial capacity of *Homo* was still set at 900 cubic centime-

ters, and the posture and gait of its species was described as being 'fully erect' (ibid).

The range of morphology within *Homo* was widened substantially in 1964 with the addition of *Homo habilis* (Leakey, Tobias and Napier, 1964). In order to accommodate *H. habilis* in their revised diagnosis of the genus *Homo*, Leakey and colleagues were forced to reduce the lower end of the range of cranial capacity to 600 cubic centimeters. Nonetheless, they adhered to the criterion of an erect posture and bipedal gait, and suggested that the possession of a fully opposable thumb and a precision grip should be added to the criteria for inclusion within *Homo*. These proposals were all consistent with contemporary interpretations of the function of *H. habilis*. However, since 1964 views about the posture, gait and dexterity of *H. habilis* have changed, and relevant new fossil evidence has been recovered. For example, many of the more recent attempts to interpret the locomotion and posture of the *H. habilis* hypodigm suggest that it was not an obligate biped (Wood, 1996; Wood and Richmond, 2000), and recent assessments of its dexterity have concluded that the case for the *H. habilis* having a modern human like precision grip is a good deal weaker than it was in 1964 (Marzke, 1997).

The systematic interpretation of 'early *Homo*' was further complicated by the proposal (reviewed and summarized in Wood, 1991) that the fossil evidence that had been accumulating within *H. habilis sensu lato* was no longer consistent with a 'single species' interpretation. One suggestion was that 'early *Homo*' was a conflation of two species, *Homo habilis sensu stricto* and *Homo rudolfensis* (Wood, 1992), and several investigations published since then have supported this interpretation (Kramer *et al.*, 1995; Grine *et al.*, 1996). The resorting of this material into two taxa yields rather different functional interpretations of the resulting species. One of them, *H. habilis sensu stricto*, has a relatively 'later *Homo*'-like, but small-brained, cranium, absolutely small chewing teeth (Wood, 1991), and a primitive-looking postcranial skeleton (Johanson *et al.*, 1987; Hartwig-Schrerer and Martin, 1991). The other, *H. rudolfensis*, has an endocranial volume that is absolutely-larger than that of *H. habilis sensu stricto*, a broader, more robust, midface, and a dentition that is absolutely larger than that of 'later *Homo*'. There are no postcranial remains reliably associated with the latter taxon (Wood and Collard, 1999a; Wood and Richmond, 2000).

THE MEANING OF THE GENUS

The genus concept has received considerably less attention from evolutionary biologists than the species concept, despite the fact that "it frequently appears that the genus is a more usable and reliable unit for classification than the species" (Simpson, 1963: 199). At the present time, there are two competing proposals for how the genus category should be

defined. The first is associated with Ernst Mayr and the evolutionary systematic school of classification. Mayr (1950: 110) suggested that "a genus consists of one species, or a group of species of common ancestry, which differ in a pronounced manner from other groups of species and are separated from them by a decided morphological gap." He went on to state that the genus "has a very distinct biological meaning. Species that are united in a given genus occupy an ecological situation which is different from that occupied by the species of another genus, or, to use the terminology of Sewall Wright, they occupy a different adaptive plateau" (*ibid.*, p.110). Thus, a genus is interpreted as a group of species of 'common ancestry' that is adaptively both homogeneous and distinctive. Mayr *et al.* (1953) concede that the phylogenetic and functional evidence may be in conflict if "unrelated species acquire a superficial similarity owing to parallel adaptations to similar environments" (*ibid.*, p.50), and in such cases they recommended the phylogenetic evidence be given precedence. But it is implicit that 'common ancestry' subsumes both monophyletic and paraphyletic groups.

The second definition of the genus is associated with the phylogenetic systematic or cladistic school of classification, which can be traced back to the work of the German entomologist Willi Hennig (1966). In this definition a genus is a group of species that are more closely related to one another than they are to any species assigned to another genus (Stevens, 1984). Under this definition a genus can only be monophyletic; it cannot be paraphyletic. This definition makes no stipulation about adaptive coherence or distinctiveness.

