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EMERGENCE OF HUMAN BEHAVIOUR PATTERNS

Archaeological tests of alternative models of early hominid behaviour: excavation and experiments

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Several rival hypotheses have been advanced regarding behavioural innovations, which may have put important selection pressures towards the development of cognitive faculties and expanded brain functions. These hypothesized changes in behaviour include increased dependence on tool-making, intensification of hunting as a subsistence activity and social patterns involving food-sharing. Archaeology constitutes one of the principal sources of evidence against which such hypotheses can be tested and the paper reports on research that has been undertaken in recent years to make the tests clear and explicit. In addition to excavation, the work reported includes experimental studies of bone fracture, experiments in the manufacture and use of stone tools and experiments on processes of site formation.

Investigators of human evolution and cultural development tend implicitly to base their interpretation on the principle of uniformitarianism. That is to say they tend to explain as many features of early hominid adaptation as possible by constructing their models from some combination of the characteristics of modern apes and the characteristics of modern humans. This mode of procedure is surely the most convenient one to adopt in the initial stages of enquiry. However, it is very important also that its limitations be recognized. As Lancaster (1968), Freeman (1968) and others have pointed out, a major part of the fascination of the study of the early antecedents of the human way of life is that we are investigating systems that have no living counterparts. Since there are no proto-humans alive today and there are no societies with proto-languages we clearly need to bear in mind the possibility that some, perhaps many, features of early hominid adaptive systems were distinctive and original.

Since the behavioural systems of early hominids would have had profound influence on brain evolution, the topic, while fraught with difficulties, is one of considerable importance. This paper offers a preliminary report on research that is designed to make the interpretation of early archaeological data on hominid behaviour more rigorous by subjecting sets of rival hypotheses to carefully devised tests. The work is being done by a team for which I am coordinator and spokesman.

Figure 1 presents a time table that indicates the first known appearance in the geological record of anatomical innovations that are a part of the human adaptive complex as we now know it. The figure presents, in a highly simplified fashion, minimum ages for important anatomical shifts in the human direction. What can be said about behavioural changes? For this, very largely we have to turn to archaeological evidence.

The ability of archaeologists to make a specific contribution to knowledge of early hominid patterns of life hinges on, but is not limited to, one particular innovation, namely hominid

Vol. 292. B

involvement in the making of recognizable implements from durable materials, most particularly stone. Once artefacts of stone began to be made they became markers for the movements and activities of their makers and archaeological inference can go beyond technology.

The upper half of figure 1 provides a time table of archaeological evidence for a series of significant technological, economic and cultural innovations.

The earliest known well documented and securely dated stone tools are those excavated by H. Merrick and J. Chavaillon from member F of the Shungura Formation at the Omo. These are almost exactly 2 Ma old. Stone artefacts that may well be about 2½ Ma old have been reported by Roche & Tiercellin (1977) from the Hadar, but we await further work for confirmation of the geological relationship and hence the age. The best studied and most informative set of very early archaeological occurrences are those of bed I at Olduvai (Leakey 1971), which

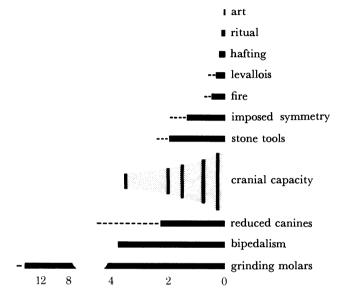


FIGURE 1. A time table showing the first known geological records of the appearance of human anatomical and behavioural traits. There is an almost complete gap in the record between 8 and 4 Ma ago.

are between 1.9 and 1.6 Ma old. Major features of the configuration discovered by M. Leakey are as fc!lows: (1) stone tools were made; (2) the behaviour of the tool makers was such that they discarded a scattering of artefacts here and there over the landscape, but also such that concentrated patches of artefacts formed in some places called sites by archaeologists; (3) some of these patches contain artefacts only, but others also contain quantities of the broken-up bones of a variety of animals, and in two cases the patch of artefacts coincides with the skeletal remains of the carcass of a single large animal. Subsequent research at Koobi Fora, Melka Kunturé, Chesowanja and Gadeb has shown that this configuration is not peculiar to Olduvai (see, for example: Isaac 1978; Harris 1978; Chavaillon 1976; Bishop et al. 1978).

