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On the Evolution of Tool-Using Behavior¹

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New archeological discoveries from the Lower Pleistocene in Africa, the advent of radiometric dating techniques, and recent observations on the behavior of free-ranging nonhuman primates can be combined to provide a fresh perspective on the evolution of tool-using behavior. The Lower Pleistocene in which relatively simple Oldowan tools are associated with small-brained forms lasted over two million years and represents over 80 percent of human history. These discoveries suggest that tool-making and tool-using are behavior patterns that emerged much more slowly in the course of human evolution than was previously thought.

THIS paper directs attention to the theoretical importance of recent discoveries and observations—especially those in primate field studies—to the interpretation of the fossil record. It is intended not as a review but simply as a discussion of the implications of recent developments.

TIME AND THE NEW METHODS OF DATING

The estimate of the amount of time occupied by the Pleistocene has steadily increased. In 1932 Keith thought that the Pleistocene might have lasted 200,000 years and the Pliocene an additional 250,000. Then for a long time the Pleistocene was estimated at one million years and the Pliocene ten times that long (Zeuner 1959). According to that view, the Pleistocene was divided into two approximately equal parts: the first 500,000 years contained at least some very simple tool traditions, but these were of uncertain date and duration; the second 500,000 years spanned three glacials and contained all the tools of the Acheulian and later tool-making traditions. With the advent of potassium-argon dating, now partly supported by the fission-track method, radiometric dates rather than relative estimates could be given for these two parts of the Pleistocene (Butzer 1964, Evernden and Curtis 1965, Fleischer *et al.* 1965). The dates and duration of the last part of the Pleistocene have not been greatly altered but the early part has been radically extended in time. The new radiometric dating suggests well over two million years ago as a probable date for the Pliocene-Pleistocene boundary, but keeps 700,000–500,000 B.P. as

likely for the onset on the First Interglacial period (Table 1). Two million years ago, according to Evernden and Curtis (1965), is a minimal estimate for the start of the Pleistocene and it may well have begun more than three million years ago. Estimates of the extent of the Lower Pleistocene, especially of the earliest part, the Villafranchian, have been the most radically affected by radiometric dating. The Villafranchian, which was once considered a relatively brief period preliminary to the major events and time spans of the Pleistocene, is now seen as lasting perhaps 2.5 million years and comprising three quarters of the total length of the Pleistocene.

While the radiometric chronology of the late Tertiary and Pleistocene stratigraphic unit is not finally settled, it is very clear that the time spans involved in the early stages of the Pleistocene have been seriously underestimated in the past. Geophysical age determinations indicate the need for a radical revision in our conception of the rate of development of tool-using abilities and techniques and in our understanding of the interrelation of tool types to the biology of their makers. At Olduvai Gorge, chopping tools, trimmed and utilized flakes, polyhedral “flaked” stones, and other utilized stones are found near the base of Bed I in layers dated between 1.9 and 1.75 million years (Evernden and Curtis 1965, M. D. Leakey 1966). From these same stratigraphic levels fossils of two distinct hominid forms have been recovered. Regardless of the ultimate classification of the hominid forms found in Bed I, there are none with large brains. Tobias’ most generous estimate for the cranial capacity of the juvenile parietal fragments is still only 725 cc. His more conservative estimate is 670 cc. (Tobias 1964).

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TABLE 1. CHRONOLOGY OF THE PLEISTOCENE
(After Butzer 1964, Evernden and Curtis 1965)

Upper	Third Interglacial (Eemian)	100,000 B.P.	
Middle	Second Interglacial (Holstein)	255,000 B.P. or more	
	First Interglacial (Cromerian)	700,000–500,000 B.P. 1,000,000 B.P.	Acheulian and later traditions
Lower	Villafranchian	2,000,000 B.P.	Oldowan tools
	(Early Villafranchian?)	3,000,000–2,500,000 B.P. ???	

