‘Is *Homo* Defined by Culture?’

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The changing face of *Homo*

THE GENUS *HOMO* was established by Carolus Linnaeus as part of the 1758 edition of his monumental review, the *Systema Naturae.* As construed by Linnaeus, the genus *Homo* subsumed two species. One, *Homo sylvestris,* was ‘nocturnal’ and was only known from Java. We now realize that *H. sylvestris* was based on the orang-utan, which has since been referred to its own genus, *Pongo* Lacépède, 1799. It was to the ‘diurnal’ species that Linnaeus attached the name *Homo sapiens.* Two of the six groups he included within *H. sapiens*, namely the ‘wild’ and the ‘monstrous’ components are of historical rather than biological interest, but the remaining ones are geographical variants drawn from the four continents, Africa, America, Asia, and Europe, known to Linnaeus.

The first fossil evidence to be included within the genus *Homo* were the remains recovered from the Feldhofer cave in the Neander Valley in Germany, which were referred to *Homo neanderthalensis* King, 1864. Thereafter, the interpretation of the genus remained unaltered until the inclusion of *Homo heidelbergensis* Schoetensack, 1908. This added a specimen with a rather more primitive mandible than had been the case for *H. neanderthalensis*, but otherwise the inclusion of this material made little difference to the perception of *Homo.* Thereafter, *Homo rhodesiensis* Woodward, 1921 and *Homo soloensis* Oppenoorth, 1932 were added to the genus, and in 1940 Weidenreich proposed that *Pithecanthropus erectus* Dubois, 1892 and *Sinanthropus pekinensis* Black, 1927 be incorporated into *Homo* as *Homo erectus.* Robinson (1961) proposed a similar solution for *Telanthropus capensis* Broom and Robinson, 1949, and subsequently Le Gros Clark (1964) suggested that *Atlanthropus mauritanicus* Arambourg, 1954 and *Meganthropus palaeojavanicus* von Koenigswald, 1950 should also be included in the hypodigm of *H. erectus.*

By the time these modifications had been made the genus *Homo* had assumed a rather different character, and it had come to subsume substantially more variation than it had done in 1940 (Le Gros Clark 1964). Even so, the lower limit of cranial capacity was still 900 cc, and the posture and gait of its member species were both ‘fully erect’. In the lit-

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erature there are many references to the use of a 'cerebral rubicon' as a criterion for membership of the genus *Homo*. Many of these discussions quote Sir Arthur Keith (1948), but his decision about the location of the rubicon was not based on the fossil record, but on the differences between the living apes and modern humans. He selected 750 cc as the rubicon because it is midway between 650 cc, the 'highest gorilla' endocranial volume, and 855 cc, the 'lowest aborigine' volume (ibid., 206). Using this, he judges the 'fossil skulls of Java' to be 'human' and the smaller-brained *Paranthropus* crania to be 'anthropoid' (ibid., 206).

Many of these criteria changed with the addition, in 1964, of *Homo habilis* (Leakey *et al.* 1964). In their 'revised diagnosis of the genus *Homo*', the range of cranial capacity had to be lowered to 600 cc in order to accommodate *H. habilis.* They also refer to an 'erect posture and bipedal gait' as well as to the possession of a 'fully opposable' thumb and a 'precision grip' as criteria for inclusion within *Homo.* These statements were all made on the basis that they were consistent with the way the function of *H. habilis* was being interpreted at the time. However, since 1964 views about the posture, gait, and dexterity of *H. habilis* have changed, and new fossil evidence has been found. For example, contemporary interpretations suggest that *H. habilis* is not an obligate biped (Wood 1996a) and the case for it having a modern human-like 'precision grip' is a good deal weaker than it was in 1964 (Marzke 1996; 1997). The result of these reassessments is that the inclusion of *H. habilis* within the genus *Homo* leaves the latter with little in the way of functional coherence.