The question then arises: what does this configuration mean? Can archaeological investigations of these material remains inform us about the adaptive patterns of early tool-making hominids? The first round of research revealed the configuration, the second is attempting to probe its evolutionary meaning.

The overall time table allows us to identify two grand puzzles that demand attention as we grope towards an understanding of the dynamics of human evolution. The first is the question of the circumstances surrounding the adoption of bipedal stance and locomotion and the **BIOLOGICAL**

MODELS OF EARLY HOMINOID BEHAVIOUR

second the nature of the selection pressures leading to a sustained trend towards brain enlargement and reorganization. From the time table it can be seen that the archaeological record as we now have it can do little or nothing to eludicate the circumstances of the shift to bipedalism, which took place at least $1\frac{1}{2}$ to 2 Ma before the date of the oldest recognizable tools yet found. On the other hand the known record of marked brain expansion and the known archaeological record coincide rather closely and it has long seemed reasonable to suggest that these two phenomena were related. That is to say, it is widely believed that some of the novel behavioural ingredients that caused the archaeological record to start forming were also significant determinants of the trend towards brain enlargement.

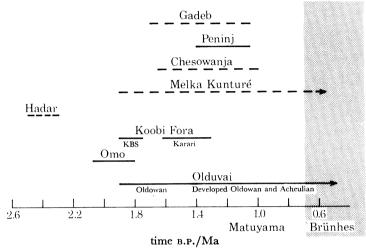


FIGURE 2. The approximate time relations among localities in east Africa yielding early archaeological evidence.

Dotted lines denote less certain age determinations.

BEHAVIOURAL INTERPRETATION: HYPOTHESES AND TESTS

At first glance the configuration just indicated seems familiar and readily interpretable. Where we see artefacts among the bones of a large animal, we quickly conclude that this is a fossil butchery site indicative of meat-eating on a large scale (Leakey 1971; Isaac 1971, 1978). Equally, the clusters of artefacts and broken bones from many different animals seem obvious to us as living sites (Leakey 1971) or home bases (Isaac 1969, 1978). But one should ask, as critics have indeed begun to ask (see, for example, Binford 1977), whether these are the only possible explanations. In adopting them without further question might we not be guilty of simply projecting familiar human-ness backwards 2 Ma? As I will briefly indicate at the end of the paper, the butchery, meat-eating, and home base interpretations are apt to get incorporated as components of far-reaching interpretations of the dynamics of human evolution. It surely behaves us to test these interpretations, to destruction if possible, before too much higher order theory is based on them.

As E. O. Wilson (1975) has pointed out, writers on human evolution have tended to be passionate advocates of one particular explanation or interpretation. However, in recent years the style has been changing in favour of the formulation of alternative or rival hypotheses, each with its own test implications that can serve to guide research. This not only turns out to be a constructive move, but also it is fun! What follows is a hasty portrait of how our research group is attempting to apply this approach. I will pose a series of problems as questions, then

179

indicate two or more possible answers or rival hypotheses plus the predictions that follow from the hypotheses. Then I will indicate the kinds of research being done to test the extent to which the predictions are met. In most instances the research is still in progress by others and so I can only whet your appetities while you await fuller reports from the investigators themselves.

(a) How did the clusters of artefacts and bones form?

Some possible explanations that have occurred to various people are as follows.

- (i) These are hydraulic jumbles in which artefacts and bones have been washed together by water currents.
- (ii) Hominid activity caused the artefact concentration and another, independent, agency, such as carnivore-feeding formed an overlapping bone concentration at some common amenity, for instance a shade tree, or a water hole.
- (iii) That the hominids caused the observed configurations by carrying both stones and bones to particular places, where artefacts were sometimes made and dropped and where bones were broken up and discarded.

