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Recognizing the Emergence of Man

Specific courses of action are necessary for identifying the traces of early man.

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A familiar portrait of early man depicts a bipedal primate who is clutching a fashioned stone in his hand while peering into the distance in search of game. If this portrait is taken as a paleoanthropological model, the demonstration of the presence of early man requires a situation where the bones of a bipedal primate and worked stone are found in the same context in an appropriately early geological setting. Since early man was a hunter, the leavings from this activity should ideally be found in close proximity. The simultaneous occurrence of man, tools, and extinct animals is so unusual that the portrait model strains the potential of the fossil record. It is a wonder that enough approximations to the ideal were found to convince 19th-century scientists of man's antiquity.

In the search for early man it is much more reasonable to expect to find stone and no bone at all. The explanation for this is clear. Bone, being much less resistant to the agents of natural decomposition, fades from the record at a much faster rate than stone does. As one goes back in time, the amount of bone relative to stone becomes infinitesimal. Even if the time factor is ignored, one expects to find more worked stone than individuals responsible for the work, for an individual must have shaped more than one implement, and the implements he made were probably shaped and eventually discarded or lost in many places.

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Without doubt, stone tools are the most abundant evidence of the presence of early man; when found in an ancient deposit, they alone are sufficient to indicate his presence. But here a difficulty arises. Stone is ubiquitous in the world; purposefully shaped stone, as compared to stone shaped by natural agencies, is rare. The farther back in time, the more unsophisticated and the closer to natural forms the forms created by man are likely to be. How to recognize the very rare purposefully shaped stone in the midst of stones shaped by natural agencies is an unsolved problem for those seeking the traces of early man. The question "When does man appear?" is answered whenever early man's products are recognized. Our concern here is with the means of accomplishing such recognition.

The problem of determining whether a group of stones was or was not purposefully shaped first arose in 1867 when Abbé Louis Bourgeois asked if certain flints or eoliths from Tertiary deposits could have been shaped by early man. The difficulty in solving the problem is best expressed by an anonymous Frenchman, who is reported to have said (*1*): "Man made one, God made ten thousand—God help the Man who tries to see the one in the ten thousand." The importance of the problem, however, has become evident only in recent years, as tools have taken on new significance for understanding the emergence of man.

At one time it was believed that, after numerous fossil primates had been discovered, a discontinuity in brain size would become apparent. This discontinuity, it was thought, would make it possible to separate the earliest hominids from other primates. Many primates have now been excavated, but no gap—no celebrated Cerebral Rubicon—has been located in the fossil record. On the contrary, the first bipedal tool-wielding primates appear to have had brains well within the normal size range for contemporary gorillas (*2*). If tools precede the enlargement of the brain—in particular, the full development of the cerebral cortex—then *commitment* to tools for survival must be the novel adaptive design that accounts for the quantum change to man. Thus, to retrieve and study early tools is to gain insight into the adaptive mechanism through which man evolved.

Further awareness of the significance of tools comes from another approach. Studies of comparative animal behavior suggest that early man differed from his contemporaries in being oriented in time, in operating in a stream of time, or in being capable of thinking about past events while anticipating the future. This idea is best illustrated in systems of communication, although it is by no means limited to this sphere of behavior. Human language exhibits displacement; we can speak freely of past events, future events, things that are out of sight, and even nonexistent things (*3*). The communication systems of other animals are undeveloped with regard to this feature, while having other features of human language. Of course, language is not preserved in the ma-

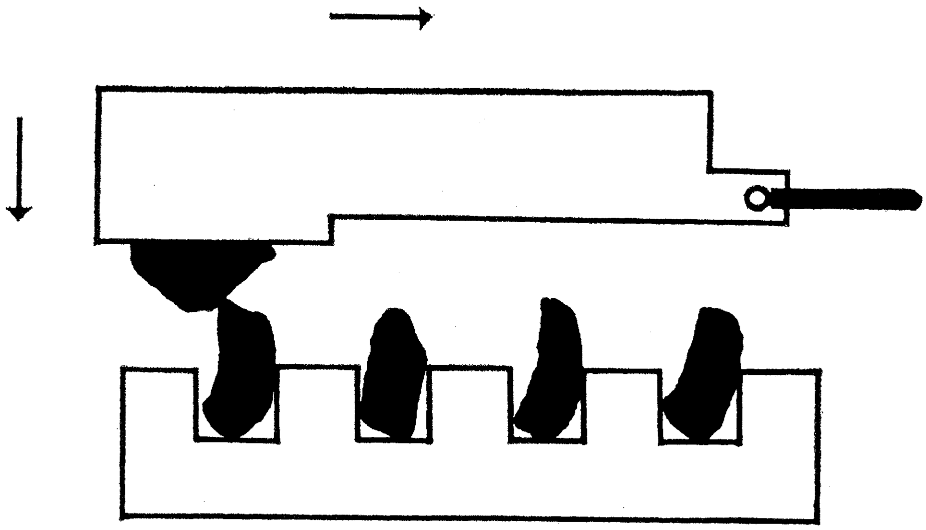

Fig. 1. Schematic representation of the apparatus used by Warren in his attempt to simulate fracture under glacial conditions. Various stones were placed in pigeonholes in a wooden frame (bottom), and a pebble was fixed to the lower part of a sled (top), which carried different weights in different experiments. In his experiments, Warren dragged the weighted sled over the stones held in the frame (*6*).

terial record, and experiments to test anticipatory behavior cannot be performed on fossils. A close analog of displacement in language, however, is found in the repetitive and systematic reshaping of matter. The manipulation of stone in a traditional way requires some memory of past experience and implies planning for the future (*3*). Clearly, purposefully shaped matter is as close an indication of anticipatory behavior, hence of the former presence of man, as can be expected to come from the ground.