It has also been suggested that the material that had been accumulating either within *H. habilis*, or in the category known as 'early *Homo*', was more variable than was consistent with a 'single species' interpretation (reviewed in Wood 1991). Subsequently, it was suggested that the 'early *Homo*' fossils were 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 interpretations of the resulting species. One of them, *H. habilis sensu stricto,* has a relatively later *Homo*-like, but small-brained, cranium, combined with a primitive-looking postcranium (Johanson *et al.* 1987; Hartwig-Schrerer & Martin 1991). The other, *H. rudolfensis,* has an absolutely-larger brain, but it is combined with a face that is unlike that of later *Homo.* There are no postcranial remains reliably associated with the latter taxon.

The origins of culture

Almost all attempts to list the features that distinguish modern humans from the living apes make reference to the complexity of modern human culture. We live with evidence of this complexity all around us, but we do not have to go far back into human prehistory before the evidence is confined to those aspects of prehuman activity that involve durable materials. Wooden tools survive for a surprisingly long time in the archaeological record (Thieme 1997), and although bone tools are rare in the Lower Pleistocene, there are grounds for concluding that the modification of bone may date back to at least 1.5 Myr (Brain *et al.* 1988). Nevertheless, most of the early evidence for human culture comprises artefacts made from stone.

The first sound absolute dating evidence for stone tool manufacture in the Lower Pleistocene came when Evernden and Curtis applied the then novel method of K/Ar dating to volcanic detritus from Olduvai Gorge, Tanzania (Leakey *et al.* 1961; Evernden & Curtis 1965). These dates confirmed the antiquity of the relatively crudely-fashioned stone artefacts, previously referred to the Oldowan Industry (Leakey 1951), that had been, and were continuing to be, recovered from Bed I at Olduvai (Leakey 1966). The Olduvai evidence retained the distinction of being the 'oldest stone tools' until the discovery of Oldowan-like artefacts at what was then called East Rudolf, in Northern Kenya (M.D. Leakey 1970; R.E.F. Leakey 1970). They were found at the KBS locality within a horizon which was apparently securely-dated to 2.4 Myr (ibid.). However, when the dating evidence was re-examined (Drake *et al.* 1980; Gleadow 1980; McDougall *et al.* 1980) it was apparent that the case for such an old age could not be substantiated, and the date for the artefacts was subsequently revised to *c.*1.9 Myr (see Brown (1994) for an excellent review of the 'KBS' dating controversy). Meanwhile, simple artefacts, mainly quartz flakes, had been found in Member F of the Shungura Formation in southern Ethiopia (Howell *et al.* 1987), and these were reliably-dated to 2.3 Myr (Feibel *et al.* 1989). Other artefact assemblages have been reported from Member E in the same formation, and these would have pushed the onset of stone artefact manufacture back to close to 2.5 Myr, but in one locality the evidence is limited to surface finds (Howell *et al.* 1987), and in the other the outcrop from which the artefacts had been excavated could not be linked securely enough to the reference stratigraphy (ibid.). Subsequent discoveries elsewhere in the Turkana Basin have confirmed the presence of artefacts at *c.*2.3–2.4 Myr (Kibunjia *et al.* 1992; Kibunjia 1994). Even more recently discoveries made at Gona, a site on the north side of the lower reaches of the Awash River, have pushed the date for stone artefact manufacture back to between 2.5 and 2.6 Myr (Semaw *et al.* 1997).

Homo and stone tools

The link between stone tool manufacture and the genus *Homo* is a long-standing one. This was made particularly explicit by Kenneth Oakley in the title of his book *Man the Toolmaker* (Oakley 1949). Indeed, in the first edition Oakley proposed that 'the problem of the antiquity of man resolves itself into the question of the geological age of the earliest known artefacts' (ibid., 3). The link between *Homo* and artefact manufacture was broken temporarily in 1959 when *Zinjanthropus boisei*, then the only hominid known from

Bed I at Olduvai Gorge (Leakey 1959), was described 'as the oldest yet discovered maker of stone tools' (ibid., 493). However, when evidence of a 'more advanced tool maker' was found (Leakey *et al.* 1964, 9), the authors adjusted the definition of the genus *Homo* (ibid., 7 and see above) to accommodate the new fossils, and thus re-established the link between stone tool manufacture and the genus *Homo.*

Some idea of the strength of that link can be gauged from the statement made by Grahame Clark in the third edition of *World Prehistory* in which he wrote that if future research produced evidence of 'a yet more advanced hominid in Bed I', then 'there would be no problem from a paleontological point of view in downgrading *H. habilis* to a variety of *A. africanus*' (Clark 1977, 22). It is clear from this statement that Clark was one of many commentators who were prepared, at least in matters related to taxonomy, to let inferences about behaviour take precedence over morphological evidence.