The Oldowan industries from Bed I are at present the oldest radiometrically dated stone artifacts, but they need not necessarily represent the very beginning of stone flaking traditions, which we can expect to extend to perhaps a quarter to a half million years earlier. At Olduvai these industries persisted into the time of deposition of the lower part of Bed II, while in upper Bed II early handaxe industries occur.² The age of the transition from Oldowan to Acheulian has not been directly determined at Olduvai³ but archeological and faunal correlations can be made with other strata for which geophysical data indicate an age of between 700,000 and 500,000 B.P. (Isaac 1965). The elementary stone techniques and poorly standardized tool-making tradition of the Oldowan appears in East Africa to have lasted at least one million years and quite probably for more than double that time with little change or advance in their manufacture or in the biology of their makers. We can assign a time span for Oldowan tools from probably earlier than 2,000,000 B.P. up to 500,000 B.P., the time when the first hand-axe cultures and the remains of larger-brained men classified as *Homo erectus* began to appear. The only possible makers of the Oldowan tools are small-brained forms (*Australopithecus*, in the broad sense).

There is reason to think that Oldowan tools were used for much longer than the 1.5 million years that passed between the lowest levels of Bed I and the beginning of the European First Interglacial period. Tools similar to the Oldowan may also date from the same or an earlier period at other African sites, such as Laetolil, Omo, Kanam, Ain Hanech, and elsewhere (Cooke 1963). Furthermore, the small

incisors and canines of *Australopithecus* suggest that members of this genus had been using tools for a very long period of time and that the use of tools had almost entirely relieved their dentition of the functions of food getting and self protection. 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. The early part of the evolution of stone tools and of man must have proceeded at a rate very different from the later stages and advances must have come very much more slowly.

To summarize to this point, the archeological discoveries from Bed I in Olduvai Gorge and the advent of new dating techniques have radically altered our conceptions of the duration of the early, primitive stages of tool using and tool making. The natural assumption has always been that tool use was so highly adaptive that once it had been firmly established as part of the normal behavior of the species the pace of evolution quickened immediately. Advances were assumed to have come in rapid succession as the brain, tool-making techniques, and cultural traditions interacted in a mutually stimulating feedback relationship. Events of the past, however, apparently did *not* move this rapidly, at least not in the beginning.

TOOL USE BY THE AFRICAN APES

In the same years that discoveries at Olduvai Gorge and advances in the techniques of radiometric dating were being made, field

workers were making new efforts to study the behavior of contemporary monkeys and apes in their natural habitats. Most of these modern field studies report very little object-manipulation in nonhuman primates except that directly involved in feeding activity (Hall 1963b, Menzel 1966). In feeding, nonhuman primates will turn over rocks, probe fingers into holes, and pull off bark or shells in search of food, but even here they are only manipulating objects and not using tools. In contrast to the findings of field workers on other primate species, Goodall (1964) has found that tool use in the chimpanzee is an important behavior pattern. Goodall (1962, 1963, 1965) over a period of six years has observed the behavior of a single population of approximately 60 free-ranging chimpanzees in the Gombe Stream Reserve in Tanzania. There can be little doubt now that tool-using performances by chimpanzees excel those reported for all other animals except man in both variety and complexity. They are also very close to man in many other measures: anatomy of the body, serum proteins, chromosome number and form, and dentition. Therefore it is not surprising that chimpanzees are closest to man in some aspects of behavior as well.