The evolutionary systematic and cladistic definitions of the genus differ crucially in the way they deal with terminal taxa that form a monophyletic group with one taxon, but which share an adaptive strategy with another taxon. For example, take the scenario that species A, B and C are monophyletic and adaptively coherent, but their sister taxon, species D, shares an adaptive strategy with a monophyletic group comprising species E, F and G (Wood and Collard, 1999a, b). How should taxon species D be classified? Should it be with species A, B and C, making the resulting genus monophyletic, but not adaptively coherent, or should it be grouped with species E, F and G, making that genus adaptively coherent, but not monophyletic? The latter option would be chosen under the evolutionary systematic definition, whereas the former option would be favored under the cladistic definition. Defining genera solely on the basis of monophyly is a tempting solution, but it is one that has its own problems. Because all species are related to one another, a genus defined on the basis of monophyly could comprise, depending on personal preference, between three species, and all the species that have ever existed. Furthermore, while a phylogenetic-based scheme would contain information

about descent, it inevitably ignores the 'modification' component of evolution and thus has a low information content (Knox, 1998).

We have suggested elsewhere (Wood and Collard, 1999a, b) that a pragmatic way of dealing with this problem is to modify the evolutionary systematic definition of the genus category so that paraphyletic taxa are inadmissible. The problem of how to classify a terminal species that forms a monophyletic group with one taxon, but which shares an adaptive strategy with another, can be overcome by recognizing it as a monotypic genus. We suggested, therefore, that a genus should be defined as *a species, or monophylum, whose members occupy a single adaptive zone*. It is important to note that, contrary to recent suggestions (Leakey *et al.*, 2001), our definition does not require the adaptive zone to be unique, or even distinctive. It just requires the adaptive zone to be consistent and coherent across the species taxa in the putative genus. Thus, for a species to be included in an existing genus we suggest the following criteria. *First, the species should belong to the same monophyletic group as the type species of that genus. Second, the adaptive strategy of the species should be closer to the adaptive strategy of the type species of the genus in which it is included, than it is the type species of any other genus.* The operative word is 'closer'; the adaptive strategy of the species under consideration does not have to be identical to that of the type species of the genus under consideration.

THEORY INTO PRACTICE

The most effective method of identifying monophyletic groups is cladistic analysis, but what strategies can we use to determine the adaptive strategies of extinct hominid species? Whatever criteria we adopt, they must be capable of being operated in a paleontological context where we seldom have direct evidence about function. Mostly functions must be inferred from morphological and other evidence, but the shorter the chain of inference, the more reliable the conclusions are likely to be.

In practice, species have been, and are being, assigned to *Homo* on the basis of four criteria. The first concerns absolute brain size. The notion of a 'cerebral Rubicon' for membership of *Homo* is closely linked with Keith (1948) who suggested 750 cubic centimetres, midway between the largest gorilla and the smallest recorded "aborigine" endocranial volumes (*ibid.*, pp. 205-6). In Leakey, Tobias and Napier's (1964) diagnosis of *Homo* the Rubicon had to be lowered to 600 cubic centimetres to accommodate *H. habilis*. The second criterion is the possession of language. Tobias (1991) has championed the link between *Homo* and the ability to communicate through spoken language. He based this primarily on evidence from endocranial casts and wrote that "in the endocranial casts of *H. habilis*, for the first time in the early hominid fossil record, there are prominences