The passage of time since Clark's statement was written has seen very little weakening of the link between *Homo* and culture. Tobias (1991) concedes that the ability to make stone artefacts may have been seen first in a 'derived *A. africanus*' ancestor of *Homo habilis sensu lato* as 'facultative' culture, but only credits the latter with 'cultural behaviour [which] must have become *obligate*' (ibid., 832). The proposal that the Chemeron temporal bone (KNM-BC1) may belong to *Homo* apparently 'made more tenable the idea that our genus is also or exclusively responsible for the origins of lithic culture' (Hill *et al.* 1992, 720), and when Kimbel and his colleagues reported the discovery at Hadar of Oldowan tools and a hominin maxilla apparently reliably-dated to 2.33±0.07 Myr, the authors referred to the discovery as representing 'the oldest association of hominid remains with stone tools, and possibly the earliest well-dated occurrence of the genus *Homo*' (Kimbel *et al.* 1996). It is clear from the emphasis of Kimbel *et al.*'s paper, and from the interest that it stimulated (Wood 1997), that the discovery of stone artefacts along with the remains of a maxilla attributed to an early hominin other than *Homo* would have evoked substantially less interest.

Tobias has long championed the link between *Homo* and the ability to communicate through spoken language (see Tobias (1991) for a review). He bases this primarily on evidence from endocranial casts and writes 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., 836). He links linguistic ability with cultural facility and claims that *H. habilis sensu lato* 'was the first culture-bound and language-dependent primate' (ibid., 840). However, despite recent claims to the contrary (Wilkins & Wakefield 1995), there is compelling evidence that function cannot always be reliably inferred from the gross appearance of the brain (Galaburda & Pandya 1982; Falk 1986; Donald 1995; Lieberman 1995; Whitcombe 1995; Gannon *et al.* 1998). We suggest that while it is attractive to link culture and language with 'the emergence of the genus *Homo* and the arrival of *Homo habilis*' and the attainment of a 'new level of organization' (Tobias 1991, 844), we caution that there is little hard evidence to support such a scenario.

How many candidates for the pioneer 'tool-maker'?

As long as human evolution was considered to be made up of a series of time-successive species, assembled in a ladder-like lineage running from an ape-like ancestor at the base of the ladder, to modern humans at the top, the identification of a tool-maker was not difficult. Indeed the possession of culture was at the heart of the 'single-species' hypothesis which was espoused by Bartholomew, Birdsell, Brace and others (eg Bartholomew & Birdsell 1953; Brace 1967) and which maintained that the principle of 'competitive exclusion' would ensure that no more than one species at a time could exploit the 'culture niche'. No matter how sound, or unsound, the principle of 'competitive exclusion' (Gause 1934), with the discovery of *Homo habilis* and *Zinjanthropus boisei* (now more usually referred to as *Paranthropus boisei*) in the hominin fossil record from Bed I at Olduvai (Leakey *et al.* 1964), and the recovery at Koobi Fora, in northern Kenya, of the remains of early African *Homo erectus/Homo ergaster* and *Paranthropus boisei* from the same strata (Leakey & Walker 1976), the 'single-species' interpretation of the early phases of the hominin fossil record became untenable.