It may well be that further observations on the behavior of gorillas in the wild will produce evidence of tool-using behavior paralleling the performances of the chimpanzees. Schaller (1963) with 500 hours of observations of the behavior of the mountain gorilla reported that he never saw gorillas use or show interest in objects except vegetation for nest building and for throwing in aggressive display. The aggressive display of the gorilla is a highly stereotyped sequence of behavior patterns that usually includes the throwing and tossing of vegetation just before a running charge (Emlen 1962, Schaller 1963). Many of the same elements, including the throwing of vegetation followed by a charge, constitute the most essential parts of the chimpanzee aggressive display. At least in this one context both species show a strong tendency to manipulate and throw objects. It should be noted that what appear to be species differences in behavior between chimpanzees and gorillas may in part merely reflect Goodall's unique long-term observations; in the first year of her study she only saw one kind of tool use, termiting. Moreover, there may have been important ecological differences between the two study areas. Schaller worked in a region of lush

evergreen vegetation of herbs and vines, where rocks, sticks, and other hard objects were rare. Food plants were abundant and everywhere at hand. The feeding pattern of the gorillas was simply a leisurely grazing through the lush vegetation. In contrast, the Gombe Stream Reserve includes valleys of dense gallery forests and higher points of open woodland and grassy slopes where wood and stone are readily available materials. Food items are often seasonal, concentrated, and hard to get. The chimpanzees make an effort to locate and to gather their food; this is exactly the sort of situation where tool use in food getting might be likely to appear. Finally, the behavior of young gorillas in captivity is very similar to that of young chimpanzees in their interest in and manipulation of objects (Schenkel 1964, Glickman and Sroges 1966). In captivity both chimpanzees and gorillas spontaneously learn to throw dirt and food with considerable accuracy at visitors.

Goodall's most remarkable observations of chimpanzee tool use are of the use of twigs and grass blades for "fishing" ants or termites out of their nests. She has collected more than 1000 of these tools and on over a hundred occasions has observed actual termiting. Chimpanzees are very efficient in getting the termites. The animal takes a piece of twig and puts it in the termite hole where the insects seize the end of the stick with their mandibles. The chimpanzee then takes it from the hole and leisurely eats the termites that are clinging to the tip. Not only do the chimpanzees use these twigs very effectively as tools but they also will frequently improve the bit of twig or grass before using it. The animal will break off a piece of vine or a twig and prepare it by stripping away any side branch or leaf that might get in the way and by breaking it to the appropriate length, which differs by a foot or more for anting as opposed to termiting. There is much individual variation in the skill and care with which a tool is made. Some animals will take nearly anything at hand; others will search carefully for just the right piece and then spend some time in preparing it. A few prepare a little pile of stems before starting to termite and some make the twig even before a nest is found. Goodall saw one male carry a termiting twig in his mouth for more than half a mile while he went from nest to nest looking for one that was ready to work.

The actual grip used to hold the twig for

termiting is standardized among adults who hold it between the thumb and the side of the bent index finger (Goodall, personal communication). Infants who have not fully mastered the adult technique may grip the tool using only four fingers and not using the thumb at all. Chimpanzees are ambidextrous in their termiting; all animals can use either hand although there may be some individual preference for one hand over the other (Goodall, personal communication). This absence of handedness may be indicative of the limitations that the chimpanzee's brain places on its ability to develop highly skilled tool use. By human standards these termiting movements and other kinds of tool-using behavior in chimpanzees always appear clumsy, like the use of tools by a human child. Tool use is learned by the chimpanzee, improves with practice, but never develops the deftness either of human skill or of highly stereotyped innate motor patterns.

Goodall was fortunate enough to observe a one-and-a-half-year-old female in the process of learning how to use the termiting twig. The infant's technique was imperfect. She made tools that were too short to more than just enter the hole; the longest was only two inches whereas the adults always use 6- to 12-inch twigs. The infant's motor patterns were imperfectly coordinated and sometimes she would jerk the twig out of the hole so quickly that the termites were knocked off. Her attention span was very short as well; she would termite for a few minutes and then break off to play. In contrast, adults often work with great concentration for more than an hour without stopping. Goodall also observed that young animals try to termite out of season in what may have been a form of play activity. She is convinced that much of the ability to termite is learned by young animals by observing the adult technique and then practicing it. She often saw infants intently watching an adult termiting and then, when the adult had moved off leaving the twig or grass blade by the nest, the infant would pick up the abandoned tool and try termiting too.