Heuristic Approaches

Debate has often accompanied claims that the work of early man has been found. How the debate has been resolved has varied with local circumstances and participants. Claims have come from different places on several continents, and each situation has required some special treatment. From the experiences of the past century, a number of approaches can be extracted.

It is impossible to list all the natural factors that might be responsible for the fracture of stone. Certainly, primary agencies include the movement of water or ice down a hill or through a depression, and differential soil movements. But other, bizarre agencies —for example, a herd of animals trampling over gravel beds—are also known to cause rocks to fracture. The first of the approaches involves observation of such natural agencies at work. Observational studies begin with locating fractured stone in an area where the possibility of human workmanship can be ruled out. The task is to describe the operation of a specific agency and to describe its effects in detail. The action and results of waves pounding the cobbles on a beach and of boulders falling from the top of a gorge and fracturing pebbles in the wall below, and the combined action of wind, gravity, lichens, and temperature fluctuations, have been observed and recorded with different degrees of completeness and precision (*4, 5*). Knowledge gained in this way can lead to the identification of natural fractures in objects thought by some to have been shaped by man. Most often, such studies have been inspired by disbelief in some claim that the work of early man had been found.

Knowledge gained from observing what has been called "the life history of boulders" (*5*) is limited, for the relevant factors are uncontrolled and difficult to define. This limitation is overcome when the problem is moved from the field into the laboratory, where, in a second approach, fracture in nature is simulated. Since fracture in nature may occur over a long time span, with vast masses of material brought into play, generalizations based on small-scale simulations require careful evaluation. Nevertheless, the results of such work clearly complement the results of observational studies. In the first decades of the 20th century the simulative approach was developed extensively by H. S. Warren, a British geologist. Warren was particularly interested in fracture resulting from glacial conditions. To perform one set of experiments (*6*), for example, he constructed a modest wooden apparatus consisting of a frame and a sled and then attempted to simulate fracture by solifluction by dragging the sled, bearing different weights in the different experiments, over differently shaped stones held in the frame (Fig. 1). Archeologically relevant experiments of this kind are, unfortunately, rare.

A third approach is that of learning about man's use of matter and the effects of such use. In this approach, a notion about the effect of using wood for the final shaping of a stone tool, for example, is examined by performing an imitative experiment. The Kon Tiki expedition is the most familiar of imitative experiments; like the Kon Tiki experiment, imitative experiments with stone show what man could have done, not what he did do (*7*). But the results of imitative experiments provide, at the very least, an additional heuristic approach for the separation of human artifacts from the work of nature.

A recent experiment both illustrates the approach and suggests the role of tools in the emergence of man. Earlier we stated that commitment to tools was the novel adaptive design that accounts for the emergence of man. If this is true, then the hands that shaped the first tools must have differed from modern hands. The evidence of comparative anatomy and the evidence of paleontology support this notion. The length of the digits in relation to the length of the thumb, the shape of the terminal phalanges of the digits and thumb, the opposability of the thumb, and other changes in the hand resulted from the selective pressure associated with the inception of toolmaking (*8*). Could the hands of early man have shaped tools, and, if they could, what might the tools have looked like? In an imitative experiment first performed in 1960 and replicated in 1962, experimenters restricted the movements of their hands to those possible for the hands of early man and then attempted to shape stone (*8, 9*). They produced forms similar to those of stones thought possibly to be early tools, but they could not make, under the self-imposed restrictions, the later, more sophisticated forms generally believed to be tools.

The Procedural Approach

The approaches discussed thus far are basically heuristic; with few exceptions, results are expressed qualitatively—often vaguely—and the application of the results to a given situation yields decisions that are persuasive but not compelling. The reception of decisions reached in this way surely depends more on feelings than on anything else. We are mainly concerned with the need for objective, impartial, publicly verifiable procedures. It is to this procedural, or course-of-action, approach that we now turn.

Let us consider an early man about to fashion a tool. First, he is able to imagine how the tool will look; second, he can predict how the object to be shaped will respond to a blow directed at it or a pressure applied to it; third, he can actualize his predictions by controlling the removal of flakes from the object. We do not mean that purpose, prediction, and control were all equally evolved and integrated in the earliest toolmakers, or that early man categorized the operations in the manner set forth; we mean only that some semblance of each operation must have been present in the production of even a simple tool.

A. S. Barnes, a physicist, in proposing the only general identification procedure that has been suggested, built on the notion that it is controlled flaking which distinguishes stone shaped by man from naturally shaped stone. Specifically, Barnes believed (*10*) that evidence of control is found in the "angle formed by the intersection of the surface on which the blow has been struck or the pressure applied and the surface of the scar left by the flake removed." This idea is foreshadowed in observational studies as well as in simulative and imitative experiments, but it was Barnes who gave it precise definition in terms of a specific angle and set out to measure that angle in groups of naturally fractured stones and stones generally believed to have been fractured by man. Although no satisfactory theory links Barnes's angle to controlled flaking, the relationship is empirically supported.