corresponding to both a well developed speech area of Broca and a secondary speech area of Wernicke. These are two of the most important neural bases for language ability in the human brain" (ibid., p. 836). *H. habilis*, he claimed, was "the first language-dependent primate" (ibid., p. 840). The third criterion is the ability to manufacture stone tools. The connection between stone-tool manufacture and *Homo* is a long-standing one, made explicit through the content and the title of the book *Man the Tool-Maker* (Oakley, 1949), and was the subject of a recent review (Wood and Collard, 1999c). For five years *Zinjanthropus* was credited with being "the oldest yet discovered maker of stone tools" (Tobias, 1991, p. 493), but the mantle was swiftly passed on to *H. habilis sensu stricto* (Leakey et al., 1964). Thereafter, the putative link between stone-tools and *Homo* has been maintained by workers such as Hill et al. (1992), and Kimbel et al. (1996). The fourth criterion for including species in *Homo* is the possession of a modern human-like precision grip based on a well-developed, opposable, pollex (Leakey et al., 1964).

It is evident, however, that these criteria are either of questionable biological significance, or they are incapable of being satisfactorily determined from the evidence contained in the hominid fossil record. The cerebral Rubicon is problematic because both the application of the concept is arbitrary and because the behavioral significance of cranial capacity without reference to estimates of body mass is unclear (e.g. Martin, 1983). Likewise, there is compelling 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 'lesion deficit' studies had implied (Galaburda and Pandya, 1982; Gannon et al., 1998; Price, 2000; Gannon et al., 2001; Gilissen, 2001). Thus, there is currently little sound evidence to link language with the appearance of the genus *Homo*. The connection between *Homo* and stone tool manufacture is also difficult to substantiate, since there is now overwhelming evidence that for much of the Pliocene in East Africa hominid species were both synchronic and sympatric. The earliest stone tools, which come from c.2.6-2.3 Myr deposits in East Africa, were almost certainly contemporaneous with both early *Homo* and *Paranthropus* (Kibunjia et al., 1992; Kibunjia, 1994; Wood et al., 1994; Semaw et al., 1997), and it is also possible that an australopith species, *Australopithecus garhi*, employed stone flakes to access animal resources (De Heinzelin et al., 1999). Lastly, functional morphological analyses of the hands of the early hominids have suggested either that a modern human-like grip is not restricted to *Homo* (Susman, 1998; Marzke and Marzke, 2000), or indicated that we cannot yet be certain about the potential range of precision grips of any of the early hominids (Marzke, 1997; Marzke and Marzke, 2000).

Elsewhere (Wood and Collard, 1999a, b), we have reasoned that in the paleontological context, adaptive grade will need to be determined differently from the way it has been approached conventionally. Many aspects of a hominid's phenotype contribute to its ability to maintain homeostasis, acquire food and produce offspring. However, not all of these can be reliably reconstructed from the fossil record. Arguably, the most important of those that can be determined using paleontological evidence are body size and shape, locomotor behavior, relative brain size, the rate and pattern of development as determined from the hard tissues, and the relative size of the masticatory apparatus. Not all of them are independent; for example body size and shape and locomotion are likely to be highly correlated, but we suggest these are at least properties of extinct hominid taxa that can be quantified and compared.

Thus, for an extinct hominid species to be allocated to the genus *Homo*, two conditions must be met. First, cladistic analyses should indicate that the species is more closely related to the type species of *Homo*, *H. sapiens*, than it is to the type species of *Ardipithecus*, *Australopithecus*, *Kenyanthropus* and *Paranthropus*. Second, the body mass and shape, the inferred locomotion, the rate and pattern of hard tissue development, and the relative size of the masticatory apparatus of the candidate species should be more similar to the strategies used by the type species of *Homo* than they are to the type species of the other early hominid genera listed above.