The hominin fossil record is now generally recognized as being more speciose than it was even 20 years ago (Wood 1996b), and there were several occasions during human evolutionary history when as many as three sympatric hominin species were extant (Figure 1). For example, at the time of what we presently understand to be the earliest evidence of stone artefacts, *c*.2.5 Myr, there are at least two, and possibly four—if we include the suggestion that *H. habilis* may be as old as, if not older than, 2.3 Myr (Tobias 1989; Kimbel *et al.* 1996; Suwa *et al.* 1996), and the possibility of temporal overlap between *Paranthropus aethiopicus* and *Paranthropus boisei* (Suwa *et al.* 1996)—hominins in the East African fossil record. However, in the light of the thumbnail sketches given above, are either *H. rudolfensis* or *H. habilis sensu stricto* so 'advanced' that we can automatically assume that one or the other, or perhaps both of them, manufactured the stone artefacts known from this time? Are they functionally comparable to *H. ergaster*, or early African *H. erectus*? If not, can we be confident that they should be included in the genus *Homo*?

Is *Homo* a good genus?

Ernst Mayr (1950) provides a good guide to what a genus is. He 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' (ibid., 110). He goes 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*' (our italics) (ibid.).

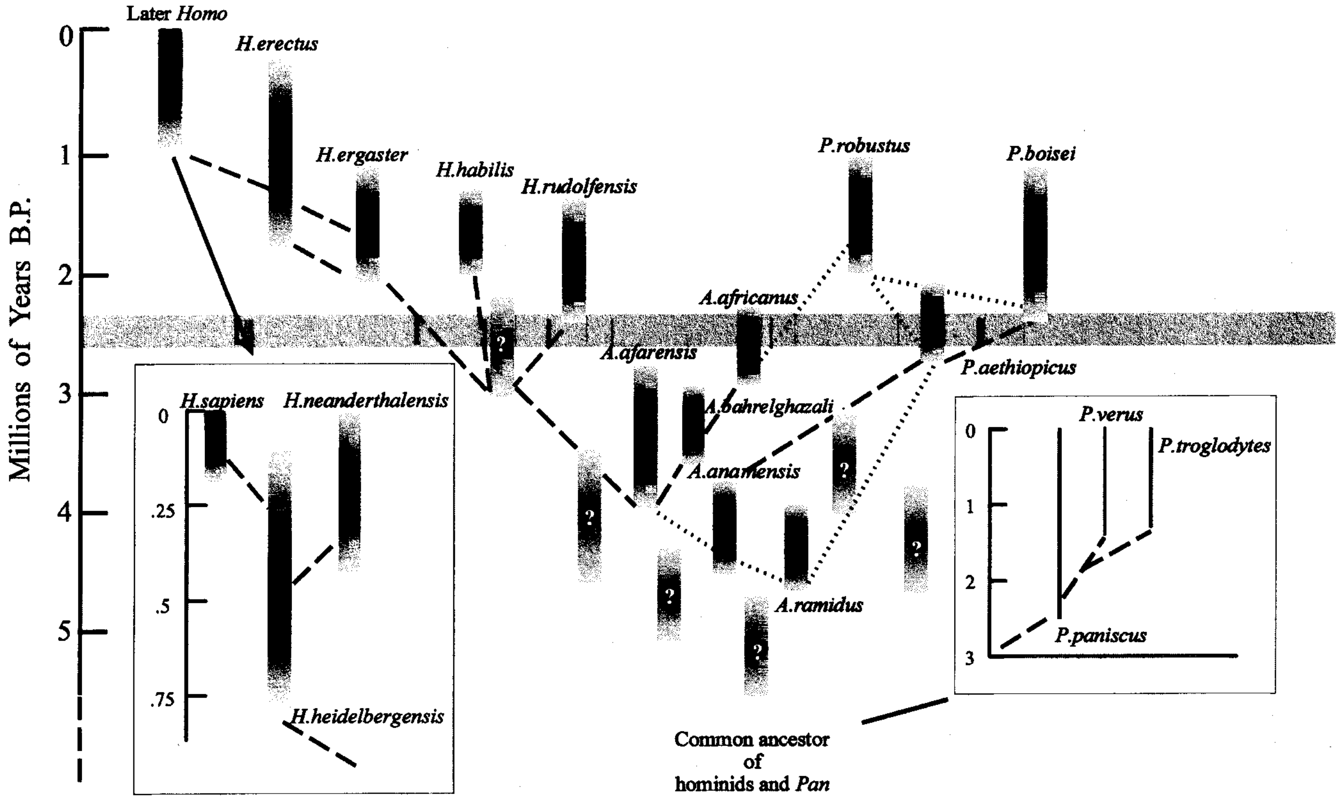

Figure 1. Approximate time ranges of hominin species groups. The columns with a question mark represent species groups that are likely to exist, but which are, for the moment, not recognized in the hominin fossil record. The horizontal grey band corresponds to the time of appearance of the earliest recognizable stone tools.

Thus, a genus has to be a group of species of 'common ancestry' that is adaptively homogeneous.

Evidence about the first of these criteria can be examined using the method of phylogenetic analysis, also known as cladistics. If all the species presently allocated to *Homo* form a well-supported 'monophyletic group', or clade, then that would satisfy one of the two necessary conditions for a genus. The second condition, that of adaptive homogeneity, can, in fossil taxa, only be investigated by looking at the distribution of morphological features which have functional and adaptive implications. How well does the genus *Homo*, as presently defined, satisfy these two criteria?

Monophyly

Although cladistic methods have been applied to the early hominin fossil record for more than two decades, since Eldredge and Tattersall's pioneering analysis was published in 1975, relatively few studies have considered the more recently recovered material attributed to 'early *Homo*', and fewer still have broken this evidence down into two taxonomic groups for the purpose of phylogenetic analysis. Of these, only Strait *et al.* (1997) conclude that the species presently included in *Homo* form a monophyletic group. The study by Lieberman *et al.* (1996) came to the conclusion that while there was evidence for linking *H. habilis sensu stricto* with later *Homo* taxa in a monophyletic group, with respect to *H. rudolfensis* there was as much evidence linking it with the *Paranthropus* clade as with that of *Homo*.