Each of these would predict the observed overall configuration, but each would predict differences in detail. The hydraulic jumble hypothesis would carry the expectation that the concentrations and their matrices would have the size-sorted characteristics and sedimentary fabric of a water-lain deposit. Under the carnivore bone accumulation hypothesis the bones would resemble carnivore-chewed assemblages in their composition and damage patterns. The hominid stone and bone transport and discard hypothesis would predict that among other things some of the bones might show specific signs (such as cut marks) of having been processed with stone knives and breakage patterns caused by hammers rather than by jaws.

All of these suggested explanations need to be taken seriously, and it should be recognized that they are not mutually exclusive. Combinations may have acted to form individual sites. Almost all archaeological horizons in east Africa were covered over and preserved by sediments deposited from moving water, albeit in some cases very gently moving water which laid down only silts and clays. This means that, even where it seems highly improbable that the concentration of materials could have been caused by hydraulic forces, it is necessary to assess the extent to which the material has been moved about before interpreting the details of arrangement.

One member of the team with which I work, K. Schick, has embarked on a programme of experimental work designed to help archaeologists assess the degree to which an excavated assemblage has been transported, winnowed or rearranged. Her work involves a wide variety of controlled observations on the processes by which material accumulates and on the effects of geological and other agencies that could cause the materials to become stratified. The results of these experiments will be used to guide interpretation of archaeologically observed configurations.

The bone assemblages from a series of sites at Koobi Fora and Olduvai have been carefully studied by H. Bunn and those from Olduvai have also been studied by R. Potts. Both have independently looked for distinctive hammer breakage patterns and for modifications such as cut marks. At some sites the results of these searches have been positive and reports on these important new findings, which meet the predictions for hominid involvement with the bones, and which effectively falsify hydraulic or carnivore causation alone, will shortly be published.

Another new finding, which helps to distinguish the three rival hypotheses under discussion,

MODELS OF EARLY HOMINOID BEHAVIOUR

181

has been the discovery by N. Toth, E. Kroll and K. Schick that at several sites numbers of stone artefacts and bones can be fitted back together again.

Preliminary plans by Kroll, who is doing detailed analyses of arrangement patterns, allow us to see that fitting pieces of stone and bone tend to be clustered in a way that would not be predicted if the artefacts and bones had simply been washed together.

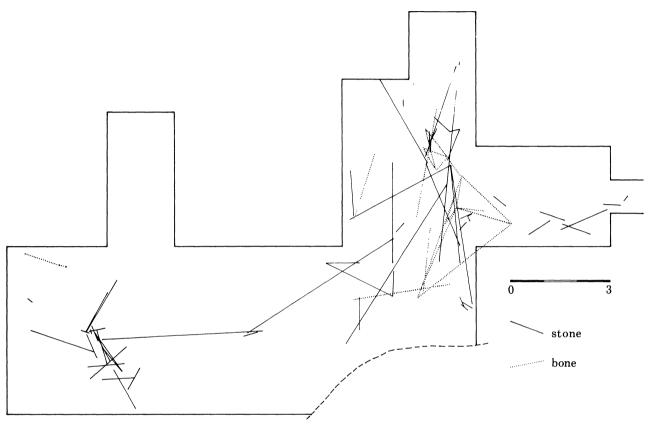


FIGURE 3. A plan of the excavated area at an early site (FxJj 50) in the Koobi Fora area. The lines join up the find places of artefact and bone pieces that fit back together. The configuration strongly implies that the hydraulic jumble hypothesis should be rejected.

(b) What kinds of hominid behaviour patterns resulted in the formation of sites?

Given the working hypothesis that the site concentrations formed through active hominid manipulation of stones and bones, the question arises, what were the hominids doing at these places?

Many of the sites are located in stoneless terrain and it is very clear that stones were carried to the locality and flaked there. As the study of conjoining pieces shows, some artefacts were removed from the immediate vicinity in which they were made. However, the accumulation of bones is not so clearly attributable to proto-human transport, since bones, while in live animals, are independently mobile! Alternative hypotheses again need to be considered.

(i) Artefacts were made and discarded at places where a variety of animal carcasses were periodically available for butchery and for breaking of bones, for instance the margin of a water hole, where animals recurrently died, or a bend in a river, where drifting carcasses washed up.