Using a simple goniometer, Barnes measured 900 angles on naturally fractured stone from 7 different localities in western Europe and 2600 angles from 16 generally accepted industries ranging in time from the beginning to the end of the Pleistocene. He found that the angle sizes in the first group were distributed as follows: 75 percent of the angles were smaller than 106°, 50 percent were smaller than 93.6°, and 25 percent were smaller than 83°. In the latter group he found that 75, 50, and 25 percent were, respectively, smaller than 77°, 69.8°, and 61.7°. Some results were stated in terms of individual collections: in each collection of naturally fractured stone at least 55 percent of the angles were 90° or greater. On the basis of this study Barnes suggested that when doubt exists about the agency of fracture in a collection of stones, angles of a third to a half of the items in question, or at least 100 angles, should be measured. If no more than 25 percent of the angles are 90° or greater, then man may be considered the responsible agent. Applying this criterion, Barnes concluded that eight collections of already suspect "Tertiary tools" or eoliths were collections of naturally fractured objects. The eoliths, as well as the specimens generally believed to be of human workmanship, were obtained from museum collections. Barnes's report appeared 25 years ago, yet, as with some other classics, the physicist's work has been neglected by anthropologists. Using his fundamental idea, we suggest below some modifications, to enhance the reliability of his method and encourage its application.

There clearly exists in Barnes's data a distinction between the distribution of angle size for all accepted tools and the distribution for all naturally fractured stones. The naturally formed angles are considerably larger, only 25 percent being smaller than 83°, as contrasted with 75 percent of the tool

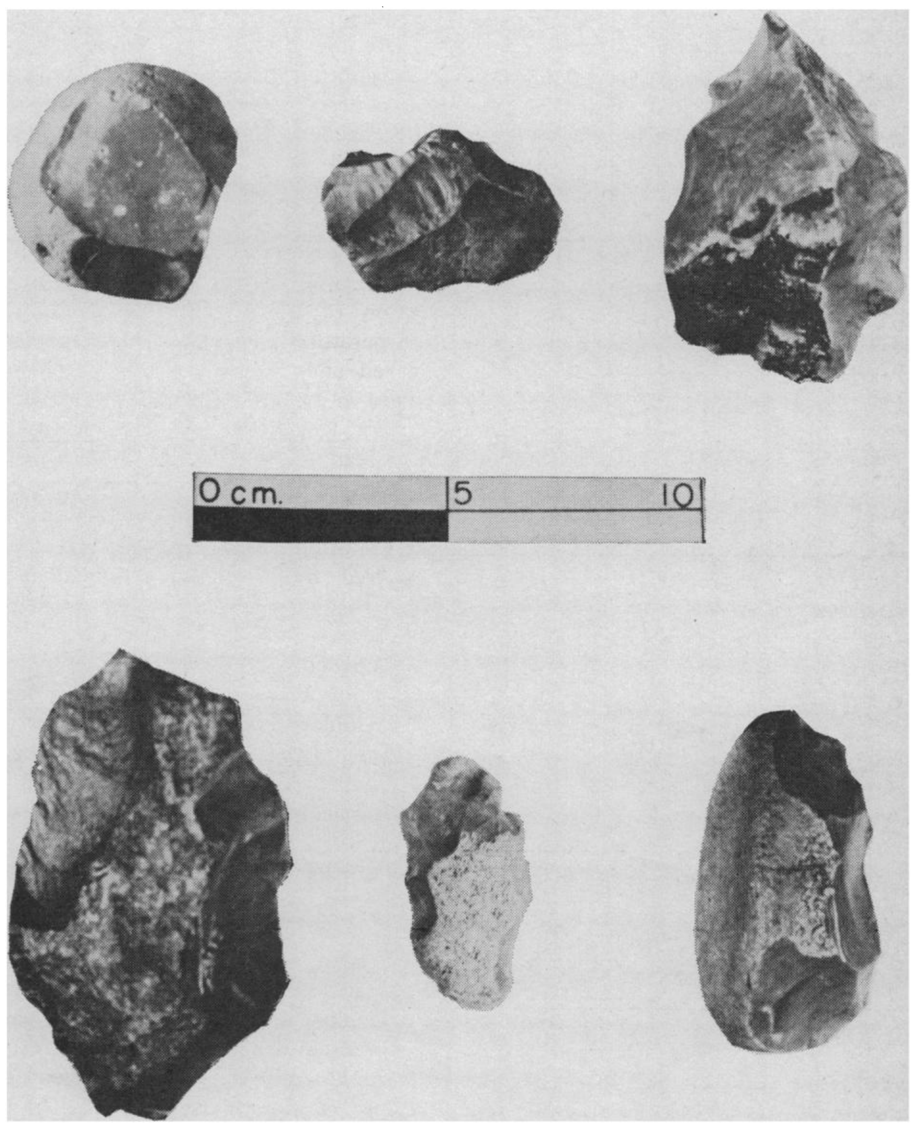

Fig. 2. Typical specimens of the postulated Tolchaco stone tool industry, collected at the Leupp Site.

angles smaller than 77°. The median for the natural angles is 93.6°; the median for the larger number of eolith angles, accepted by Barnes as the result of natural fracture, is 92°. This suggests the possibility that the median for naturally formed angles is at or very near 90°, the center of the possible range. Angles produced by toolmakers, however, have the considerably lower median of 69.8°. Similarly, Barnes's criterion for designating a collection an industry—no more than 25 percent of the angles 90° or larger—rules out collections for which the median for angle size is definitely more than 90°.

A group of naturally fractured stones from a particular environment may not be representative of all naturally fractured stones, as they have been subjected to a limited number of phenomena. Their angle measurements may display a bias, although, it is to be hoped, not as great a bias as that introduced by man. Bias can be seen in Barnes's data, where of the eight eolith collections, the percentage of angles of 90° or larger is as much as 35 percent lower in one collection than in another. To make sure that a bias is due to man, one should compare the angles of the stones showing this bias with the naturally formed angles of stones comprising the environment. This requires determination of the angles of all other stones in the area under consideration as well as of stones believed to constitute the industry. The distributions should be compared in order to make sure that the angles of the postulated industry are significantly smaller and that fewer of them—and at most, 25 percent of them—are 90° or larger.

