20%). Alexander and Player (1965) have also stated that the southern race, *simum,* has sparse body hair white the northern has no hairs, only follicles. Groves (1975) suggests that the northern may be longer-legged and shorter-bodied than the southern, but this is not based on any data.

A BRIEF PALAEONTOLOGICAL HISTORY AND COMPARATIVE ANATOMICAL STUDY OF THE RECENT RHINOS OF AFRICA

Summary of presentation by Claude Guerin
(Universite Claude Bernard ——Lyon)

Information on this subject has been published by Guerin (1980).

The black rhino (*Diceros bicornis)*

The lineage begins in the upper part of the middle Miocene, about 12 million years ago, with
Paradiceros mukirii known from Fort Ternan (Kenya) and Beni Mellal (Morocco). The genus *Diceros* appears later in the upper Miocene and is known at that time in Spain, Greece and Turkey with *D. pachygnathus,* In Turkey with *D. neumayri,* and in Tunisia and Italy with *D. douariensis.* The first of these three very large Miocene species may be the ancestor of the white rhino, *Ceratotherium.*

The species *D. bicornis* appears during the Pliocene about 4 to 5 million years ago, and is known in more than 20 sites of Pliocene up to middle Pleistocene age, especially Hadar (Afar) in Ethiopia, Omo (Mursi, Usno and Shungura formations) in Ethiopia, East Turkana in Kenya, Laetolil and Olduvai In TanzanIa. More sites of upper Pleistocene and Holocene age are recorded. However, the material is always rare and the fossil form has not yet received any precise taxonomic status. Anatomical differences between the fossil and extant forms are minimal. Thus the fossil form warrants no more than a subspecific status.

I have studied about 60 adult skulls and more than 30 postcranial skeletons of *D. bicornis,* most of these being of Groves' (1967) medium-sized East African forms: subspecies *ladoensis, michaeli* and *brucii.* It is not easy to distinguish between these subspecies, whereas *minor* appears to be smaller-skulled and *bicornis* exceptionally large-skulled. I have not been able to study *chobiensis* and *longipes.* Statistical analyses show that, from the data I collected, *D. bicornis* is homogeneous, with rather normal variability (see Guerin, 1980). The various subspecies appear to constitute a complicated cline.

The white rhino *(Ceratotherium simum)*

The lineage of the white rhino Is much more recent than that of the black. The genus

Ceratotherium appears during the Pliocene with *C. praecox,* a species defined in 1972 by Hooijer and Patterson with material from Kanopol and Ekora in East Africa. The same year Hooijer described abundant material of the same species from Langebaanweg In South Africa. I have studied the material from Chemeron formation (Lake Baringo) and a good deal of material from Hadar (Ethiopia) and from Laetolil (Tanzania). The species is now known in 11 localities of East and South Africa.

The recent species *C. simum* appears about 3 million years ago. it is classically held that there are two fossil subspecies, C.s. *germanoafricanum* from East Africa and *C.s. mauritanicum* from North Africa. I have studied material of *germanoafricanum* from Afar, East Turkana, Olduvai, Omo, Rawi and sever minor locations, and *mauritanicum* material from Ternifine (0.8 million years), Ain Hanech (1.5 mIllion years) and other minor localities. The postcranial material shows clear differences between the fossil and the recent subspecies.

For the two recent forms, *simum* and *cottoni,* I have been able to find only about 30 skulls and 12 postcranials, and many were without specified origin. In fact, only 16 skulls and 8 postcranial skeletons were certainly from *cottoni,* and 8 skulls with 2 postcranial skeletons from *simum.* Hence the results are little more than an indication of differences. On average, *simum* has a skull slightly larger than that of cottoni, with a lower and broader skull roof, and a differently-shaped occipital surface (confirming observations of Groves, 1975). Comparison of fossil forms with the complete sample of recent species shows that the skull of *C. praecox* Is shorter, broader and lower, while the skull of *C.s. germanoafricanum* seems like that of a gigantic white rhino with comparatively narrower occipital surfaces, broader cheek teeth and correspondingly narrower palate widths. A comparison of limb elements again shows *germanofricanum to* be like a giant white rhino, while *mauritanicum* has similar (or exaggerated) proportions to *C. praecox,* being dissimilar to recent white rhinos and *germanoafricanum.*