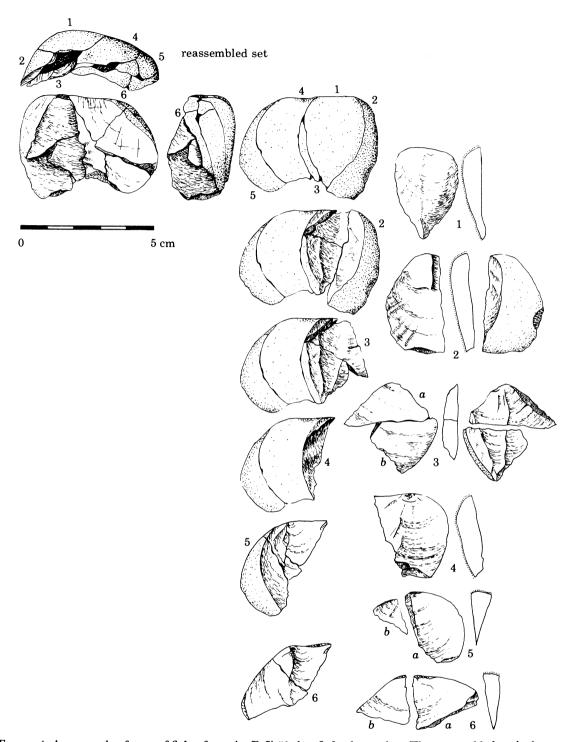


FIGURE 4. An example of a set of flakes from site FxJj 50 that fit back together. The reassembled set is shown at the top and successive stages of disassembly are set out below. The flakes can be seen to have been struck from the margin of a water-rounded cobble. After the striking of the flakes, the cobble would have had the form of a chopper, but this had been removed from the vicinity where the flaking was done.

MODELS OF EARLY HOMINOID BEHAVIOUR

183

(ii) Bones and meat from many different carcasses were carried to a central locality at which the manufacture of stone artefacts was also carried out.

At the present time I cannot offer decisive evidence to prove false either of these alternatives. However, given the considerable diversity of species at some of the sites, and given their varied physiographic settings, such as flood plains on the shores of lakes for the Olduvai FLK Zinj site, and flood plains on channel banks for FxJj 50, one is inclined to regard the first explanation as less credible.

If the second hypothesis is adopted, then this implies the transport of food, a behaviour common in birds and bees but rare among mammals and almost unknown in primates other

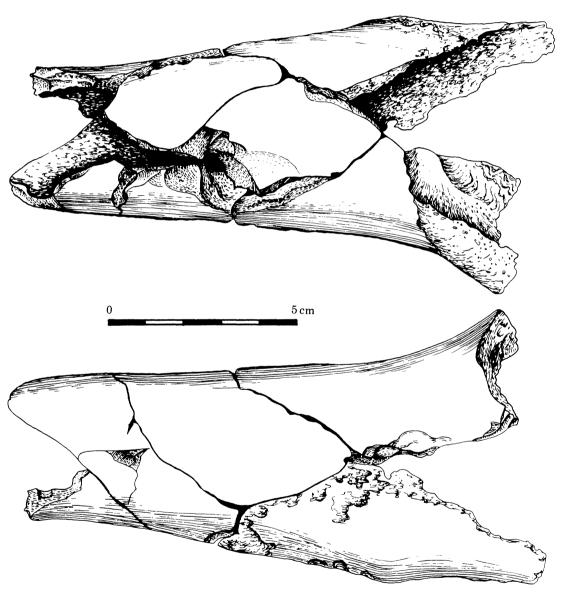


FIGURE 5. An example of pieces of bone that fit back together. The reassembled set has been identified by H. Bunn as a humerus shaft from a large alcelaphine antelope. Experimental evidence strongly suggests that the fracture of the shaft was induced by a hammer blow. Part of what is almost certainly the articular end of this same bone was also found at the site and this has scored lines on it that seem to be cut marks inflicted by the sharp edge of a stone tool.

than humans. Whether the food was transported for sharing among an entire social group or simply for the feeding of the young would be an important follow up question, to which we can as yet offer no answer, or even any potential tests.

