A consideration of some aspect of the behaviour and ecology of the early hominids

P. R. Lattin

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SYNOPSIS.

In this paper, I have considered certain aspects of the ecology and behaviour of the early hominids in the light of the available literature on this subject. The first section discusses the place, nature and significance of the early hominids in the overall history of the hominid line, as well as discussing the possibility that it was a change in the habits of the ancestral hominids, brought about by altered environmental circumstances that encouraged the selection of modifications for more efficient bipedalism. The second section reviews the arguments that have been put forward by Reynolds in support of his contention that human society arose from an ape-like system of open groups. Although agreeing with much that he has written on this topic, I have questioned the validity of some of his views on the openness of pongid and early hominid society. The third section discusses the cultural capacities of the various early hominid forms with reference to the palaeontological evidence and the known tool-using abilities of other, especially sub-human primate, species. Moreover, it draws attention to the behavioural preadaptedness of these creatures for developing tool-using habits, as well as reviewing the arguments that have been expressed on whether tool-using arose from agonistic displays or food-getting habits. The fourth section deals with the feeding habits of the early hominids, and argues that vegetable foods were the staple diet of the early hominids, as they are of tropical hunter gatherers, with only relatively small, though significant, additions of other items. The final section constitutes a general appreciation of the behaviour and ecology of the early hominids, with special reference to the arguments expressed elsewhere in this work.

P. R. LATTIN

A CONSIDERATION OF SOME ASPECTS OF THE BEHAVIOUR AND ECOLOGY OF THE EARLY HOMINIDS.

M.A. Thesis, 1969.

CONTENTS.

PREFACE.

In the last decade, new discoveries in the fields of palaeontology and primate behaviour, together with the work of scholars in other related fields of enquiry, have considerably modified our ideas about the possible nature and circumstances of the early hominids. Indeed, interest in the many different aspects of man's evolutionary history is more intense today than it has ever been in the past, and research workers in many different disciplines with different aims and methods are almost daily contributing to our overall understanding of this subject, and especially of those anatomical and behavioural changes which have enabled man to become the most successful of living species.

Any attempt at a comprehensive treatment of the nature and significance of the early hominids would obviously require a far more detailed approach than is possible within the framework of this thesis, and even then it is arguable whether a satisfactory synthesis of the vast amount of data on this subject could hope to be achieved by one individual. As such, this thesis attempts no more than a consideration of some aspects of the ecology and behaviour of the early hominids, and though the limitations of such an approach will be obvious to the reader, and need not be set down here, it is to be hoped that I have at least identified some of the complex issues which face investigators in this subject.

With respect to the terminology I have employed in this paper, the words protohominid and early hominid have been used synonymously in view of the fact that no general agreement has been reached on a collective term for the early relatives of man. The word australopithecine has been used specifically to refer to those forms which have been included in the genus Australopithecus by Tobias (1967), and the word hominine to the forms Homo habilis (Leakey et al. 1964), Telanthropus and Pithecanthropus (Tobias 1962). I realize that this terminology is perhaps open to question as there is still some dispute on the precise taxonomic status of these various forms; at the same time these terms probably reflect the views of most authorities in this field today. In discussing the fossil evidence pertaining to a particular form, I have used the term by which it is generally known in the literature (sic Telanthropus Homo habilis, Paranthropus, Zinjanthropus) rather than the taxonomic category to which various scholars have assigned it.

The references that I have cited in the text are numbered individually, and their details recorded at the end of each section. A complete bibliography of all the literature referred to in the text as well as the other works that have been consulted in the preparation of this work can be found at the back of the volume. The notes which I have included on various points relating to the text have been marked with an asterisk, and may be found at the foot of the page on which they occur.

Finally I should like to thank all those who have assisted me directly or indirectly in the preparation of this thesis. Especially I would thank Dr. Sunderland for his encouragement and advice at every stage in the preparation of this work, and to Mrs. Foulds for the time and care that she has taken in typing the manuscript.

EARLY HOMINID SYSTEMATICS.

The protohominid forms of the Early and ~~upper~~ early Middle Pleistocene were small bipedal ground living creatures inhabiting savannah or woodland savannah type country. Between four and five feet in height, they probably weighed from 60 to 120 pounds, depending on the species and sex to which they belonged. The most significant of the anatomical features which distinguished them from the apes was their habitual erect posture (achieved by modifications to the pelvis, to the spinal column, to the position of the foramen magnum etc., as well as to obvious changes in the foot and ankle; reduced prognathism; jaws and teeth whose morphological pattern was fundamentally of the hominid type (curved contour of the dental arcade, small canine teeth, lack of diastema etc.,); and a brain relatively, though not absolutely larger than the living apes. They possessed a primitive lithic culture and though mainly vegetarian in diet, probably supplemented this food with insects, larvae, fish, crustacea, reptiles and small or immature mammals. They are most famously associated with Olduvai Gorge in Tanzania and the South African fossil bearing sites, though their remains have also been found at other sites in East and North Africa, in the Middle East, and contentiously in the Djetis beds of Java.

Until recently, the ascription of each major fossil discovery to a new species or genus presented a confusing picture, and obfuscated the morphological relationship between the different forms. Thus, at one time, a number of different genera were claimed for this one group of fossil hominids, and variously named Plesianthropus, Paranthropus, Telanthropus, Zinjanthropus and Australopithecus. Although even today there is no final agreement on the number of genera and species in this group, generally they are thought of as comprising one genus (Australopithecus) and two species (africanus and robustus).

However, this simple taxonomic scheme is complicated by the discovery of two fossil forms, one in South Africa (Telanthropus) and the other in East Africa (Homo habilis) which appear to be anatomically more advanced than the other protohominids of this period. Fossil remains of Telanthropus were unearthed in Middle Pleistocene deposits at Swartkrans in sympatric and synchronic association with fossils of the type Australopithecus robustus. Robinson considers that this hominid form shows distinct morphological differences to the other australopithecines and considers it to be a hominine (Homo erectus).[1] However, other authorities do not agree with this viewpoint, and consider that its differences are no more than might be expected to occur between members of a single species, and accordingly, they assign it to the taxon Australopithecus africanus. However, the rest of the fossil-bearing sites have clearly distinguished the two australopithecine sub groups in time, and if Telanthropus were to be included in the taxon Australopithecus africanus, this would definitely associate the two types - robust and gracile - both synchronically and sympatrically. In the past, Australopithecus africanus has generally been thought of as an Early Pleistocene form, and Australopitheous robustus as a Middle Pleistocene form, based mainly on the evidence from the South African fossil sites, where these creatures were first discovered. However, the discovery of Zinjanthropus boisei in Early Pleistocene deposits at Olduvai Gorge has upset this neat temporal dissociation of the two forms. Zinjanthropus is generally considered to be a representative of the taxon Australopitheous robustus, though recently Tobias has affirmed his conviction that it is specially distinct from the other two australopithecine forms.[2] Whatever one's conclusions may be there is no disputing that a more robust form of australopithecine was living in East Africa in the Early Pleistocene.

In 1960, Leakey discovered the skull of another hominid in Bed I at Olduvai, about a foot lower in depth than the Zinjanthropus skull, though some distance away from it. This skull, which has variously been presented as the first evidence of murder in history, as Pre-Zinjanthropus and finally as Homo habilis, apparently approximates in many of its morphological characters to the hominines, (Homo erectus and Homo sapiens) rather than the australopithecines. Leakey distinguishes it absolutely from the other protohominid forms of the Early Pleistocene and considers it to be directly ancestral to man.[3]

Various interpretations of the palaeontological evidence have been put forward at different times. Basically there are three different ways of looking at it. One is to lump all the various forms together with only specific or sub-specific distinction between them and place them in the genus Homo. The more robust (primitive) individuals might, from this standpoint, be considered extreme types who were either genetically isolated from the main line of human evolution, or selected out over a period of time. Another and more generally accepted interpretation is that which classifies the protohominids of this period (including Homo habilis but excluding the later euhominid Telanthropus) into one genus (Australopithecus) and two species (africanus and robustus). However, some authorities, such as Robinson, make a generic distinction between the two types, classifying the gracile forms as Australopithecus* and the robust forms as Paranthropus.[4] In this context, it does not really matter which classification is adopted. The gracile forms, in this scheme, represent the progressive line in hominid evolution and are thus man's direct ancestors. The more robust forms represent a conservative line doomed by their specialisations to eventual extinction. All the same, it is thought that these two lines must have had a common ancestor in the Pliocene. Such an interpretation therefore would place Homo habilis on the progressive line along with other gracile forms and Zinjanthropus boisei on the conservative line with the robust forms.

A third way of viewing the evidence would be to distinguish the

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*Recently Robinson has dropped the generic category Australopithecus, in favour of placing all the gracile forms in the genus Homo. (Robinson 1965).

advanced forms Homo habilis and Telanthropus absolutely from the other protohominids of this period, and place them on the direct line of evolution which led to man. The rest of the protohominids could then either be lumped together, or distinguished into gracile and robust forms with a common ancestor in the Pliocene. Whatever scheme is adopted they would be off the main line of human evolution. In this case Ramapithecus may either have been the common ancestor of all the Pleistocene protohominids, or only of the advanced forms Homo habilis and Telanthropus.

These three interpretations are, of course, not the only ways of looking at the available evidence. However, it may be inappropriate at this time to posit fixed evolutionary schemes, as the palaeontological data are susceptible to so many different interpretations. One solution to this dilemma might be merely to distinguish those forms that, at the moment, seem most likely to be the early forebears of man, and to place them on or close to the main line of human evolution. This would realise an evolutionary series similar to the third scheme outlined above, starting in late Miocene times with the form Ramapithecus (including Kenyapithecus wickeri) and progressing through Homo habilis and Telanthropus to Homo erectus and finally to modern man himself.

The major features of hominid systematics in the Early and Middle Pleistocene period are thus fairly clear. However, in order fully to appreciate the importance of these creatures in the overall history of man's evolution, it is necessary to know something at least of their distant forebears in the Oligocene and Miocene periods.

The Fayum beds in Egypt have produced the greatest variety of Oligocene primates discovered at a single site, and testify to the fact that even at this early date, the primates had differentiated into a number of distinct species, including some forms that must have been the remote ancestors of the higher primates living today. Yet, by the close of the Eocene epoch, the primates, who had then been in existence for 30 million years, had evolved into nothing more advanced than a few primitive lemur-like and tarsier-like creatures. The remarkable evolutionary development which led to the appearance of a wide variety of Anthropoidea or true monkeys in the Oligocene is scarcely documented in the fossil record, though to account for such diversity of monkey like creatures in the Oligocene epoch demands that the evolutionary changes which led to their appearance must have begun in the lower Eocene.

Four species of primates discovered at the Fayum sites are of particular interest. The first is the form known as Oligopithecus, which, on the basis of its molar teeth, Simons places on or near the evolutionary line that led to the living Old World monkeys - the cercopithecoids.[5] Another fossil form, Propliopithecus, has been classified within the super-family Hominoidea - to which men and the great apes belong - and though at one time considered to be ancestral to the gibbon, is placed by Simons, because of its generalized morphology, on or near the evolutionary line that led to the living Pongidae and man.[6] Moreover, the discovery of Aeolopithecus, which resembles the modern gibbon far more than Propliopithecus, appears to indicate that even at this date the gibbon lineage was distinct from the other Hominoidea. Lastly the form Aegyptopithecus, appears to be closely related to the Miocene and Pliocene dryopithecines, which, like Propliopithecus, would place it on or near the ancestral line which led to the East African Miocene ape Proconsul, and the living Pongidae.

There is, then, evidence from Oligocene times, that even at this stage the Hominoidea had become differentiated from the other Primates, and indeed, it appears quite likely that the hominoids themselves had split into at least two lines, the one leading to the living Hylobatidae (gibbons and siamangs) the other to man and the living Pongidae (chimpanzees, gorillas and orang-utans).

A great variety of fossil hominoids have been found in Miocene deposits throughout the Old World. They range in size from forms no larger than the modern gibbon to forms as large, if not larger, than the gorilla of today. However, though many of these forms have at one time or other been considered to have been on or close to the ancestral line of evolution which led to man, Simons and Pilbeam have recently undertaken a complete reassessment of their place in hominoid systematics with the following important conclusions for this paper.[7] That the fossil form Ramapithecus found in the Siwalik hills, India, and the form Kenyapithecus wickeri discovered by Leakey at Fort Ternan, be placed in a single genus, Ramapithecus. Further that as it is difficult on the fossil evidence available at the moment to distinguish Ramapithecus from the Pleistocene hominid Australopithecus, this creature must be considered as man's almost certain ancestor of 15 million years ago. The foreshortened face, rounded dental arcade and small canine tooth of Ramapithecus are all characteristically hominid traits, and distinguish it completely from the other apelike forms which lived at this time. They further place all the dryopithecine fossils found in Europe, Asia and Africa, with the Proconsul forms of East Africa and with Sivapithecus of India into a single genus Dryopithecus. This lumping of so many spatially distinct fossils into one cosmopolitan genus has not been enthusiastically received by everyone, though generally this rationalization of a perplexing wilderness of genera and species has been welcomed with relief. Certainly it has made it easier to see the possible connection between these Miocene hominoids and the living apes. For instance, this classification makes the Dryopithecinae a sub-family of the family Pongidae and divides them into three genera, Dryopithecus, Gigantopithecus (an immense form from China) and Aegyptopithecus (the Oligocene form that would appear to be close to the ancestral lineage of the African Miocene ape Proconsul).

The best idea we have of what the dryopithecines looked like, come from the Proconsul deposits in East Africa, and especially the fossil remains of the gibbon sized Proconsul africanus. These include two partially complete skulls, and some limb bones including parts of a foot and a forelimb with a hand, and have permitted scholars to piece together a fairly accurate portrait of this creature. Simons describes the result thus -

> "The picture that emerges from the study of this material is that of an advanced catarrhine, showing some monkey-like traits of hand, skull and brain, but hominoid and even partially hominid characteristics of face, jaws and dentition. The foot and forelimb are also more suggestive of some ape-like adaptations - including an incipient ability to swing by the arms from tree-branch to tree-branch - than they are of either arboreal or ground dwelling Old World monkeys."[8]

This creature is considered by some scholars to be on the ancestral line which led through Ramapithecus and Australopithecus (sensu lato) to Homo erectus and eventually to modern man. The other two Proconsul forms, P. nyanzae (a chimpanzee-sized creature) and P. major (a gorilla-sized creature) are generally reckoned to be on the ancestral line that led to the living Pongidae.

Though the Pliocene is not well documented in the fossil record, it may be assumed that the differentiation of the pongid and hominid stocks continued throughout this epoch and resulted in the protohominid forms of the Early Pleistocene which have been found in such relative abundance at Olduvai and elsewhere in Africa and the Middle East.

The possible relationship of the Pleistocene protohominids to the later evolution of man has been discussed earlier; whatever one's particular conclusion may be, it is almost certain that at least one of these forms was on the direct evolutionary line which led through Homo erectus to Homo sapiens. Furthermore Homo habilis seems to be the obvious candidate as man's direct ancestor of the Early Pleistocene, though this form may itself have differentiated from one of the other australopithecines (A. africanus or A. robustus) at an earlier date. On the other hand it may have evolved separately from the form Kenyapithecus wickeri (Ramapithecus). Finally the tentative nature of these schemes must be emphasized, for the palaeontological data posit many difficulties of interpretation. For instance, the fact that some of the Olduvai fossil material has been subjected to absolute dating techniques when there is no similar evidence so far available for any of the South African fossils, makes cross association between them difficult, while cross association between continents is even more difficult. Moreover, the results of recent biochemical tests seem to indicate a far more recent common ancestor for man and the living apes than the palaeontological evidence suggests is possible. For instance, Sarich and Wilson have argued that if the change of the serum albumins in apes and man is comparable with that of other proteins in other species then man and the African apes must have had a common ancestor as recently as 5 million years ago.[9] However, the value of biochemical and cytological studies as evolutionary time clocks is still questionable at this stage, though obviously their potential significance for the future development and clarification of primate systematics is enormous.

Having briefly described the different protohominid forms of the Early Pleistocene, and discussed their position in the overall history of hominid evolution, it is important to know why these primitive man-like creatures have been accorded such special attention. The reason is largely historical. Until recently, palaeontologists and others interested in human evolution, were looking for rubicons that absolutely distinguished man from his ape-like ancestors. The most obvious of these rubicons was brain, though others such as upright posture, culture etc., were also sought. However, as more and more information came to light about the anatomy and culture of our primitive forebears, it became more and more obvious that there was no discontinuity, no absolute break between man and his ancestors, just as Thomas Huxley had so unwaveringly averred in the wake of the Darwinian revolution. In tracing back man's evolutionary lineage, it should be obvious that each successively remote form will tend to have more traits common to the ancestral stock from which the apes and man evolved, than traits which are distinctively hominid in character. From another point of view, in the light of their common origin, man and the apes share a number of characters common to both of them, and as one goes back in time through the lineages of these two families, the pool of characters common to both lines will increase until that point at which representatives of the converging lines cannot be distinguished. However, though these basic tenets were accepted in theory, often they were not applied in practice, and the tracing of man's evolutionary line was commonly based on hypothetical and preconceived ideas about what man's direct ancestors must have been like. The result of this tendency is well documented in the history of the discovery of man's fossil forebears. One form after another was placed off the main line of human evolution because it did not fit in with the prevalent ideas of the time, while the Piltdown skull which so estimably 'aped' what specialists in the field were, perhaps unconsciously, looking for - a big-brained, ape-jawed man - was commonly believed to be man's direct ancestor. However, a number of different factors eventually led to a re-appraisal of man's likely evolutionary history, and many of the known fossil forms came to be seen not as aberrant forms off the main line of human evolution, but rather as stages in its successive hominization. The factors that brought about this change occurred over a relatively long period of time, and it is only recently that there has been any broad agreement on the major features of hominid evolution. The discovery of the South African australopithecines was a first stage in this process. Subsequently the discovery of the Olduvai fossil forms, the perfection of absolute dating techniques, the many field-studies of free-living primates, the discovery that culture was neither the sole prerogative of man nor by itself the product of a large brain, and the complete reappraisal of hominoid systematics initiated by the work of Ernst Mayr, and continued by Simons and Pilbeam among others, all in their several ways contributed to this new enlightenment. The exposure of the Piltdown skull as a forgery should have finally laid the ghost of rubiconism. That it has not entirely disappeared today testifies to the strong emotional appeal of this doctrine, and the conservatism of a cultural tradition which in almost every society has always distinguished between man, that is us, the group, the tribe, the culture, or all men generally, and them, the rest of the natural world, known or unknown.

The obvious significance of the australopithecines was apparent from the outset, though initially, their importance was blurred by the controversy which arose over their proper taxonomic status. However, once it was established that these small-brained, bipedal forms were on or close to the main line of human evolution, and that moreover they used and manufactured a variety of tools, their position became all the more fascinating. Here were bipedal creatures with a brain hardly larger than the modern chimpanzee, living in open or woodland savannah, making tools and hunting a variety of small animals. Furthermore, they contradicted almost every previously held assumption about the appearance of man's Pleistocene ancestors, and the possible relationship between a large man-like brain and the manufacture of tools. No wonder Dart and his fellow colleagues in South Africa caused such an academic furore! Yet, ironically, the revolution which the Australopithecinae caused, has eventually led to their own eclipse as the really significant link between man and his hominoid ancestors. In recent years, as more and more fossil remains of this form came to light, especially remains of the advanced hominid Homo habilis, their basic anatomical similarity to man became more obvious. Indeed, some authorities would now like to see them placed in the same genus as man himself. Despite the smallness of their brains, they possessed to a varying degree almost all those anatomical features which distinguish man, and the recent discovery of a big toe bone even seems to indicate that at least one of these Early Pleistocene forms possessed man's characteristic striding gait (Napier).[10] Thus, these creatures which were once considered to be close up to the point of divergence between the hominid and pongid ancestral lines, are now seen to be far more than half-way to man. As this is so, it is obvious that we shall have to look to still earlier forms to find those incipient and critical changes of anatomy and behaviour which started the hominid line along its own unique evolutionary pathway. The discovery by Leakey in Upper Miocene deposits at Fort Ternan of the forms Kenyapithecus wickeri, which may also have been a tool-user of sorts, could provide some of the answers.

The foregoing discussion of the appearance, place and importance of the Pleistocene protohominids is a necessary introduction to any consideration of their social and cultural behaviour. Moreover, two of the features that have been mentioned - sic their tool-using ability and their bipedal posture - were of the utmost behavioural significance in the evolutionary success of the hominid line, and must be treated accordingly. Their technological and cultural capabilities are discussed separately elsewhere, and the rest of this introductory section is devoted to an examination of the origin and adaptive significance of bipedalism.

That the australopithecines were characteristically bipedal is certain for their long bones and pelves show anatomical modifications consonant with an habitual erect posture. However, this is not to say that their bipedalism was either particularly efficient or particularly graceful. Its essential peculiarity has been described by Napier as follows -

> "For Australopithecus walking was something of a jog trot. These hominids must have covered the ground with quick, rather short steps, with their knees and hips slightly bent; the prolonged stance of the fully human gait must surely have been absent. Compared with man's stride, therefore, the gait of Australopithecus was physiologically inefficient. It calls for a disproportionately high output of energy; indeed, Australopithecus probably found long-distance travel impossible".[11]

Although the australopithecines were imperfectly bipedal, recent discoveries at Olduvai, suggest that in fact the advanced hominid, Homo habilis, was more efficiently bipedal than the other contemporary hominid forms. Accompanying the lower jaw and other bones of the pre-Zinjanthropus juvenile (Homo habilis) discovered by Leakey in Bed I at Olduvai was found the foot of an adult female. Although it was incomplete, the heel and ankle had survived as well as a greater part of the structure of the foot. Day and Napier, who studied the foot in detail, while concluding on the basis of a functional analysis that it was habitually bipedal, in the absence of the terminal bones of the toe could not say certainly whether or not it possessed man's characteristic striding gait.[12] Less cautiously, Leakey asserted that

> "this foot is well within the range structurally and morphologically of the feet of present day men and women."

and went on to say that

> "the evidence suggests most strongly that in evolution, the foot, and with the foot upright stature, came before the development of the hand."[13]

The foot was, of course, much smaller in size than that of present day women.

In 1961, a big toe bone was discovered at Olduvai in a slightly higher layer than that which produced the habiline fossils, with

> "characteristics that are found only in modern man and that can with assurance be correlated with a striding gait" (Napier)[14]

It is not known, however, whether this toe bone comes from Zinjanthropus or Homo habilis, though in view of the many other anatomical similarities between Homo habilis and man the indications are that it belongs to him rather than Zinjanthropus.

The fact, then, that at least one hominid in the Early Pleistocene period possessed man's unique striding gait is of great significance, for it shows that the basic modifications necessary for erect posture must have begun at a much earlier date. The necessity of finding some of the lower skeleton of Kenyapithecus wickeri or other related forms thus becomes more urgent, as at present, it is impossible to predict accurately just how far this form may have been modified for erect posture. However, it appears more likely now that this creature, which Simons considers to be "almost certainly man's forerunner of 15 million years ago"[15] was at least partially modified for bipedal locomotion.

At this point, it may be useful to examine how behavioural factors can affect the direction of natural selection, and in this particular context the anatomical modifications which led to erect posture. Probably the clearest statement of the importance of behaviour in the evolutionary development of different species has been made by Sir Alister Hardy in his book "The Living Stream". In this work, he follows Lamarck in stressing the importance of a change of habits in the subsequent evolution of a species, though he does not accept that learned behaviour can, per se, be transmitted from one generation to the next. He writes -

> "If a population of animals should change their habits (no doubt often on account of changes in their surroundings such as food supply, breeding sites etc., but also sometimes due to their exploratory curiosity discovering new ways of life, such as new sources of food or new methods of exploitation) then, sooner or later, variations in the gene complex will turn up in the population to produce small alterations in the animals' structure which will make them more efficient in relation to their new behaviour pattern; these more efficient individuals will tend to survive rather than the less efficient, and so the composition of the population will gradually change. Thus evolutionary change is one caused initially by a change in behaviour." (p.170)[16]

Later he goes on to say -

> "...the concept of survival value .... is not sufficient. It leaves out the live animal and concentrates too much on what it is and too little on what it does. It would appear to be glaringly obvious that what an animal does, or tries to do, can determine what characters are of survival value i.e. can decide the direction of natural selection." (p.186)[17]

He illustrates this point by noting that a mutation causing slight webbing in a non-swimmer will not subsequently cause an accumulation of genes making for the habit of swimming. Furthermore he quotes from a paper written by Dr.(Mrs.) Ewer emphasizing that

> "evolutionary change does not have to 'wait for the right mutation to turn up': the first advance will always be made on the basis of changes in frequency and reconstruction of genes already present in the population with new variations bringing up the rear by continuously replenishing the pool of variability.
>
> This evolutionary plasticity at the level of the population applies to all characteristics, both structural and behavioural. Behaviour, however, generally has much more plasticity at the level of the individual than has structure. The adaptability of behaviour to varying environmental conditions gives it a 'factor of safety' allowing an immediate behavioural response to be made at once to a changed situation without the necessity of waiting for appropriate changes in the genetical structure of the population. Thus behaviour will always tend to be one jump ahead of structure, and so to play a decisive role in the evolutionary process".(p.187)[18]

Sir A. Hardy's hypothesis then is briefly this. That in the evolutionary modification of a species external change comes first - that is to say the animal does not change its behaviour in a random or arbitrary manner for no reason. However, it is generally because of the plasticity of its behaviour that the animal can adapt to an external change rather than because of chance structural modifications. Subsequently selection begins to operate and those who can adapt best to the changed circumstances tend to survive. Finally comes the process known as 'genetic assimilation' or 'organic selection' in which the efficiency of the behavioural response is gradually built up by genetic modifications until in the end a genotype results in which the environmental learning is no longer required.