Chimpanzees are not the only primates that like termites, and Goodall has seen baboons near chimpanzees while they are at work. Baboons are eager to eat termites, but they have never been observed trying to fish for termites themselves. The baboons do occasionally watch the chimpanzees termiting but not as intently as do young chimpanzees who will

peer at working adults for minutes at a time (Goodall, personal communication).

Termiting is a seasonal activity, coming just before the termites begin their nuptial flights, which occur about eight times for each termite heap over a period of four months or more during the rainy season. During most of the year the termites are protected by a concrete-like shell that covers their nests, but for the flights the workers tunnel out to the surface. After each flight, the holes are sealed over until the next. Chimpanzees are able to scratch off the thin covering at the end of the tunnel and thus, by using the fishing technique, are able to eat termites throughout the entire season. Birds, monkeys, and other animals can feast on the termites only during the actual flights. The simple technique of fishing for termites assures the chimpanzees of a protein-rich diet for several months out of every year without competition from other species, and the inability of the baboons to imitate the chimpanzee behavior robs them of the extra protein.

Termiting is only one example of tool use by chimpanzees. Goodall saw them make sponges for dipping water out of crevices and boles of trees that were too small to let them put their faces down to the water. They would take a handful of leaves, chew them slightly, dip the wad into the water and then suck it. Goodall tried the same thing and found it seven to eight times more efficient than the technique used by many nonhuman primates of dipping the hand or fingers into water and letting the water drip into the mouth. Besides using leaves as sponges for drinking water, chimpanzees use them to wipe water or dirt from the body or sticky substances from the fingers. This use of objects to groom the body is more unusual than it seems. Although some species of bird are known to rub ants in their feathers as a part of grooming and elephants sometimes use objects to scratch themselves, man is the only animal reported to habitually use objects in grooming (Hall 1963b).

One other way in which chimpanzees use objects as tools is in aggressive display (Kortlandt and Kooij 1963, Goodall 1964). This behavior is particularly interesting because it suggests that tools for defense may have been developed just as early in man's history as tools for foodgetting. Random throwing of objects—anything that comes to hand such as stones, sticks or other vegetation—is a common element in the excited displays

of many primates, and chimpanzees are no exception (Hall 1963b). They tend to throw things when meeting other groups after a separation or when being annoyed by baboons (and probably by predators, Kortlandt and Kooij 1963). Sometimes an animal will even take some care in aiming the object; instead of just tossing it into the air, he will throw it toward the animal at which the display is aimed. Goodall saw chimpanzees aim and throw stones, both overhand and underhand, at baboons and at humans as part of such a sequence of aggressive display. This behavior pattern is significant because, as Washburn (1963b) has pointed out, it suggests the possible first steps in the evolution of weapons. If an animal is displaying to intimidate an aggressor, object throwing as a part of that display is effective whether he hits the other animal or not. If the total display is not intimidating enough, the chimpanzee is still able to flee or to fight with his canines. It is easy to imagine how the ability to develop skill in aimed throwing of sticks and rocks could gradually evolve until it became so effective that the creature need no longer rely on his canines. Only then would the selective pressure on large canines be relaxed and a behavior pattern, defense with weapons, could ultimately replace the behavioral and morphological pattern of defense by fighting with canines.

These examples of tool use in chimpanzees, when taken together, provide a good starting place for answering questions about how and why tools were used by man's earliest ancestors. It is true that some birds and other mammals use tools, but in any one tool-using species there is likely to be only one kind of tool. There is no nonprimate that uses such disparate objects as termiting twigs, leaf sponges, and stone projectiles. And, conversely, in the chimpanzee there is no single, highly evolved, stereotyped sequence of movements of the sort common in other vertebrate tool users such as the deft twist of a cactus spine used by finches to dig grubs from bark or even the much more complex but still relatively stereotyped patterns of nest building found in many mammals. In the chimpanzee there is a far more generalized tendency to manipulate objects and to use them in many different situations. And, if Goodall is correct, these different ways to use tools constitute a tradition based on biology but trans-

mitted from adults to young by observational learning and practice.