Another important question that arises as we pursue this chain of investigation is the matter of the amount of time and the number of site usage episodes that formed early sites. Were the assemblages of artefacts and bones at such living sites as the Olduvai FLK Zinj site or FxJj 50 and FxJj 20 at Koobi Fora deposited as refuse during a single sustained period of occupancy or did they accumulate as a result of a long drawn-out series of short return visits, with each visit leading to the discard of an increment of refuse?

We know of no simple measures of duration and recurrence of occupancy, but patient work may help to put limits on the mode of accumulation. For instance, the degree of preburial bone weathering would allow one to distinguish bone assemblages that had taken many years to accumulate. H. Bunn has concluded that, at least at some of the early sites, subaerial weathering is not apparent on most bones, probably implying accumulation over no more than a year or so.

Another line of attack follows deductive logic. If at the majority of early hominid sites usage bouts were brief and short, there might also be many 'mini-sites' scattered about, places where activities lasted a few hours or a day or so and led to the deposition of just a few artefacts and other refuse items. We have begun to look for these and have indeed found some, but the sample areas searched and the series excavated need to be much enlarged before any judgement of the relative frequency of mini- and maxi-sites can be reached.

The early sites have been variously called occupation sites, living sites, home bases etc. All these are loaded terms that involve many tacit backward projections of the familiar forms of modern Homo sapiens patterns. For instance, even if food was carried to these places and if tools were made and used there, they need not have been sleeping places. In her spatial analysis of the sites, E. Kroll is seeking to formulate questions such as these and to seek discriminants between various possible modes of site usage and formation.

(c) What do the early stone tools themselves teach us about the organisms that made them?

Within our team this problem is being studied in a variety of ways. J. W. K. Harris and I are testing for correlations between the characteristics of assemblages and the characteristics of the environmental context in which each variant set was discarded. This is being done in the hope of identifying distinctive habitat-specific activities. We have also looked for evidence of change through time (Isaac & Harris 1978; Harris 1978). In pursuing this work it became clear that we needed to know whether the early artefact assemblages represent opportunistic leasteffort solutions to the problem of obtaining sharp edges from stone, or whether, as in most late prehistoric and modern assemblages, there was a fairly elaborate set of culturally defined, arbitrary artefact forms. Different archaeologists can look at the same assemblage and come up with quite different judgements on this question. Approaches other than laboratory sorting were clearly needed to resolve this uncertainty.

In addition we realized, as did many other workers, that if we are to move towards an understanding of the adaptive significance of tools in early hominid life, we need to ascertain first the uses to which they can be put, and secondly to seek evidence of how they actually were used.

Both the complexity of design problem and the problem of function called for a combination of experiments and close scrutiny of the sets of excavated ancient artefacts. A start on this large

MODELS OF EARLY HOMINOID BEHAVIOUR

185

and important task has been made for the project by N. Toth, who has learned to replicate all of the artefact forms so far recovered from the early sites at Koobi Fora using the same raw materials as were used between 1½ and 2 Ma ago. He will be reporting his specific findings elsewhere, but it appears that the features of the early stone artefact assemblages can be accounted for as the application of an opportunistic, least-effort strategy applied to locally available forms of stone. Even such apparently fancy forms as the Karari scraper need be no more than this.

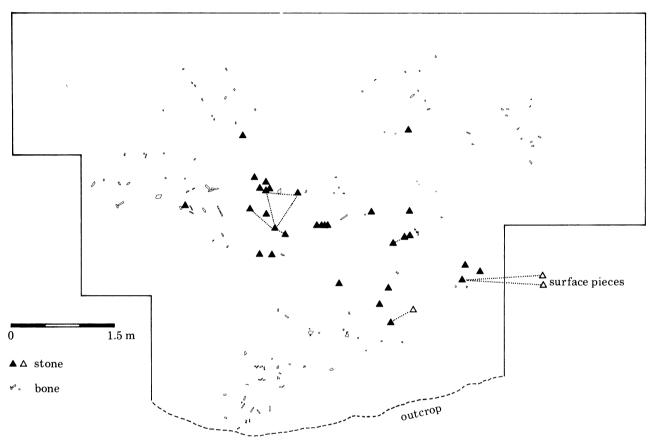


FIGURE 6. An example of the disposition of finds at a mini-site of the kind that our research group is now searching out and excavating. At this one (FxJj 64), stone flakes, derived from the knapping of just three or four stones, form a cluster superimposed on a scatter of bone fragments. Such sites have the advantage that they may represent a single bout of activity during one visit to the locale, lasting from between an hour or so to a day or so. This example was found by A. K. Behrensmeyer and excavated by F. Marshall.