Now in the light of this hypothesis it is possible to say that changed behaviour patterns were crucial to the evolution of erect posture and that they must have arisen initially in response to an external change in the environment. Further because of the antiquity of man's characteristic striding gait which has been traced back at least as far as the Early Pleistocene, the processes which led to its development must have begun as far back as the Miocene period and possibly earlier still. What was the vital external change in this instance? There are really two possible answers. One is the classic theory which argues that man's direct ancestors were pushed out of the retreating primary forests by the ancestors of the living apes; forced to live in the open savannah they developed new patterns of behaviour and an erect posture. However, the known palaeontological evidence indicates that this expatriation must have begun at least as far back as the Miocene, and the dryopithecine forms of this period do not show the more extreme branch-swinging specializations of the living apes. This is an important point as the theory implies that man's ancestors were competing for an ecological niche similar to that occupied by the great apes of today, yet this does not appear to be substantiated by the fossil record.

The other answer, and the one I prefer myself, argues that the ancestors of man and the living great apes did not formerly occupy a closed-forest habitat, but that they lived in an open-forest environment on the edge of the primary forest. With the retreat of the primary forests, man's primitive forebears competed with the ancestors of the great apes for occupation of the increasing amount of open woodland and were so successful that they forced the other hominoids back into the retreating forests. Indeed, it may well be that it was at this time that a progressive hominid line diverged from the ancestral line which eventually led to the living great apes. This line of argument appears to be supported by a variety of evidence. Firstly, Simons has written in a personal communication to Reynolds that

> "The common ancestor of the larger apes and man could have been pre-adapted by behaviour, not morphology to bipedal branch-walking and to arm-swinging in the trees. From this there are two obvious locomotor pathways, one towards increased arm-swinging as in Pongo, and to a lesser extent in Pan and Gorilla, and the other towards human bipedalism.."19

This fits in well with the sort of environment posited above for the common ancestor of man and the great apes, that is a habitat on the edge of the primary forest, as it does also with the hypothesized subsequent evolution of the pongid and hominid ancestral lines. Napier has expressed his doubts about the implications of the first theory which suggests that bipedalism was the result of the extrusion of man's forebears on the open savannah. He considers that this mode of locomotion is far more likely to have arisen in woodland savannah. Such a habitat he argues

> "has enough trees to provide forest foods and ready escape from predators. At the same time, its open grassy spaces are areas in which new locomotor adaptions can be practiced and new foods can be sampled. In short, the woodland-savannah provides an ideal nursery for evolving hominids, combining the challenge and incentive of the open grassland with much of the security

> of the forest. It was probably in this transitional environment that man's ancestors learned to walk on two legs. In all likelihood, however, they only learned to stride when they later moved into the open savannah."[20]

Finally the work of Kortlandt and Kooij on the tool-using ability of chimpanzees suggests that their ancestors once inhabited a more open environment.[21] Indeed chimpanzee populations can still be found in open habitats where they are not hunted by man. Their conclusions are based on the inherent throwing and club-using abilities of chimpanzees which, they believe, cannot be explained if they have always lived in forest habitats where they would have had neither the opportunity nor the purpose to develop these skills. If their hypothesis is correct, then the ancestors of man and the living great apes may indeed have been fringe-forest-living creatures and may all have possessed an incipient culture and tool-using prowess. However, the favourable adaptations which led to bipedalism in the hominid line gave these forms an immense advantage over their quadrupedal competitors and allowed them to move out further and further into the open savannah while the forebears of the living Pongidae were forced back into the forests.

Now if the second hypothesis explains the possible external changes that led to a change in the habits of the ancestral hominid stock, it does not say what these new habits may have been, and which of them were crucial to the development of erect posture. Behaviourally, one of the most significant factors in the change from a peripheral forest environment to an open woodland environment is the necessity of covering sometimes considerable distances on the ground from one source of food to another. Both Reynolds[22] and Kortlandt[23] observed that even forest-living chimpanzees tend to move from tree to tree on the ground and have an intricate network of 'chimp tracks' along which they travel from one place to another. However, the undergrowth in a forest often entails walking for long periods doubled up in order to get under projecting branches, through thickets etc., and obviously there would be neither opportunity nor advantage in chimpanzees walking erect in such conditions. However, in more open habitats, such as the plantation on which Kortlandt centred his study in the Eastern Congo, chimpanzees frequently walk on two legs; indeed Kortlandt considers that 10 - 15 per cent of the distance covered by these apes in the plantation was achieved by this mode of locomotion. Further, he noted that -

> "Apparently they walked bipedally in order to have their hands free - for example to carry or eat fruit or to gain a better view of their surroundings."[24]

Other workers, particularly Lawick-Goodall,[25] have confirmed these findings. All this would seem to corroborate the hypothesis that the ancestors of both man and the living chimpanzees were not primarily tree-living creatures. However, despite the fact that chimpanzees tend to move from place to place on the ground, Reynolds has estimated that the chimpanzees of the Budongo Forest spend between 50 and 75 per cent of the daylight hours in the trees for the obvious reason that most of their food is to be found there.[26] However, in a woodland-savannah habitat the amount of time spent on the ground would necessarily increase as the trees would be further apart, and it would take longer to move from one to another. Furthermore, the actual density of tree-food in any one area would tend to be less, and thus discourage large group combinations at a feeding site. At the same time, such a habitat might encourage the exploitation of new food sources on or near the ground.

With all this in mind, two behavioural adaptations to woodland-savannah life stand out in importance, and must have been crucial in encouraging the selection of structural adaptations towards more efficient bipedalism in the hominid line. Further, both are mentioned in the quotation from Kortlandt above. One is the freeing of the hands and the other the necessity of gaining a better view of one's surroundings.

The freeing of the hands for the carriage and manipulation of objects, whether food or tools must have been of enormous adaptive advantage to any woodland-savannah living creature. For instance, Lawick-Goodall has observed that chimpanzees may carry chosen twigs or vine stems for as much as half a mile from one termite nest to another.[27] Now if the ancestral hominid stock habitually carried a wooden stick as a means of defence against predators and possibly as a digging tool as well, a two legged mode of locomotion would be far more convenient than a three-legged or quadrupedal gait. Furthermore, erect posture would mean that they could carry chosen foodstuffs for a considerable distance before consuming them. The effective use of a club, as also the aiming and throwing of stones, must really be executed in an upright position, and the experiments of Kortlandt and Kooij on the club-using behaviour of chimpanzees indicates that they habitually adopt this stance for that purpose.[28] Schaller's recent study, The Deer and The Tiger, has, moreover, shown how important a factor predation may be for ground-living primates, noting that 20 per cent of leopard scats and 6 per cent of tiger scats contained langur hair.[29] The vulnerability of the relatively small ancestral hominid forms to such attacks would have been considerably minimized by determined object throwing or club-wielding displays, and the effectiveness of these displays would have increased in proportion to the efficiency of their ability to stand and run bipedally.

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SOCIAL ORGANIZATION .

Until recently, our ideas of primate sociology were largely based on a small number of field studies which it is now clear tended to give a distorted impression of primate society. They promoted a view of primate social organization held together by sexual attraction and dominated by draconian power structures based on the principle that 'biggest is best'. However, the many field studies that have been undertaken in recent years have emphasized among other things the diversity rather than the similarity of primate social organization; moreover they have shown that sexuality is not the key to sub-human primate sociability and that the importance of dominance hierarchies in the social structure of a group vary from species to species, and even from group to group within a species.

Any attempted analysis of protohominid sociology is almost bound by its very nature to be contentious. In the absence of direct evidence, one is forced to rely on the indirect evidence provided by living communities of sub-human primates and the few remaining hunter-gatherer societies which still exist today. As the relative importance of the many variable factors that affect primate organization are even now a matter of dispute, there is a constant danger of using comparative evidence that may be completely inappropriate to the protohominid situation. Moreover, the observations of field workers themselves may be open to question, not so much in the actual details observed, but rather in the emphasis which the observer may place on certain, and possibly unrepresentative, aspects of the total social climate. Observer bias, however unconscious, is therefore itself a variable which must be reckoned with. However, on the available evidence it would appear that protohominid society was probably a society of open groups bound together by ties of friendship and kinship. As in this respect I subscribe to the views expressed by Reynolds on protohominid social organization it may be well to summarize his own theories about the development of protohominid society; thereafter I can add some comments of my own.

Reynolds argues:

1. That in view of the recent common ancestry of man and the large apes certain social behaviour patterns of the living Pongidae which are not normally found in other Old World monkeys, must also have been characteristic of the first protohominids and have preceded later adaptations to a savannah ecology. These include
    a) a nomadic aterritorial way of life in which the distribution and availability of food primarily determines the movements of individuals and groups.
    b) a system of open groups formed by the temporary association of individuals drawn together by ties of friendship based on like age or sex, sexual attraction, mother-offspring relationships and possibly sibling relationships as well. Within this flexible and constantly changing group structure, mothers and their immature

offspring form the basic and independent social units of the community.

c) individual choice in sexual relationships, with little or no rivalry between males for the possession of oestrus females.

d) tendency of adult males to roam about by themselves or in small active groups and in so doing to discover new sources of food etc.

e) certain unique behaviour patterns as for instance use of tools, use of weapons, drumming and dancing, and the making of beds.

2. That the remaining hunter gatherer communities of modern man show a remarkable similarity in their social organization to the societies of the living apes; this supports the likelihood of a continuity of behavioural evolution from a common ancestor.

3. That over the course of millions of years, from late Oligocene times onwards, the protohominids emerged from the forest edges and became more distinct in their specializations and more organized in their social groupings. Whereas the mothers and infants initially remained on the forest edges, gathering vegetables and fruit, the wandering bands of adult males began to co-operate in game drives, in scavenging large carcasses etc. Children stayed with their mothers and formed play groups of age mates, and at adolescence the young males and occasionally the young females as well, joined the roaming bands of adult males in their exploratory expeditions.

4. That during the Pliocene period, between Ramapithecus and Australopithecus, the protohominids left the retreating primary forests and became mainly savannah-living creatures.

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5. That mothers and infants now lived on the open savannah along with the adolescents and adult males, and were partially dependent on meat provided by the males. With food and water sources more widely spaced, there was a decrease in population density, which in turn encouraged the formation of more constant groupings, probably composed initially of related mothers and their offspring and one or two elder males. These groups lived in favourable locations close to water and spent most of their time foraging for vegetable foods.
6. That as time went on the roving bands of adult males became specialist hunters and providers of meat for the less mobile mother-offspring units from which in turn they often received stored vegetables.
7. That when technology had progressed to the stage where individuals could hunt alone, the smallest economically viable units at times of maximum dispersion became a nuclear family of a male, a female and her offspring. However, the development of exclusive sexual partnerships probably did not come about until relatively later in the history of the hominid line.
8. That many of the characteristic features of present day society stem from the stage when permanent or semi-permanent settlement began. These include territorial behaviour, inter-group aggression, rigid structures of authority, strict sexual mores etc.

Although this summary is all too brief a statement of the detailed views Reynolds has put forward in two articles, it more or less covers the major points of his argument.[1,2] Now, though, as I have mentioned above, I concur with his view that the protohominids lived in an open community of small interacting bands and that "at no stage did inbreeding, territorial hominid hordes range the savannahs"[3] yet I cannot agree with all the opinions he has expressed.

To start with I would not emphasize apparent differences in the social behaviour of Old World monkeys and the living apes to the extent that he has done. Many of the behavioural characteristics which he considers particularly distinguish pongid society are in fact present to a varying degree in other primate societies as well. Moreover, it may be doubted whether some of these patterns of behaviour, in the terms that he has described them, are generally common to the large apes anyway. For instance, he has written, with regard to the great apes that

> "None of them has a fixed range beyond which a group rarely wanders, and which may be routinely travelled, as in baboons for example"[4]

However, Schaller has observed that gorilla groups appear to have some boundaries beyond which they do not roam.[5] Thus, although groups move about in an irregular pattern from day to day, and do not occupy an exclusive range, yet there appears to be some kind of behavioural inhibition that stops them from leading a completely nomadic life. The boundaries may well be defined by social tradition; alternatively they may be the result of an innate tendency to remain in an area with which individuals are familiar and in which they feel 'at home', tendencies that would, of course, be reinforced by social learning. In this regard it is interesting to note Leonard Williams' observations on a captive colony of woolly monkeys. They are of course highly territorial in their behaviour, and in this respect completely dissimilar from the large apes. Yet the way in which they familiarize their environment by chest rubbing displays (mostly performed by dominant males) is particularly instructive. Such chest rubbing displays impart on the object rubbed a scent from glands located on the chest. Williams noted that any new object such as a ball would be ceremonially chest rubbed, and moreover that when he first extended the monkeys' territory into the trees in his garden, Jojo, the dominant male, spent two days testing the strength of branches, breaking off those that were unsafe, and generally familiarizing the environment, both for his own and the troops' benefit, by chest rubbing branches, trunks, poles etc. etc. Thus familiar scents provide comfort and security to troop members; conversely the absence of familiar smells or the presence of unfamiliar smells make them wary and cautious.[6] Although there is nothing akin to scent marking in gorillas or the other large apes, the same behavioural tendencies may be equally manifest in them, in that they will be wary of entering areas with which they are not familiar. Indeed, most mammals, whether they are territorial in their behaviour or not, generally spend their lives in an area and even an ecological niche far more limited than they are capable of occupying. As such, it would imply a vast behavioural discontinuity between the large apes and the other mammals if they too did not favour areas and objects and habits etc. with which they were familiar, and to treat with caution unfamiliar places, objects, etc.

Again Reynolds has written that

> "Among Old World monkey groups there is nothing comparable to the exploratory males found among the large apes".[7]

Yet it is by no means clear from the available evidence that exploratory males are either particularly characteristic of pongid society, or that isolate or group-living males are not found among other higher primate species. The limited field data on orang-utans in association with their relatively small population density does not really permit any such generalization about the social behaviour of adolescent and adult males - only that social groups, other than mother-offspring units, are highly unstable in composition and duration. Moreover, there is no indication from Schaller's field observations that the activities of adult male gorillas are exploratory, only that solitary adult males are sometimes found living apart from any groups.[8] This is no more remarkable in itself than the many other examples that have been recorded of adult or sub-adult males living a solitary existence in other Old World monkey species - as for instance by Jay in langurs,[9] Koford in rhesus monkeys[10] and Immanishi in Japanese macaques.[11] Furthermore, isolated as solitary male gorillas are from the daily routine of band-living members, it is difficult to see how their hypothesized 'exploratory behaviour' would be of benefit to anyone but themselves for, as Schaller has remarked, a group's movements are largely determined by the leader, and besides,the activities of a solitary gorilla without any permanent band allegiance could hardly be imitated by other gorillas.

With respect to chimpanzees, both the field-observations of Reynolds[12] and of Lawick-Goodall[13] confirm that all-male or mixed male and childless female bands are a common feature of their society. Moreover, these bands are far more mobile than other group formations - especially those made up of mothers and offspring - and move on to new sources of food sooner than other groups. All the same, it is contentious to suggest that such behaviour is only found among chimpanzees (and possibly the other large apes). For instance, DeVore and Washburn have remarked of the highly integrated societies of savannah-living baboons that

> "While the centre of the troop moves slowly along, the adult and older juvenile (subadult) males and adult females sometimes move rapidly ahead to a new feeding spot. This may separate them from the rest of the troop by a quarter of a mile or more and they may not rejoin the troop for 30 minutes or an hour. Although peripheral adult males may make such a side trip alone, or in small groups, other troop members will not leave the troop unless accompanied by the males. Healthy 'solitary males' observed during the early part of our study later proved to be troopmembers who had left the troop for a short while."[14]

Now although on the face of it, this description appears to be remote from the kind of group formations found among chimpanzees, yet it suggests some interesting parallels. If one takes into account that these baboons depend on a highly integrated social structure for their survival, and that their ecology is completely dissimilar from that of the forest-living and largely fruit eating chimpanzees, who moreover face little danger from predation, then the behaviour of peripheral males and females in reaching new food areas first and of adult males wandering off by themselves for short periods of time, either singly or in groups, is not altogether unlike the behaviour attributed by Reynolds to exploratory bands of adult males in the large apes.

How far pongid society is an open group society depends to a large extent on what one means by open or closed in terms of the overall structure of a society. For instance, while Reynolds admits that gorilla groups are far more stable social units than those of chimpanzees, he argues that

> "even in gorillas a sense of community is apparent. For example, some adult males seem to prefer a wandering life, attached to no particular group. Such males are temporarily accepted in established groups without hostility. Sometimes two groups happen to be foraging in the same place and they may join up for a day or two; or they may simply stare at each other and go their separate ways. In either case it is clear that gorillas, like chimpanzees and orangs, recognize ties of relationship which extend beyond the immediate group."[15]

However, it is not at all clear that in staring at each other without engaging in overt hostilities, gorillas are recognizing "ties of relationship which extend beyond the immediate group." Intense staring in all the higher primates, including man, generally indicates either threat or apprehension or a combination of both. It certainly does not indicate amiability. Moreover Schaller notes that the kind of behaviour patterns which result from the meeting of two groups or of a solitary male with a group, varies from situation to situation, and he suggests that those groups which mix amicably together when they meet may be close kin. He furthermore remarks that gorillas only change groups very occasionally.[16] It would appear therefore that gorilla bands are not completely open groups, and that their relations with other gorilla bands or single gorillas may depend on whether or not they have previously established ties, certainly of kinship and maybe of friendship as well, between them. In this regard it is interesting to note the following description of the behaviour of proximate baboon troops in Uganda made by Rowell

> "the troops were spread along a river, so that each had only one neighbour either side. The best-known troop had quite different relationships with each of its two neighbours. With its upstream neighbour it occasionally joined forces to go to some rather distant fruit trees, and they would sleep in trees only a few hundred yards apart. Older juvenile males and the occasional adult male sometimes moved between the troops. The downstream neighbours rarely met the middle troop: When they did each side stared at the other intently and then one or other withdrew. The downstream troop had a closer relationship with its downstream neighbour and sometimes slept in the same neighbouring trees. It was a large troop (over fifty) and occasionally split into sub-groups which followed different routes for all or part of a day, but as far as I could tell always rejoined at night. One interpretation would be that the first two troops had divided relatively recently, and that the other was in the very early stages of division."[17]

Now this account indicates that traditional ties of association, whether of friendship or kinship, can be an important factor in determining the kind of behaviour which may arise when two groups, who normally move about by themselves, meet. Descriptively, it is similar in many respects to Schaller's observations of the varying patterns of social behaviour which accompanied the meeting of two gorilla groups - in some cases amiable interaction, in others intense staring followed by the withdrawal of one or other group. If gorilla groups are not then altogether open societies, it may be that chimpanzee groups too are open only to individuals who have previously established some kind of relationship with each other. If this hypothesis is correct then it places an entirely different complexion on the social organization of the large apes, and on any consequent evaluation of the possible nature of protohominid society.

It has been suggested, then, that previously established ties of kinship or friendship are an important factor in determining the nature of social interactions between different groups of the large apes. The more stable social groupings of gorillas are perhaps a result of their particular feeding habits, for, generally, they have abundant sources of food readily at hand. Chimpanzees, however, relying as they do primarily on fruits and buds for the bulk of their food supply, must often scatter far more widely in their foraging activities. Moreover it may be that this dispersion has led field workers in the past to see far less social organization in chimpanzee communities than, in fact, exists within a local population of this species. A primate species that lives in spatially coherent troops and/or which occupies a limited area, is relatively easy to observe as a unit, and the nature of its intra- and inter-group behaviour patterns can be fairly readily assessed. However, the fissional habits of chimpanzees in the exploitation of available food resources make it far more difficult for a field worker to establish the overall basis on which social interactions between individuals and groups occur, and the extent to which an underlying social structure may affect the movements and behaviour of individual sub-groups. Thus it may be that if the movements and social interactions of a local population of chimpanzees could be observed in toto, they might appear far less random than various field workers have intimated, and display considerably more overall social organization. Indeed there are various indications from the available field evidence on chimpanzees that this may be so.

Kortlandt has observed that among the chimpanzees he studied, there was one very old male chimpanzee to whose unquestioned authority all the other chimpanzees deferred -

> "All his whims and fancies were indulged, and even the biggest of the senior males sought his company."[18]

Kortlandt also observed that the two most frequent kinds of group aggregation were sexual groups that consisted "mainly of adult males and childless females, but often included a few mothers and children," and nursery groups of mothers and their juvenile offspring that were sometimes accompanied by one or two adult males. He remarked of these groups that neither seemed to be fixed or controlled in any way, with individuals constantly coming and going between groups, the groups themselves often merging or splitting. However, he noted that the behaviour of the two kinds of aggregation were marked by different behaviour patterns, and that the sexual groups roamed over a larger area than the nursery groups, who seemed to rely far more on the plantation paw paws for the bulk of their diet.

In the main, both the observations of Lawick-Goodall and Reynolds confirm these social behaviour patterns, though Lawick-Goodall's long term field study has provided far more detail on the habits and behaviour of chimpanzees than the shorter studies of Kortlandt and Reynolds. For instance, she was able to break down the particular composition of groups far more precisely than Kortlandt, and found that out of 350 occasions on which it was possible to assess a group's composition, 30 percent were mixed groups, 28 per cent males and single males, 18 per cent mature and adolescent males and females and 24 per cent females and young.[19] Unfortunately, however, these figures only show the number of occasions on which certain types of aggregation were observed, and not the number of occasions on which certain individuals were characteristically found together, nor the circumstances of the aggregations - for example whether mixed groups occurred more frequently at times when a lot of food was available in a small area. However, the general observations of both Lawick-Goodall[20] and Reynolds[21] have confirmed that at certain seasons when a rich supply of food is concentrated together, chimpanzee aggregations tend to be much larger than at other times. Lawick-Goodall also noted the importance which ties of primary kinship play in the social behaviour of chimpanzees and that long after the period of necessary dependance, children will often return to their mothers. This association of mothers and their offspring may also help to establish ties of lasting friendship between siblings, for in moving around together, they will have frequent opportunities first to establish and later to reaffirm close social bonds with one another. The importance of such relationships has also been observed in other social contexts as well. For instance, Lawick-Goodall found that mothers and children tend to support each other in any dispute with other members of the community. Moreover, sub-adult males will defer to their mothers in feeding situations where they would not tolerate such behaviour in another female.[22] Kinship relations have also been found to be an important factor in the social behaviour of other higher primate species, as for instance among rhesus macaques (Sade, Koford)[23,24] and among Japanese macaques (Immanishi).[25] Sade especially had noted that the social groupings of rhesus macaques on Cayo Santiago Island are largely governed by kinship relations; mothers spend most of their time with their offspring, and the children themselves tend to stick together long after they have reached maturity.