Since the items representing a postulated industry or representing the environment are only a part of that industry or environment, the number of angle measurements must be sufficient to permit statements about the populations as a whole. Barnes does not consider the environment but, with reference to postulated industries, states that the angles of one-third to one-half the items available, or at least 100 angles, should be measured. However, the number of angles measured should depend on the statements to be made and the degrees of confidence sought. Let us assume that the entire postulated industry and the entire environment each contain at least 1000 angles distributed not very differently from the normal, and that the angle measurements are representative of the respective populations. In order to state that A percent of the angles are 90° or larger and that B percent are smaller than 90°, and to make this statement with a probability of $1 - \alpha$ that A has a maximum relative error of ϵ, the number of angle measurements must be at least t^2B/ϵ^2A. Here t is the argument corresponding to the value $1 - \alpha/2$ of the normal probability integral and ϵ is not very small (*11*). Similarly, the probability is $(1 - \alpha)$ that the mean of the n measured angles is within ts of the mean of the population, where s is the estimated standard error of the mean (*12*, p. 197).

The degree of confidence in any comparison of the postulated industry and its environment depends on the number of angles measured in each. For example, a comparison can be made of the means of both sets of angles. If

$$\left| \frac{M_1 - M_2}{\left(\frac{s_p^2}{n_1} + \frac{s_p^2}{n_2} \right)^{\frac{1}{2}}} \right| > t,$$

where M_1 is the mean of the n_1 angles of the environment, M_2 is the mean of the n_2 angles of the industry, and s_p^2 is the population variance estimated from the combined samples, the measurements may be interpreted as representing populations with different means, and the probability that this interpretation is incorrect—that the means are in fact the same—is only α. If the quantity is less than or equal to t, no conclusion can be reached (*12*, p. 238).

In sum, the modified procedure to test for the existence of a postulated

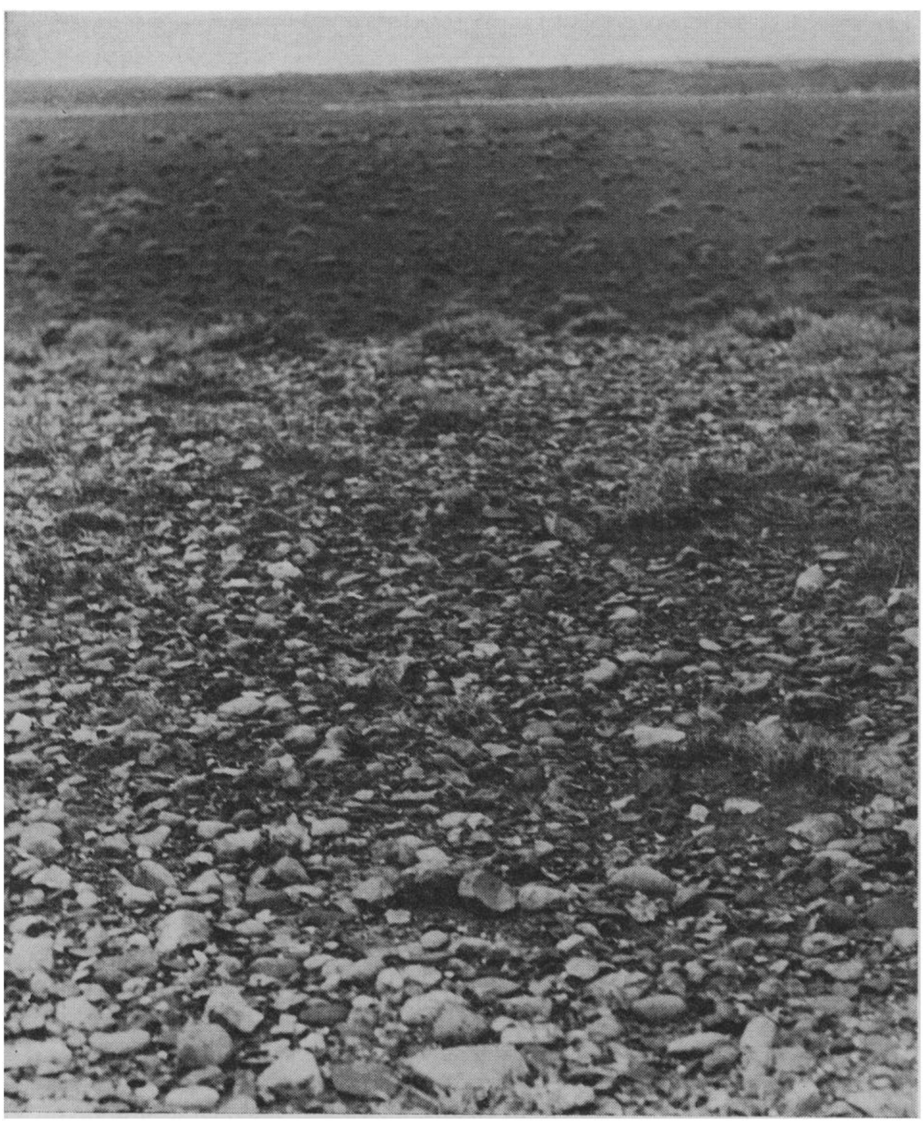

Fig. 3. The dense gravel pavement that constitutes the Leupp Site.

industry requires a field collection method that yields a representative sample of stones of the industry and of its environment. The hypothesis that some of the stones represent an industry is verified if the distribution of angle sizes for these stones is distinct from that for stones of the environment, and if the sizes are generally smaller; if the mean is distinctly less than 90°, and less than the mean for stones of the environment; and if the percentage of angles of 90° and larger is less than 25 percent and less than the percentage for stones of the environment. The procedure is intended to be used where isolation of an "industry" has already been made, or can be made, on the basis of criteria other than the small angles of the stones in question.