In the investigation of function, Toth and other members of our group have demonstrated that by means of simple flakes and core tools it is perfectly possible to perform all the most basic functions that in ethnography and later prehistory are necessary to the human way of life: branches can be chopped off and then sharpened so as to form a digging stick or spear; a simple carrying device such as a bark tray can be prepared; and animals, even very large pachyderms over which the non-human carnivores have great difficulty, can be cut up.

These experiments, together with those done by P. Jones and the late L. Leakey (Jones, this symposium) and by others, go a long way to confirm the view that the discovery of how to obtain sharp-edged tools had great potential adaptive significance. Among others, they facilitate access to energy-rich food types such as meat and deep tubers.

186

G. L. ISAAC

However, what early tools might have been used for and what they actually were used for are not necessarily the same things. N. Toth has tackled this also, working with L. Keeley, a pioneer researcher on the distinctive wear patterns that are induced on stone by contact with such materials as wood, bone, hide, meat and plant tissues of various kinds. As Keeley and Toth will report in due course, preliminary examinations seem to imply that several different varieties of use wear are evident on chert flakes from the Koobi Fora Formation.

The finding, by H. Bunn and R. Potts, of cut marks on bones represents still another important class of evidence regarding the function of some early tools.

In the preceding part of this paper I have given examples of the kinds of research question that our research group, among others, are pursuing. By way of conclusion I now want to deal briefly with how these kinds of archaeological enquiries connect with the overall interdisciplinary study of human evolution. As I mentioned in the introduction, two grand puzzles can be recognized, and it is to the second of these that archaeological data seem most relevant, namely the puzzle of how natural selection acted to initiate and sustain a prolonged trend in the human ancestral lineage towards the enlargement and reorganization of the brain.

Since the time of Darwin, a succession of more or less vague and speculative explanations has been advanced. Two stand out as particularly prominent, 'tool-using' and 'hunting'. The tool-using line of explanation, though widely invoked, is seldom stated very explicitly. Presumably it involves the notion that novel genetic configurations that endowed some small-brained, bipedal early hominids with superior abilities in making and using tools enabled the carriers of these genotypes to leave more surviving offspring. The argument runs on to the effect that, since many tool making and tool-using skills need to be culturally transmitted, the adaptive importance of tools led to the establishment and elaboration of culture in general (cf. Lancaster 1968; Tobias, this symposium).

The hunting theory has been recounted in dramatic terms by writers such as Dart, Ardrey and Morris and in more restrained terms by, for example, Washburn & Lancaster (1968) and by Campbell (1966). It argues that, for savannah-living hominids, gaining increased access to a new food resource, meat, was the main selective advantage and that successful access was facilitated by mutations favouring the use of tools, enhanced foresight and cunning, and by mutations favouring communication and cooperation, especially among males.

Very recently, various workers, including myself (Washburn 1965; Hewes 1961; Lee 1979; Lancaster 1978; Isaac 1978), have been involved in making explicit yet another line of explanation, food-sharing. This subsumes tools and hunting, adds some other components and then goes on to argue that it was the adoption of a whole integrated complex of behavioural innovations that in each generation gave individuals, or perhaps kin groups, with somewhat more versatile brains, a crucial advantage over their contemporaries.

The investigations outlined in the body of this paper are all aimed at helping to distinguish the relative credibility of these and other rival large-scale overarching theories of the evolutionary dynamics of human brain enlargement. The information that we now have does not make it seem that the earlier approximations, 'tool-using' and 'hunting' are wrong, only that they are seriously incomplete. For instance, use of stone tools could only have become important as a part of a whole series of social, reproductive and dietary changes (cf. Parker & Gibson 1979).