Now as I have mentioned above, these observations may indicate a more organized community structure in chimpanzees than perhaps field workers have previously recognized. It is apparent that mother-offspring units generally frequent a more limited area than the more mobile groups of adolescents of both sexes, and adult males. This would seem to be an obvious corollary of their reduced mobility. Furthermore, by remaining within a fairly well defined area throughout the year, they form an inner range of activity which serves as a focus to the social behaviour of the community as a whole. As they are the effective breeding units of the populations, the wandering males must rejoin them from time to time if propagation is to be effected. Moreover the males probably tend to rejoin those groups containing individuals with whom they have previously established ties of friendship or kinship, as for instance in a brother joining his sister or son joining his mother. Furthermore during their relatively long childhood, young chimpanzees become thoroughly familiar with the area within which their mothers normally range, and would naturally feel most secure and at home here, and thus be drawn back to it by ties of deep attachment as well as personal friendship. The older and less active males, unable or unwilling to keep up with the more mobile groups of adolescents and young males, tend to remain either with or in the vicinity of the slower moving groups of mothers and children Here, their dominant position viz a viz females, their long experience and their presence at the natural centre of the group's activities combine to give them a position of considerable authority and respect, as Kortlandt observed (see above).

This interpretation of chimpanzee society, suggesting as it does a central body of females, juveniles and elder adult males surrounded by adolescents and young adult males is similar in some respects to the social behaviour of gorillas, though on a vastly increased scale. Thus, unlike gorillas, the particular feeding habits of chimpanzees and the nature and distribution of the food on which they rely, tends to disperse them in small foraging groups and except at certain seasons discourages the formation of either particularly large or particularly stable group formations. Yet withall, the community contains a centre, composed of small interacting mother-offspring groups and elder males, who normally forage only within a certain range, and an extended periphery of young subadults of both sexes and young adult males, some of whom travel considerable distances in their search for available food sources. As large group aggregations only occur on those occasions when a plentiful supply of food is to be found in a small area, it is at these times that peripheral members will most often tend to be drawn back into the forum of community life, and to renew old ties of amity and affection and perhaps to establish new ones. Furthermore the social stimulation and excitement that is produced when many individuals are moving around together induces, as Lawick-Goodall has observed, a greatly increased amount of reproductive behaviour,[26] which in turn tends to strengthen the social bonds between the various members of the community as a whole.

From this standpoint, therefore, the mercurial nature of chimpanzee groupings observed by the various field workers may be seen as a constant fission and fusion among the peripheral groups of adolescent males and females and adult males that make up the extended perimeter of chimpanzee society. Similarly, the more constant associations of mothers and children, accompanied occasionally by elder adult males, alternately swell into mixed groups of all ages and sexes and then return once more to their former proportions as elder offspring, siblings and age mates join them for a time, and then move off elsewhere. Moreover the mother-offspring groups themselves constantly combine and recombine in different formations depending on the nature and distribution of food within a particular area and their own personal whims or desires. The wide prevalence of chimpanzee tracks observed both by Kortlandt[27] and Reynolds[28] would seem to confirm an overall pattern and cohesion to the foraging activities of the society as a whole, for they could not have been made by the random wanderings of nomads. This is all the more certain in view of the fact that Schaller found no such traditional pathways used by gorillas,[29] which accords with their apparently aimless wandering life and the nature of their feeding habits. It is likely, therefore, that these chimpanzee tracks are traditional pathways from one known feeding area to another, and that they are customarily used by all the chimpanzees within a local population, and especially by those members who live within a posited inner range of activity.

Now the kind of social organization that I have suggested for chimpanzees also makes good ecological sense. In utilizing peripheral resources of food and only coming into the range normally occupied by mothers and juveniles and elder adult males at times of optimum feeding conditions, the more mobile and active members of the community do not use up the resources of food on which the less active members depend for their livelihood. The social behaviour of gelada baboons in the face of scattered food resources offers an interesting analogy to the patterns of dispersion found among chimpanzees. Thus, Crook found that gelada, like hamadryas, baboons live in a society based on the one male group and though herds occasionally form, they only do so in optimum feeding conditions. Subadult males and adult males without harems generally collect into all male groups, and tend to move around and feed by themselves, and to wander further away from the crags on which their ultimate safety depends, and to which they return every night. Commentingon this behaviour Crook remarked that

> "A large 'multimale' troop moving over dispersed food sources has females in direct competition with males at any one site. This is acceptable if the food supply is adequate. However, where food supply is sparse, it appears essential that the females, as the effective breeding units, should have a high proportion of the available food. Under these circumstances the social units are formed of 'one male' and 'all male' groups. Within a one male group at any one food source the proportion of food available to the females is high, because only one large mature male is present. The all male groups, which tend to range along the canyon away from the cliff line, may occasionally exploit the same food sites but if so it is usually at a different time to the one male group."[30]

The arguments that I have expressed here suggesting an overall pattern to the social behaviour of chimpanzees, who make up a local population of the species, do not violate the detailed observations of the various fieldworkers in any way. However, they do attempt to rationalize the fissiparous and mercurial nature of chimpanzee groups in a manner that accords both with their known ecology, and the need for some overall structure to the activities of the community as a whole in the exploitation of available food resources. Without such ordering, a completely unadaptive pattern of foraging activity would result, in which the more mobile and active members of the community -

and the least important to the continued survival of the species - would rapidly eat up the available food supply in a particular area before moving off elsewhere, leaving the less mobile members behind to feed on what was left. Such behaviour could only result in complete disaster for the species as a whole. There must therefore be a more than fortuitous logic to the characteristic patterns of dispersion and aggregation found among chimpanzees that in normal circumstances allows all members of the community, and especially the less active mothers and offspring, access to sufficient supplies of food throughout the year. Unlike chimpanzees, the foraging activities of gorillas approximate more closely to those of other ground living species, such as the macaques and baboons, and like them, they tend to form stable groups as the nature of their food exerts no pressure on them to disperse very widely.

In view of this discussion, it is possible to suggest that the protohominids may have had a social organization different in some respects from that indicated by Reynolds. I have argued elsewhere (see section on Early Hominid Systematics) that the progressive hominid line probably evolved from a hominoid ancestor that was not solely arboreal in its habits, and which frequented a woodland savannah habitat that encouraged the development of bipedal locomotion. It is probable that the feeding habits of the ancestral protohominids were similar in many respects to those of the living chimpanzees, though perhaps without so heavy a bias on tree-borne food. Thus both Lawick-Goodall[31] and Reynolds[32] have noted that chimpanzees find up to 90 per cent of their food in the trees; consequently they spend most of the daylight hours above ground (between 50 per cent and 75 per cent according to Reynolds).[33] However, the progressive modifications for an increasingly efficient bipedal gait in association with the more open habitat in which they probably lived, suggests that the ancestral protohominids spent far less of their time in the trees, and far more of it foraging for food growing on or near the ground. Yet, in spite of their largely ground living existence, it is unlikely that they developed the kind of stable group aggregations typical of gorilla society, for unlike these creatures, their food was probably subject to considerable seasonal variations, as well as being more widely dispersed. It is probable therefore that like chimpanzees they lived in small interacting groups that fluctuated in size according to changes in the nature and distribution of food. Furthermore the groups which made up a local population probably occupied a definite range, from which normally only active young male members of the community strayed very far. I have argued that both chimpanzee and gorilla groups are generally open only to those individuals with whom ties of amity and affection have previously been established, and it seems reasonable to consider that this same behaviour was characteristic of the early protohominids as well. Thus although the protohominids living in broken woodland were not territorial in the sense that they occupied a defended area, it may well be that they treated with caution any unknown individuals or groups whom they came across on the perimeter of their customary range of activity.

For a number of different reasons, the change from a woodland or fringe forest habitat to open savannah, which may have occurred as early as Upper Miocene times, probably led to the formation of more stable social units. To start with, as mother-offspring groups would have been the most vulnerable as well as the most valuable members of the community, they would have required some kind of protection from predators. This could have been achieved in a number of different ways of which one example is the integrated troop formations of savannah living baboons and macaques in which the vulnerable females and infants are protected by the dominant adult males of the centre and the subadult and less dominant males of the periphery. The one male groups characteristic of patas monkey society illustrate another possible way of coping with potential predators; in this case the male distracts the attention of the intruder by elaborate running and leaping displays while the rest of the group 'freeze' (Hall).[34] However, such a social defence mechanism could only be effective in relatively small and inconspicuous animals - which the protohominids were not. Both these social defence mechanisms, however, illustrate the important part that adult males play in defending the more vulnerable and less mobile females and infants. It may be assumed, therefore, that it was the adult males in protohominid society who were the protectors of the group, and that a strategic position close by the mothers and infants was all the more vital for them in view of the increased dependence of infants on their mothers. In this regard Clark has noted that -

> "The responsibility of protecting the Australopithecine juveniles is emphasized by Dart's (1948) and Robinson's (1956) studies of the deciduous dentition, which show that the young were dependent upon their parents for nutrition and protection for several years, as are human young."[35]

Now it is obvious from their anatomy and from the fact that the mothers would have been considerably handicapped in having to hold young infants in their arms that the protohominids could not have run away from possible predators. They must, therefore, have relied on the adult males to scare off any potential predators, and, as in the large apes, this was probably achieved by means of fiercesome displays that included a good deal of noise and the hurling about of objects either at, or in the general direction of, the intruder. It is even possible that they used clubs against predators as, according to Kortlandt, do savannah-living chimpanzees when confronted by a leopard.[36]

The threat of predation alone would, therefore, have tended to close up foraging groups into more spatially integrated units and encouraged the constant association of adult males with mother-offspring units. However, though from this point of view large integrated troops along the lines of the savannah-living baboons would seem to be the most effective means of coping with predators, it is unlikely that the protohominids formed very large group aggregations, except at particularly beneficent seasons when a great deal of food was situated within a small area, or in dry seasons when the whole of a local population would have collected round the remaining water holes. It is more likely that they foraged in small groups during the day, returning at night to refuges such as cliffs or trees that afforded some protection against predators. Within the normal range occupied by a local population there would be various refuges of this kind which these creatures would occupy at different times according to seasonal variations in the location of food. Moreover, such refuges were probably located close to water, for as Leakey has pointed out

> "You can carry solid objects, once you are standing upright; you can carry meat, you can carry bone, you can carry skins and you can carry stones to make stone tools with, but our hands are insufficient to carry water in an adequate quantity. There were still no vessels in which to carry water, so man lived by the edges of lake shores."[37]

One might imagine, therefore, that the mixed groups of mothers and juveniles accompanied by elder adult males usually foraged in the close vicinity of these refuges, and that the younger males and adolescents roamed further afield in their search for food. At times of maximum dispersion, therefore, the smallest social unit would have been that composed of one or two related mothers and offspring and attendant elder males. Thus it may be that it was the necessity of having a male continually present with mothers and their children when the local population of a particular area was spread out gathering widely scattered food, which encouraged the formation of pair bonds within the wider community. These bonds would probably not at first have been very well defined, and elder males may periodically have changed from one group to another, though generally a personal preference for the company of one female, whether through ties of amity or kinship, would have tended to produce the constant association of one male with one or more particular females, who themselves may have been closely related - sic either sisters or mothers and daughters. However, it is unlikely that the protector males exercised exclusive sexual rights over the females they were accompanying, and other males, especially at times of large group aggregations, would probably have had access to them. That it was the elder males who generally accompanied the mothers and infants would have been a) because they were not willing or able to travel so widely or so rapidly as younger males in the search for food and b) because their age and experience would have qualified them best to undertake the role of guardians.

Now Reynolds has argued that

> "when technology had progressed to the stage where individuals could hunt alone, the smallest economically viable unit at times of maximum dispersion became the nuclear family of a male, a female and her young."[38]

Yet it is not clear why such groups could not have been formed before the development of a primitive hunting technology unless meat was an essential and even substantial part of the protohominid's diet. However, I have argued elsewhere in this paper (see section on Feeding Habits) that the protohominids must have been largely vegetarian, and that what hunting they did do could perfectly well have been done with their hands, for the fossil record indicates that, as among living baboons and chimpanzees, most of the victims of the Early Pleistocene protohominids were relatively small or immature animals. Leakey himself has demonstrated the possibility of catching small mammals with his bare hands and has noted furthermore that

> "There is certainly no sign of any lethal weapon amongst these artefacts of the earliest toolmakers."[39]

Thus immature and small animals along with such 'slow game' as mice, lizards, frogs, chameleons etc. could have been killed by both males and females without the aid either of other individuals or of primitive weapons. Any larger animals that were killed by these creatures were probably caught either at those times when large groups were moving about together, or by roaming bands of young males.

In view of the fact that the protohominids were largely vegetarian feeders and that what meat they did consume could normally have been killed with their bare hands, it does not seem to me that the need for reciprocal food sharing - that is the exchange of vegetables gathered by the women for meat hunted by the men - provided the behavioural foundations of human life, as many authors have averred. Rather I think it more probable, as I have suggested above, that it was the necessity of having a male continually present with mothers and their children at times of maximum dispersion that led to the formation of pair bonds. Such a pattern of social organization is, after all, found among other higher primate species, as for instance in patas monkeys and gelada and hamadryas baboons. Of course these group formations must not in any way be confused with pair bonds as there is no exclusive partnership here between one male and one female, but rather a harem group composed of females and their attendant young with a male overlord. However, it may be that this kind of adaptive social organization to scattered food sources was the initiating cause of those behavioural, anatomical and cultural specializations that led to the formation of permanent pair bonds in man. Moreover, such an answer is a far simpler explanation of the known facts than any hypothesis which argues that pair bonding arose from a hunting way of life and the need for reciprocal food sharing. Furthermore, the prolonged dependence of infants on their mothers would have tended to increase the necessity of having one particular male constantly present with a mother and her children, rather than ephemeral associations of males and females which may have resulted in females with young infants being left unprotected when the population was widely dispersed. This in turn could well have led to the development of year round sexual receptivity in the female which would have helped to stabilize and strengthen the bond between _a_ male and _a_ female.

From this viewpoint, therefore, the characteristic association of one male with one (and occasionally more) females and their young preceded the development of a hunting way of life; furthermore it behaviourally preadapted the protohominids to the special requirements of a hunting economy, which depended for its success on previously established bonds between particular males and females. Without such a pre-established pattern of social behaviour, it is difficult to envisage how the largely vegetarian ancestral protohominids, with a social organization similar in many respects to that of the living apes, developed into the skilled hunters of the Middle Pleistocene, while retaining a relatively open outbreeding society of small groups bound together by ties of amity and kinship.

It is likely, then, that the protohominids of the Early Pleistocene lived in small family groups composed of mothers and their children with attendant males that came together or dispersed according to seasonal variations in the nature and distribution of food. The individuals who together made up a local population of the species probably occupied a definite range within which they normally moved and in which the sources of food and their seasonal occurrence were known to everyone. Small foraging parties at times of maximum dispersion were probably formed most often on the basis of kinship ties between either the females or the males, though at times of large group aggregations, new alliances may have been established, and when the community dispersed again, changes in the individual membership of family groups - especially among the adolescent and subadult members - and in the association of one family group with another may well have occurred. Moreover such large aggregations at times of optimum feeding conditions probably served to establish a sense of community between all the various individuals inhabiting one locality, and may have resulted in them treating with caution or hostility any unknown individuals or groups with whom they came in contact.

In many respects this pattern of social organization is found among the few remaining societies of hunter gatherers which still exist today. These communities are made up of bands which normally occupy a particular territory that varies in size according to the nature of the environment in which it is located. The bands themselves are composed of nuclear families who come together or disperse in small sub-groups according to variations in the abundance and distribution of food. In this regard, Marshall has observed that !Kung Bushman bands were normally only seen in their entirety during the tsi season and at the end of the dry period when they stayed together near the permanent water-holes. At other times the bands were dispersed throughout various parts of their territories.[40] Steward, writing of the Basin-Plateau Indians of South-West America, noted that

> "As food shortage was always a real danger it was necessary that families harvest alone or in the company of not more than one or two families."[41]

All the same, the family was not always the maximum economic unit, for the males of different family groups would sometimes co-operate together to hunt game. Moreover

> "Several plant and animal species occurred in such great quantities in certain localities during short periods that, even when they were not taken co-operatively, they drew large numbers of families to such localities."[42]

Similar patterns of fission and fusion have been observed among Mbuti Pygmy bands by Turnbull,[43] while other recent studies or restudies of existing hunter-gatherer societies (of which a brief review can be found in Reynolds)[44] have confirmed the generality of such social behaviour patterns in the face of constantly changing economic circumstances.

Generally speaking one normally acquires membership of a band either by being born into it or by marrying into it, though in some societies, individuals and nuclear families may also join a band through personal choice as long as the other band members agree. As band exogamy is is usually the preferred form of marriage in these communities, the constant exchange of individuals between neighbouring bands serves to establish a web of consanguineous and affinal kinship ties over the whole community, within which individuals and nuclear families may freely come and go. Shifting band composition is therefore the general rule in these societies, and while individuals normally reside within the territory of the band to which they belong by birth, marriage or choice, they will often travel to visit friends and relations in neighbouring bands.

The rules governing unauthorized tresspass by members of one band on the territory of another may often reflect underlying ecological pressures. Thus the extent of a band's territory may usually be defined in terms of its sufficiency to provide enough food for its members throughout the year; as this is so, territorial trespass for specific food finding purposes is the exception rather than the rule. Occasionally, however, local shortage of an especially important or desired food item may induce members of one band to invade the territory of a neighbouring band. With respect to this, Turnbull has noted of the Mbuti Pygmies that

> "The only cases of uncondoned tresspass known to me are instances when a band has found itself short of honey during the brief honey season, and has invaded its neighbour's territory and actually set up temporary camp there. This was considered inexcusable only because permission was not first sought."[45]

In this regard also it is interesting to note Marshall's observation that among !Kung Bushman bands it is the veldkos (field foods) that are most jealously guarded while hunting rights are far less rigidly enforced. This may well reflect the relative importance of veldkos in the subsistence economy of !Kung bands, as, according to Marshall, 80 per cent of their food is made up of veldkos.[46] Moreover the !Kung are by no means exceptional in their heavy reliance on vegetable items, for as Meggitt has observed

> "a vegetarian stress seems to be one of the prime distinguishing features of hunting, fishing, and gathering economies."[47]

Thus among hunter gatherers who live in bands associated with a particular region or territory, it is the fixed and traditional sources of gathered food that are normally identified with individual and band rights, whereas game, which is constantly on the move from one band's territory to another, cannot be claimed exclusively by any band until it is actually killed. The ambivalent status of such 'moving food' may partly explain the somewhat uncertain 'rights' of hunters who have pursued game across a territorial boundary, as also, the reason why hunter gatherers generally treat this kind of tresspass far less seriously than the unlicensed and premeditated pilfering of 'fixed foods'.

However, among certain groups of hunter gatherers, as for instance the Basin Plateau Indians of South-West America, the food supply is so uncertain and so variable from one season to another and from year to year that neither bands nor individual families exercise permanent territorial rights over particular areas. Indeed the impoverished nature of the environment necessarily demands that individual families normally function as independent economic units while variations in the supply and distribution of food often requires them to reside in different localities in successive years. Although temporary groupings of people occur at certain beneficent seasons - for instance during the pine nut harvest - the most permanent associations of families are found at winter encampments where certain families habitually remain during those months when there are no food plants to be had, and when they are forced to subsist on what they have managed to store (Steward).[48]

It is apparent from this discussion that the social organization of hunter gatherers is in certain respects strikingly similar to that of chimpanzees as for example in the dispersion and aggregation of local groups or bands according to seasonal variations in the nature and distribution of food and also in the importance attached to primary kinship bonds in the characteristic association of one individual or family group with another. In consequence it is perhaps reasonable to assume that similar patterns of behaviour were also a feature of protohominid society. However as well as obvious similarities there are many differences of which perhaps the most significant, in the context of this discussion, are those associated with the division of labour by age and sex, the practice of reciprocal food sharing, and the position of the nuclear family as the basic unit of economic activity. In view of the known meat-sharing habits of chimpanzees, and the fact that male chimpanzees normally do the killing of small or immature animals (Lawick-Goodall),[49] it is possible that food sharing habits and a certain amount of labour division were also characteristic of protohominid society. Such food sharing habits, other than those directly associated with maternal behaviour, may first have arisen among members of the more stable groups of elder males and females and their infant and juvenile offspring that formed the basic social and economic units of protohominid society. Membership of these groups was probably determined by mutual ties of primary kinship or friendship, and the close social and affectional bonds that must have existed between these individuals would have provided a natural basis for the development of food sharing practices. Moreover in view of the fact that mothers and their dependent offspring would have been the least mobile members of the community and also the most in need of protein, and as as adult or elder adolescent males may have done most - if not all - of the scavenging or killing of small and immature animals, food sharing may initially have taken the form of flesh 'hand outs' by the adult or subadult males to the women and children. From such habits as these it would have been but a short step to the development of truly reciprocal food sharing habits in which vegetables gathered by the women were exchanged for meat hunted by the men. However for such a behavioural adaptation to have been of much consequence in the economy of the early hominids would have required far more specialization of labour than probably existed among them, and thus it may not have been until the development of more sophisticated methods of hunting in the Middle Pleistocene, associated with the habitual killing of relatively large and mature animals, that reciprocal food sharing practices became of major adaptive importance in the social and economic behaviour of man's early relatives.

In conclusion it has been argued here that the protohominids of the Early Pleistocene probably lived in small interacting groups that came together or dispersed according to fluctuations in the distribution and supply of food. These groups at times of maximum dispersion were probably composed of one or two females with their infant and juvenile offspring and attendant elder males, and in this respect at least may have resembled the kind of group organization found among the largely ground living gorilla. Although it is unlikely that permanent pair bonds between particular males and females were present at this stage of human evolution, it may well be that individual males habitually accompanied particular maternal groups at times of maximum dispersion and that these groups possessed a strong sense of communal identity viz a viz the rest of the community. Of interest in this respect is Schaller's observation that

> "gorillas have very strong attachments to members of their own group, probably because they feel more secure and content among intimate friends

and relatives than among more casual acquaintances."[50] The lasting importance of primary kinship ties both among hunter gatherers and the large apes suggests that such ties must also have been an important factor in the characteristic association of individuals and groups among the early hominids. Moreover although it is likely that protohominid society was based on a system of open groups, as among both hunter gatherers and the large apes these groups were probably open only to individuals with whom ties either of friendship or kinship had previously been established.

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CULTURE AND TECHNOLOGY

The history of hominoid tool-using has been traced back certainly as far as the Early Pleistocene, and there is every indication that it must have occurred further back even than this. Indeed, Leakey has recently found smashed mammalian bones in the same Upper Miocene deposits at Fort Ternan from which remains of Kenyapithecus wickeri have been taken.[1] The smashed bones, including a skull, have depressed fractures of a kind that could have been made by a blunt instrument, and Leakey has discovered a lump of lava in the same deposit showing several battered edges that has every appearance of having been used for this purpose. Now Leakey, more than anyone else, save possibly Dart, knows what artificially fractured fossil bones look like, and the usual argument that has been used time and time again to contradict such 'wild' claims as this - sic, that these fractures may have been caused by natural means in the course of fossilization - seems particularly inappropriate. Furthermore, a free-living chimpanzee has been observed to use a rock to crack open a palm-nut kernel (Beatty),[2] and on the basis of the fossil remains, Kenyapithecus seems to have been at least as capable as the modern chimpanzee. At the same time, an isolated piece of lava is far too meagre evidence in itself to justify attributing tool-using prowess to this creature. Moreover, as no post-cervical remains of Kenyapithecus have been found it is impossible to say whether the hands could even have manipulated tools, though on the face of it, it is reasonable to think that they could.

That the Early and Middle Pleistocene hominids were both tool-users and tool-makers is indisputable, though initially there was a considerable amount of controversy over the cultural and technological capabilities of these hominid forms (see discussion in section on Diet). However, though it is now clear that at least some of the hominid types living at that time were capable of making lithic tools, there is still a great deal of speculation as to precisely who was responsible for their manufacture.

In South Africa the only stone tools associated with Australopithecus (sensu lato) come from Mid Pleistocene deposits at the Sterkfontein Extensio site and at Swartkrans, where remains of Paranthropus (A. robustus) and Telanthropus have been found. Sonia Cole considers that the tools are early Chellean in type, and that Telanthropus was responsible for their manufacture.[3] She argues that if Paranthropus made tools at all, they would have been Oldowan pebble tools, similar to those discovered by Leakey in Early Pleistocene deposits at Olduvai Gorge. However, it is now uncertain who was responsible for the manufacture of these pebble tools at Olduvai. Originally Leakey considered that Zinjanthropus boisei made and used them,[4] but recently his discovery of the advanced hominid form Homo habilis in the same Early Pleistocene deposits has led him to revise his earlier opinion, and he now believes that this last creature was mainly responsible for the Oldowan pebble culture.[5] All the same, he does not consider that Homo habilis was the only Early Pleistocene toolmaker, but rather that this form or a close ancestor of this form in the Pliocene originated the idea, and that Zinjan-thropus copied them. Thus he has written

> "From a close study of the stone tools that were found on the Zinjanthropus floor with the Zinjanthropus skull, the best made are less well made than the average tools found at a much lower level at the place where the human remains represent the other type of creature (Homo habilis).* We think that it is more probable that Zinjanthropus was copying the tools of the other type of creature who probably invented the idea, but we cannot say for certain."[6]

All the same, this variety may be due solely to differences in skill between the members of a single population, and if, as some authors aver, Zinjanthropus was a victim of habiline predation, then such an interpretation is even more likely.