Using these conditions as criteria, what evidence is there that *H. erectus*, *Homo ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis* and *H. rudolfensis* share a functionally-coherent adaptive strategy that is closer to that of *H. sapiens* than it is to the adaptive strategies of the type species of extinct hominid genera? We have reviewed this evidence elsewhere (Wood and Collard, 1999a), and concluded that on the basis of the available information, the adaptive strategies fall into two broad groups. The first group has a relatively low body mass, a body shape that in terms of thermoregulation is interpreted as being better suited to a relatively closed environment, and a postcranial skeleton that suggests a combination of terrestrial bipedalism with proficient climbing. The first group (with the exception of *Ardipithecus*, and perhaps *Kenyanthropus*) also has relatively large chewing teeth and jaws, and a dental developmental schedule that was more ape-like than modern human-like. This broad grouping may subsume more than one adaptive strategy, but taxonomic and other implications of this are beyond the scope of this review. The second group has a larger body mass, a more modern human-like, open-habitat adapted, physique, and a postcranial skeleton consistent with a form of locomotion similar to that practiced by modern humans (i.e., terrestrial bipedalism with a limited ability for adult climbing). The chewing teeth and jaws of the second group are relatively smaller, suggesting they were

apparently adapted to a diet which, when ingested, had similar mechanical properties to that of *H. sapiens*, and the rate and pattern of its dental and skeletal development were more modern human-like. It is noteworthy that relative brain size does not group the fossil hominid genera in the same way. This suggests that the link between relative brain size and adaptive zone is more complex than is conventionally assumed (Deacon, 1990).

With varying degrees of certainty, species with reasonably adequate fossil records within *Australopithecus* and *Paranthropus*, together with *H. habilis sensu stricto* and *H. rudolfensis*, can all be assigned to the first group, whereas *H. erectus*, *H. ergaster*, *H. heidelbergensis* and *H. neanderthalensis* can be assigned to the second. We presently know too little about *Ardipithecus ramidus* and *Kenyanthropus platyops* to be confident about even an approximate assessment of their adaptive strategies. When these observations are combined with the uncertainty over the phylogenetic relationships of *H. habilis* and *H. rudolfensis* (Wood and Collard, 1999a, b) it is clear that the species currently assigned to *Homo* do not form a monophylum whose members occupy a single adaptive zone. In other words, with the hypodigms of *H. habilis* and *H. rudolfensis* assigned to it, the genus *Homo* fails to measure up to the criteria for a genus.

Our initial solution, which was to recommend that the two displaced taxa, *H. habilis* and *H. rudolfensis*, be transferred to a new genus, did not survive the reviewing process. We thus recommended the most conservative alternative taxonomy, which was that the two taxa should be transferred, or returned, to *Australopithecus* (Wood and Collard, 1999a). This only increases the likelihood that *Australopithecus* is a paraphyletic group, thus making it an even more 'flawed' genus, but until we have the means to generate a reliable hominid phylogeny there is little point in redistributing the species presently allocated to *Australopithecus*. Moreover, until we have a reliable phylogeny, we cannot know whether the facial resemblances between *Australopithecus rudolfensis* and *Kenyanthropus platyops* justify the transferring the former species to *Kenyanthropus* (Leakey *et al.*, 2001; Lieberman, 2001). Nor can we be certain whether *Australopithecus habilis* can be accommodated within any existing hominid genus. We were encouraged by some colleagues to associate sir Wilfrid Le Gros Clark's name with any new genus for *A. habilis*, and we hope this proposal will be heeded if the need arises.

CONCLUSION

Hominid systematics is often criticised for being arcane and irrelevant, but the reality is very different. Sound, logical, taxonomic hypotheses are the bedrock upon which the foundation of all biology, especially paleobiology, is built. Although alpha, or species, taxonomy generates most

interest, the genus is also an important taxonomic category. We readily accept that even though we have tried to base our generic criteria on data which can be obtained from the hominid fossil record, the data are sparse. In some cases the data are so limited that it is impossible to make any meaningful estimate of within-taxon variation, so we cited only estimates of the mean in our initial, inevitably condensed, publication (Wood and Collard, 1999a). Clearly, as improved methods of analysis and new fossil evidence make more data available, our taxonomic hypotheses can be reexamined to see whether they are consistent with the new evidence. Taxonomies are, after all, just hypotheses. However, they need to be evaluated just as intensively as the other types of hypotheses generated by palaeontologists.

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