The Procedure Applied

Courses of action are best explored by direct application. A suitable situation for applying the procedure just summarized was found on a hilltop near Leupp, Arizona. The sole hint of prehistoric man's presence at Leupp is so crude a postulated industry that the difference between the stones in question and naturally fractured stone cannot be taken for granted. The earliest habitation of Leupp was remote in time from the emergence of man, and Leupp is far from areas where early man is known to have developed, but the objects found there fit the theoretical model for early tools.

Beginning in 1934, identification of a "primitive stone industry," called the Tolchaco Industry, was made along the Little Colorado River. The human origin of this "industry" is questioned by its very proponents, who use such terms as *crude* and *haphazard* to describe it (*13, 14*). "Since many of the implements are very crude," states one supporter (*14*), "the question naturally arises, 'Are they man-made or just the phenomena of nature?' " They are man-made, according to the same author, because the implements, found in gravels on the tops of hills, do not occur on all hills in the area, are found in the surface only, and show signs of having been sharply struck. For us at least, these criteria are not sufficient.

A number of hills near Leupp are cited in the files of the Museum of Northern Arizona as locales of the Tolchaco Industry. No specimens of the industry had been collected from some of the designated hilltops, and from this group we selected one hill —the Leupp Site—for intensive study. The archives of the museum contain implements of the postulated industry, collected by various investigators over a considerable period and from various places. We used these specimens as prototypes in identifying at the Leupp Site what others had identified as the Tolchaco Industry. Typical specimens of this industry from the Leupp Site are shown in Fig. 2.

The Leupp Site looks similar to many of the usual gravel pavements found in desert lands; no bones, fossil or recent, are present, and there are no hearths (Fig. 3). Two plants, saltbush and rabbitbush, grow conspicuously in the midst of the pebbles, which are predominantly chert. The altitude at Leupp is approximately