Thus the palaeontological evidence indicates, if nothing more, that stone tools were widely manufactured in Africa during the Early and Middle Pleistocene. Indeed stone tools similar to those found at Olduvai have been discovered, along with the remains of an advanced hominid (possibly Homo habilis) at Ubeidiya in the Jordan Valley.[7] As the lithic tools are generally associated with the more advanced hominid types (Homo habilis and Telanthropus) it is perhaps reasonable to think that these creatures manufactured them. Thus it may well be that Telanthropus made the stone tools found at Swartkrans. At the same time, Zinjanthropus may have been a stone-tool maker as well. As most scholars place Zinjanthropus along

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* Words 'Homo habilis' my addition.

with Paranthropus in the taxon A. robustus, if Zinjanthropus was capable of making pebble tools in the Early Pleistocene, then it is at least possible that his more recent successors in South Africa in the Mid.Pleistocene could have made the tools which have been found there. Moreover, it has been established by Napier that the australopithecines had a power grip and possibly a precision grip as well, and were thus capable, anatomically at least, of manufacturing pebble tools.[8] However, as these South African tools have been evaluated as early Chellean in type, and as Chellean artefacts are normally associated with Pithecanthropines of the Mid. Pleistocene period, the argument for Telanthropus as their maker becomes very strong, and is given even more authority in view of the fact that the only other implements discovered at South African sites have been Dart's osteodontokeratic tools.[9*]

In any case, the claims of Zinjanthropus to have been any more than a potential tool-maker rest entirely on Leakey's assertion that there is evidence of a more or less advanced lithic culture associated with the two Early Pleistocene hominid forms that have been found at Olduvai. However, Tobias does not appear to concur with this opinion, and considers that the Australopithecinae could not achieve the highest implemental frontier of Khroustov (1964) that is to use a tool to make a tool.[10] If this is so, it would place even the manufacture of pebble tools outside

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[*] A discussion of the significance and controversial nature of osteodontokeratic tools may be found in the section on Feeding Habits.

their scope. At the same time, it is well known that previous attempts to make an absolute distinction between the capabilities of progressive man-like forms and other creatures have always failed, and it is perhaps optimistic to expect this distinction to be any more valid than the previous ones. Tobias argues, however, that if Zinjanthropus

> "was the victim of the more skilled hominine hunters of Olduvai, then the presence on the habiline living floors of his skeletal remains <u>without bone and horn tools</u> would be understandable."p.240[11]

Yet even this opinion is open to question, as Leakey first introduced the type skull of the form later described as Homo habilis as evidence of the first known murder in history, and thus it is possible that Homo habilis himself may have been the prey and not the predator. Equally well the depressed fractures found in one of the Makapansgat skulls, in the habiline skull, and in various Pithecanthropine skulls in China may all be evidence of a long tradition of cannibalism and intra-specific aggression.

The contradictory nature of the evidence becomes even more striking if one considers that chimpanzees are said by Kortlandt to use clubs against leopards in savannah or broken savannah type country,[12] and that with a little practice captive chimpanzees can achieve almost as good an aim with a stone or a rock as a man (Morris).[13] Now if savannah-living chimpanzees sometimes use clubs against potential predators, and can be taught to 'shy' as accurately as a man, how much more likely is it that all the various Early Pleistocene hominid forms were capable of at least these abilities, and could easily have 'aped' the fairly primitive technological advances of proximate populations whether of their own species or not. Such a conclusion is not put forward as an easy solution to this very complicated question; on the basis of comparative evidence, however, it seems unlikely that habitually bipedal hominid forms were not capable of clubbing or throwing. The clubbing behaviour of chimpanzees is always performed in an upright position. Moreover the remarkable display of the threatened gorilla which includes at the end a powerful bipedal run, demonstrates how grounded apes tend to react in threat situations. In any aggressive or defensive encounter, the ability to leave one's hands free to grapple with an opponent can be very useful, especially if one is ill-endowed with a natural armament of claws and teeth, and more so still if one of the free hands is used to wield a club. At the same time an upright position tends to exaggerate one's size and, if accompanied by screams, might well daunt any potential predator. Certainly anyone who has witnessed the fiercesome display of a threatened gorilla would testify to its effectiveness. All this may corroborate Dart's thesis that the club was the major offensive and defensive weapon of the early hominids. If this was the case, then the pebble tools would mainly have been used for purposes other than hunting or self-protection - that is for cutting and scraping meat etc. This is still more likely in view of the fact that Oldowan pebble tools would probably have been of very limited value as defensive weapons, and that for throwing, unworked lumps of stone or rock would have been as good if not better than the pebble tools. Moreover

Leakey himself has remarked of the Oldowan tools that "there is certainly no sign of any lethal weapon amongst these artefacts of the earliest toolmakers."[14] The idea that the early hominids were club-hunters and occasionally stone throwers is given qualified support by Dart's own investigations.[15] For instance, he has noted that the depressed fractures found in many baboon and hominid skulls in South African fossil-bearing deposits are of two distinct types. Some "are so sharply sular and depressed that they appear to have been caused by impacts of stone." Others at the Makapansgat, Taungs and Sterkfontein sites show "double-depressed (or double valleculated) cranial fractures" and were found in association with

> "double-ridged ungulate humeri, such as fitted, and in all likelihood regularly caused these fractures."[16]

In sum it may be argued that all the hominid forms of the Early and Middle Pleistocene periods used tools to as great, if not a greater extent, than the living apes. This conclusion is supported among other reasons by the apparent correlation that exists today between tool-using - especially clubbing and throwing behaviour - and savannah or broken woodland environments in the chimpanzee. Moreover field observations appear to indicate that they tend to walk or stand bipedally more often in open environments than in forest environments in situations not directly concerned with the procurement of food - for instance, to see whether or not it is safe for them to cross an area of open ground (Kortlandt).[17] Furthermore, they often use this method of locomotion in order to leave their arms free to carry food for short distances (Kortlandt; Lawick-Goodall).[18,19] Not only were all the Pleistocene hominids habitually bipedal but they also inhabited a savannah or woodland savannah environment.

In the final event, the question of which hominid forms made stone tools and which did not can only be resolved by considering the inferred ecology of each population and the fact that it would have been meat eating forms who would obviously have found the manufacture of pebble tools most useful for cutting up their prey etc.

Ecologically, there are, perhaps, three possible explanations of the known evidence. One is that the advanced hominid form Homo habilis was, by Early Pleistocene times, mainly a savannah living creature, and occupied a completely different habitat from the other hominid forms. If his remote ancestors in the Miocene had been creatures similar to the form Kenyapithecus wickeri, it is possible that he had an established hunting and bone-smashing tradition, and that his partially carnivorous diet included other primate species, especially non-forest living populations. It is known that both chimpanzees and baboons sometimes kill other primate species with which they come in contact (Lawick-Goodall; DeVore and Washburn),[20,21] and it is at least as likely that Homo habilis did the same. As the other hominid forms were also bipedal, and thus probably inhabited an open or semi-open habitat, they would have been the most natural primate victims of this form, along with the savannah-living baboons, and this appears to be given some support by the skull fractures exhibited by baboon and hominid forms in Early and Middle Pleistocene deposits. The Zinjanthropus remains discovered at Olduvai, and the remains of Paranthropus found at Swartkrans, according to this interpretation, would then be the victims of habiline or telanthropine predation. But this does not account for the fact that the juvenile skull described by Leakey and later designated Homo habilis, itself shows a depressed fracture of the skull which probably caused its death.[22]

Another explanation is that Zinjanthropus and Homo habilis (or Paranthropus and Telanthropus) occupied the same habitat and generally speaking the same ecological niche. In this case they would have been ecological competitors and would constantly have come into aggressive contact with one another which may have resulted in deaths on both sides. However, the more advanced form Homo habilis may have been socially better organized and culturally more sophisticated, using a wide range of stone, wooden and bone tools in daily life. They may even have used a digging stick to assist their foraging activities, which would have greatly increased their food-getting ability, and placed them at a distinct advantage over their less sophisticated rivals. Moreover, these advanced hominids may have been so successful in their social and cultural adaptations to savannah life, that the conservative australopithecine line, unable to compete with them effectively, either died out, or was forced back into ecologically less desirable areas not occupied by Homo habilis.

It is even possible that the numerous reports made by people who claim to have seen man-like creatures in remote and inaccessible areas, may indicate that remnant populations of a conservative hominid line still exist today (see Sanderson).[23]

Finally, the various hominid forms may all have been inhabiting the same natural environment, but occupying different ecological niches. This argument has been put forward by Robinson, among others, to account for the discovery both sympatrically and synchronically of Paranthropus and Telanthropus at Swartkrans. The same principle of course applies to Zinjanthropus and Homo habilis at Olduvai. Robinson argues that whereas Paranthropus was a vegetarian creature of limited cultural attainments, Telanthropus was a hunter, and that it was he who made the early stone tools that have been found in South Africa.[24] However, Tobias disputes Robinson's evaluation of the primarily dental evidence pertaining to his hypothesis that Paranthropus was a vegetarian form[25] and certainly it is unlikely in view of the occasional predatory behaviour of living chimpanzees and savannah-living baboons, that Paranthropus was entirely vegetarian. Moreover, as Robinson considers that Zinjanthropus belongs to the same taxon as Paranthropus, such a view could not explain the habiline skull fracture, unless one posits either very high intra-specific aggression and territorialism in this form, or that all hominid forms in the Early Pleistocene had at least an osteodontokeratic culture, and defended themselves against potential predators in the hypothesized manner of savannah-living chimpanzees when faced by a leopard. Both these explanations are, of course, feasible. It may be that none of these three interpretations are correct or that parts of all of them occurred at different times in different places and in different circumstances.

Now the possibility that a club-like stick or bone was the main tool of our primitive forebears is supported by a great deal of indirect evidence. Furthermore, this indirect evidence is even more important than usual in view of the fact that wooden tools are seldom preserved by fossilization. Firstly, as I have argued elsewhere in this paper, vegetable foods must have constituted the major portion of the diet of the early hominids. In this case, the first priority of any marginal forest or savannah-living creature would be to compete successfully for the available resources. Now these early hominids could never have competed for the surface vegetation with the vast herds of ungulate species which roamed the savannahs. However, baboons have managed to find a successful ecological niche in the open-savannah by concentrating to a large extent on sub-surface roots and rhizomes which are all that remains after the ungulate herds have cropped the surface vegetation. A creature which could extend this range of foods and facilitate their collection by the use of a simple digging stick, would obviously have stood at an immense advantage to one which merely fiddled for roots with its hands. That the savannah inhabiting form Homo habilis at least may have used such a tool is possible. Moreover, in this case, occupation of a similar habitat, and reliance on similar sources of food by baboons and early hominid forms, would not necessarily have resulted in the competitive exclusion of one or other species, for their ecological niches would not have been exactly the same. The total population of hominids would have been very small, and their range would have been considerably larger than that of baboons (especially in those forms that possessed a striding gait). Moreover, their range would probably have included broken woodland at seasons when fruits were abundant and their diet may also have included a relatively substantial amount of meat. However, there would necessarily have been some direct competition between the two populations for the available resources, and the fractured baboon skulls that have been found in Early and Middle Pleistocene deposits may testify to the ecological pressure of these early hominid forms on the baboon population.

Secondly, all known hunter/gatherer populations use a digging stick in their foraging activity, and as their way of life probably coincides to some extent with that of early hominid populations, then it is reasonable to think that these early forms possessed similar simple foraging equipment. Furthermore, the living Bushmen, who are probably far more skilled hunters than the early hominids and have more sophisticated weapons, get only 20 per cent of their food from hunting. The other 80 per cent is made up of veldkos or field foods (Marshall).[26]

Lastly, the living great apes are familiar with the manipulation and use of sticks in their daily lives. They use twigs to poke into termite mounds (Lawick-Goodall),[27] and to get at underground bees' nests (Merfield and Miller),[28] while each night they habitually make nests in which to sleep. The use of robust sticks as clubs has also been ascribed to them (Kortlandt),[29] while one gorilla was reported by Pitman to have used a stick to pull some fruit within his reach.[30] Furthermore, Lawick-Goodall has observed that chimpanzees will even carry carefully selected sticks or vine stems for as much as half a mile from one termite nest to another.[31] The extension of this stick-using behaviour to uncovering roots and rhizomes is not difficult to envisage; nor is the habitual carriage of such a stick for this purpose. Moreover a single robust stick which can be used effectively for either digging or clubbing would be far less cumbersome and far more useful than a lot of small pebble tools. In all probability, pebble tools were made and used only at living sites or at the scene of a large kill and then discarded. This is not to suggest that suitable stones may not have been brought to a living site for subsequent manufacture. However, unless they possessed some sort of receptacle or string bag in which to put these tools, they would have been very impracticable to carry for long distances; especially if the group was either foraging or hunting.

Any discussion of the cultural technology of early hominid populations would be incomplete if it confined itself merely to a description of those creatures who may have possessed a stone, wood or bone tool culture, without considering the context and significance of culture and tool-using generally, and the possible ways in which it may have arisen.

The ability to use tools is not a sole prerogative of man, nor even of the higher primates. For instance, various birds, including the Egyptian vulture, two species of Gallapagos finches (Camarhynchus pallidus and Camarhynchus heliobates) and the bower-bird - as well as the sea-otter, have been observed to use tools. With the exception of the bower-bird - which uses fruits to stain the stems of its bower - the tool-using activities of these species are used to get at food sources that would otherwise be inaccessible to them.

Observations on the tool-using abilities of sub-human primates had, until recently, mostly been confined to captive animals. Especially famous in this respect are the remarkable series of experiments undertaken by Köhler in the second decade of this century, which though primarily intended to investigate the cognitive processes of the great apes, clearly demonstrated how chimpanzees could solve relatively difficult problems involving the manipulation and modification of objects.[32] Since then the remarkable versatility of the great apes, and of the chimpanzees especially, in manipulating various kinds of machines has become abundantly obvious, but until recently there was little evidence that they used tools in their natural habitat. However, the work of Lawick-Goodall in the Gombe Stream Reserve has revealed that chimpanzees do make use of, and may even modify, tools for specific purposes.[33] Thus she has observed them to use a "sponge" of chewed leaves to sop up water from rain pools, bunches of grass or leaves to clean themselves of detritus or other waste matter, and vine stems or twigs to "fish" for termites. Other investigators have reported further examples of tool-using in the great apes. Beatty observed chimpanzees in Liberia breaking open palm-nuts by hammering them with rocks,[34] and Merfield and Miller have described how chimpanzees in Cameroon poke long twigs into underground bees' nests to get at the honey.[35] Pitman reported seeing a gorilla using a stick to pull fruit within its reach,[36] while recently Davenport has observed one orang-utan constructing an overhead shelter against the rain.[37]

The mere fact, however, that a number of different animal species make use of tools in their natural environment does not, of course, indicate that these actions have analogous behavioural origins. Thus tool-using habits may be determined largely by innate factors, even though a certain amount of trial-and-error performance of the action may increase it's effectiveness. In man, tool-making and tool-using are largely the result of learning, whether by individual trial-and-error, insight, or imitation, and cannot therefore justifiably be lumped together with the tool-using performances of species whose manipulative habits are genetically controlled. Moreover, the question of habits, and social traditions as a specific category of habit, inevitably raises the general question of culture. As man's tool-using and tool-making performances are generally speaking part of his culture, obviously one cannot satisfactorily discuss his technological capacities, nor those of his hominid forebears, without knowing something of the nature of culture, and the origin and spread of cultural traditions.

Culture refers not only to objects and tools, but includes other social traditions as well, such as communication and food preference. Milner and Prost have referred to a definition of it as "learned and shared behaviour",[38] and if this definition is accepted then it includes the social traditions of many sub-human animals species. For instance, the song of some English songbirds such as the blackbird appears to be innately determined (male birds brought up in isolation sing a perfect song) while the song of other birds such as the chaffinch and skylark must first be learned from other members of the species (Haldane).[39] Another example of social tradition may be found in tits, whose habit of opening milk bottle tops has spread, apparently by imitation, right through the tit population of Europe (Fisher and Hinde).[40] Such evidence as this would seem to contradict Dobzhansky's statement that

> "There is no culture* without human genes; a capacity for culture is a species character of Homo sapiens, in the same sense as a body temperature close to 37°C and a 9 months pregnancy term are species characters."[41]

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* By culture, Dobzhansky would appear to mean "an organized group of learned responses characteristic of a particular society" (Linton 1955) See T.Dobzhansky, 1962, Mankind Evolving, Yale University Press,pp59.

All the same there is obviously a vast difference between the sophisticated and various social traditions of man and the opening of milk bottle tops by tits. Yet it is not important in this context how many or how few social traditions one species may have, but rather the fact that neither the bottle-opening behaviour of the tit, nor the multifarious traditions and customs of man, are innately determined. However, in certain circumstances, a social tradition may be assimilated into the genetic code of a species, and may thereafter be passed on from generation to generation by genetic means rather than by imitative learning. In his book, The Living Stream, Sir Alister Hardy described the possible way in which this may be brought about. He believes that the direction of evolution is largely controlled by behavioural factors. That is to say, the behaviour patterns of a species generally determine whether or not a random mutation is preserved. Thus he writes

> "Surely, it is more likely that genetical changes may have been selected to give by new nerve-cell associations, a built-in inherited behaviour pattern to replace that of a learned habit, than that a chance change in the nervous mechanism (by mutation) may have produced a new form of behaviour which can be used with advantage to the animal."(p.195)[42]

In elaboration of this point, he quotes from an article written by Dr. Ewer on the same subject -

> "In the evolution of a fully innate behaviour pattern evoked by a releaser ... it is difficult to imagine that the process could begin otherwise than with the making of an approriate response, probably imperfectly performed and subject to trial and error, and with learning of a simple conditioning type involved in the determination of the situation in which the response is

> made. From this stage there will be rapid selection, on the one hand for more perfect performance of the motor responses, and on the other for the shortening of the conditioning period, provided the environmental stimulus (or some special part of the total stimulus situation) remains constant.... this should result in the building up of a genotype giving the motor responses in more and more perfect form, with the learning period more and more curtailed. The final result will be the innate pattern evoked by its releaser. But may not imprinting represent a penultimate stage on this route, a stage in which the motor response has been perfected and the learning period has become vestigal but has not yet disappeared."(p.196)[43]

Thus elaborate instinctive behaviour patterns may have arisen from new habits being passed by organic selection (or genetic assimilation) into the genotype of a species.

The genesis of new behaviour patterns by an individual or species can only arise within certain well defined physiological limits - that is to say, what a creature is obviously determines to a very large extent what it can do. Thus, in their natural environment creatures can only evolve new behaviour patterns within a given framework of inherited tendencies and dispositions, whatever these may be. Furthermore, for a new habit to become traditionally established within a population, it must generally be of adaptive advantage to the species, though this need not necessarily be the case.

However, if it is true that what a creature is largely determines what it can do, it is also true that what it does is generally far less than it is capable of doing. Thus Waddington has written

> "Animals - and the following considerations do not apply so directly to plants - are usually surrounded by a much wider range of environmental conditions than they are willing to inhabit. They live in a highly heterogeneous 'ambience' from which they themselves select the particular habitat in which their life will be passed."[44]

Each creature then in a very real sense selects its own personal environment, and though obviously the collective environment of individual members of an individual species will tend to coincide, yet the personal responses of each member of a species to the ecological niche which it is inhabiting will tend to be different. Moreover the range and variety of responses which an animal may make in its natural environment will tend to increase the more intelligent it is, and the less specialized it is anatomically and ecologically. This, perhaps, is the main reason why social traditions are found more abundantly among certain species of higher primates than elsewhere in the animal kingdom. Furthermore the degree of man's behavioural flexibility in the face of different and changing environments must certainly be one of the most significant reasons for his evolutionary success.

At this stage, it may perhaps be useful to review and comment on some of the points I have made in the last few pages. Firstly, social traditions are not exclusive to man. They have been found to occur both among primate and non-primate species though never to the same extent or with such variety as in man. The idea that culture is a distinguishing character of man is another example of the all - or - none doctrine of man's evolutionary history and cannot be justified on the known evidence. The obvious point must be made again that man is an animal, and distinct from the rest of the animal world in degree, not in kind. Such specializations as a large brain and bipedal posture may have enabled him to become the most successful of living species, yet the enlargement of the brain and possibly even a striding gait postdated the earliest known technological examples of cultural forms that were once considered to be man's sole possession - such as tool-making. However, though social traditions are found among non-human species, even complex behaviour patterns involving the manipulation of objects may be determined largely by innate factors. Thus the ability to use tools in a particular context may be learned individually by each member of a species, but need not necessarily be so acquired. Lawick-Goodall has clearly demonstrated that the egg-smashing behaviour of the Egyptian vulture is largely determined by innate factors, with the ostrich egg acting as the "releaser".[45] This may also be true of the tool-using performances of other non-primate species - the sea-otter, the bower bird, and the two species of Darwin finches - though perhaps the evidence for this is not so unequivocable as in the case of the Egyption vulture. However, as Hardy has said, even innate behaviour patterns probably arose from learned habits being passed by genetic assimilation into the instinctive equipment of a species.

New habits arise from the variable responses of individual members of a species to their total environments. These responses, though largely governed by innate factors and limited by the ecological niche in which a species lives, will nevertheless be different in different individuals, as a result of their different life histories. Thus, as in man, a creature's behaviour is the product both of learned habits and innate dispositions, though obviously the greater the learning ability of a species generally, the greater will be the effect of experience on the individual life patterns of its members, and the greater will be the variety of behavioural responses shown by them.

Animals have a tendency to explore their own particular environments, and this exploratory behaviour will occur most frequently in those areas - anatomical, behavioural or ecological - with which they are most familiar and to which they are most drawn by innate disposition. Thus, it is perhaps not surprising that tool-using behaviour whether in primate or non-primate species is generally found among populations who are predisposed towards the manipulation of particular aspects of their environment. For instance, sea-otters have frequently been observed playing with rocks and shells, throwing them from one paw to another for hours at a time. That an individual otter, or indeed a succession of individuals, should have discovered by 'trial and error' a means of opening crustacea with stones is not altogether surprising. Furthermore, that they should use these stones in the way they do - floating on their backs with the stones resting on their chests as an anvil - is a logical adaptation of existing behavioural tendencies. Thus, they usually swim on their backs when not in a hurry, and they sleep on their backs in the kelp-beds. Moreover, it is normal practice for mothers to shelter infants on their chests. Again, it is not surprising to find that several avian species are tool-users, for most birds are manipulators by hereditary disposition, and perform often considerably complex instinctive actions, for instance, in the construction of their nests. That their innately determined manipulative actions should occasionally have been adapted to serve other ends in the better exploitation of their environment is not improbable, prima facie, though obviously the likelihood of the learned habit of one individual becoming the social tradition of a population is altogether more uncertain, and would explain the relative scarcity of this phenomenon.

With regard to manipulative ability, it is also pertinent that these skills are generally found in species that rely especially on their visual sense in the perception and interpretation of their environment. The performance of even simple manipulative actions involving the use of tools is very difficult without adequate visual cues regarding length, mass, breadth and other linear and spatial relationships. Visual acuity characterizes most species of birds, and among this group too, manipulative skills are generally highly developed. A highly developed visual sense (including stereoscopic vision) along with manual and pedal dexterity in the manipulation of objects, is also characteristic of most primate species.