Archaeological research has shown that many early artefacts occur jumbled up among the

broken bones of edible animals. Does this circumstantial evidence really imply that the early hominids were hunting in a serious way? I have already indicated the existence of new evidence that tends to sustain the hypothesis that the tool-making hominids were eating meat and marrow. However, there are more ways of obtaining flesh and bone than by hunting and killing. We need to consider scavenging as an alternative. There are aspects of the bone assemblages associated with early artefacts that would be more plausibly predicted under the scavenging hypothesis than under the hunting hypothesis (cf. Vrba 1975; Schaller & Lowther 1969). Most tropical modern human gatherer-hunters catch and consume quantities of medium to smallish animals, which size range it is unusual to obtain by scavenging. However, the archaeological bone assemblages from Olduvai (Leakey 1971) and from Koobi Fora (H. Bunn, personal communication) are dominated by bones from medium to large animals, precisely the size range of carcasses that do provide scavenging opportunities (Vrba 1975). The relative importance of these two alternatives remains to be explored in further research.

However, even if meat-eating and hunting are adopted as reasonably well documented components of early hominid behaviour, the hunting hypothesis remains far from satisfactory as a comprehensive explanation of the basis for the evolution of the human brain-mind-culture complex. For instance, what were the females and children doing while males hunted?

The food-sharing hypothesis would predict the following as having been important: tools, transport of food, meat-eating, gathered plant foods, division of labour and the existence of places at which members of a social group would reconvene at least every day or so and at which discarded artefacts and food refuse would accumulate. The archaeological configuration observed at Olduvai and at Koobi Fora fits many of these predictions.

This line of explanation has important potential for helping us to understand the complex dynamics of the last 2 or 3 Ma of human evolution. It has already been adopted in such widely read popular books as *Origins*, written by Leakey & Lewin (1977). However, it is a hypothesis, not an established truth. This is why our research group has systematically sought to test it by attempting to prove its predictions false. However, there are important gaps: we assume that plant foods were the dominant source of energy and nutrition for the early Pleistocene hominids, but, beyond the preliminary findings of A. Walker in his studies of tooth wear (this symposium), we have few ways to test that assumption or to ascertain when gathering with postponed consumption of plant foods began. One member of our group, J. Sept, intends to attack an aspect of the problem by studying the feeding opportunities that are represented in modern analogues of the situations in which field evidence shows that early hominids lived, made tools and died.

Once the food-sharing system had been established the theory predicts that it would have produced steady selection pressure in favour of capabilities for developing social systems based on reciprocity. There are clear potential cross ties here between this theory and the recently enunciated theories of the evolution of social tendencies through the mechanism of kin selection (Hamilton 1964; Trivers 1971; Wilson 1975).

The food-sharing line of explanation is not an entirely new suggestion, but until recently it was implicit rather than explicit. In 1975 I sought to rectify this by stating clearly the thesis that the early tool-making hominids lived in social groups that manifested division of labour and practised food-sharing at home bases (Isaac 1976). Many people took this to mean that the early hominids must have been relatively placid, cooperative, gentle creatures who lived essentially human lives, less a few trappings of cultural elaboration. This does not necessarily follow, and I return to the point made at the outset: there are no living counterparts of the early

hominids and we should expect that, as we refine our information about them, more and more distinctive and unexpected features may appear. To illustrate this let me close by pointing out that recent research on finger bones (Susman et al. 1979) and shoulder joint (Vrba 1979) strongly imply that the hominids of 2 Ma ago, though adapted to bipedal locomotion, were also well adapted for tree climbing. It is entirely possible that they did not sleep at their so-called home bases but that they slept in trees.