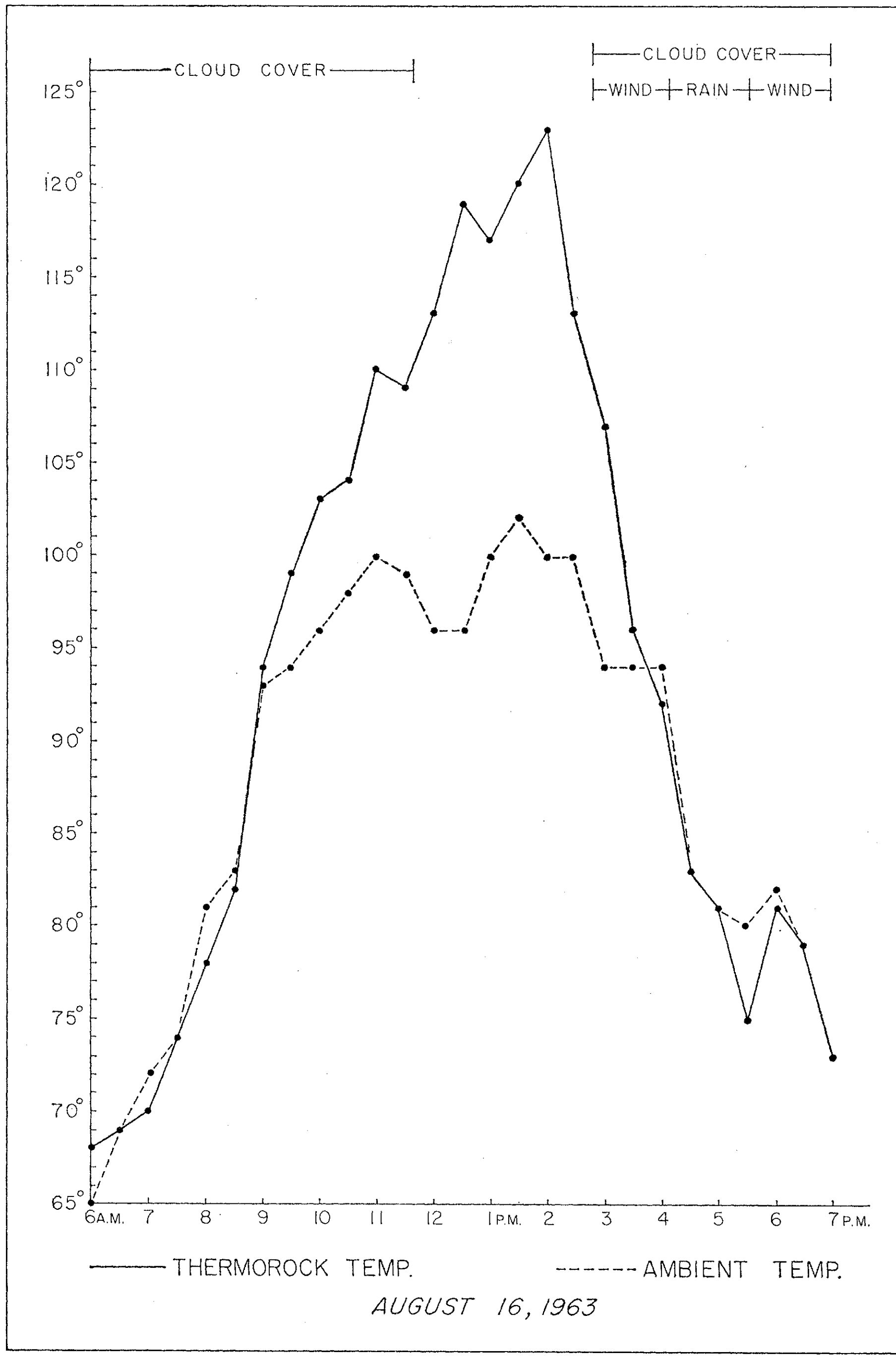

Fig. 4. Records of the temperatures within a pebble and of the ambient temperature during a 13-hour period. The temperature of the pebble ("thermorock temp.") was obtained by embedding a thermometer in the pebble. The prevailing atmospheric conditions are indicated by labels at top.

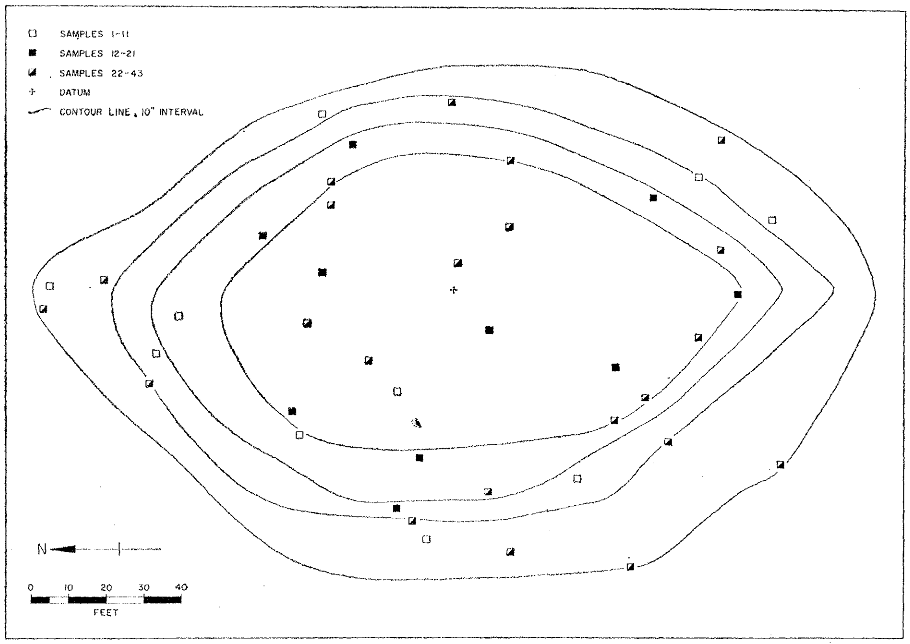

Fig. 5. Contour map of the Leupp Site. The initial collection consisted of all items (samples 1–11), from the 0.6- by 0.6-meter sampling areas, which did not pass through a screen of 1.27-centimeter mesh. The collection on which the discussion of the angle-size distribution is based consisted of fractured pebbles with measurable angles (samples 1–43) from the same areas, which did not pass through the 1.27-centimeter mesh.

1350 meters, but midday summer temperatures above 100°F (32°C) are common. Familiar desert atmospheric phenomena probably produce enough stress to account for some natural fracture. Just how much stress may be involved is suggested in the record of temperature changes within a single pebble during a typical summer day (Fig. 4). The record was obtained by embedding a thermometer in the rock.

If sampling procedures are not entirely unknown in archeology, they are rarely used. Here, for gathering data about the gravel pavement, we used systematic cluster sampling. A grid of squares representing areas of 0.6 by 0.6 meter was laid over a contour map of the site (Fig. 5). For each population considered, the sample consisted of all the items, within selected clusters, that did not pass through a screen of 1.27-centimeter (½-inch) mesh. The number of items differed for the various clusters and for the several populations considered. Use of the individual elements as collection units would have been a formidable task, since several overlapping populations were involved, none of which had an implicit order that could be utilized. The clusters were selected systematically. The advantage of systematic sampling for surface collections is that no sizable portion of the surface will be unrepresented. The method is particularly useful, in dealing with land and its cover, where the population is not necessarily homogeneous but is influenced by the characteristics of the terrain (*15, 16*). The initial cluster was selected randomly, and subsequent clusters were chosen at equally spaced intervals. Since the items in the clusters are correlated to some extent, the derived estimates for the several populations should show a sampling variance greater than the variance for independently selected items. On the other hand, systematic sampling, in appropriate situations, leads to smaller variance than entirely random sampling (*15*), but this effect may not be sufficient to compensate for the greater variance resulting from the use of clusters (*17*).

An initial sampling at the Leupp Site led to the description of the approximately 600,000 pebbles and parts of pebbles constituting the gravel pavement (Fig. 5, samples 1 to 11). The majority of the specimens exhibit no fractures, a greater number show no measurable angles, and a still larger number cannot be identified as belonging to the postulated industry. Specifically it can be stated with 95-percent confidence that at least 83 percent show no flaking, at least 95 percent have no measurable angles, and, at most, 1.5 percent are identifiable as belonging to the postulated industry. Of the pebbles or parts of pebbles that exhibit some flaking, at least 8 percent can be identified as belonging to the industry.