It is also of interest in this context to note the apparent correlation which exists between learning ability and hue discriminability in the primate order; thus Harlow has written -

> "It is a matter of established fact that as we go from catarrhine monkey to anthropoid ape to man, the ability to see in the long wave portion of the spectrum progressively improves (Grether 1939,40). Indeed, if we exclude the spider monkey, learning ability and hue discriminability within the primate order would be almost as highly correlated as learning ability and complexity of cortical structure."[46]

Moreover he also remarked that

> "If one plots a curve showing difference thresholds as a function of wave-length, the curves for pigeons and man are almost superimposable."[47]

and added later that

> "recent studies have shown that the pigeon has a wider range of behavioural capacities (Ginsburg 1957, Reeves 1919) than had previously been believed, and it is more than possible that the pigeon and other birds are more capable of solving moderately difficult learning problems than many mammals. Finally the primates as an order are pre-eminent over all other mammals both in terms of their visual capabilities and their capacity for learning."[48]

Thus, that some avian species and some species of higher primates have tool-using abilities in common may be less remarkable in view of certain common aspects of their behaviour and physiology - such as, for example, a heavy reliance on visually perceived data, an ability to see in the long range portion of the spectrum (which perhaps is correlated to learning ability) and an instinctive urge towards object-manipulation. However, without considerably more comparative evidence than is available at this time, it would be rash to stress too heavily the possible physiological and behavioural correlates of avian and primate tool-using abilitie

There remains one significant feature of socially learned behaviour - sic the way in which new habits are disseminated through a population (especially a social-living population of higher primate) - which has not yet been discussed, and it would perhaps be useful to examine this topic now.

For many years, Japanese workers have been conducting long term field studies on the Japanese macaque, and one of the most important aspects of their research programme has been the insights which they have obtained into the origin and transmission of social traditions among a free-living primate species. The social traditions on which they have reported have to do with the acquisition of new feeding habits. They have found that a new eating habit is normally originated by one individual through trial and error investigation of his environment, and then imitated by other members of the troop (Immanishi).[49] For instance in one troop, a one and a half year old female began washing sweet potatoes before eating them, and this habit quickly spread to her playmates and some of their mothers (Kawamura).[50] Once the mother learned the habit, it was always passed on to her offspring. Furthermore, the family to which the originator belonged was the first in which all the members washed sweet potatoes. However, none of the adult males in this troop learned the habit, yet, in another troop, where candy eating was initiated by two to three year old youngsters, the habit spread not only to the immediate maternal family of these youngsters and their playmates, but also to certain of the adult males. These adult males were in the habit of looking after selected infants during the breeding season when their mothers were bearing forth new children, and the candy-eating habit was passed on to them by their adoptees. The sub-adult males who had least to do with the young were, not surprisingly, the last to learn the habit. The fact that there was no tradition of paternal care among the adult males of the troop possessing the 'sweet-potato-washing' subculture may therefore largely explain why none of them learned the habit.

However, sub-cultures are distinguished not only by the degree of transmission but by the rate of transmission as well. Thus after eighteen months only 51.2 per cent of the candy-eating troop had learned the habit, while the habit of wheat-eating spread through the whole of another troop in just four hours (Kawamura).[51] Apparently the reason for this remarkable difference in propagation rate was due to the status of the individual who first initiated it, and the subsequent direction of its propagation through the troop. Thus the wheat-eating habit was originated by an adult male, and copied first by the alpha male and subsequently by the alpha female and her family. In consequence the habit rapidly spread downwards through the troop. The candy-eating habit on the other hand was spread upwards through the troop and though readily travelling along lines paralleling the mother-offspring relationship and later the adult male-adoptee relationship, was yet held back by a society organized from the top.

The principle that a new habit will travel more easily and more quickly through a troop from top to bottom than vice versa has been widely corroborated. For instance collaborators of Robert Yerkes observed that chimpanzees tended to copy only higher ranking members of their species.[52] A low-ranking individual was removed from a group of these apes and taught to take bananas from a feeding apparatus; having mastered the technique, both he and the apparatus were brought back into the group. None of the higher ranking members of the group bothered to learn how to work this apparatus, but simply used their superior status to deprive him of the fruits of his labour. However when the highest ranking was removed and taught how to use the feeding apparatus, on his return, the other chimpanzees closely watched his actions and soon learned to imitate him.

There are then two conditions which must usually be satisfied for a new habit to spread through a given population. First of all, the habit must generally be imitable by all the members of the group. Now the ability of each individual to master the whole of a group's cultural traditions is generally characteristic of all sub-human animal species and to a great extent this principle must also have applied to the cultural traditions of the protohominids.* However, this is not to infer

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* Yet even at this stage it is possible that specialist traditions were a feature of protohominid society. For instance Kortlandt and Kooij (1963) noted that zoo investigations have shown that the frequency and accuracy of throwing behaviour in the great apes is substantially greater in males than in females. It may be then that weapons of offence and defence among the protohominids were customarily used and manufactured by the adult males.

that an individual may be either more or less adept in say the manipulation of a tool. All species are eventually composed of individuals and no known population in the animal world is so genetically uniform that every individual within it is an exact copy of every other individual. However, even though genotypes may sometimes be the same, phenotypes never are.

Secondly among social living primates, there are certain optimum pathways along which a habit may be transmitted. The mother-offspring relationship is an obvious example of this; so is the pathway which parallels the hierarchical structure of a group. Now, as mentioned above, individuals pay more attention to the activities of the dominant males (or females) than to the activities of the sub-dominant individuals.* Thus Schaller has remarked of the mountain gorilla that

> "Every independent animal in the group appeared to be aware of the leader, either directly or through the behaviour of animals in his vicinity. Cues reflecting a changed pattern of activity were patterned after the leader. Thus the entire daily routine - the distance of travel, the location of rest stops, and the time and place of nesting - was largely determined by the leader."[53]

This 'attention binding' by the dominant individual is of course found in other contexts and other animals orders as well. For instance, the human tradition of patronage is an example of such 'attention-binding'

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* A detailed discussion of the concept of 'attention' as applied to the study of primate social behaviour can be found in Chance (1967) and Virgo and Waterhouse (1969)

in which a supplicant uses the superior rank of an individual to support him and/or his work. Another example of this 'authority' factor is recorded by Lorenz. He writes -

> "The expression movements of a high-ranking jackdaw, particularly of an old male, are paid much more attention to by the colony members than those of a lower-ranking, young bird. For example, if a young bird shows fright at some meaningless stimulus, the others, especially the older ones, pay almost no attention to his expressions of fear. But if the same sort of alarm proceeds from one of the old males all the jackdaws within sight and earshot immediately take flight. Since, in jackdaws, recognition of predatory enemies is not innate but is learned by every individual from the behaviour of experienced old birds, it is probably of considerable importance that great store is set by the 'opinion' of old, high-ranking and experienced adults."[54]

On the basis of this discussion, some tentative conclusions about the nature of culture and the origin of tool-using and tool-making among the protohominids may now be made. Culture defined as "learned and shared behaviour" occurs to a greater or lesser extent in other species besides man. However, White has defined it as

> "an extrasomatic temporal continuum of things and events dependent upon symboling"[55]

and as such it probably excludes the social traditions of all non-human species. Such a viewpoint however necessarily implies a quantum break between the specific abilities of man and the abilities of the rest of the animal world. In the words of White "man and culture originated simultaneously."[56] However, elsewhere in this paper, I have questioned the validity of rubiconism as a useful philosophical starting point to interpreting man's place in nature, and certainly cultural rubisonism has no greater attraction for me than any of the other arbitrary criteria that have been put forward as absolutely distinguishing man from the apes. Language is a biological event in the evolutionary history of man, in the same way as bipedal posture, and its importance lies in the adaptive advantage which it gave to the progressive human line. However, just as the structural modifications for erect posture were probably 'selected' by foregoing behavioural adaptations, so the expansion of that part of the brain, which controls speech must have been encouraged by patterns of behaviour long antedating its actual development. Moreover, the ability to speak could only have arisen among a species with considerable stability of social organization and characterized by long standing social traditions.

With reference to the specific question of early hominid technology, it is clear from the discussion of social traditions in primate and non primate species that behavioural and anatomical predisposition were of crucial importance in the development of manipulative habits. In this context Washburn has recently remarked that

> "It has been noted that monkeys of the genus Cebus appear to learn object manipulation easily (Vevers and Weiner 1963) but Thorrington (1967) has shown that extensive manipulation of twigs and branches is a normal part of the feeding behaviour of these monkeys."[57]

The considerable manipulative skills of the great apes in both natural and artificial environments are thus especially significant in the light of the known and inferred tool-using abilities of the early hominids; furthermore many of the apes' manipulative skills occur in relation to food sources that would otherwise be unobtainable - eg. termiting with vine stems (Lawick-Goodall),[58] pounding palm-nut kernels with stones (Beatty),[59] and pulling fruit within reach by means of a stick (Pitman, Köhler).[60,61]

In freeing the hands from locomotory duties, bipedalism enabled tools to be used in a greater variety of contexts as well as making it easier to carry objects from one place to another. I have argued elsewhere that selection for more efficient bipedalism was initiated by the development of new patterns of behaviour, and that moreover these new habits were originated by euryphagous ancestral protohominids inhabiting woodland savannah. These habits may have been to do with the carriage of food from one place to another, or to allow better visual perception of the immediate environment at ground level, or a combination of both factors. It is unlikely that the use or manufacture of tools played any significant role in directing the course of human evolution at this stage, though the experimental studies of Kortlandt and Kooij with chimpanzees in threat situations[62] certainly suggest that the effective use of objects in agonistic displays may have been considerably enhanced by adaptations favouring more efficient bipedalism.

The subject of agonistic displays raises an important question which has been widely debated for many years - did man's cultural technology first develop from tool-using or weapon-using habits? The issue itself is made more difficult to answer by the metaphysical implications that have been attached to it, relating as it does to the nature of man himself. Some authors of which Ardrey is popularly the best known exponent,* contend that man has primarily been successful because of his predatory adaptations, and would therefore argue that tools were first used and manufactured as weapons. This view has some support from field and experimental observations of the living great apes, (for instance the experiments of Kortlandt and Kooij with chimpanzees)[63] as also from the palaeontological record which has revealed both the primitive hunting tools** and the victims of man's distant forebears.

Now although the various exponents of this theory differ considerably on matters of detail, and in their interpretation of the available evidence, nevertheless they all agree that human tool-using and tool-making probably arose from agonistic displays that included the picking up and throwing of objects. Such displays in our closest living relatives, the great apes, have been widely reported in the available literature, as, for instance, by Schaller in gorillas,[64] Kortlandt[65] and Lawick-Goodall[66] in chimpanzees and Davenport in orang-utans.[67] Moreover, all these displays, however ritualized, involve the use of branches or vegetation, which may either be scattered randomly about, or directed at

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* see Ardrey, 1961, African Genesis, London:Collins.

**The tools associated with the Oldowan lithic culture were probably not weapons as such, but rather choppers, scrapers, cutters etc. for butchering the carcasses and cracking open the long bones and skulls of animals that had been killed by other means, or else scavenged.

the particular creature who occasioned the display. Kortlandt and Kooij have noted of chimpanzees that such displays generally occur when these apes are in a strongly ambivalent state of mind balanced between fear and aggression.[68] Furthermore they consider that whereas agonistic throwing behaviour is probably instinctive in the great apes, any aiming component has to be learnt individually, and Morris, among others, has shown just how well chimpanzees at least can learn to throw. Thus Morris taught chimpanzees how to use a coconut shy scaled down to take grapes, and found that "their accuracy after only a few trials was almost at the human level."[69] Moreover Lawick-Goodall has observed free-living chimpanzees drive off baboons by throwing stones at them.[70] Those authors, then, who subscribe to the view that early hominid tool-using arose from agonistic behaviour patterns would probably argue that man's early relatives, like the living apes, characteristically used 'objects-in-display' as part of their behavioural response to threat situations, and that it was the development of purpose and direction in the object throwing component of these displays that led to the development of habitual tool-using habits and later still to the modification of objects for specific tasks. Moreover aimed throwing at potential predators - or for that matter aimed clubbing - may, by transference of learning, have been carried over into other types of behaviour, as for instance in driving off carnivores or vultures from a kill, or even in knocking down small animals. Thus 'weapons' of defence would have given rise to 'weapons' of offence, and in so doing have immeasurably increased the efficiency of early man's hunting and scavenging activities.

However, there are several objections to this hypothesis which, taken together, cast some doubt on whether weapon-using habits did, in fact, have primacy in evolution over other kinds of tool-using behaviour. Firstly, although in 1963 the late Professor Hall claimed that

> "tool-using as a feeding adaptation occurs
> in several different types of animals but has
> so far proved very rare in monkeys and apes",[71]

the recent field observations of Lawick-Goodall have established that chimpanzees of the Gombe Stream Reserve not only use tools to get at food sources that would otherwise be inaccessible to them, but may even modify tools for this purpose. Furthermore, she is convinced, as a result of her studies, that termiting is learned by young chimpanzees from first watching and then imitating the behaviour of adults, and that though at first they are unskilful performers, as for instance in making tools that are too short or in jerking the twig out of the hole so quickly that the termites are knocked off, they become increasingly proficient with practice.[72]

Lawick-Goodall has also observed that they will make a sponge out of chewed leaves to sop up water from rain pools. These observations, taken together with the other instances in which free-living members of the large apes have been reported to use tools in order to extend the scope and variety of their food supply, do not substantiate Hall's statement that "tool-using as a feeding adaptation is very rarely found in the higher primates." Furthermore, whereas chimpanzees have been observed to use tools in a variety of different feeding situations, non-primate tool-users have generally been found to use them in only a single feeding context eg. mollusc-smashing by sea-otters. Moreover, although the tool-using performances of non-primate species appear to be largely determined by innate factors, it is likely that at least some of the tool-using habits of chimpanzees are purposive, and that these habits are first learned by imitation from adults and thereafter improved by practice. In sum, the fact that chimpanzees, and perhaps the other large apes as well, use and modify objects for specific food-getting purposes, and that these habits are individually learned from other members, clearly demonstrates that they have evolved a primitive traditional 'technology' based on patterns of behaviour that are not primarily agonistic in origin.

Secondly, the only instances of tool modification that have been observed in free-living chimpanzees have been in circumstances other than those associated with agonistic patterns of behaviour, although, given a choice, chimpanzees may select one particular kind or type of display object in preference to another (Kortlandt and Kooij).[74] This suggests that the early hominids may have first begun to modify objects in order to extend the scope and variety of their food-supply, rather than to make primitive weapons with which to defend themselves against predators. Furthermore, even if the early hominids did first develop tool-using - that is throwing - habits from their use of objects in agonistic displays, this does not necessarily imply that tool-modification also derived from the same behavioural source, for selected, though unmodified, stones, long bones, horns, sticks etc. would have been sufficient in themselves for defensive and offensive purposes - at least so far as the Early Pleistocene hominids are concerned.

Thirdly none of the lithic tools associated with the Oldowan cultural period are offensive weapons, but rather implements for the dismembering and butchering of carcasses that had been killed by other means. Furthermore, as it is unlikely that these primitive tools would have been much use as defensive weapons, it must be considered very improbable that they were ever used for this purpose.

Fourthly, the animal remains that have been found on the living floors of the Early Pleistocene hominids are generally of small or immature creatures, similar in type and size to the kind of animals which are killed by living baboons and chimpanzees. As Leakey has demonstrated the possibility of catching small antelope with his bare hands,[75] and as this is the manner in which both baboons and chimpanzees catch their prey, it is not unlikely that most of the early hominids' flesh food was also caught without the aid of hunting weapons. Thus, although tools would not have been of much advantage to the early hominids in the actual capture of their prey, they would have been particularly useful in dismembering them and breaking open the long bones and skulls for the marrow and brains. Furthermore, cutting tools would have made it both easier and safer for man's early relatives to scavenge from the kills of carnivores by allowing them to cut off joints of meat which could then be carried to safety before being eaten. All these hypothesized lithic tool-making and tool-using habits, based on the palaeontological evidence, were specifically feeding adaptations, and moreover feeding adaptations that enabled them to increase the amount of food they were able to obtain from the carcasses of animals that had already been killed by other means.

In the light of this evidence, it is perhaps reasonable to consider that systematic tool-using and tool-making habits in the human line were first developed in contexts unrelated to the agonistic use of objects either as offensive or defensive weapons. However, this is not to suggest that the spontaneous and emotive use of objects in threat situations may not have preceded the development of tool-using habits, nor that these emotive displays did not eventually give rise to the habitual use and manufacture of weapons for defensive and offensive purposes. At the same time, as it is quite likely that the early hominids used weapons in contexts other than those related to agonistic patterns of behaviour, it may be that the use of weapons as specific feeding adaptations may have had evolutionary precedence over the use of weapons for defensive or offensive purposes.

In sum, as chimpanzees have been observed to use tools in three different behavioural contexts - sic in agonistic displays, as for instance in the use of clubs against potential predators (Kortlandt and Kooij),[76] in procuring food items that would otherwise be unobtainable, as for instance in using vine stems to 'fish' for termites (Lawick-Goodall),[77] and in grooming behaviour, as for instance in using a bunch of grass to clean themselves of detritus or waste food (Lawick-Goodall),[78] it is probable that the protohominids' tool-using and tool-making habits covered at least as broad a behavioural compass. Moreover besides the many Oldowan lithic tools that have been discovered on their living floors, it is quite likely that they also used a variety of wooden and bone tools, and may especially have developed the use of a digging stick to facilitate the collection of subsurface roots and rhizomes on which, at certain seasons, they may have largely depended for their staple diet.

In the past, a great deal of attention has been paid to the critical importance of tool-using habits in the evolutionary success of the hominid line; however, although it is true that tool-using habits permitted man's early relatives to better exploit the potential resources of their environment, it must also be remembered that tool-using behaviour was only one of a number of factors that gave adaptive advantage, and that the ability both to use and manufacture tools is not in itself the reason for man's present extraordinary place in the natural world. Concomitant behavioural, anatomical and even ecological changes have been at least as important in the progressive development and success of the human line of evolution. Thus there has been much speculation as to why chimpanzees, who are readily able to master a great many instrumental and tool-using techniques in captivity, have not developed these abilities in their natural environment. The answer, in part at any rate, must lie in their ecological circumstances, and the fact that their forest habitat and the bountiful supplies of food to be found there throughout the year offer them few inducements to innovate and develop new patterns of behaviour. They are, in fact, particularly well adapted to a nomadic forest or mixed forest and woodland way of life.

The adaptive sufficiency of the early hominids' primitive technology to their particular ecological circumstances and the lack of any inducement to further develop and advance their tool-making habits must also have been an important factor in the incredibly slow rate of technological change during the Early and early Middle Pleistocene periods. Moreover the subsequent development of more sophisticated hunting weapons probably arose in response to environmental changes that led the early relatives of man to alter their behaviour in the direction of more meat-eating habits. In this respect it is interesting to note Clark's comment that it was the drier interpluvial periods that seem to have been associated with times of cultural 'speed-up'

> "... when less favourable living conditions stimulated man's powers of invention toward improved methods of securing food ..."79

In conclusion, an attempt has been made in this section to relate what is known about the cultural status of the early hominids and especially their tool-using and tool-making abilities, to a general appraisal of the nature, occurrence and transmission of social traditions among both primate and non-primate species. In particular I have stressed the importance of behavioural and anatomical predisposition in the development of tool-using habits, and the fact that these habits are adaptive rather than fortuitous behavioural mechanisms. Thus, once a new and favourable balance has been achieved by a population or species in relation to the particular habitat it is occupying, there is considerable inertia against any subsequent behavioural innovations in conditions of social and/or environmental stability. Indeed this factor of "adaptive inertia" must have been one of the most important reasons for the generally slow rate of technological development among man's early relatives.

With respect to the particular issue of whether weapon-using or tool-using habits had precedence in evolution, I have argued that tool-using habits probably had primacy of origin, though in view of the fact that chimpanzees have been reported to use tools as weapons, as specific feeding adaptations, and as grooming devices, there can be no absolute certainty about this.

In fine, though the possession of culture is one of the most significant and characteristic features of man, culture is certainly not a sole prerogative of the progressive human line of development; yet, even at this early stage of hominid evolution, social traditions both in specific tool-using or weapon-using contexts, as also generally in behaviour and feeding habits, must have clearly distinguished them from any other life form on this planet.

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FEEDING HABITS.

During the last few decades the question of predation has caused a great deal of controversy in discussions on protohominid behaviour. For years it was assumed that man's distant forebears, like man's close-living relatives, the chimpanzees, were amiable, forest-living primates, subsisting on a diet of wild fruit and berries. More recently, however, there has been an almost complete reversal in ideas about the physical and social aspects of our hominid ancestors, and almost complete agreement that hominid forms living in the Pleistocene and possibly even as far back as the Pliocene and the Miocene were at least occasional predators. This revolution in thought has come about as a result of a complex change in our direct and indirect knowledge of the higher primates, for there is available today a range of factual data that in scope and depth, belittles the data available even twenty years ago. Discoveries in palaeontology and of new and more sophisticated methods of dating, the revolution in the systematics of the Hominoidea and Hominidae and detailed field research in animal behaviour and particularly primate behaviour, have all contributed to this revolution.

It would be superfluous here, to relate the history of the 'Predatory Controversy' especially as the literature on this subject is easily accessible, and has been popularly reviewed by Ardrey, in his book, 'African Genesis'.[1] However, there are certain points which bear more lengthy consideration within this debate of which probably the most important concern the writings of Professor Dart and the reactions of his professional colleagues to them. It was Dart who really started the whole controversy with his contention that Australopithecus was a hunter and the possessor of an osteodontokeratic culture. Unfortunately, however, Dart made it much easier for his critics to lampoon this view of protohominid behaviour by writing up his research in purple prose of the most lurid kind, as illustrated in the following extract:-

> "... man's predecessors differed from living apes in being confirmed killers; carnivorous creatures that seized living quarries by violence, battered them to death, tore apart their broken bodies, dismembered them limb from limb, slaking their ravenous thirst from the hot blood of victims and greedily devouring livid, writhing flesh."[2]

This apart, the real issues at stake were metaphysical rather than scientific, and concerned man's idea of man whether within or without the evolutionary scheme. Man had generally been thought of, even in the post-Darwinian era, as an all or none creation, a product of evolutionary process, yes, but a super-species to boot. Despite the revolutionary work of Darwin many of his successors schematically seemed to think of evolution as rather a staircase to man than as a family tree, and that invention and intelligence were the sole prerogatives of man. The 'great leap forward' was the evolution of man's big brain, and it was brain, rather than any other character, that distinguished man, not only taxonomically from the apes, but in kind from every other life form on this planet. It is easy to see why in this case, the Piltdown forgery was so successful (a man's brain with an ape's jaws? indubitably the missing link!). The evidence which exposed the Piltdown skull as a forgery was published in 1953 (Weiner et alii)[3] and though it took several more years before Dart's thesis was generally accepted, the psychological barriers to belief had been broken. The idea of a big-brained, ape-jawed proto-man was finally repudiated and the readiness to accept a lesser heritage more widely accepted. Truly, we were now creatures of this world.

However, the battle was neither so easily, nor so quietly won, as perhaps I have inferred. Dart's thesis was alternately attacked and defended by a multitude of protagonists on a number of different fronts. For instance, the evidence pertaining to the vast accumulation of mammal bones, which, for Dart, confirmed the predatory nature of the australopithecines, led others to suggest that it was the work of hyaenas or porcupines. Both these suggestions were assiduously contested by a combination of statistical and morphological evidence and field observation. (Dart; Hughes;)[4,5]

Until recently, this particular controversy had died down, with Dart et alii, if not victors, at least masters of the evidence available at the time. However, in 1967, Dr. Sutcliffe, of the British Museum, who previously had excavated the site of a prehistoric hyaena cave in Devon and found it to contain an overwhelming majority of hyaena remains (quite unlike the Makapansgat deposit) made a trip to East Africa for the purpose of collecting material for comparison with the remains of British hyaena dens. He investigated a number of dens at Neveya in Uganda, at Kajiado in Kenya and in the Ngorongoro Crater in Tanzania. He found, both within the dens and in their vicinity, a great variety of species including cattle, buffalo, elephant, rhino, hippo, zebra, wildebeest, buck and even human skulls (at Kajiado). It appeared that most of the bones within the dens were associated with the feeding of young hyaenas who had gnawed them; outside the dens however, the bones tended to be splintered and looked very similar to Dart's osteodontokeratic tools. Further, wildebeest jaws had been gnawed at both ends, and at the bottom, making them almost indistinguishable from the photographs of australopithecine scrapers (Hillaby).[6] This evidence contradicts earlier statements by Dart and others, that investigations of several dens of living hyaenas by Hughes, 'had failed to uncover a single broken bone'.[7] If one also considers the fact that recent field research has revealed the hyaena to be a pack hunter of remarkable ferocity, Dart's thesis begins to look, as it did to begin with, no more than an inspired guess.

Certainly, the evidence now is not so overwhelmingly in favour of Dart as it was before. However, there is much that is difficult to contest - the statistical analysis, the fractured baboon skulls, and the known osteodontokeratic artefacts from other Early and Middle Pleistocene sites.