Chimpanzees use tools in an impressive number of different situations, when they are compared with the rest of the animal kingdom in this respect (Hall, 1963b). By far the most common types of tool use in vertebrates are in feeding behavior or in preparation of nests or dens. The use of objects in self-grooming is almost unknown in animals and in aggressive display it has been observed only in monkeys, apes, and man. Goodall's single population of chimpanzees performed more complex kinds of tool use, and in a wider variety of situations, than has been observed for any other animal; that is true even though tool use is a very small part of their behavior repertoire and is a comparatively rare event. This small group of apes over a period of a few years was seen to use tools in agonistic display, in aimed throwing, in a variety of food-getting situations, in drinking, and in self-grooming. Perhaps the making of nests or sleeping platforms should be included in this list too, since it is very similar to these other forms of tool use in that objects are manipulated and modified to perform some important activity better—in this case the nest is a tool for sleeping.

CHIMPANZEE LEARNING OF TOOL-USING TRADITIONS

It would be interesting to know why chimpanzees seem to be able to learn the use of objects more readily than do many other primates. There are important biological limitations on learning abilities that vary from species to species and do not reflect differences in intelligence so much as differences in specialization. Hall (1963b) has argued that in themselves tool-using performances give no indication of relative intelligence. A finch that uses a cactus spine to extract grubs is no more intelligent than other finches; the species has simply evolved a behavioral pattern rather than a morphological pattern to aid in its feeding. Nevertheless, chimpanzees do have large brains and the great apes have a much longer maturation period than do other non-human primates; certainly both these characteristics are related to greater learning abilities.

Undoubtedly there are many factors that contribute to the ontogeny of such an important adaptive pattern as the use of objects as

tools. Schiller (1957) and more recently Chance (1960) have emphasized the importance of certain motor patterns occurring in the tool-using performances of captive chimpanzees that appear to be largely determined by heredity and that require only the opportunity for play for their perfection. For example, the tendency to manipulate sticks, to lick the ends, and to poke them into any available hole are responses that occur over and over again in captive chimpanzees. These responses are not necessarily organized into the efficient use of sticks to probe for objects but they probably form the basis of complex motor patterns such as termiting.

Certain kinds of human-like tool use such as overhand and underhand throwing are easier for an ape than for a monkey. The anatomy of the shoulder girdle of man and the apes enables them to throw or toss objects using powerful movements, something which is much more awkward and difficult for a quadrupedal monkey (Washburn and Jay 1967). In contrast, differences between chimpanzees and monkeys in manipulative abilities of the hands are based not so much on anatomical differences in the forelimbs as on the brain and the ability to learn different kinds of object manipulations. The hands of monkeys and apes are equally suited to picking up a stick and making poking or scratching movements with it but differences in the brain make these much more likely behavior patterns for the chimpanzee.

Another factor, one that may be just as important in tool use as genetic tendencies toward motor patterns, is the degree to which chimpanzees can learn by observing the activities of other animals. Hall (1963a) has emphasized that observational learning is rarer in nonhuman primates than one might expect and that the ability to learn in this way varies tremendously according to the task to be learned and the context in which this learning takes place. Monkeys and apes seem to have greater abilities in this direction than do most other mammals, and Hall has suggested that these abilities are most often demonstrated when the animals are in the relaxed, protected atmosphere of a social group formed of animals linked by close affectional bonds. This is a situation that is common in the natural environment of monkeys and apes, but it is rarely duplicated in the laboratory. Monkeys and apes learn emotional attitudes,

such as fear of particular objects or situations, with great ease from other group members as might be expected in animals for which group life is an important adaptive mechanism (Hamburg 1963).