In order that the distribution of angles on the fractured stone might be studied, the collection was increased (Fig. 5, samples 1 to 11 and 12 to 43). The populations of concern were the measurable angles on specimens identified as implements and the measurable angles on the remaining specimens. Of all the pebbles or parts of pebbles with measurable angles, those that do not fit the prototype for the industry are about three times as numerous as those that do. However, objects identified as belonging to the industry show a higher average number of measurable angles per specimen, and, therefore, the number of angles for objects from the environment ("environment angles") is only about twice the number for objects from the postulated industry ("industry angles").

The distribution of the industry angles is shown in Fig. 6*A*; the distribution of the environment angles, in Fig. 6*B*. The *A* distribution is distinctly different from the *B* distribution and generally lower. With 95-percent confidence it can be stated that the percentage of angles in each 10° interval differs for the two populations. The percentage of angles smaller than 60° is at least 24 percent higher in distribution *A* than in distribution *B*; the percentage of angles larger than 80° is at least 38 percent higher in *B* than in *A*. At most, 4.1 percent of the industry angles are larger than 90°, while at least 27 percent of the environment angles are larger than 90°. Hence, the percentage of angles larger than 90° for objects from the postulated industry is considerably below the percentage for objects from the environment, and well below 25 percent. The mean for the environment angles is 82.7° (maximum error, 7.4°; confidence level, 95 percent), while the mean for the industry angles is 66.5° (maximum error, 8.7°; confidence level, 95 percent). With 99-percent confidence it can be stated that the populations show different means such that the mean for the industry angles is considerably lower than the mean for the environment angles (*19*). Thus we conclude that prehistoric man was present at Leupp.

The Recognition Problem

If recognition presents difficulties for the paleoanthropologist, he can take comfort in the knowledge that he is not alone. The recent controversy about the possible existence of extraterrestrial biogenic particles in carbonaceous chondrites, for example, is couched in arguments that are commonplace in discussions about early industries (*19*). In a consideration of threshold phenomena, like those discussed here, it is not surprising to find even closer parallels in problems such as that of recognizing the early fossil evidence for the beginning of life. It is instructive to recall the reception awarded early claims of the discovery of Precambrian fossils, made prior to the refinement of biogeochemical techniques. Take the case of *Brooksella canyonensis*, a jellyfish named in 1941. The specimen, or a photograph of it, was presented to specialists, who ". . . varied in opinion from one pronouncing it undoubtedly a medusa to the opposite that it is positively inorganic." And the defense of those who supported the organic nature of Precambrian *B. canyonensis* bears unmistakable resemblance to the usual nonprocedural defenses offered by those who argue for the existence of early industries (*20*).

Whatever the phenomenon under consideration may be, the recognition problem can be posed in a general form: given a set, is or is not a particular subset of sought events present within it? When the characteristics of the sought events are assumed to be known, the problem is to isolate them, if they are present, from other events. An example is that of searching for a particular message and being able to say, if and when a message is received, that it is the message sought and not a different one, or something without meaning. For our purposes the fact that the message was unintentional is irrelevant; irrelevant too is the fact that the message may have started on its way over 1 million years ago. If a subset has been singled out for attention by some unspecified means, the problem becomes that of determining whether it meets the required characterization. The characterization may be in terms of individual events or, as in the procedure discussed above, in terms of the entire subset of events. If for any reason the sought events are not characterized, we are dealing with another variety of the recognition problem, and the magnitude of the task is increased considerably.

Especially where the emergence of man is at issue, the core of the problem is characterization of the sought events. The transformation of the inorganic into the extraorganic, like the prior transformation of the inorganic into the organic, may have left few material traces until after the transformation was well advanced. Yet, traces that do exist will not be recognized if their characterization is too narrow to allow for the variations inherent in gradual change. Too gross a characterization will hinder recognition by admitting the inclusion of extraneous events. It follows that an ideal characterization, one that gives the greatest chance of success, must go beyond the single characteristic given here and include a balanced variety of factors.

Perhaps some of these characteristics can be established from the intuitive knowledge won after more than 100 years of experience with collections generally accepted as industries. The heuristic approaches discussed above are another potential means of characterization. Intuitive knowledge and heuristic studies might yield characteristics that are certain (that is, characteristics that can be causally connected with tool manufacture), others that are usually but not necessarily present, and still others that exclude naturally fractured stone but do not assure human workmanship. Any of these approaches might contribute toward building an a priori tool characterization; for example, characteristics established with varying degrees