I have dwelt at length on the hyaena controversy as in many ways this was the most crucial factional contest in the whole debate. Another argument concerned whether or not Australopithecus was a maker of stone tools. In 1959 Mary Leakey found the skull known as Zinjanthropus boisei in Olduvai Gorge, on a living floor in association with pebble tools and the bones of a variety of small mammals, and reptiles. Apparently, therefore, the ape-man was not only a possible tool user and tool improvisor, but also a maker of stone tools as well. Certainly he was a predator - or was he? Washburn had earlier raised the question of whether the australopithecines were the hunters or the hunted, and had concluded that they were the hunted and that their bones had been brought to the fossil bearing deposits by hyaenas.[8] After all, an apparently more advanced hominid - Telanthropus - lived in South Africa in the Middle Pleistocene and he might both have been the progenitor of the Middle Pleistocene lithic culture and the hunter of the australopithecines. In 1961, Leakey found in Bed I, at Olduvai, not far from where Zinjanthropus had been discovered, and about a foot lower in depth, skull fragments of a form that was later to be designated Homo habilis. So now, not only was there the confusing position of Telanthropus in South Africa, but at a much earlier date, there was living in East Africa a contemporary of Zinjanthropus, whose skull capacity (680 ccs.) closely approached the range of Homo erectus. Was it he who was the tool maker, and was Zinjanthropus perhaps a victim? The position is still somewhat confused at this time, and there remains some doubt about the particular cultural capacities of these various hominid forms. However, morphological analysis of the fossil characters of the australopithecines has shown that their post-cervical skeleton was very similar to man's, that they were possessors of the power grip and maybe the precision grip as well[9] and finally, that their reduced dentition and absence of developed canines implies a tool using prowess of considerable antiquity.

Palaeontology is not the only discipline which has furnished evidence of predatory behaviour in the protohominids. Field studies of primate behaviour have shown that both baboons and chimpanzees are occasional predators. It may be argued that if predation is a factor in the feeding behaviour of living chimpanzees and baboons then, in view of the anatomical evidence pertaining to the protohominids it is more than likely that they too, were to some extent, predaceous in their feeding habits. The fact that hunting is the most common motif of the ancient cave artists, that weaponry or culinary objects are the most common artefacts of paleolithic archaeological excavation, and that hunting seems to be a behavioural syndrome as powerful in our complex Western society as it is among the Bushmen, seems to add up to a triumphal avowal of Dart's belief in man's predatory nature, an avowal moreover that is now largely implicit in the work of most contemporary scholars in this field.

However, there is a great deal of published evidence from a variety of different fields which suggests that the predatory habits of the early hominids may have been overemphasized by writers who were justifiably anxious to convince a largely sceptical audience that man's distant forebears were not solely vegetarian in their diet.

Ecological analysis offers primatologists a way of quantifying field observations of, for instance, feeding habits that in the past have often been based on data that was not necessarily an accurate representation of food preferences or of the actual amount each food item comprises in a total diet. Thus, it has been reported that both chimpanzees and baboons are occasional predators, the former at least on monkeys and bushpig (Lawick-Goodall)[10] and the latter at least on monkeys and young antelope (DeVore and Washburn).[11] Now it is clear that these instances were observed only very infrequently, though before either of these findings were published, Dart had claimed that baboons both killed and ate other animals.[12] He even published a photograph of a baboon doing just this but his material was largely disregarded. Dart claims that meat-eating is a dietary necessity for baboons, and that they not only kill more frequently than is commonly believed but that they do so intentionally. DeVore and Washburn on the other hand, claim that baboon predation is largely fortuitous, and that for instance, a baboon walking across the savannah may stumble across a young antelope and kill it but that he has no predatory intention before seeing the game.[13] Dart however considers that baboons search an area with the specific intention of finding a quarry, an opinion that is supported by Capt. Potter, who was at one time the Game Conservator for Zululand. In a letter to Dart he maintained that he had

> "repeatedly witnessed during the previous twenty years apparently organized hunts (by baboons) which often result in the death of the intended."

Further he stated as his firm belief that

> "baboons do more damage to bird life (eggs and young birds) and also to young buck of the smaller species than all the other vermin put together."[14]

Despite the fact that both baboons and chimpanzees are known to be at least occasional predators, no one to my knowledge, has followed up this singularly important evidence. Thus, are baboons and chimpanzees predaceous throughout the year or only at particular seasons (for instance when antelopes drop their young?). Are there regional differences either qualitatively or quantatively in the predatory behaviour of these two species? Thus, does predation depend on the numbers of available prey, or the lack of competition from other predators, or local custom, or lack of other food resources, or what? Again, just what are the fatality figures for predation by baboons, and how important is predation in both the seasonal and annual diet of these species? These are just some of the questions that must be answered and until they are answered satisfactorily, many of the speculative hypotheses that have been put forward by various authors can neither be accepted nor disproved.

Now, the victims of baboon and chimpanzee predation are, so far as is known, not incompatible with the type and size of animal found in association with Zinjanthropus at Olduvai. Further, the length of time that a living site was occupied can drastically affect the interpretation of known facts, and so far as I know, no irrefutable evidence has come forward of a living site used during a known time period that indicates that the early hominids were any more than 'bounty' hunters - that is to say, hunting was an addition to, not the basis of, protohominid feeding habits. In large, this pattern is to be found among the hunter-gatherers of today except in extreme habitats such as the Arctic. Until primate predation has been satisfactorily studied and compared with the known feeding habits of hunter-gatherers, and to what palaeontological evidence there is, it will be impossible to use the word 'hunter' or 'hunting' with any useful meaning. If for instance, baboon predation is a dietary necessity to maintain full physical health, as Dart suggests, then baboons may be called hunter-gatherers, just as meaningfully as Bushmen. In this context it is interesting to note that though, in many countries, the bulk intake of food may be considerable it is the small amounts of fish and meat which maintain a fit community rather than one suffering from malnutrition. It would also be useful to know how far other primates differ from ourselves in their feeding requirements, and what the really essential food components are in the diet of different human and non-human primate populations. Only when questions such as these have been answered satisfactorily will it be possible to ascribe to the word 'hunter' both a specific meaning - i.e. one who hunts - as well as an ascriptive meaning - i.e. one who exists by hunting. It has been said that baboons are popularly thought of as vegetarians and that their carnivorous habits have been largely overlooked. Inversely, it may be said that man (in Western society) is popularly thought of as a meat eater and it has not been appreciated just how far he is a vegetarian. However, 95 per cent of the total calory intake of the world's population per annum, is in food items other than meat.

Considered from the standpoints of biological evolution and ecology it is unlikely that predaceous habits in themselves were of major adaptive importance in the early hominids successful exploitation of a savannah habitat. It is well known that every species of organic life in the world occupies a different and generally speaking, original place in the ecosystem of any one area. In the animal kingdom, for instance, species have evolved as adepts of various food resources which are occasionally so specific - like the restricted eucalyptus diet of the koala bear or the bamboo diet of the panda bear - that even the slightest environmental changes may entail the evolutionary extinction of the entire population. Simpson states that it is improbable that every ecological niche is filled at any one time, and that whether or not an ecological niche is filled depends not only on environmental configurations but on the prior existence of organisms who could exploit the available niche.[15] Now hominoids are not primarily hunters, nor are they particularly well adapted anatomically to exploit an ecological niche that involves a considerable amount of meat-eating. For instance, Eiseley has pointed out that man's stomach is not that of a true meat-eater, for he does not possess the powerful digestive acids of the genuine carnivore.[16] As a result, neither he nor his remote ancestors could possibly have ingested large quantities of raw flesh; this could only have been done after the invention of fire for cooking purposes. The first reliable evidence for the existence of hearths comes from Middle Pleistocene deposits at Choukoutien associated with Homo erectus, and even then the fires may have been built for non-gastrological reasons such as warmth or defence.

Furthermore, Schaller has observed that even specialist predators like the tiger find hunting an arduous and time-consuming business. In the course of his study at Kanha National Park he observed twelve complete stalks by tigers of which only one was successful.[17] Pack hunters seem to experience equal difficulties in killing their prey. Thus Mech observed seventy seven attacks on moose by a pack of wolves on Isle Royale over a three year period, but only six animals were killed; in one day alone, the pack chased moose fifteen times without securing a single victim.[18] Of course, when these carnivores eventually do make a kill, they are able to eat relatively large quantities of raw flesh that would be impossible for a species which had not evolved appropriate gastric specializations to deal with it.

In view of these considerations, it would seem that even largely savannah-living hominids of late Pliocene or Early Pleistocene times could not primarily have been flesh-eaters. They must have relied to a greater or lesser extent on vegetable foods.

However, to suggest that the early hominids were not primarily hunters, is not to suggest that they displayed no predatory behaviour whatever. Though, as I said above, the palaeontological evidence is still somewhat enigmatic, it would appear that the protohominids relied for their meat diet mostly on small game. Now this is significant in a number of ways. To start with, it is known that a total biomass per square kilometre varies for different habitats, and that in East Africa, the largest ungulate biomass per square kilometre is to be found in the open savannahs on the edge of the Congolese forests - 23,550 kgs per sq. km on the Rwindi-Rutshuru Plain (Albert National Park) and 18,800 kgs per sq. km in the Queen Elizabeth National Park (Bourlière)[19] Of these amounts, 70 per cent plus, is made up of two species, the hippo and the elephant, and 95 per cent plus if the buffalo is included as well. However, the biomass per square kilometre for the Nairobi National Park and the Serengeti Plain is considerably lower than in the two previous instances - 13,215 and 4,692 kgs per sq. km respectively - and its composition is entirely different in so far as it is the small ungulates that make up the majority of these figures (Bourlière).[20] This may well indicate that by Early Pleistocene times at least, and possibly even earlier, many of the protohominids were living in the open savannah, for it was only there that their prey, as evidenced by the fossil material at Olduvai, were to be found in any great numbers. All the same, it must be remembered that, except for a dry period at the top of Bed I, the climate associated with Bed I and Bed II at Olduvai was somewhat wetter than exists today. This is shown, among other things, by the discovery of fossil bones belonging to ancestors of the forest and swamp-living okapi and sitatunga (Bed I) and to crocodile and hippopotamus (Bed II). Moreover, a shallow fluctuating lake seems to have existed, except during the dry period, throughout these times (Cole).[21]

It is probable then that though principally vegetarian in their diet the early hominids were euryphagous creatures, and that their feeding habits were similar in many respects to the savannah-living baboons of today. Now baboon skulls are fairly commonly found among protohominid fossil deposits and often display skull damage that may have been inflicted with a club or other blunt instrument. Lawick-Goodall (National Geographic Film) has shown chimpanzees fighting with baboons over a hand-out of food, and it would probably have been with baboons that savannah-living hominids would have tangled in their search for food.

The other fairly frequently occurring mammal associated with protohominid fossil deposits, other than an ungulate, is the hyaena, which, too, a euryphagous hominid may be expected to have come into close and sometimes hostile conflict. All carnivores are to some extent scavengers - for instance in the Ngorongoro Crater, lions let hyaenas do most of their killing for them, driving away the hyaenas from their kill, and not allowing them back until they themselves are sated (Kruuk)[22] - and hyaenas probably, are greater scavengers than any. But, man also is a scavenger, whether it be manifested by Bushmen, following a lion around its range to share in its kills (van der Post),[23] or by Hippies in California building freak-out towns from refuse dumps.

At the same time, scavenging has its own specialists as well, such as vultures and many different kinds of insects, and in the face of this specialist competition and that of various carnivores looking out for an easy meal, it would have been difficult for savannah-living hominids to show any appreciable returns from this activity. Moreover, DeVore and Washburn have observed that East African savannah-living baboons show no interest in carrion or actually avoid it, and have concluded that

> "primates with habits similar to those of baboons could get meat hunting far more easily than by scavenging."[24]

However, other considerations suggest that the early hominids may have been occasional scavengers. Firstly, though their pebble-tools would not have been very useful either for defending themselves or killing other creatures, they would have been indispensable for quartering a carcass, especially in view of the fact that they were naturally ill equipped with fangs or claws to tear a carcass to pieces. This then may have been the purpose for which they were made. Moreover, these tools would have been most useful in cutting up the carcasses of fairly large animals which they probably could not have killed themselves, but which they may have been able to scavenge. Secondly, the brains and marrow contained in the skulls and bones of large creatures could only have been opened by animals, such as hyaenas, whose teeth were capable of cracking open robust bones. However, the early hominids could also have gained access to this nutritious food-source by using stones, and the great variety of smashed mammalian bones and skulls found in Early and Middle Pleistocene deposits associated with protohominids, may support this conclusion. Further Leakey has recently found similarly smashed bones at Fort Ternan in association with the Miocene form Kenyapithecus wickeri that could well indicate a marrow and brain eating tradition of considerable antiquity. Moreover, he has found a battered lump of lava with these fossils which has every indication of having been used for the purpose of smashing open skulls.[25] It is arguable, therefore, that a certain amount of scavenging was undertaken by savannah-living hominids. As a result, they would have come into contact with hyaenas, not only when scavenging themselves, but also as scavengers at their own hunting triumphs. This, of course, may have provoked some uninhibited retaliation.

Paleontological evidence regarding the amount, kind and frequency of predation in the protohominids, is especially difficult to interpret, for though it appears certain that the early hominids were definite predators of 'slow game' and young antelopes, it is debatable whether or not they tackled anything larger. At first, the fossil materials from South Africa, and the discovery of Zinjanthropus in association not only with the bones of generally small and young animals but also with lithic tools led most people, including Leakey himself, to the conclusion that Zinjanthropus was a tool using hunter.[26] However, his later discovery of what is now known as Homo habilis made him revise his former opinion and claim that this more advanced hominid was in all probability the tool maker of Olduvai Bed I, and that Zinjanthropus may have been his victim.[27] The fact that the Miocene form Kenyapithecus (dating back about 14 million years) used stones to break open skulls, and that this creature long antedates Zinjanthropus suggests that the latter may well have developed crude stone tools for use as cutters, choppers, scrapers etc. The difficulty is that at this time one cannot say just how technologically sophisticated the various types of early hominid were, especially as their taxonomic relationship to each other have not been definitely resolved. However, there is some evidence of a more and less advanced lithic culture in Bed I at Olduvai which suggests that both Zinjanthropus and Homo habilis made tools, though with different degrees of competence(Leakey).[28]

It is now generally agreed that the spear was the major hunting weapon of the Middle Pleistocene, first with one end sharpened to a point and hardened by fire (a later modification), and then with a stone or bone head. Furthermore Dart favours the club as the major offensive and defensive weapon of a hypothetical osteodontokeratic culture in the Early

Pleistocene,[29] and Kortlandt has shown that savannah-living chimpanzees today will attack leopards with clubs.[30] Lawick-Goodall has observed chimpanzees using twigs and grass stalks to catch termites,[31] while other reported instances of tool using in the great apes, include for instance, poking sticks into underground bees' nests (Merfield and Miller)[32] and hammering palm nuts with stones (Beatty).[33] One might infer from all this that wood (or bone) was used far earlier than stone as a tool. Further, both chimpanzees and gorillas display considerable manipulative skills in the use of wood in the wild (such as their skill in nest building) and the potential for far more in test conditions. Nevertheless, wood, unlike stone, is far less likely to be preserved for later examination. If chimpanzees and gorillas can build nests by a method of elementary weaving it is but a step to making string bags and baskets, while a stick, sharpened at one end, may be used for a variety of different purposes, whether or not it is intended primarily as a club, digging stick or spear. We may presume, then, that wooden tools were, for a considerable time, the basic technological equipment of the protohominids.

If this is so, the remark of DeVore and Washburn to the effect that a simple digging stick or stone would immeasurably increase the efficiency with which baboons could gather sub-surface roots and rhizomes becomes especially significant.[34] Further, these authors also remarked that the baboons' concentration on sub-surface food items allows them to feed in an area which has been denuded of surface vegetation by the many ungulates which share their habitat. In itself, this would suggest a strong reliance by savannah-living hominids on this same source of food, and more certainly so when one remembers that hunter-gatherers often rely on rhizomes, roots and tubers for a large part of their diet, and that their task is made both more simple and more productive by the use of digging tools.

However, the picture is complicated by Robinson's contention that morphological analysis of the fossil material indicates that Paranthropus (A. robustus) and Australopithecus (A. africanus) are generically distinct from each other, and that the morphological differences between them are largely explicable by differences in their respective diets.[35] Thus he considers that whereas the robust form was a vegetarian the gracile form was both an omnivore and a meat eater. However, Tobias has recently re-examined the evidence pertaining to this particular issue, and has come to very different conclusions from those expressed by Robinson.[36] He considers that on the available evidence, no generic distinction can be made between the two forms, nor can any satisfactory conclusion be reached on qualitative differences in their respective diets.

Robinson's case rests on three main points. Firstly, that the cheek teeth of Paranthropus are larger in size than those of Australopithecus, and that there is a greater disparity in size between the cheek teeth and the anterior teeth of Paranthropus than between the same teeth in Australopithecus.[37] However Tobias, while admitting that the mandibular canines of Australopithecus are significantly larger than the mandibular canines of Paranthropus, and that six out of ten cheek teeth in Paranthropus are absolutely larger than those of Australopithecus, disagrees with Robinson that disparate reduction of the frontal teeth was a contributory cause of this difference. He considers that both the maxillary and mandibular incisors and the maxillary canines are approximately the same size in both groups. He concludes that the real cause of the disparity lies in an enlargement of the maxillary cheek teeth in Paranthropus and in the larger mandibular canine of Australopithecus, and adds that

> "such a differentiation in the size of the cheek teeth, of itself, provides no evidence of major ecological or adaptive radiation."[38]

Secondly, Robinson asserts that the enamel on the occlusal surface of Paranthropus' teeth is chipped which he correlates with similar chipping in the teeth of baboons and which he ascribes to the action of particles of grit in the diet.[39] Tobias affirms this chipping but notes that it is 'not confined to, nor even commoner in, the Paranthropus material'.[40] He suggests that particles of grit would be unlikely to cause such chipping, and that they are far more probably the result of chewing on hard material such as bones. Thirdly, Robinson reckons that Paranthropus displays a 'considerably thickened bone around the molar roots' which indicates "that crushing and grinding was the main function involved." However, Tobias argues that

> "since Paranthropus, has on the average, larger dental crowns and roots than Australopithecus, it is to be

> expected that the alveolar bone would be thicker or more robust."

and goes on to say that some of the Makapansgat jaws

> "have very robust alveolar processes, comparable with some of those encountered in Paranthropus."[42]

Other points raised by Robinson in defence of his thesis - differences in dental variability and brain size and brain quality - are also disputed by Tobias and need not be related here. The validity of Robinson's thesis, in the terms that he has stated it, is thus very much more doubtful in the light of Tobias' recent reappraisal of the evidence. However, on the face of it, there is every reason to think that two closely related co-existing protohominids would have exploited different ecological niches. Furthermore, his thesis nicely accommodates some known facts that are at present only contentiously explained - for instance, the association of Paranthropus and Telanthropus in Middle Pleistocene deposits at Swartkrans, and of Zinjanthropus and Homo habilis in Early Pleistocene deposits at Olduvai. Moreover, if Paranthropus (or Zinjanthropus) was a vegetarian and Telanthropus (or Homo habilis) a meat eater, then the latter may have preyed on the former. At the same time both forms may have been competing for the same ecological niche, which eventually would have resulted in the competitive exclusion of one or other of them - in this case probably Paranthropus/Zinjanthropus. Yet as fossils associated with both Zinjanthropus and Homo habilis have been found in Bed I and Bed II at Olduvai, and as the difference in time between the earliest and the latest synchronically associated remains of the two forms is at least half a million years, they could not have been very close ecological competitors.

Certainly it would be inappropriate at this time to make an authoritative statement on possible ecological differences between different groups of co-existing hominids. However, it should be remembered that man himself, without speciation, consumes a vast range of food items, that are in some populations occasionally as specialised, if not more so, than the posited food specialisations of Paranthropus and Australopithecus. Further, when such specialisations are made the basis of a contention that sets out to establish generic distinction between two hominid forms, the conclusion must to some extent be suspect. A change in the physical environment of a behaviourally flexible omnivorous primate may very well have occasioned a change in its feeding habits and might, to some extent, have modified its morphology in the same way that the physical environment has to some extent modified the species Homo sapiens in different parts of the world. Moreover, it has been found that Japanese macaques vary from group to group in their feeding habits; each group develops its own particular menu and this menu may differ quite considerably from the menus of neighbouring groups of the same species (Kawamura).[43]

Though I find the idea of man as an omnivorous and largely vegetarian species attractive, the fossil record poses some fairly awkward questions for such a viewpoint. Firstly, why did man evolve an upright stance if his major food source remained on or near the ground? A baboon, with his quadrupedal gait can fiddle for roots and glean grasses both more easily and more comfortably, than can man, and could perfectly well use a digging stick in that position. Bipedal locomotion, on the other hand, facilitates hunting enormously. Everyone must have seen pictures of a ferret or otter sitting up on its hind legs, or have observed a cat similarly sitting up to get a clearer view of some distant object, especially if there is grass, or some other visual barrier in the way. Behaviour such as this is vital to any hunter that relies mostly on its eye-sight and stalking skill to kill its prey. Certainly, bipedalism would confer a selective advantage on any hominid hunter and would encourage him to use his free hands for carrying weapons or other tools. Further, the mechanical advantage conferred by bipedalism in the use of weapons, would be equally if not more important, for only bipedally could a club be wielded in a manner likely to cause gross physical damage, while bipedal posture is essential for throwing wood or stone effectively on the ground. The selective advantage of bipedal posture for a primate without an anatomically specialised armament of claws, teeth etc., is undeniable. Moreover, Napier has put forward the intriguing suggestion that the greater energy requirement of inefficient bipedalism may have led man's remote ancestors

> "to alter their diet in the direction of an increased reliance on high-energy food-stuffs, such as the flesh of other animals.[44]

However, in the course of this discussion I have mentioned a number of reasons for thinking that the predatory aspect of protohominid feeding habits may have been overemphasized in the past, and the following considerations would seem to support this view.

Kortlandt has observed that chimpanzees adopt a bipedal posture when coming from forest to more open ground apparently in order to see whether it is safe for them to proceed.[45] A propensity for bipedalism would have been selectively advantageous to savannah-living hominids in that it would have allowed them more easily to espy any danger from predators. Beyond this it would have facilitated the carriage of food from one place to another, as also the ability to carry not only food, but such items as a digging tool as well. In this context it is interesting to note that a large proportion of the reported instances of bipedalism in chimpanzees and other sub-human primates have been in food carrying situations. Bipedalism then would have been as favourable an adaptation for a largely vegetarian primate in savannah or woodland savannah as it would have been for a hunting one. As primates generally are vegetarian feeders not flesh eaters, it is therefore reasonable to think that selection for upright posture was initiated by visual and transportative habits related to a gathering economy.

Numerous speculations have been made on the kind of society in which the early hominids lived, some authors favouring open groups, others a more closed social system. Whichever it was, the degree of communal co-operation in the food quest is unknown, as also whether or not there was any division of labour. From indirect (anatomical) evidence it may strongly be argued that there was some division of labour for the narrowing of the birth canal as a result of bipedal posture and the increase in relative size of the brain made it necessary for an infant to be born earlier, and thus more helpless, which would necessarily have entailed longer and more intensive care on the mother's part. One might imagine then that mother-offspring groups were by far the most vulnerable section of early hominid communities. It may be added here that both Reynolds[46] and Kortlandt[47] have observed that chimpanzee mothers and children are the least mobile elements in the food-quest, always arriving last at a new feeding place and leaving last, while the more mobile groups of males and young adults, both male and female, may possibly act as the food-finders, announcing the discovery of food by raising, in Reynolds' words, an 'immense hulabaloo' (but see section on Social Organization). In a savannah environment it would have been suicidal, in view of the generally slow reproductive potential of man, to have exposed females and their offspring to the constant threat of predation, without the protection of adult males. The mother-offspring element in a relatively large savannah-living primate could not then have been left unprotected, nor could it effectively have joined in the hunting activities of a highly mobile band of predator hominids - if there ever was such a creature living in the open savannah. Furthermore, for reasons I have already given, they could not have relied for their food solely on meat brought back to them by members of a hunting group, who in turn could not have relied solely on their hunting successes to sustain them, let alone a number of female and infant dependants. Mother-offspring groups must therefore have gathered most of their food, either as part of a larger group composed of all ages and sexes, or as a distinct group occupying a site which provided them with ready protection and sufficient resources of food and water while more mobile sections of the community engaged in hunting and foraging elsewhere.