Since the two Pleistocene subspecies seem to be very different to each other and from the recent ones, *germanoafricanum* probably deserves full species rank and may be the ancestor of the two recent forms; *mauritanicum,* which has no descendants, seems closer to their common ancestor, *C. praecox,* and probably also deserves species rank. The two recent subspecies are clearly distinct from each other and seem to be In the course of a speciation process. More postcranial material, particularly from southern Africa, Is required to help verify this.

BIOCHEMICAL INVESTIGATIONS OF RHINO SYSTEMATICS

Summary of presentation by Matthew George
(Howard University)

A comparative study was undertaken of genetic differences between individual northern and southern white rhinos, and a black rhino. This study was based on comparisons of mitochondrial DNA (mtDNA), which is a useful means of Investigating closely related species since 1.) the molecule Is maternally Inherited, thus complications arising from paternal contributions and recombination events (which affect nuclear DNA) are avoided; 2.) the molecule evolves very rapidly (5-10 times faster than nuclear DNA) so that if differences exist between races they are more likely to be detected than through other methods.

After purification of mtDNA molecules extracted from liver and spleen tissue of the three animals, these were subjected to digestion by 21 different restriction enzymes (which cut the mtDNA at specific sequences of nucleotide units). The cleaved fragments were separated electrophoretically. With most of the restriction enzymes, the migration patterns of mtDNA of the black rhino were different to those of the two white rhinos, while comparison of the two white rhinos showed 13 patterns to be identical and the remaining 8 different.

Analysis of these data indicate that the white rhinos differ by 4% In their nucleotide sequence and they both differ by 7% from the black rhino, If rhinoceros mtDNA changes at a rate of 2% per million years as has been shown in primate mtDNA, the divergence time between the white rhinos is 2 million years, and between either of the white rhinos and the black

rhino is 3.5 million years. The estimated time of divergence between the two species agrees well with fossil evidence (Hooijer, 1969), but the two million year divergence time for the two geographically separated subspecies is surprising; the mtDNA analysis suggests that little or no gene flow has occurred between the races for this period.

The intraspecific variation in mtDNA observed here in the white rhino is consistent with levels of intraspecific variation found in other species such as macaques, apes, rodents, sheep and goats. The intergeneric difference (7%) for the mtDNA of *Ceratotherium* and *Diceros* is somewhat lower than observed in mtDNA studies on other taxa.

We may tentatively conclude that, whereas morphological divergence between *simum* and *cottoni* has been slow (due perhaps to similar selection pressures or convergent evolution), the mtDNA analysis exposes significant genetic differences in these two forms. A second *C.s. simum* individual's mtDNA was subsequently studied, with essentially similar results. However, more sampling is required, in particular to verify the basic level of intraspecific variation in a particular race of white rhino, so that we can be certain that the differences between the northern and southern races are not in fact normal intraspecific polymorphic differences. in addition to increasing the sample size (ideally about 10 rhino from each race should be studied), the number of restriction enzymes could also be increased. *Comments by Oliver Ryder (Zoological Society of San Diego)* While the analysis of mitchondrial DNA of northern and southern white rhinos displays clear differences, no significant differences have been elucidated from protein electrophoretic studies carried out at the University of California, San Diego (A. Merenlender and D._Woodruff). Twenty-six presumptive loci were examined from five northern white rhinos, 14 southern white rhinos and five black rhinos (all *michaeli).* The electrophoretic difference between the northern and southern forms was approximately one-tenth that between white and black rhinos, whereas the. mitochondrial DNA studies had shown a difference between the northern and southern races which was about one-half of the mitochondrial DNA differences between the white and black rhinos.

