modified by interacting with the foreign antigen.

Immunologists argued over these competing hypotheses for years, but could not resolve the issue without a clear view of the nature of the receptor. The cloned genes should be helpful in this regard, too. For example, they can be transferred independently to see how each alters the specificity of the recipient cells for foreign or histocompatibility antigen.

Meanwhile, Kappler and Marrack have evidence in favor of the altered self hypothesis. To prove that the first monoclonal antibody they identified was directed at the receptor molecule and not at some associated structure, they used it to screen some 400 additional T-T hybridoma clones. The antibody reacted with one with the same specificity for foreign antigen as the original clone against which the monoclonal antibody was directed. "The reaction with antibody predicted the specificity for antigen," Marrack says. The second clone also had the same cross-reactivity with histocompatibility antigens as the original, suggesting that a single receptor was recognizing both.

A complete T cell receptor may include more than the protein heterodimer identified by the monoclonal antibodies, however. "The interesting thing about the structure (the heterodimer) is that it could be demonstrated to be noncovalently linked in the membrane to what is now an old friend, T3," Reinherz says. T3 is the designation for a surface protein on all mature T cells that was identified by Reinherz and Stuart Schlossman of the Dana-Farber Cancer Institute in studies aimed at defining the surface molecules characteristic of the different types of normal and abnormal lymphoid cells. T3 appears late in differentiation, when the cells are becoming immunocompetent. It is apparently not directly involved in antigen recognition as its structure does not vary from clone to clone.

But antibodies against T3 block the antigen-specific activation of T cells. In addition, antibody against T3, which has been bound to Sepharose beads, activates T cells, just as the bound monoclonal antibodies to the heterodimers activated the appropriate cell targets. These results suggest, Reinherz says, that the T cell receptor for antigen is a complex of the cell-specific heterodimer with T3.

Additional proteins on T cell surfaces influence the reactivity of the cells with their targets. A molecule designated T4 (in the human, L3T4 in the mouse) is needed for recognition of class II histocompatibility antigens and one called T8 (or Lyt 2 in the mouse) is required for recognition of class I antigens. Antibodies to T4 and T8 do not block specific antigen-induced activation of T cells, indicating that they are not part of the receptor for antigen. However, they may increase the overall avidity with which the T cell binds to its target, perhaps by recognizing a framework region of the appropriate histocompatibility antigen or some other nonvariable component on the target cell surface.

In any event, T cell interactions with their partner or target cells are clearly complex. Their study will be greatly facilitated by the identification and isolation of the T cell receptor molecules and their genes, work which should supply the hitherto missing link of immune cell interactions. The immunoglobulin receptors of B cells have been well characterized by now. The histocompatibility antigens, which are among the target molecules recognized by T cells, are well on their way to being understood (*Science*, 27 May, p. 937). Soon the same may be said for the T cell receptor for antigen.

—**Jean L. Marx**

Archeological Analysis Gets Some Teeth

A BASIC program has been developed that generates a mortality profile of ungulate species from tooth data in a fossil collection

Prehistoric sites frequently yield what even to the most experienced eye looks like an unpromising jumble of bones and stones. Without sound, objective methods of analysis there often remains considerable doubt over the paleontological and archeological significance of such sites. Focusing on teeth rather than bones, Richard Klein and Kathryn Cruz-Uribe of the University of Chicago have recently described* a technique that will help unjumble even some of the most meager collections of fossils.

The Chicago workers' specific interest with their technique is to be able to determine the age distribution (or mortality profile) of individuals of ungulate species represented in a fossil assemblage. Pat Shipman, a paleontologist at Johns Hopkins University, notes that obtaining reliable and detailed mortality profiles is extremely important in archeology and paleontology. "This technique," she comments, "gives a better shot at age profiles than anything else."

The basis of Klein and Cruz-Uribe's technique, which is a refinement of a model developed by British ecologist Clive Spinage, is the cumulative wear that teeth suffer through an animal's life. The use of teeth in establishing age profiles confers two distinct benefits.

First, as Shipman notes, the accuracy with which the degree of tooth wear can be measured compared with other age-related processes in the skeleton, such as fusion of epiphyses in bones, allows a much finer time resolution. "With tooth wear you can divide the lifespan into tenths as against only fifths or sixths with other methods."

The second benefit derives from the much higher rate of preservation of teeth in fossil deposits compared with other parts of the skeleton, which are softer and more likely to disintegrate. "Mandibles have an order of magnitude better preservation than other parts of the skeleton," says Shipman. "And single teeth have an order of magnitude better preservation than mandibles." The extension of age profile analysis to relatively impoverished fossil collection is therefore considerable using a technique that utilizes single teeth.

The ability to construct age profiles of fossil accumulations is crucial to an understanding of the nature of the accumulation, a perspective that was developed by Björn Kurtén and Leigh Van Valen in the 1950's and 1960's and more recently by Elizabeth Vrba at the Transvaal Museum in Pretoria, South Africa, and by Klein. As Klein and Cruz-Uribe explain in their recent *Paleobiology* paper, modern interpretations of age profiles refer to two theoretical models.

In one model the mode of death of the individuals in the assemblage is considered to be the result of some kind of

Paleobiology* **9, 70 (1983).

catastrophe, such as a flash flood, an epidemic, or a volcanic eruption. The age distribution of fossil bones in the collection reflects the age distribution of animals on the hoof: successively older age classes contain progressively fewer individuals. If this type of mortality profile is found in indisputable association with archeological remains one inference is that hunters had been able to drive herds of prey animals to their deaths or carry out mass slaughter in some other fashion.