Now, any kind of labour division, however elementary, may have involved a certain amount of food sharing. Sahlins affirms that food-sharing is not found in any sub-human primate other than in the sense that a dominant animal may make a subservient one refrain from or give up eating a choice food morsel.[48] However, both Lawick-Goodall[49] and Köhler[50] have observed instances of one chimpanzee sharing food with another. Lawick-Goodall's observations are all the more interesting in that they arose as a result of predatory activity. She has drawn attention to the fact that when an adolescent male makes a kill, the carcass is torn apart and shared among all the chimpanzees present; on the other hand when the prey is in the possession of an adult male, no such sharing occurs, even if there are more dominant adult males present. The other members of the group sit round the successful hunter "watching the meat with longing eyes, holding out their hands palm uppermost in a begging gesture."[51] The reaction of the male to these suppliants varies - some adults ignore them completely, others give a certain amount away. Now, the first kind of sharing mentioned above obviously falls within the terms of Sahlins' statement; the latter kind, however, seems to indicate a different kind of behavioural response altogether, and much closer to the human idea of sharing as a voluntary gesture.

In this context, it is interesting to compare these findings with observed instances of predation in baboons. DeVore and Washburn witnessed the actual killing of a young Thomson's gazelle by an adult male baboon, and have described the event as follows:

> "an adult male baboon grabbed it, brought it above his head, and slammed it to the ground. He immediately tore into the stomach of the gazelle and began eating. Beginning with the most dominant males, five of the six adult males in the troop participated in eating this gazelle, and two hours later, only skin, teeth and large bones remained. The viscera were eaten first, followed by the flesh, and finally the thin brain case was bitten open and the contents carefully scooped out with the fingers - bits of skull being pulled through the teeth and licked clean."[52]

In the course of their study, they also saw five or six other instances of predation, in one of which an adult male baboon who had killed a half-grown African hare was harried by two more dominant males in the troop as well as a pair of tawny eagles. However, he managed to elude his terrestrial and airborne pursuers and consume most of the prey himself. From these observations it would appear that the sharing of meat among baboons is determined by dominance ranking to a far greater extent than among chimpanzees, which is in character with their generally more authoritarian social structure.

In both chimpanzees and baboons, it is the males - whether adult or subadult - who seem to engage in predatory activity. Furthermore, the only documented case of a female capturing an animal was by Washburn at Victoria Falls. He saw a female catch a vervet monkey and hold it in her mouth. However, "she was apparently bewildered by the situation and soon released it unharmed."[53] This may well indicate that female baboons, unlike male baboons have not developed flesh-eating habits, and thus do not know what to do with prey even when they have it literally in their mouths. Certainly all the recorded instances of baboon flesh-eating by DeVore and Washburn have been among males. At the same time it may be that the vervet monkey, similar in many respects to an infant baboon, in this case released conflicting drives of maternal care and hunger in the female. This would, of course, explain her observed confusion and subsequent release of the monkey unharmed.

All this suggests that the predatory activities of protohominid populations were primarily conducted by adult or subadult males, and that therefore there was a certain amount of labour division. However, there would have had to be a far greater degree of sharing than exists among living chimpanzees or baboons for this division to be of much importance. As voluntary meat-sharing has been observed only among chimpanzees, and as apparently their groups are often composed on the basis of sibling, mother-offspring or friendship ties, sharing would probably have occurred first within the framework of these groups. The importance and lasting nature of sibling and mother-offspring relationships in the higher primates beyond the period of necessary dependance has been widely reported by field workers in recent years. It may be, therefore, that protohominid society was composed of small groups of related individuals or friends, similar in many respects both to the societies of living chimpanzees and human hunter-gatherers. Moreover, like most living hunter-gatherers, vegetables and other field-foods, including insects and slow game, probably composed the bulk of their diet.

Unfortunately, much of the material that exists on the diet of hunter-gatherers is unquantifiable and, whereas a great deal is known of the extent and variety of food items in their diet, very little is known about the amount that each food item contributes to the total diet. However, Marshall has estimated that 80 per cent of the Bushman's food consists of veldkos (field foods) and that the known sources of these foods and their seasonal occurrence are well known to everyone.[54] A !Kung Bushman territory must provide enough veldkos to sustain the group and thus the gathering potential of a territory is far more important than the hunting potential. Anyway, hunting is an exhausting and time-consuming occupation and a successful hunt may take days rather than hours. Marshall estimates that on average a !Kung band gets only 15 to 18 large animals per year. One can easily imagine why, in such circumstances, the veldkos are so important, and are more jealously guarded than the hunting rights to a territory. Meggitt has also emphasized the importance of vegetarian items in the diet of tropical hunter-gatherers, commenting that

> "a vegetarian stress seems to be one of the prime distinguishing features of hunting, fishing and gathering economies."[55]

Among living groups of hunter-gatherers in Australia, even on the northern coast where game and fish are abundant, he has calculated that vegetables make up 70 per cent to 80 per cent of the peoples diet, and that the women collect most of it.

It is important to emphasize, however, that generalizations about the diet of hunter-gatherers are extremely difficult to make, for they depend not only on habitat factors but on traditional customs and food preferences as well. It is easy to remark that the habitat in which an Eskimo lives forces him to subsist almost entirely on meat and fish. However, environmental factors alone are not the only determinants of eating habits. Turnbull has noted in his book on the Mbuti Pygmies that

> "At all times of year there is in the forest an abundant supply of mushrooms, roots, berries, nuts and herbs, some fruits and some leafy vegetables."[56]

yet the Pygmies are ardent hunters and kill enough game for some of the meat to be exchanged for plantation foods and village utensils. Moreover, these kills are made in an area where the total biomass of game animals is fractional compared to that of more open woodland or savannah.

Yet the Mbuti Pygmies with their economic ties to a Negro village are perhaps unsatisfactory examples in that their village-band relationship may have encouraged hunting activities which were formerly not so pronounced. All the same it demonstrates that in a tropical forest women can gather almost all the food necessary to keep a small band alive, and this in itself may have encouraged the men to become specialist hunters.

Two other food-sources which may have been of some significance in the diet of the protohominids may briefly be mentioned here. They are insects and honey. Both non-human primates and men are known to practice entomophagy to a greater or lesser extent. Of special interest are the observations on entomophagy in chimpanzees by Lawick-Goodall,[57] in baboons by DeVore and Washburn,[58] and in human populations generally by Bodenheimer.[59] Lawick-Goodall has seen chimpanzees feeding on two types of gall, on two species of ants, and on termites. The termite - and ant-eating habits both involved the use of sticks or twigs to reach the hidden quarry. Though obviously the total quantity of insects eaten by chimpanzees is minimal compared to that of vegetarian foods, yet there is one season of the year when they become an especially important part of the chimpanzees diet. This is at the beginning of the rainy season when

> "for a period of as long as nine weeks, the chimpanzees feed for one or two hours daily on a species of termite common in the area."[60]

In this context, DeVore and Washburn have also observed that though baboons will eat a wide variety of insects, they only become a significant part of their diet during an insect glut. Thus when Nairobi National Park was invaded by "army-worm" caterpillars, the baboons fed on them almost exclusively for about ten days. Other species capitalized on the invasion as well, for in one small area they saw not only 3 baboon troops totalling 188 animals feeding on the caterpillars, but several troops of vervet monkeys and about 300 Maribou storks. They noted moreover that

> "the different baboon troops fed very near each other, and the other animals, without incident. All were gorging themselves on the caterpillars; several baboons were timed picking up 100 army worms per minute, and continuing at this rate for about 10 - 15 minutes without a break."[61]

Now, this insect-glut feeding compares very closely with the entomophagous habits of tropical hunter-gatherers, for though they consume a small amount of insects throughout the year, it is only at particular seasons that they become especially important food items. The B~~u~~ogong moth harvest is a particularly well known example of this, and during the months of November, December and January its multitudinous presence on the Koskiusko Plateau attract~~s~~ed a vast number of Australian Aborigines from different tribes to feed on it. Moreover McCarthy has commented that during this time the Aborigines become quite sleek and plump.[62] Many other examples of the entomophagous habits of hunter gatherers are cited in the literature and need not be set down here. However, anyone who doubts its widespread occurrence among both hunter-gatherer and agricultural populations should refer to Bodenheimer's classic account of this subject.

The fact that a concentrated food source attracts large numbers of potential feeders is an obvious and well known aspect of the ecology of animal populations. Moreover, it is also apparent that for large primates, insects would only be worth the time and trouble of collecting where and when they occurred in quantity (and/or size). However, there are two points connected with the entomophagous habits of primates that are of particular significance. One is the generally rich calorific content of these insects, and the other is the value of sticks or twigs to get at them.

Now Bodenheimer has argued that examination of the actual insects eaten in large quantities by man shows that they are precisely those which are rich in animal proteins in animal fats and in calories. In this regard he cites especially the termites which are eaten in vast quantities in tropical Africa, Asia and America, when the winged sexuals swarm out of the nests. Furthermore he notes that this emphasis on the winged sexuals is

> "physiologically well-founded, as the swollen abdomen, especially of the females, is rich in fats and proteins, in contrast to the much poorer body composition of the neutral castes."[63]

It is the winged sexuals also that are taken by the chimpanzees of the Gombe Stream Reserve.

The second point concerns the use of tools. In 1937, Noyes suggested that the idea of tools first occurred to man through the difficulty his ancestors found in opening termite hills;[64] in the light of Lawick-Goodall's recent findings[65] this theory may be less far fetched than it sounds. The first repeated observations of free-living chimpanzees using and modifying tools were made by Lawick-Goodall in the Gombe Stream Reserve; moreover the tools were being used to get at the winged sexuals in termitaries. Obviously without the aid of a stick both termite hunting and ant-nesting would be considerably less rewarding for chimpanzees. Moreover, many of the insects eaten by man, and especially by tropical hunter-gatherers, are found either under the earth or inside trunks, branches or roots, and could not be reached without the aid of sticks and/or stone (latterly metal) axes. For instance, Bodenheimer quotes the following extract, from a book by Dr. Basedow, on how witchetty grubs are caught

> "The witchetty grub is extracted from its hiding place by means of a light hooked stick. This implement is 10 - 15 cm long and is usually cut from a small pronged twig, one arm of which is left the required length, the other cut short and sharpened to form the hook. The stick is inserted into the hole occupied by the witchetty grub, hook foremost and pushed in until the grub is penetrated; then it is withdrawn, the hook bringing the grub with it. As the hole is usually small at its entrance, the bark is first cut away to a small depth with a tomahawk in order to avoid the constriction when the grub is being withdrawn. The witchetty-hook is known throughout central and southern Australia."[66]

The protohominids may then have developed their tool-using and tool-making prowess from using sticks and twigs to open termite mounds, antsnests and beesnests. Moreover it may have been their success in endeavours such as these which encouraged them to experiment with using tools for other purposes, and especially to uncovering the roots and rhizomes which probably made up a large part of their diet.

Honey-eating has been observed among chimpanzees in Cameroun by Beatty and again the use of sticks was seen to be a crucial part of the food-getting operations.[67] The predilection of hunter-gatherers for this food is well known, and Bodenheimer has even gone so far as to say that -

> "Many primitive peoples, such as the Pygmies, would not be able to survive in their last refuge in the tropical forests if they were not able to live mainly on honey. Half a kilo of honey provides the daily calorific requirements, while the addition of bee-maggots as a rich source of proteins, as well as of fats, as well as of vitamins and minerals make honey a well-balanced food, especially as considerable quantities of pollen are taken simultaneously."[68]

Elsewhere he stresses its rapidly energising components and also its medicinal and bactericidal properties. He remarks furthermore that

> "A Paleolithic cave drawing from Arana in Spain gives a vivid picture of a Paleolithic man collecting honey from a wild bees nest on a rock face,"[69]

and adds that it is almost identical to a sketch which Spittel (1924) made of a Veddah taking honey from a rock in the forests of Ceylon.

Now though one may question Bodenheimer's claim that honey is the food on which Pygmies rely most heavily for their continued existence, yet its general importance has recently been corroborated by Turnbull. Indeed, he remarks that -

> "There is a craving for honey during the season that never seems to be satisfied. No amount of alternative foods, even meat, can reduce this passion for honey."70

Although it would be tedious to detail any more instances of this well-known and widespread feeding habit, it is necessary to have emphasized its particular dietary importance for hunter-gatherers. Moreover, most of the points I have made regarding entomophagy in primates - sic rich nutritional content, the utility of sticks in its recovery etc. - apply to honey eating as well.

In sum, if chimpanzees will poke twigs into underground bees' nests to get at the honey, and will use vine stems to 'fish' for the winged sexuals inside termitaries, and if savannah living baboons will seize the opportunity of gorging themselves on a sudden glut of caterpillars, and as, furthermore, both insects and honey are widely consumed by hunter gatherers, and apparently have been for several thousand years at least, it is not unlikely that euryphagous hominid forms would also have exploited these same food items. Moreover the frequently 'hidden' location of insects within trees, or underground etc., may well have led the early hominids to develop simple wooden or lithic tools in order to get at them more easily. Indeed, the likelihood that such tool-using habits may, in fact, have been present in the early hominids is considerably increased in view of their known bone and skull smashing propensities, as also the fact that chimpanzees both manufacture and use tools in similar food-getting contexts.

Several important points emerge from this general discussion of the possible feeding habits of the early hominids. To start with, the evidence from both comparative and direct sources suggests that the Early Pleistocene hominids were all, to a greater or lesser extent, omnivorous in their feeding habits, though it is likely, that members of both phyletic lines - sic gracile and robust - relied on vegetables and fruits for the greater part of their food supply. How far the robust and gracile forms were differentiated in the ecological niches they occupied cannot be precisely determined at this time, either on morphological grounds or from the palaeontological evidence, though the principle of 'competitive exclusion' would necessarily imply that co-existing sympatric hominids must have had different feeding habits, unless they were ecological rivals. However, in view of the close phylogenetic relationship of the robust and gracile forms, as also their morphological dissimilarities and their long association in time, it must be considered very unlikely that they were, in fact, ecological rivals, even though representatives of the two lines may sometimes have come into aggressive conflict with each other. In sum, it is perhaps reasonable to think that members of the progressive human line were more catholic in the range of food items they consumed, and that their predatory activities were both more extensive and more various than those of the robust forms. All the same, as it is known that the food lists of a single higher primate species may markedly differ from one local population to another, it is not unlikely that local populations of the early hominids also differed from one another in their particular feeding traditions, and that these differences may have been as great between local groups of one or other hominid form as they were between individual members of the two lines generally.

The predatory habits of the early hominids were probably confined mainly to the capture of small or immature animals, and to scavenging the remains of larger animals from the kills of carnivores. For instance the creatures that have been found on the living floor where Zinjanthropus was discovered, include the remains of birds, amphibians, snakes, lizards, rodents and immature pigs and antelopes; moreover the evidence here shows that all those bones which may have contained marrow have been deliberately smashed open (Leakey).[71] The fact that smashed mammalian bones have also been found in association with the very early proto-hominid Kenyapitheous, suggests a particularly long standing habit of marrow and brain eating among the early hominids as also that a variegated and partially carnivorous diet has been characteristic of the hominid line from an early stage in its development - as it is also in the living chimpanzee today. In this regard too, it is interesting to note the frequent occurrence of aquatic creatures such as crabs, fish and turtles on the living floors of man's early relatives (Dart, Leakey),[72,73] and especially so when one considers that most of the camp sites of the early hominids have been found by the sides of lake shores. Such habits as these not only confirm the behavioural flexibility of the early hominids in exploiting novel sources of food, but also illustrate how ready they were to adapt their feeding traditions to the particular resources of their immediate environment. Moreover these foraging activities would appear to contradict Washburn and Lancaster's assertion that

> "During most of human history, water must have been a major physical and psychological barrier and the inability to cope with water is shown in the archaeological record by the absence of fish, shellfish, or any other object that would have required going deeply into water or the use of boats. There is no evidence that the resources of river and sea were utilized until this later preagricultural period..."[74]

In conclusion, therefore, it seems likely that the food lists of the early hominids - and especially those of man's direct ancestors - were considerably more varied than the food lists of any living subhuman primate species, save possibly the baboon/macaques, who, other than man, have been the most successful of living primates in adapting their behaviour to a considerable range of environmental and climatic conditions. However, unlike these monkeys, the early hominids probably foraged in small groups and only came together in larger aggregations when food was locally abundant in one area or in the dry season when all the various members who made up a local population, would have collected together round the remaining water sources. The bipedal habits of these forms would have enabled them to carry back food items - and especially joints of scavenged meat or the carcasses of small or immature animals they had killed themselves - for later consumption at their camp sites, and perhaps even for distribution among other members of the local group.

Moreover the development of simple lithic, wooden or bone tools for specific food getting purposes would have enormously increased the efficiency with which they were able to exploit the potential food resources of their environment.as also the variety of food items available to them. In short, their pattern of foraging may have been similar in many respects to that of tropical hunter gatherers living today though without the same emphasis on hunting by the men, for it was probably not until the development of better hunting techniques and of larger and more stable social groups in the Middle Pleistocene that the hunting rather than the gathering of game became a really important factor in the economic organization of man's distant forebears.

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CONCLUSION.

At this stage it may be useful to review some of the points I have raised in the preceding pages and relate them to what is presently known about the nature and habits of the early hominids.

The history of man's evolution from late Oligocene times onwards occurred against a background of climatic and geomorphic changes that considerably modified the nature of the physical environment. The retreat of the primary forests during late Miocene times was an especially important factor in the emergence of the progressive hominid line, for it opened up areas of woodland and woodland savannah that must have encouraged the development of more ground-living habits in a number of ancestral primate species, including the early relatives of man. Over the course of millions of years the ancestral protohominids would have spent more and more of their time on or near the ground, and these ground-living habits would have encouraged the selection of anatomical modifications that better adapted them for a largely terrestrial existence. Moreover as Napier has remarked, woodland savannah would have provided an ideal nursery for the progressive development of modifications leading to more efficient bipedalism,[1] and it seems reasonable to think that the early protohominids were already habitually bipedal forms before they emerged onto the open savannah in the Pliocene or Early Pleistocene. Indeed, the bipedal habits that they developed in this environment may well have been of crucial importance in preadapting them both behaviourally and anatomically for their subsequent successful exploitation of a savannah habitat.

During Pleistocene times the variable climatic conditions associated with the pluvial and interpluvial periods of Africa and the glacial and interglacial periods of Europe also played a critical part in man's evolutionary history. For instance, with respect to Africa, Clark has observed

> "that it was during times of climatic change, and in particular, of drier or non-pluvial climatic conditions that the most rapid changes in technology occurred."[2]

Elaborating this point he noted that the drier periods, which seem to have been associated with times of cultural 'speed-up', were

> "of relatively short duration compared with the intervening wet periods, when new ideas and new forms were able to spread with greater ease throughout the continent and when less favourable living conditions stimulated man's powers of invention toward improved methods of securing food and more comfortable living quarters. . . . . On the other hand, as soon as technical ability permitted (that is to say, from the end of the Earlier Stone Age onwards), the long periods of wetter climate made for stability, slow development and isolation of groups, and so resulted in a number of contemporary regional cultural variants."[3]

To what extent the pluvial and interpluvial periods in Africa can be correlated with the successive advances and retreats of the ice in higher latitudes is still a matter of dispute, though it seems likely, as Cole has observed,

> "that pluvial periods in the tropics were broadly contemporary with glacial periods elsewhere."[4]

Furthermore, as it seems probable that the general pattern of rainfall distribution was much the same in Pleistocene times as it is today (Cole),[5] there is some difficulty in evaluating how much wetter the wetter periods were than the drier ones, as also the effect that these changes had on the ecology of different localities, for whereas a moderate increase in precipitation could have had far reaching effects on the biosphere of one area, a similar increase elsewhere may have had relatively little or no effect on the existing environment. Though further discussion of the climatic and geological background to man's evolution would be out of place here, it is necessary to have given at least some indication of the part that climatic variations have played in the course of man's development, and especially of the way that changed environmental conditions have, at various stages, led members of the progressive hominid line to change their behaviour, first in the direction of more ground-living habits and much later to developing an increasingly efficient hunting-and-gathering technology.

The palaeontological evidence indicates that there were a number of early hominid forms living in Africa during the Early Pleistocene, though how far these various forms differed from one another behaviourally and morphologically, and what phylogenetic relationship they have to sapient man, are still matters of debate. However, it now seems fairly certain that at least three distinct hominid forms existed at this period, of which Homo habilis is the most advanced and almost certainly man's direct ancestor. The other two hominid forms - sic Australopithecus robustus (Zinjanthropus boisei) and Australopithecus africanus (including the Taung skull, Australopithecus prometheus and Plesianthropus transvaalensis) must therefore have been reproductively isolated from the progressive human line of evolution at this stage, though it is possible that all three hominids had a common ancestor as recently as the late Pliocene period, and that the Upper Miocene form Ramapithecus (including Kenyapithecus) represents a still earlier common stage of evolutionary development. On the other hand Ramapithecus may represent an early stage of differentiation between the more gracile and robust lines of hominid evolution, and that later still, the gracile line itself gave rise to the progressive human line which subsequently evolved independently through Homo habilis and Homo erectus to Homo sapiens. Such an evolutionary scheme as this would account for the closer morphological resemblance of Australopithecus africanus to Homo habilis than of Australopithecus robustus to Homo habilis, as the robust form would have been genetically isolated from the ancestral human line for much longer than the gracile form, and would thus be expected to have developed more divergent characters.

Tobias, on the basis of his own analysis of the evidence regarding the phylogenetic relationships of the various early hominid forms, recognizes

> "two apparent hominid lineages in the Lower and Middle Pleistocene: one line was seemingly specialising away from the main hominising trend and comprised A.boisei → A.robustus. The other line comprised Australopithecus africanus → Homo habilis → later Homo, and seems to have been the main line of structural hominisation and of cultural evolution."[6]

At the same time, he cautions that at this stage of our knowledge, it is impossible to say whether or not these two lines were completely isolated from each other genetically during the Pleistocene period, and that there may have been some transference of genes between the less hominized members of the gracile line (Australopithecus africanus) and members of the more robust line. Such gene transference might at least partially explain

> "the 'gracilisation' of Australopithecus boisei into the later and somewhat toned down Australopithecus robustus.",[7]

as well as accounting for those features in the Makapansgat specimens of Australopithecus africanus that are reminiscent of Australopithecus robustus.

The presence of a number of apparently distinct hominid forms in the Early and Middle Pleistocene periods suggests that they must have occupied different ecological niches, especially in those instances where two different hominids are known to have co-existed together in one place (as at Olduvai with Zinjanthropus boisei and Homo habilis), for as Mayr has observed

> "The principle of 'competitive exclusion' would prevent sympatry if there were not considerable ecological divergence."[8]

However, although on ecological grounds, it is reasonable to suppose that the different hominids were distinguished in their feeding habits, Tobias has recently questioned the morphological grounds on which Robinson has based his contention that there was

> "an adaptive difference of considerable magnitude between the Paranthropus phyletic line and the Australopithecus - hominine one."[9]

Tobias considers that the morphological differences between respective members of the robust and gracile phyletic lines are far less pronounced than Robinson has claimed, and that the differences which do exist are not in themselves indicative of vegetarian feeding habits among the robust forms.[10] Moreover, as recent field studies have established that the largely fruit-eating chimpanzee will occasionally catch and eat small mammals as well as feed on several types of insect (Lawick-Goodall),[11] and as local groups of a single higher primate species may anyway differ considerably from each other in the food items they consume, depending on the kind of habitat in which they are living and the particular feeding traditions of the group, it may be assumed that the early hominids in general were no less willing or able to vary their diet according to their environmental circumstances and to seasonal fluctuations in the availability and distribution of food.

Unfortunately, the evidence from the living floors associated with the various hominid forms does not help to clarify the issue. For instance, the skull of Zinjanthropus was found on a living floor in association with the

> "remains of birds, amphibians, snakes, lizards, rodents, and immature pigs and antelopes." (Cole).[12]

Moreover, in contrast to the rest of the fossil remains at this level, the skull was nearly complete and showed no signs of having been deliberately smashed or broken; as a result, Leakey concluded that the animal bones represented the discarded debris of meals that had been eaten by Zinjanthropus.[13] However, his later discovery of the advanced hominid, Homo habilis, at a slightly deeper level than that at which Zinjanthropus was found, with the fossil remains of

> "many tortoises, many birds, a number of cat fish and also tilapia together with some large mammals and many smaller ones"[14]

raised the possibility that Homo habilis was responsible for the animal remains on both living floors. Furthermore, detailed examination of the distribution of bones on the Zinjanthropus living floor clearly showed that

> "the Zinjanthropus skull, like other larger specimens, was on the outskirts of the site, and makes it possible that it was, like these other specimens, the remains of a meal." (Leakey)[15]

At the same time, it is strange, in view of the fact that even the Miocene form Kenyapithecus broke open animal bones and skulls to get at the marrow and brains, that the Zinjanthropus skull, if indeed it represents the remains of a meal, was not also smashed open. Moreover, as only parts of the habiline skull have been recovered and as Leakey considers that this particular individual was killed by a blow on the head, it may be that the advanced hominid, far from being the hunter of Zinjanthropus, was in fact his victim.