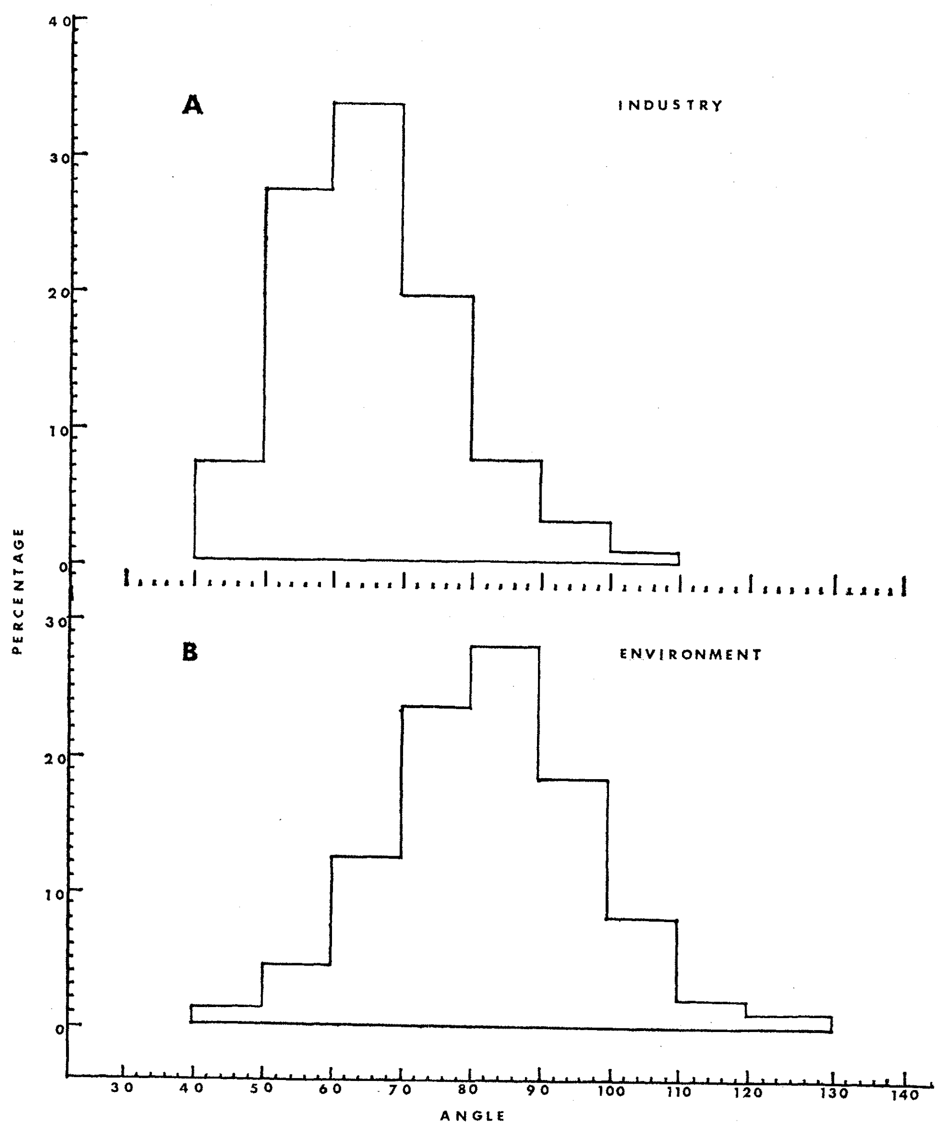

Fig. 6. Distribution of angle size for (*A*) stones of the proposed industry and (*B*) stones of the environment at the Leupp Site.

of certainty might be considered in combinations which would yield conclusions carrying differing confidence estimates. For any of this to happen, private, subjective experience must be made objective.

But success may still be elusive, for subtle reasons related to the investigator's capacity for delineating the sought events. The selection of characteristics can be too closely tied to cultural or personal prejudices—for example, a prejudice favoring symmetry or another favoring uniformity. This, we believe, is what Warren, the experimentalist, expressed when he wrote (*6*): "If we knew nothing of the matter, and were shown a perfect crystal of a diamond and rough piece of broken brick, I think we should imagine that there was more evidence of human design in the crystal with its perfect regularity of form and its polished facets, than there was in the brick." History provides cautionary examples, such as the case of the 18th-century microscopists who saw miniature human beings in spermatozoa because they expected them to be there, and the contrasting behavior of those who, in peering through the first telescopes, lacked the imagination to grasp what they beheld.

Summary

Recognition of early human industries takes on significance with the realization that commitment to tools is the novel adaptive design accounting for the emergence of man. The most abundant evidence for the emergence of man consists of the stones that he refashioned. But recognizing these objects is a problem, as they are both rare and similar to the stones of the environments in which they occur. Because the validity of a procedural, or course-of-action, approach to the problem of recognition can be demonstrated, such an approach is preferable to the intuitive and heuristic approaches that have dominated attempts to deal with the possible traces of early man.

We have modified a course of action proposed 25 years ago and have explored its potentialities by applying it to a case where an industry had already been identified by subjective means. Although the problem of recognition is found in many fields, it is most difficult where characterization of the sought events is itself a task, as it is in this case and in other investigations where threshold phenomena are the object of the inquiry.

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19. See, for example, F. W. Fitch and E. Anders, *Science* **140**, 1097 (1963).
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21. We are grateful for the hospitality and cooperation extended to us by the staff and administration of the Museum of Northern Arizona, Flagstaff, during the summer of 1963. The field work was aided by a Cornell University Faculty Grant. Clement W. Meighan of the University of California, Los Angeles, provided valuable criticism.

Dominance and Diversity in Land Plant Communities

Numerical relations of species express the importance of competition in community function and evolution.

R. H. Whittaker

Natural communities are mixtures of species which are unequally successful. In a given community one or a few species, the dominants, overshadow all others in their mass and biological activity and may strongly affect conditions of environment for other species. The community also includes other species which are of intermediate abundance or rare, and it is the number of these less conspicuously successful species which primarily determines the community's diversity—its richness in species. When species are arranged in a sequence from most to least important, they form a continuous progression from dominants through intermediates to rare species. This article is an inquiry into the form and meaning of these progressions in plant communities on land, based on field data from Great Smoky Mountains National Park. A number of "laws," interpretations, and models to fit such progressions have been offered (*1–10*); curves expressing four major hypotheses are shown in Fig. 1. Much of the discussion that follows concerns the fact that the relations are less lawful, orderly, and consistent than ecologists might wish. They are no less significant for all that, in relation to both ecology and evolution.

Two approaches to measurement need to be distinguished, although they are often closely related. (i) Species-diversity may be measured on the basis of numbers of species in sample units large enough to include some minor species. In terrestrial communities relations of species numbers to sample areas are complex; but, within limits, numbers of species increase approxi-

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