These results all relate to cladistic analyses that include only craniodental evidence. While it would be unwise to speculate about the results of studies that are not yet undertaken, it is worth bearing in mind that if the scope of the analysis was widened to include postcranial characters, then given even the little we know about the postcranial skeleton of *H. habilis sensu stricto* (Johanson *et al.* 1987), it is unlikely that this taxon would be part of a *Homo* clade, since its postcranial skeleton is at least as primitive as that of *A. afarensis* (Hartwig-Schrerer & Martin 1991).

Adaptive homogeneity

In an analysis which is reported elsewhere (Collard & Wood in press) we have examined information about early hominin taxa which reflect their body shape, locomotor behaviour, and the size of their neocortex, and we have analysed data which provide information about diet. We reasoned that one way of assessing how many adaptive strategies are represented in hominin evolution is to look for major differences in the way in which the component species go about maintaining homeostasis, acquiring food, and producing offspring. We also reasoned that a species' mode of locomotion, dietary choices, brain size, and the shape and size of its body would be significant factors in determining how it achieved homeostasis, an adequate food intake, and reproductive success.

While the importance of locomotion and diet is obvious, the significance of brain size and, especially, body shape and size requires some explanation. Brain size appears to determine the principal social interactions that are involved in reproduction (Dunbar 1992; 1995; Aiello & Dunbar 1993). Body shape is closely linked to temperature regulation, water balance, and habitat (Wheeler 1991; 1992; Ruff 1991; 1993; 1994; Ruff & Walker 1993). Ruff (1993) notes that in closed, forested environments with limited direct sunlight and little air movement a tall, linear physique loses its advantages. Moreover, humid environments decrease the usefulness of a relatively large surface area for evaporative cooling by sweating.

We assessed information and morphometric evidence for seven African early hominin species: *Australopithecus afarensis*, *Australopithecus africanus*, *Paranthropus robustus*, *Paranthropus boisei*, *Homo habilis*, *Homo rudolfensis*, and *Homo ergaster*. Other early hominin species, including *Ardipithecus ramidus* (White *et al.* 1994; 1995), *Australopithecus anamensis* (Leakey *et al.* 1995), and *Paranthropus aethiopicus* (Walker *et al.* 1986), were not considered, since at the time of the study their published fossil records were, and still are, too sparse. As functional inferences about fossil taxa can be made only by analogy with extant species, we also considered evidence for *H. sapiens* and *Pan troglodytes*.