Thus it is not clear whether both of these hominids were meat eaters or only one of them; nor whether one hominid preyed on the other, and if so, which was the hunter and which the hunted. Indeed it is possible that aggressive interactions between the two hominid forms may have resulted in deaths on both sides. All that can be said for certain at this time is that at least one form was partially carnivorous, and that in view of the subsequent course of man's evolution, it is probable that the more hominised form was the hunter. However, as both baboons and chimpanzees may occasionally catch and eat small or immature creatures, it is by no means impossible that both hominid forms included a certain amount of flesh in their diet, and that this amount varied from one local population to another, according to the nature of the environment in which they were living and the particular feeding habits of the group to which they belonged.

Anyway, as I have argued in the Section on Feeding Habits, it may be that the predaceous habits of the early hominids have been overemphasized in the past, and that the reason man's hominid ancestors were so successful in exploiting a savannah habitat was rather because of the catholicity of their feeding habits than because of their carnivorous propensities. Furthermore, as all the early hominids must have relied on vegetable items for the bulk of their diet, it is possible that the use of a simple digging stick to get at subsurface roots and rhyzomes was adaptively more important to the successful exploitation of the savannah than the development of flesh-eating habits. This conclusion is based on a variety of comparative and direct evidence.

First of all vegetable foods comprise between 70% and 80% of the diet of tropical hunter gatherers living today (Meggitt),[16] and these people are probably far more adept hunters and possess a more sophisticated hunting technology than the Early Pleistocene hominids. Thus, in a full year, Marshall has estimated that a !Kung Bushman band kills only 15 - 18 large animals, and has observed furthermore that territorial restrictions on hunting are far less rigidly enforced than those associated with the areas of veldkos (field foods) owned exclusively by each band.[17] Secondly, man's stomach is not that of a true meat eater, and his ancestors of the Early Pleistocene would not have been able to digest large quantities of raw meat, without cooking it first. Thirdly, hunting is both a time consuming and arduous way of earning a livelihood, and the early hominids, without a social organization at least as developed as that of living hunter-gatherers, could not have spent hours, let alone days, hunting down one animal. Fourthly, the absence of any lethal weapon among the stone artefacts of the early hominids, suggests that what hunting they did was performed either with their bare hands, or with the aid of clubs or natural stones. The stone tools associated with these creatures are rather for butchering a carcass than for killing it, which suggests that the larger animals found on the living floors may have been scavenged, and that the tools were used to cut them up and to break open the long bones and skulls for the marrow and brains. Furthermore, the majority of animal remains associated with the early hominids come within the category of 'slow game' that could simply have been picked up, or of immature larger animals that could have been caught or clubbed without the necessity of a long chase.

Fifthly, the animals that are killed and eaten by baboons and chimpanzees are generally small or immature mammals (young bushpig, various species of immature antelope, monkeys, etc.) and in this respect coincide very closely with the known flesh-eating habits of the early hominids. Moreover as the total amount of meat eaten by chimpanzees and baboons is relatively insignificant compared to the vegetable items that make up the bulk of their diet, it may be that the carnivorous habits of the early hominids also only accounted for a very small proportion of the food that they ate. Now, as I have mentioned above, tropical hunter-gatherers rely on vegetable foods for between 70% - 80% of their total diet (Marshall puts the figure at 80% for the !Kung Bushmen).[18] Although there are no accurate estimates of the proportion of meat in the diet of baboons and chimpanzees, it is obviously very small. For instance, Lawick-Goodall has said that 90% of the food eaten by chimpanzees of the Gombe Stream Reserve is found growing in the trees.[19] The other 10% must therefore be made up of vegetable items that are found growing on or near the ground and various kinds of insects, etc, as well as meat. The actual percentage of meat in their annual diet cannot therefore be more than 5% and probably considerably less - i.e. 1% - 2%. Now it is not certain what percentage of the meat eaten by the !Kung is made up of large animals and what percentage made up of 'slow game', though it is likely that at least half of the total amount of meat they consume is made up of larger animals hunted by the men. Thus perhaps between 5% and 8% of the !Kung's diet is composed of small or immature animals - having deducted a certain amount from the 20% that is made up of non-vegetable foods to account for such items as honey, grubs etc. This figure then, is not much greater than the percentage of meat, made up of small or immature animals, in the diet of savannah-living or forest/woodland-living chimpanzees. Thus the greatest difference in the carnivorous habits of hunter-gatherers and living chimpanzees and baboons is in the number of medium or large mammals that are killed by hunter-gatherers. Now, as the animal remains that have been found on the living floors of the early hominids are most frequently those of small or immature creatures, then, in view both of the proportion of meat in the total diet of chimpanzees and baboons, and the proportion of 'slow game' in the total diet of hunter-gatherers, it is unlikely that more than 5% - 10% of the early hominids diet - including such items as scavenged meat and the marrow and brains contained in long bones and skulls - was made up of flesh foods. Thus it was probably not until the development of more sophisticated hunting techniques in the Mid Pleistocene period which made it easier to kill relatively large and mature animals, that the amount of meat in the diet of man's direct ancestors increased to anything like the amount found in the diet of tropical hunter-gatherers living today. Such a conclusion is at least partially corroborated by the fact that the first definite evidence we have of the hunting and killing of larger game animals comes from the Bk II living site in Bed I at Olduvai Gorge, associated with Chellian man, and which probably postdates the early hominid living floors of Bed I by over one million years (Leakey).[20] From the available evidence therefore it seems fairly clear that the early hominids must have relied on vegetable items for most of their food, and that their technological skills may first have been used to extend the scope and variety of potential food sources other than meat. However in view of the fact that both baboons and chimpanzees, who are largely vegetarian feeders, will sometimes kill and eat small animals it is by no means unlikely that all the various early hominid forms were at least occasional predators, and further that the amount of flesh they consumed varied from one local population to another according to the particular feeding traditions of the group and the kind of habitat that they occupied.

The importance which many authors have attached to the evolution of a hunting way of life* often suggests, either overtly or by implication, that the development of flesh-eating habits were by themselves an important determinant of many of the characteristic social and behavioural features of man. However such a viewpoint seems to miss the essential reason for the evolutionary success of the human line, which has been in the application of flexible and relatively unstereotyped patterns of behaviour to the exploitation of a wide range of different habitats and furthermore that this behavioural adaptability has permitted man's ancestors to survive at times and in circumstances that would have been impossible for a more specialized animal. Moreover a definition of man's essential 'humanity' in terms of his success as a predator does not seem to recognize a) that even before the rapid increases both in brain size and cultural sophistication, members of the progressive human line were at least occasional meat eaters, and that their later exploitation of more varied meat sources was an adaptive shift to changing environmental circumstances in degree not in kind, and b) that many of the features which particularly distinguish man from the other primates such as bipedalism, manifold tool-using and tool-making habits, enlargement of the brain and permanent association of particular males to particular females, were already either completed or in process at the early hominid stage of evolution. To take but one example of the way most

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* See for instance Washburn and Lancaster's article on 'The Evolution of Hunting (1967).

scholars have emphasized the importance of hunting in man's behavioural and anatomical evolution, it has been suggested that pair bonds arose from the reciprocal food sharing behaviour of meat-laden males and vegetable-laden females. However, as I have argued elsewhere in this paper, the association of particular males with one or more females probably preceded the development of specialized hunting habits, and resulted rather from their particular ecological circumstances and the necessity of protecting females and their dependent children from possible predation than from the requirements of reciprocal food sharing practices. Moreover it is likely that the close association of males and females, and the lasting ties of friendship between primary kin, far from being the result of a hunting way of life, in fact pre-adapted the early hominids to the special requirements of a hunting/gathering ecology.

If the development of hunting behaviour in itself does not explain many of the more significant features of man's behaviour and anatomy, this does not imply that the adaptive exploitation of flesh foods was not an important factor in the progressive development of the human line, for in stimulating man's powers of technological invention, it permitted him to occupy a range of habitats that would have been impossible for a more specialized feeder. However, it must be emphasized that along with changes in his hunting technology and hunting skill, there were probably also significant developments in his gathering activities, associated not only with the use of a digging stick, but perhaps even with the collection of various vegetable foods that required some kind of preparation before being eaten. Indeed, it may be that adaptive developments in the gathering potential of early man were as important a factor in his successful exploitation of a savannah habitat, especially at times of decreasing rainfall, as developments in his hunting behaviour. Such a belief is supported by the fact that during the interpluvial periods the biomass of game animals in savannah or other open habitats would probably have decreased and animals would therefore have been harder to kill; at the same time the amount of suprasurface vegetable foods would also have decreased. Thus the gathering of subsurface roots, rhizomes and tubers and the seasonal exploitation of widely separated supplies of vegetables and fruits would have been as necessary to the survival of the early hominids as developments in their skill as hunters. The ecology of tropical hunter gatherers living in arid or marginal environments is especially relevant in this context, for they must perforce range over a wide area in order to collect sufficient vegetable foods to sustain them throughout the year. Moreover, while reduction in the biomass of game animals per unit area obviously requires them to exploit a large hunting territory, the widely scattered distribution of vegetables also requires them to exploit a large foraging area. Thus the dramatic increase in the size of area over which local groups will roam in arid or marginal environments as compared to other environments, such as forest or parkland, is as important a corollary of the availability of vegetable foods as it is of game animals. Increases in the size of the home range of the early hominids may therefore have been as much to do with the nature of their gathering activities as they were to do with their development of organized hunting.

In sum, in view of the differences that exist in the feeding habits of sympatrically living chimpanzees and gorillas it is likely that the different hominid types of the Early and early Middle Pleistocene periods were also differentiated in the nature and variety of food items they consumed, and that the more robust forms were perhaps more exclusively vegetarian in their feeding habits than the more gracile forms. However, as contemporary higher primate species also differ considerably from one local group to another in the food items they consume, depending both on the particular traditions of the group and the nature of the environment in which they are living, differences in the feeding habits of local populations of the early hominids would have been no less marked. Moreover it has been argued here that an omnivorous diet was characteristic of the progressive human line of evolution from a very early stage in its development - sic Kenyapithecus has been found in association with smashed mammalian bones (Leakey)[21] which appear to indicate that even at this stage, a variegated and partially carnivorous diet was a feature of man's very early hominid ancestors. Furthermore the success of the progressively more hominised forms of the Early and early Middle

Pleistocene periods in exploiting a savannah habitat during times of considerable climatic and geomorphic change was not solely a result of their developing skill as hunters, but rather their generalized ability to utilize a wide range of food items, including a greater variety of vegetable foods.

With respect to the particular cultural status of the early hominids, there now seems little doubt that all of them were at least tool-users, though whether all of them were tool-makers, and which forms were responsible for manufacturing the lithic tools that have been found on their living floors has yet to be clearly resolved. For instance, Leakey first assumed that the lithic tools discovered in association with the remains of Zinjanthropus were made by this creature,[22] though his later discovery of an advanced hominid form, Homo habilis, also in association with Oldowan tools at a slightly lower level than that at which Zinjanthropus was found, led him to revise his former opinion and claim that Homo habilis was in fact the tool-maker of Olduvai Bed I.[23] However examination of the lithic tools found on the Zinjanthropus floor has revealed that

> "the last made are less well made than the tools found at a much lower level at the place where the human remains represent the other type of creature (Homo habilis)*" (Leakey)[24]

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* Words 'Homo habilis' my addition.

Thus it may be that both these forms were lithic tool-makers, though with differing degrees of competence; on the other hand these differences may simply be the result of differences in individual skill, or of juveniles inexpertly attempting to copy the tool-making habits of their seniors.

The only lithic tools that have been found in South Africa come from Middle Pleistocene deposits at the Sterkfontein Extension site and at Swartkrans. Although there is no general agreement on who made these artefacts, as they have been described as early Chellian in type (Cole),[25] it is probable that a more advanced hominid form, possibly Telanthropus, was responsible for their manufacture. Oldowan-type tools have also been found in Early Pleistocene deposits at Ubeidiya in the Jordan Valley (Stekelis),[26] and here again it appears likely on the evidence of the associated hominid remains that their manufacturer was an advanced hominid belonging to the same taxon as Homo habilis. All the lithic tools that have been found in these sites seem to have been culinary objects rather than hunting weapons, and the assumption must be, therefore, that these early relatives of man were still relatively unsophisticated hunters, relying on their bare hands, or on clubs or stones to do most of their killing. Moreover, it is likely that these tools would have been most useful for cutting up the carcasses of larger animals that they had scavenged and in breaking open long bones and skulls for the marrow and brains that they contained.

The use and manufacture of various bone and horn tools have also been ascribed to the early hominids of this period, and Dart especially has championed the existence of a widespread osteodontokeratic culture among the gracile hominids associated with Early Pleistocene deposits in South Africa at Taung, Makapansgat and Sterkfontein.[27] However, although Dart's detailed statistical analysis of the various fossil remains at Makapansgat indicate that these remains were more than a haphazard assemblage of bones, and that there appears to have been some purpose in their collection, Oakley is

> "unable to accept any of the bones which I have examined from the Limeworks Breccia as showing any undoubted stigmata of having been used as tools or weapons."[28]

Moreover the only undoubted bone tool that has been discovered in Early Pleistocene deposits comes from Olduvai Gorge and is associated with the more advanced hominid, Homo habilis. At the same time, as Kenyapithecus, dating back some 14 million years, appears to have used a lump of lava to break open animal bones (Leakey),[29] there would have been ample scope and opportunity, during the period of time separating this very early hominid from the hominid forms of the Early Pleistocene, for them to have developed bone-using habits. Indeed one might imagine that these habits developed from the tendency of juveniles to pick up and play with animal bones left lying around after a meal and that this familiarity with the use of bones at the level of play may later have been extended to other behavioural contexts as well. There is then a fair probability that osteodontokeratic tools were used by various hominid forms at this time, though there may have been considerable differences in the skill with which they were modified for use, varying from finely worked bone tools such as the one found at Olduvai in association with Homo habilis, to the simple detachment of jaws, teeth and horns for cutting and scraping meat which may have been the limit of cultural sophistication attained by the gracile forms discovered in South Africa.

In view of the fact that the early hominids both used and manufactured bone and stone tools, and as living chimpanzees have been reported to use and even modify twigs and rocks in a number of different behavioural contexts, there is every likelihood that the bone and tool industries of the early hominids represent only a small part of their wider cultural and technical abilities. Thus it is likely that if they used stones to break open long bones and skulls, and cutters to dismember a carcass, that they also used digging sticks to assist their foraging for subsurface roots and rhizomes, and may even have invented string bags or other kinds of receptacles to further increase the special advantages of bipedal locomotion in the carriage of objects or food from one place to another.

In the light of the available evidence it appears fairly certain therefore that all the hominid forms of the Early and early Middle Pleistocene periods made and used a variety of wood and bone tools, though perhaps not all of them were lithic tool makers. Yet, whatever may have been the individual cultural status of the various hominids, there is little doubt that the more advanced forms, represented by Homo habilis in East Africa, and Telanthropus in South Africe, were the most culturally sophisticated and that they were responsible for manufacturing most of the lithic tools that have been found in the fossil deposits of this period.

Elsewhere in this paper, I have stressed the importance of behavioural and anatomical predisposition in the development of tool-using and tool-making habits among the protohominids, and especially of the importance of such generalized higher primate features as stereoscopic vision, manual dexterity, and the manipulation of objects, and of such particular hominid features as bipedal posture, a brain relatively though not absolutely larger than the great apes, and at least a power grip. However, predisposition is not sufficient in itself to explain the phenomenal development of tool-using abilities and of other social traditions in the progressive human line; such developments in skill must have been brought about by changes in the habits of the early hominids that were themselves brought about by changes in their environmental circumstances. With particular reference to the climatic changes of the Pleistocene epoch, obviously the successive pluvial and interpluvial conditions of tropical Africa and the broadly synchronic glacial and interglacial conditions of the northern hemisphere, must have been one of the most decisive factors in early man's increasing skill as a tool-maker, and that during the drier interpluvial periods especially, there must have been considerable selective pressure for the more efficient manufacture and use of tools in a wide variety of behavioural and ecological contexts. However the development of early man's abilities as a tool-maker took place over a relatively long period of time, and were the result of a complex series of selective interrelated changes in his anatomy, behaviour, social organization and ecology. In this regard, Lancaster has observed

> "an estimate of two million years of tool-use prior to hand-axe cultures and Homo erectus is undoubtedly conservative. This would mean that the stage of human evolution in which small brained men used pebble tools and walked bipedally lasted at least four times as long as have all the subsequent stages."[30]

The reasons for this very slow initial development in tool manufacture are related not only to the obvious anatomical (manual) and intellectual limitations of these early hominid forms but also to various limiting aspects of their ecology and behaviour. For instance, the development of general manipulative skills and tool-using habits is related to the amount of free time that an animal has to practice and develop these skills. Thus if a species spends most of its time either looking for or actually consuming food, it will obviously have little chance to develop manipulative and tool-using habits. The richer the natural environment in which a species is living and the less time it has to spend actually foraging for food, the more time it is going to have to play around with various objects and to develop a special facility in manipulating a variety of different objects in a variety of different behavioural contexts. Of special interest in this respect is Crook's observation that differences in the behaviour of proximate populations of doguera and gelada baboons appear to be related to differences in their food supply. He has written

> "The geladas, eating small objects of low apparent nutritional value, may spend up to 70% of their time at certain times of day, in getting their food. Doguera baboons, by contrast, which eat larger, more nutritious morsels mainly in woodland, spend comparatively little time feeding and much more time wandering about, manipulating objects and playing. This appears to account in part for their ability to learn complex habits - such as the removal of spines from leaves and fruit of Prickly Pear. They have time in which to educate themselves and the young have time to learn by observation. The more stereotyped gelada behaviour is imposed by its feeding economy."[31]

Again, with respect to the large apes, one of the principal reasons why chimpanzees have developed greater facility than gorillas in the manipulation and use of objects may be because of the nature and variety of their menu in comparison to the unexciting diet of the largely pith-eating gorilla, and the fact that fruits are far more stimulating objects to play with and manipulate than vegetable stalks and leaves.

From this point of view then euryphagous early hominid forms inhabiting a savannah or woodland savannah environment and eating a small but significant percentage of rich and nutritious food items such as bone marrow and brains and meat and fish would certainly have had as much time on their hands as the living large apes in which to experiment with and manipulate various objects. Why then the slow development in technological skills? There are a number of reasons for this of which perhaps the most obvious is that they had reached the limits of their physical and intellectual competence. Related to these limitations of body and mind is the factor of 'adaptive inertia', whereby once the early hominids had reached a favourable ecological balance in their exploitation of a particular habitat in conditions of environmental and social stability, selective pressures for increased intelligence and manipulative skill would have ceased to operate - or at least ceased to operate very dramatically. Another important reason must have been the actual nature of their society which was probably made up of small groups that only came together when there was a plentiful supply of food available in one area. Most of their time would thus have been spent foraging together for food in widely separated small communities that probably never exceeded a dozen or so members. Within these small groups individuals would probably have collected most of their own food, though there may have been some division of labour in which the females remained in protected places close to water where they could forage in relative safety while the males went off and scavenged meat from the carcasses of larger animals or did some simple hunting of their own. Whatever the facts of the matter, it is certain that there was little or no necessity for individuals to cooperate together either in hunting or in gathering food. The relative isolation and small size of these groups and the nature of their feeding habits would then have provided little scope or incentive to the development of more sophisticated tool-using and tool-making habits. However subsequent changes in the ecology of these groups which may have encouraged the formation of co-operative hunting parties and local bands perhaps two or three times as large as before, could well have stimulated early man's powers of invention, as also to have increased the chances of new skills being copied and improved by other individuals either of the same or of neighbouring groups. In short, as the scale and diversity of man's economic activities increased, so too did the scale and diversity of his culture.

The palaeontological evidence would seem to corroborate many of the details of this hypothesis. Thus the faunal remains associated with the early hominid living floors in Bed I at Olduvai indicate that while one or both of the hominid forms found at this level were meat eaters, their carnivorous diet was mostly made up of small or immature animals (Leakey),[32] Moreover from the size of the floors themselves and the distribution of tools over them, it is clear that the occupants were both few in number and transient in residence (Clark).[33] One might imagine therefore, that these lake shore living hominids lived in small nomadic groups, and that though they consumed a wide range of food items including fish, small mammals and reptiles, they subsisted mainly on individually gathered vegetables and fruits. There is certainly no evidence that any collective cooperation was required in the food quest. However, the later BK II and SHK sites at Olduvai associated with Chellian Man present a very different picture. The tools found at this level indicate that

> "artifactual material now occurs in greater abundance than previously, that there are more classes of tools in the assemblages, and that these show the beginnings of formalization in the types of tool. The same chopper-chopping tools, bashing stones and small irregular cores or polyhedrals occur as were found in Bed I, but now there appear also true polyhedral stones, a large number of flake tools, often with abruptly retouched edges, and the hand axe." (Clark)[34]

It is clear, therefore, that by this stage early man had become a far more proficient tool maker and that moreover the tools he made were both more varied and more functionally specialized than those associated with the earlier hominid forms of Bed I. If Chellian man was culturally more sophisticated than the earlier hominid forms, excavations at the BK II site reveal that he was also a more skilled and efficient predator and that he

> "hunted and killed large animals, which he probably drove into swampy and boggy ground and despatched by stoning and any other means open to him (Leakey 1958). These animals were, moreover, cut up and

> eaten at the site of the kill where the implements for doing this were also manufactured, as can be seen by the abundance of tools and waste littering the banks of the gully where the game had been trapped. Such a method is used in Africa up to the present day and, to be successful, demands group action (Smith,1920).* It indicates, therefore, that Chellian man was already a reasonably accomplished and communally organized hunter, which would seem to imply a considerable intellectual advance over the earlier and basic cultural stage." (Clark)[35]

Thus, from the evidence of the living floors at Olduvai Gorge, it is apparent that there were marked differences between Chellian man and the earlier hominid forms in social organization, cultural attainments, and eating habits (as reflected, for example, in Chellian man's killing of larger game animals) and moreover that these differences were probably the result of changes in the environmental circumstances of man's early relatives that caused them to change their habits in the direction of larger groups, and the collective hunting of game. Subsequently these changed habits would have encouraged the selection of anatomical modifications for increased skill in the manipulation manufacture and utilization of objects, whether for tool-using or weapon using purposes.

To conclude. In this paper, I have attempted to appraise certain aspects of the behaviour and ecology of the Early and early Middle Pleistocene hominids in the light of the available written evidence from

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* SMITH, W.E., and DALE, A.M., 1920, The Ila-Speaking Peoples of Northern Rhodesia, London:MacMillan.

both comparative and direct sources. While there are many obvious limitations to such an approach, it is to be hoped that at least some idea has been given of the possible nature and circumstances of these early relatives of man. Moreover, in spite of the many uncertainties that still surround certain features of their behaviour and ecology, as also their precise place and significance in the evolutionary history of man, it is clear that in many respects they are far closer to man than they are to the living apes; it is perhaps reasonable therefore, as some scholars have done, to include them along with the later hominines and modern man in the genus Homo. In their possession of a relatively large brain, habitual erect posture, and generalized tool-using and tool-making abilities, they are in many ways a less proximate link with man's more remote hominoid ancestors than was previously believed, and it is to still earlier forms that one must look in order to find those incipient changes in behaviour and anatomy that started man's early relatives on the path of their subsequent and highly successful evolutionary development.

Man's emergence as a super species is directly related to the fact that at certain critical points in his evolutionary history, he has been sufficiently unspecialized anatomically and sufficiently adaptable behaviourally to change his habits to suit the new circumstances and potentialities of his environment. He is, as Morris has observed, the supreme opportunist from a family of opportunists.[36] At the same time he has also had the luck to be in the right place, at the right time, with the right behavioural and anatomical characters, and no more so than at the beginning of the Pleistocene epoch when, as man emergent, he was sufficiently well advanced intellectually and sufficiently well equipped anatomically to be able to adapt his behaviour to the changing circumstances of his environment, and so to become, through successive stages of hominisation, man transcendant.

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