Other, more complex kinds of observational learning in monkeys and apes are much more rare. Frequently the activities of one animal will stimulate another animal to do the same thing, but this sort of social facilitation is often merely a matter of a focusing of the attention of the second animal on a stimulus that then elicits a parallel response. For example, Hall (1963a) reported an experiment in which a young baboon, raised in captivity, was released near a wild troop. The young animal had been fed the diet of a pet and was unfamiliar with the wild foods of the area in which it was released. It learned how to dig for bulbs and roots by watching the other animals closely and then going over and digging beside them, but, as Hall emphasized, it did not learn how to dig, but rather where and for what to dig. The ability to mimic a novel motor pattern demonstrated by another animal has not conclusively been shown for any nonhuman primate except the chimpanzee. Studies of captive chimpanzees (Köhler 1925, Yerkes and Yerkes 1929, Hayes and Hayes 1952) point toward their considerable abilities in all the forms of observational learning mentioned above, ranging from the simpler kinds of attention focusing to something that must be genuine imitation of novel motor patterns. It is likely, then, that both these factors—the existence of simple hereditary motor acts that form the basis of more complex motor patterns of tool use and the ease with which one chimpanzee can learn by observing the activities of another chimpanzee—play important roles in the development of tool-using traditions within local populations of chimpanzees.

Tool-using behavior by chimpanzees is remarkable in the multiplicity of forms it takes, but it is very different from human use of tools in degree if not in kind. Chimpanzees, like men, both use and make tools, but man's brain is highly evolved and highly specialized to learn many different skilled uses of objects. For a species to depend on tool use as a way of life—for obtaining food and for defense—such tool use must be skillful. A spear has to be thrown just as skillfully as a baboon wields its canines in fighting, or the behavior pattern

could never replace the morphological pattern in agonistic situations. Skill is a matter of evolutionary changes in the brain that do not fossilize. There are really only two indirect lines of evidence of skill from the past: (1) relative brain size of the tool makers and (2) the tools themselves, in the techniques by which they were made and in the complexity and specializations of the tool assemblages. The specializations of modern man's brain that allow him to learn many different skilled uses of tools may have come relatively late in the history of tool use, perhaps not until *Homo erectus*, when the rate of change in tool traditions became so rapid and when a major increase in cranial capacity occurred. The slow pace of evolution in tools and in their makers before that time may well reflect a lack of ability to use them skillfully.

The tool-using behavior of chimpanzees suggests the kind of ape ancestor that might be postulated for the origin of the hominid line—an ape that used tools for many different reasons and in many different ways, no matter how insignificant the tool, like leaf sponges, or how undramatic, like termiting twigs, or inefficient, like a clumsily swung stick. The more kinds of tools this ape used the more likely his ancestral role, because it would have been the accumulated influence of many reasons for using tools and many ways of using them that would have taken selective pressure off the specific situation, the specific tool, and the specific movement. Selective pressure was put on a hand that could use many tools skillfully and on a brain capable of learning these skills. Natural selection would then have acted upon a broader category of behavior, one involving the brain, the hand, many objects, and a wide variety of social and ecological situations and problems. The evolution of skilled tool using marks a major change from the kind of tool use that is incidental to the life of a chimpanzee to the kind that is absolutely essential for survival of the human individual.

PROBLEMS OF INTERPRETATION IN THE EVOLUTION OF TOOL USE

Chimpanzee tool-using behavior raises the question of how many millions of years of this sort of casual tool use and object manipulation by apes has existed. It also raises the problem of whether the ancestors of chimpanzees and man used tools before their separation or

whether tool use evolved independently in the two species. Any reconstruction of evolutionary events can be guarded against the possibility of parallelism and convergence only by an evaluation of the degree of similarity between two species in as many different and unrelated systems as possible. The greater the number of similarities that can be found, in as many unrelated biological systems as possible, the higher the chances that one is dealing with true genetic affinities between species and not superficial similarities due to parallel evolution. A large number of such similarities between two species also suggests a shallow time depth of separation in which minor and random differences have not had a chance to accumulate.