The mortality profile associated with the second model is one in which young and old individuals are overrepresented in relation to their numbers in live populations. "Such a profile will contain those population members who die of starvation, accidents, predation, endemic diseases, and other routine, attritional mortality factors that affect the very young and the old most heavily." Again, in an archeological context such a profile might imply that people had been scavenging victims of attritional mortality or had actively hunted those most vulnerable individuals—the young and the old—in the standing population.

Klein has worked extensively in archeological settings in South Africa and has seen both types of mortality profiles in two different species represented in a Middle Stone Age site, the Klasies River Mouth Cave. Fossil remains of eland, which are known to be readily herded and driven, display a rather typical catastrophic profile. Cape buffalo, which are considerably less biddable than eland, appear as an attritional profile. In both cases, explain the Chicago workers, teeth of the youngest individuals are probably somewhat underrepresented because, compared with those of adults, they are more likely to disintegrate.

The need for reliable mortality profiles in fossil assemblages is therefore clear, but the question has always been, how do you get it?

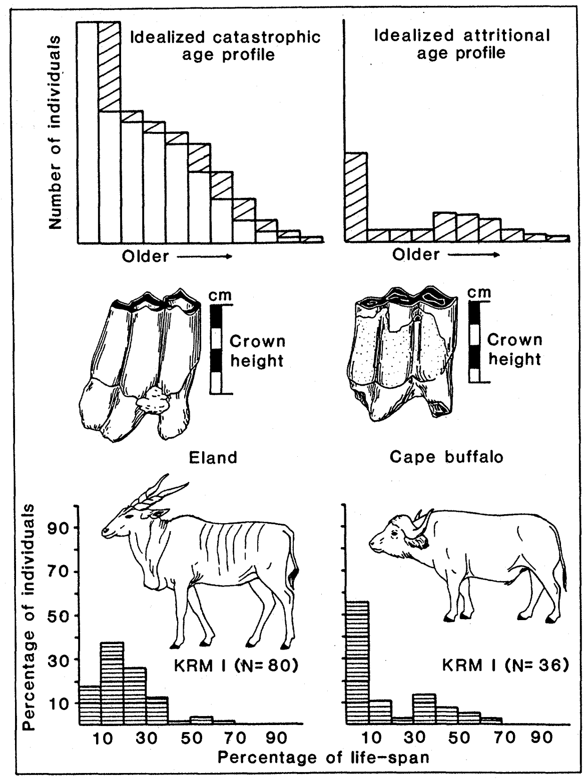
It so happens that the cementum in the roots of many ungulate species is deposited in discrete annular rings, analogous to tree rings. And, just as trees can be dated by counting the rings, the age of an ungulate tooth, and therefore its owner, can be determined by ring counting (given the appropriate adjustment for the age at which a permanent tooth might erupt). But, alas, not in fossil teeth, as the mineralization process tends to blur this neat record. In any case, the technique requires that the tooth be destroyed in the process, an act of paleovandalism that most paleontologists and archeologists are reluctant to commit.

Probably the most common method of deriving age profiles in ungulate assemblages has been based on an evaluation of the overall pattern of dental eruption and wear. By comparing fossil dentitions with living members of the same species, or to closely related species if the fossil species is now extinct, some kind of subjective estimate of age can be reached. "An obvious difficulty with the subjective method is that different investigators may produce somewhat different results," suggest Klein and Cruz-Uribe. "A more serious difficulty in applying it to fossil material is that it generally requires complete or nearly complete demimandibles or maxillae. In many fossil samples, including most of those with which we have experience, complete or nearly complete demi-jaws are less common than isolated teeth."

Given that it is preferable to work with isolated teeth, and that the neat annular rings of the living tooth become obscured in the fossil, the task is to be able to utilize some other secure, age-related property of teeth. As an ungulate continuously wears its teeth down while chewing throughout its life, often to the point at which they are completely abraded away, a measure based on wear is a good bet. Once fully erupted, an ungulate's permanent teeth initially wear at a high rate, because the surfaces are relatively rough. As the surfaces wear down they become smoother; this steadily reduces the rate at which further wear occurs.

The relationship between age and degree of wear is therefore not simple and so far no one has thoroughly described the process mathematically. Nevertheless, based on extensive field observation Spinage was able to develop a simple formula that gives a good approximation. The datum for any particular tooth is the crown height—that is the distance between the occlusal surface and the line separating the enamel of the crown from the dentine of the root. Given data points for an unworn crown and the age at which the crown is completely worn away (at which point is the "potential ecological longevity," as wildlife biologists term it), the age of any tooth, and therefore its owner, can be calculated. (Various adjustments for the sequence of deciduous to permanent teeth must of course be made.)

Although the formulation appears to be reliable it is, comments Shipman, "an extremely tedious process to perform." The tedium, note Klein and Cruz-Uribe, is a source of all too easy error. Moreover, says Shipman, "many people who have an interest in deriving age profiles from fossil collections simply do not know about the Spinage formula." What Klein and his colleague have now done is refine and test the formulation in the process of writing a BASIC program that generates a mortality profile divided into 10 percent-of-potential-life-span intervals. The program, say the Chicago workers, "should substantially reduce the tedium and possibility of error." It will also make the Spinage method of analysis more widely accessible to a community that thirsts for these kinds of insights.—ROGER LEWIN



Mortality profiles, past and present

An idealized catastrophic mortality profile (blank bars) is shown top left; the number of individuals who die between successive age classes is shown as hatched bars and is displayed as an attritional profile top right. At center are lower third molars showing the measure used by Klein and Cruz-Uribe. Bottom left shows the mortality profile of eland at the Middle Stone Age site of Klasies River Mouth Cave (KRM 1), which roughly conforms with a catastrophic profile. Cape buffalo remains from the same cave show an attritional profile.