Information about, and relevant data for the interpretation of, early hominin species is frustratingly sketchy. What is known, however, suggests that these species can be divided into two broad adaptive categories (see Figure 1). One of these is characterized by a combination of facultative bipedalism and an ability to move effectively in trees; a diet which was considerably more mechanically demanding than those of *H. sapiens* and *P. troglodytes*; a low to moderate encephalization quotient; and a body shape which in terms of thermoregulation was best suited to a relatively wooded environment. The other adaptive strategy is characterized by a form of locomotion which is much more similar to that practised by modern humans, ie obligatory bipedalism with a limited ability to climb within trees; a diet which had similar mechanical properties to those of *H. sapiens* and *P. troglodytes*; a moderate encephalization quotient; and a physique which would have been adaptive on the open savannah. With varying degrees of certainty, *A. afarensis*, *A. africanus*, *P. boisei*, *P. robustus*, *H. habilis*, and *H. rudolfensis* can all be assigned to the first group, whereas among the early hominin taxa, only *H. ergaster* can be assigned to the second. Among the first group there is substantial morphological variation, and there are several clades subsumed within it. It is possible that additions to the fossil record, together with appropriate analyses, may show that it consists of species which sample more than one adaptive strategy.

In sum, the data we reviewed suggest that *A. afarensis*, *A. africanus*, *P. robustus*, *P. boisei*, *H. habilis*, and *H. rudolfensis* were, to use Andrews' (1995) phrase, 'bipedal apes'. They spent much of their time moving about in trees, were equipped with a brain that was little bigger in relative terms than that of *P. troglodytes*, had an omnivorous diet which included a greater proportion of difficult-to-process items, such as seeds, than that of *P. troglodytes*, and would have found it easier to live in relatively wooded habitats than in the open. The data also suggest that *H. ergaster* should be recognized as having a different adaptive strategy from that of *A. afarensis*, *A. africanus*, *P. robustus*, *P. boisei*, *H. habilis*, and *H. rudolfensis*. While still relatively unencephalized, *H. ergaster* appears to have been a fully committed biped, whose adaptations allowed it, if necessary, to venture into the open savannah. It also had a diet that was no more mechanically demanding than those of *H. sapiens* and *P. troglodytes*.

Conclusions and implications

For a variety of reasons it is no longer tenable to regard the possession of culture and membership of the genus *Homo* as synonymous. There are several grounds for abandoning this simplistic association. Firstly, stone tools are a poor proxy for 'culture'. They just happen to be durable, and if they are to be surrogates for 'culture', then 'culture' has to be redefined and qualified to reflect this. Secondly, what we can infer about the functional capabilities of two of the taxa presently included in *Homo*, namely *H. habilis sensu stricto* and *H. rudolfensis*, suggests that there are few grounds for regarding them as so 'advanced', that they are the only possible candidates for the manufacture of the stone artefacts. The fossil record of the postcranial skeleton of the early hominin upper limb is generally poor, but there are sufficient hand bones preserved to fuel a lively debate about whether it would have been possible for hominins other than those in *Homo* to make tools (Susman 1988; 1994; 1998; Marzke 1997), and research aimed at trying to understand the role of the hand and forearm muscles in stone tool manufacture (eg Marzke 1997; Hamrick *et al.* 1998) promises to generate testable criteria against which such judgements can be made. However, even if it could be demonstrated that *H. habilis sensu stricto* and *H. rudolfensis* could make tools, it is clear that their inclusion in *Homo* strains the latter's credibility as a genus. Their inclusion probably violates the requirement for monophyly, and almost certainly weakens the claim that all the members of the genus *Homo* occupy the same location in the 'adaptive landscape'. We suggest that species should only be included in the genus *Homo* if they share the reduced teeth and jaws, the derived body shape and the morphological manifestations of a commitment to terrestrial bipedalism that are apparently first seen in the hominin fossil record in early *African H. erectus/H. ergaster.*

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Abstracts

J. DESMOND CLARK

Grahame Clark and World Prehistory: A Personal Perspective

This paper traces the development of Grahame Clark's concepts of human cultural and biological evolution and identifies some of the factors that enhanced the depth and scope of his horizons from regional and national to international and global prehistory and interrelated behavioural traits of modern human populations of our present world.