Anatomical affinities between man and the apes have long been recognized both in dentition (Le Gros Clark 1962) and in the anatomy of the shoulder girdle (Grand 1964, Washburn 1963a). Washburn (1963a) noted that similarities between man and apes in the shoulder girdle involve fine details in a series of highly specialized modifications of the shoulder, elbow, and wrist joints. The full complement of these modifications was not present in the apes of the Miocene and may not have been established until the Miocene-Pliocene border, perhaps 13 million years ago. Washburn argued that man is likely to have separated from the African apes sometime in the early Pliocene, perhaps several million years after the establishment of a modern shoulder girdle in the family Pongidae.

The number of similarities between man and the great apes is extremely impressive. Besides the affinities in dentition and the anatomy of the shoulder girdle mentioned above, man is closer to the great apes than to any other animal in susceptibility to special kinds of viral disease (Hsiung, Black, and Henderson 1964), in blood groups (Franks 1963), and in the glands of the axilla, the form of the hair follicles, the chemicals found at the ends of nerves, and many other details of the skin (Montagna and Ellis 1963).

The African apes are often specifically cited as being the most similar to man and the orangutan has never been mentioned as being closer to man than are the African apes. In respect to chromosome number and form, the chimpanzee is almost identical to man with only one extra set of acrocentric chromosomes (Klinger *et al.* 1963, Chiarelli 1962). Dunn

TABLE 2. CHRONOLOGY OF THE EVOLUTION OF TOOL-USING BEHAVIOR

GEOLOGICAL TIME DIVISIONS	RADIOMETRIC AGE ESTIMATES	TOOL-USING SPECIES OF PRIMATES	TYPES OF TOOL-USING TRADITIONS
Pleistocene	700,000-500,000 B.P.	<i>Homo erectus</i> (1 species only)	Hand axe and later traditions
	2,000,000 B.P.	<i>Australopithecus</i> (more than 1 species)	Oldowan industries
Pliocene	13,000,000 B.P.	Pongid and Hominid (many species)	Unskilled, ape tool use (hypothetical)

(1966) compared the internal parasites of man and apes and found that man and the African apes shared in common a much greater number of species of parasites, especially the host-specific ones, than do the Asiatic apes and man. Man living in the tropical forests of Southeast Asia shares many more species of helminths with African apes than with the Asiatic apes who are living in the same forest. Thus even when sharing his habitat with the Asiatic apes, man carries the internal parasites of the African apes. Goodman (1963) came to the conclusion that man and the African apes are so similar in their serum proteins that *Pan* and *Gorilla* should be classified in the Hominiidae, whereas *Pongo* should be left in the Pongidae. Other workers on primate hemoglobins (Zuckerkanndl 1963, Buettner-Janusch and Buettner-Janusch 1964, Hafeigh and Williams 1966) agree on the close affinities between man and the African apes as opposed to the Asiatic apes but do not take such an extreme taxonomic position. Sarich (1966) in a quantitative assessment of differences among the apes and man in serum albumins and gamma globulin found that man was very similar to the African apes and much less closely related to the Asiatic apes. The order of magnitude of these differences suggested a separation between man and the African apes going back perhaps 8 million years and a common ancestor for all modern apes and man coming from the Miocene-Pliocene border. There is no reason to think that all the different biological systems mentioned above are either genetically or functionally linked. Thus, an evolutionary change in one of these systems should not necessarily involve corresponding changes in the others. So many similarities between these systems can only be interpreted

as reflecting close genetic relationships between man and the African apes, a relationship in which the time of separation is small enough that minor or random differences have not had a chance to accumulate.