REFERENCES (Isaac)

- Bishop, W. W., Hill, A. & Pickford, M. 1978 Chesowanja: a revised geological interpretation. In *Geological background to fossil man* (ed. W. W. Bishop), pp. 309-327. Edinburgh: Scottish Academic Press.
- Binford, L. 1977 Olorgesailie deserves more than the usual book review. J. anthrop. Res. 33, 493-502.
- Campbell, B. G. 1966 Human evolution. Chicago: Aldine.
- Chavaillon, J. 1976 Evidence for the technical practices of Early Pleistocene hominids: Shungura Formation, lower Omo valley, Ethiopia. In *Earliest man and end environments in the Lake Rudolf Basin* (ed. Y. Coppens, F. C. Howell, G. Ll. Isaac & R. E. F. Leakey), pp. 565-573. Chicago: University of Chicago Press.
- Freeman, L. G. 1968 A theoretical framework for interpreting archaeological materials. In *Man the hunter* (ed. R. B. Lee & I. DeVore), pp. 262-267. Chicago: Aldine.
- Hamilton, W. D. 1964 The genetical evolution of social behaviour II. J. theor. Biol. 7, 17-52.
- Harris, J. W. K. 1978 The Karari Industry: its place in East African prehistory. Ph.D. thesis. University of California, Berkeley.
- Hewes, G. W. 1961 Food transport and the origins of hominid bipedalism. Am. Anthrop. 63, 687-710.
- Isaac, G. Ll. 1969 Studies of early culture in East Africa. Wld Archaeol. 1, 1-28.
- Isaac, G. Ll. 1971 The diet of early man. Wld Archaeol. 2, 278-299.
- Isaac, G. Ll. 1976 East Africa as a source of fossil evidence for human evolution. In *Human origins: Louis Leakey and the east African evidence* (ed. G. Ll. Isaac & E. R. McCown), pp. 121-137. Menlo Park: W. A. Benjamin. Isaac, G. Ll. 1978 The food-sharing behaviour of protohuman hominids. *Scient. Am.* 238, 90-108.
- Isaac, G. Ll. & Harris, J. W. K. 1978 Archaeology. In Koobi Fora research project, vol. 1 (ed. M. G. Leakey & R. E. Leakey), pp. 64–85. Oxford: Clarendon Press.
- Lancaster, J. B. 1968 On the evolution of tool-using behaviour. Am. Anthrop. 70, 56-66.
- Lancaster, J. B. 1978 Carrying and sharing in human evolution. Hum. Nature 1 (2), 82-89.
- Leakey, M. D. 1971 Excavations in Beds I and II, 1960-1963. Olduvai Gorge, vol. 3. Cambridge University Press.
- Leakey, R. E. F. & Lewin, R. 1977 Origins. New York: E. P. Dutton.
- Lee, R. B. 1979 The !Kung San. Cambridge University Press.
- Parker, S. T. & Gibson, R. 1979 A developmental model for the evolution of language and intelligence in early hominids. In *The behavioural and brain sciences*, vol. 2, pp. 367–408. Cambridge University Press.
- Roche, H. & Tiercellin, J. J. 1977 Discovery of an old lithic industry in situ in the Hadar Formation, Central Afar, Ethiopia. C. r. hebd. Séanc. Acad. Sci. Paris D 284, 1871-1874.
- Schaller, G. B. & Lowther, G. R. 1969 The relevance of carnivore behaviour to the study of early hominids. SWest. J. Anthrop. 25, 307-340.
- Susman, R. L. & Creel, N. 1979 Functional and morphological affinities of the subadult hand (O.H. 7) from Olduvai Gorge. Am. J. phys. Anthrop. 51, 311-331.
- Trivers, R. L. 1971 The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35-57.
- Vrba, E. 1975 Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraii from the fossil Bovidae. *Nature*, *Lond*. 254, 301–304.
- Vrba, E. S. 1979 New study of the scapula of Australopithecus africanus from Sterkfontein. Am. J. phys. Anthrop. 51, 117-130.
- Washburn, S. L. 1965 An apes-eye view of human evolution. In *The origin of man* (ed. P. DeVore), pp. 89-107. New York: Wenner Gren Foundation.
- Washburn, S. L. & Lancaster, C. S. 1968 The evolution of hunting. In *Man the hunter* (ed. R. B. Lee & I. De Vore), pp. 293-303. Chicago: Aldine.
- Wilson, E. O. 1975 Sociobiology: the new synthesis. Harvard: Belknap.