BERNARD WOOD and MARK COLLARD

'Is *Homo* Defined by Culture?'

When the genus *Homo* was established by Linnaeus in 1758 it was described as consisting of two species components referred to as 'diurnal' and 'nocturnal'. We know now that 'nocturnal' Man referred to the orang-utan, which is now included in a separate genus, *Pongo*. The description of the second, 'diurnal', species, which Linnaeus called *Homo sapiens*, recognized six subgroups of which four were living, continental-based, geographic variants. It was more than a century later that the first fossil species, *Homo neanderthalensis* King, 1864, was added to *Homo* and since then other species referred to the genus have made it morphologically more inclusive.

Arguably the greatest single step in this process of relaxing the morphological criteria for including fossil species in *Homo* was made exactly a hundred years after the addition of *H. neanderthalensis*, when in 1964 Louis Leakey, Phillip Tobias, and John Napier proposed that gracile hominin remains from Olduvai Gorge, Tanzania, be included in the genus *Homo* as *Homo habilis*. Since then the hypodigm of *H. habilis* has accommodated specimens which have stretched the variability within that species to the point where many believe that the fossils attributed to it sample not one, but two species, *H. habilis sensu stricto* and *Homo rudolfensis*.

In this paper we trace the increasing inclusivity of the genus *Homo* and relate it to the apparently ever greater antiquity of stone tool manufacture. We also review the criteria for recognizing genera and examine whether our present understanding of the genus *Homo* conforms with the two main criteria, namely monophyly and adaptive homogeneity. We review the evidence for monophyly and refer to the results of an examination of a range of functionally-related variables to assess the adaptive levels of early hominin species.

Our conclusion is that the boundaries of *Homo* should be reset so that it includes early African *Homo erectus*, or *Homo ergaster*, and excludes *H. habilis sensu stricto* and *H. rudolfensis*. This would mean that the manufacture of stone tools would no longer be restricted to members of the genus *Homo*. However, we would contend that this has been an untenable association ever since the realization that synchronic taxa have existed in East Africa for much of the early phases of hominin evolution for which there is also evidence of stone artefact manufacture.

JOHN PARKINGTON

Western Cape Landscapes

The Atlantic coast of the western Cape is host to a vast quantity of archaeological sites of the past 100,000 years. Ecological studies of Middle and Late Stone Age sites provide opportunities to explore the development of behavioural patterns. The multitude of painted shelters and caves in the western Cape allow us to glimpse the systems of belief that structured early societies.

RHYS JONES

Dating the Human Colonization of Australia: Radiocarbon and Luminescence Revolutions

Dating the early colonization of Australia has for long been at the forefront of prehistoric archaeological enquiries. This paper reviews the historical progression from conjecture to fact, amplified by increasingly sophisticated methods of dating, and identifies those sites now acknowledged to be of paramount importance to a greater understanding of human colonization of the continent.

BRIAN FAGAN

Grahame Clark and American Archaeology

Grahame Clark exercised a seminal influence on American archaeology at a critical stage in its development. His ecological and subsistence researches in the Cambridgeshire Fenland and interest in settlement archaeology were known to but a few American scholars of the 1940s and 1950s. However, the publication of *Prehistoric Europe: The Economic Basis* (1952) and *Star Carr* (1954) came at a time when Americanists were turning from culture history to processual archaeology. Clark's analyses of environment and subsistence played a vital role in the formulation of some of the basic tenets of the so-called 'new archaeology' of the 1960s. His field researches provided a practical component to the influ-