The lack of divergence in many different systems strongly supports the idea of an end of the Miocene or early Pliocene (but no earlier) division between man and the African apes, somewhere on the order of 10 million years ago. If this is so, then it may be worth considering the possibility that casual, unskilled tool use might have been typical of many species of apes during the Pliocene. It should be remembered that the late Miocene and early Pliocene represent a time when apes were abundant, diverse, and widely spread over much of the Old World (Simons 1963a, 1963b). Fossil apes have been found in Europe, Africa, India, and China—a much larger geographical distribution than that of the modern apes, which live only in restricted areas of Africa and Southeast Asia (Simons and Pilbeam 1965). The number of different forms of apes was also much greater than today. From a single site, Rusinga Island in Lake Victoria, there are at least two species from the genus *Dryopithecus* as well as one or more species of gibbonlike apes. The modern apes are only remnants, survivors of a time when the family was highly successful and diverse. Table 2 suggests that a kind of unskilled ape tool use continued without major changes for millions of years and has continued down to the present in one or more of the surviving, descendant species of ape.

The onset of the Pleistocene witnessed the emergence of perhaps one or more forms of bipedal hominid that, although possessing relatively small brains, had come to rely on

tool use for much of their food getting and defense. Clearly, specializations in the hand and especially the thumb (Napier 1962), the reduction in the canines and incisors (Robinson 1963), and bipedalism (Napier 1964), all point toward the importance of tools to their way of life. Both the small brains and the tools themselves suggest a lack of skill in the way these tools were made and used. These hominids of the Early Pleistocene should not be thought of as merely forms transitional to man. They were highly successful, judging by their wide geographic distribution, and they lasted without major changes in either anatomy or tool traditions for a long time, perhaps 2.5 million years. Then, about half a million years ago, a rapid rate of evolutionary development in brain size and complexity of tool assemblages seems to have begun. This later period is associated with the emergence of a single species of tool user, *Homo erectus*, dominating much of the Old World. Remnant species of ape also survived but with quite restricted geographic distribution. Perhaps a new efficiency in the skilled use of tools effectively closed the niche to competition. It probably left no room within the broad niche created by tools for separate species to develop specialized applications. Any possibility for different kinds of tool users—perhaps an open savanna, a woodland, and a forest form (a possibility that may have been realized in *Australopithecus* during the Early Pleistocene)—disappeared and a single species of Hominid, using various tool traditions, spread across the Old World. The increase of efficiency and skill with which tools were used, a trend that probably began in the early Pliocene, may well have been associated with a gradual decrease in the number of primate species able to command a portion of the niche open to tool users. At an early, inefficient stage many species may have tried using tools with variable degrees of success but, as skill and efficiency increased, the competition between tool-using species also increased and the possibility of many forms sharing the niche disappeared.

SUMMARY

Our conceptions of the conditions under which tools first evolved have been radically altered by recent archeological discoveries, new methods of dating, and primate field studies. All point toward a single conclusion—

that in itself tool use does not cause a major change in the history of a species. Man is not the only primate to use tools and probably many species of ape have in time past used tools to some degree. The new radiometric dating by potassium-argon and fission-track methods indicates that the Early Pleistocene lasted for at least 2.5 million years and that during that time small-brained men used simple tools with little change or advance. The rapid acceleration of cultural advances, once traditionally thought to be a natural consequence of tools of any sort, came late in the history of tool use and was probably associated with specializations in the human brain that allowed the skilled use of many different kinds of tools. This evolutionary advance occurred in only one genus and species, *Homo erectus*, that preempted the entire niche once open to a number of different kinds of tool users. As Oakley (1954) argued some years ago, it is the skill with which man uses his tools that best reflect man's specializations for a human way of life.

NOTES

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² The early handaxe industries are designated Lower or Early Acheulian, the term Chellean having been abandoned by workers in many parts of Africa (Biberson 1961, Mason 1962, Leakey and Leakey 1965).

³ There is only a single sample from Olduvai for which dates ranging from 500,000–300,000 B.P. have been published (Hay 1963, Evernden and Curtis 1965).

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