Additional samples of northern white rhinos have been obtained from animals in captivity at Dvur Kralove, Czechoslovakia and will be subjected to mitochondrial DNA analysis. Additionally, chromosome studies of both black and white rhinos are very limited and should be undertaken. Both of these projects are underway in research supported by the Zoological Society of San Diego and the Ellen B. Scripps Foundation.

The phylogenies derived from fossil, electrophoretic, and mitochondrial DNA studies agree, but questions arise over the rates of evolution and times of divergence between the taxa. It is known that the rates of divergence in different animal lineages vary greatly and it would seem that the genetic loci studied by protein electrophoresis may have a particularly slow rate of evolution in rhinos in comparison to other vertebrates. This is consistent with the mitochondrial DNA findings. The fact that the protein electrophoretic studies indicate that genetic distances between the northern and southern white rhino are no more than those that can be expected in a single randomly mating population, while the mitochondrial DNA studies indicate longstanding genetic isolation, may be due to the difference in rates of evolution of nuclear genes (assayed by protein electrophoresis) a mitochondrial DNA or they may be due to a rehybridization event. Limited breeding occurring between rejoin populations that had been separated for some time has led merging of nuclear genes with retention of mitochondial DNAs of only a single population. Generally, the phenomena require recent genetic interaction of the previously separated populations.

While conservation decisions may need to be ma immediately, a clearer understanding of the systematics both white and black rhinos will require further studies chromosomes, protein electrophoresis, mitochondrIal a nuclear DNA genes.

Comments by Don Melnick (Columbia University)
In applying genetic methods to conservation goals we must be careful to avoid placing too much importance on subspecies designations and, instead, assess the distribution of genetic, morphological and ecologic variation throughout a species' range. It is these variants that we wish to conserve in the most efficient, cost-effective w and not the somewhat arbitrary taxonomic distinction between so-called subspecies.

With this in mind, it is necessary to investigate the distribution of genetic diversity (Nel, 1973) across the remaining black rhinoceros populations, in order to establish how much of the species variability can be attributed differences within populations as opposed to difference between populations. This will help us avoid some of the difficulties which have arisen in interpreting the results oft white rhino studies.

The relevance of genetic diversity analysis to rhino conservation in Africa can be Illustrated by an example of two Asian primate species (Melnick, 1987). Only 5% of the genetic diversity found among rhesus monkeys across Asia can be attributed to differences between animals in different regions. The remaining 95% of species diversity is intrapopulation diversity that can be found in any single region. In contrast, 41% of the genetic diversity found among long-tailed macaques can be attributed to difference between regional populations of this species. Hence, if the strategy were devised to conserve the greatest amount on genetic diversity in these primates it would entail the conservation of many more regional populations of the long-tailed macaque than the rhesus monkey. Given the scarcity of resources available for the conservation of the black rhino, we need to determine which of these two types of genetic structure exist.

With the assistance of the New York Zoological Society, the AAZPA and the AERSG, a genetic survey of the black rhino has commenced, with the aim of analyzing mtDNA and bloc proteins in reasonably-sized samples from populations different parts of Africa. Thus far, blood samples from 3 individual black rhinos have been collected in Zimbabwe by P. du Tout, sampling is underway in Kenya and some samples may also become available from South Africa. Sampling very opportunistic, since it usually depends on translocation exercises. It may be very difficult if not impossible to get samples from central Africa. In addition to the wild-caught rhinos, we have collected, with the help of participating zoo blood samples from 12 captive rhinos of Kenyan origin. protocol for tissue collection has been developed and ha been circulated to those who may be in a position to obtain samples.

ECOLOGICAL ADAPTIONS OF RHINOS

Summary of discussion

N. Owen-Smith noted that the feeding ecology of northern white rhinos may well differ to that of the southern white rhinos. The latter graze on short, nutritious grasses while the northern animals live in a wetter habitat, with long fibrous grasses. K. Hillman-Smith confirmed that this is a possibility but relevant research has not yet been undertaken in Garamba National Park. Casual observations indicate that