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Determination of pedigrees and taxa of primates by protein electrophoresis

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Accurate identification of the parentage and taxa of animals held in a collection is essential to their optimal display and management. Without knowledge of the species, subspecies, and even geographic population or evolutionarily significant unit (ESU: Wharton, 1985) to which a specimen belongs it can be of little value in our attempts to conserve natural biota. Breeding of animals of unknown or unrecognised taxa may fail because of partial or total reproductive barriers between unidentified species (de Boer, 1982), or at best will produce additional

animals of dubious value. Without knowledge of pedigree, attempts to avoid the deleterious effects of inbreeding (Ralls *et al.*, 1979; Ralls & Ballou, 1983) are frustrated. Yet zoos often acquire animals of uncertain parentage, geographic origin and even species identification. This is because records can be lost, discarded or never instituted at the time of capture or birth; such events may occur during transactions with either animal dealers or (less often) other zoos directly, or occasionally during staff transitions.

Whereas most natural history museums would consider specimens lacking information on capture locality to be worthless for systematic study, zoos frequently have little choice in acquiring such animals and tend to designate the species and subspecies on the basis of cursory examinations of external anatomy. These taxonomic determinations are used for breeding plans, public education and entry into national and international studbooks and databases (e.g. *International Zoo Yearbook* and the International Species Inventory System (ISIS)) which provide bases for scientific investigations of the species' biology and the effects of management programmes. Finally, the taxonomic guesses and uncertain pedigrees are often transmitted with the animals during transactions and the receiving institution may have no knowledge of the basis for the designation. It would be reasonable for zoos to question the taxonomic status and pedigree of many of the animals in their care.

One approach to ascertaining parentage, determining correct taxonomic classifications and simultaneously increasing our knowledge of the evolutionary distinctiveness of problematic taxa is the analysis of protein polymorphisms by electrophoretic techniques (Ryder *et al.*, 1981; Chambers & Bayless, 1983; Wayne *et al.*, 1986). Small samples of blood or tissue can be analysed for variants unique to a species, subspecies, population or lineage by placing a homogenate into a gel made of starch, agarose or acrylamide, separating the proteins according to electrical charge by applications of high voltage across the gel and then staining proteins with specific biochemical stains. At the Chicago Zoological Park (Brookfield Zoo) electrophoretic analysis of blood proteins has been useful in the identification of taxa and pedigrees of several primate species.

SULAWESI MACAQUES

The macaques inhabiting the Sulawesi (Celebes) islands in Indonesia form a confusing array of morphological types. Fooden (1969) recognised seven subspecies from north to south: *Macaca nigra, M. nigrescens, M. hecki, M. tonkeana, M. maura, M. ochreata* and *M. brunnescens*. Based on observations of apparent hybrids at species boundaries Groves (1980) proposed to include *nigrescens* as a subspecies under *nigra, hecki* under *tonkeana* and *brunnescens* under *ochreata*. Kawamoto, Takenaka & Brotoisworo (1982) examined genetic variation among the Sulawesi macaques by gel electrophoresis of blood proteins and found genetic similarity to correlate well with geographical proximity. The genetic differentiation between the Sulawesi macaques was comparable to that reported for species of non-Sulawesi macaques but typical of differences found among conspecific populations of non-primate species (Nozawa *et al.*, 1977; Kawamoto, Shotake & Nozawa, 1982; Kawamoto, Takenaka & Brotoisworo, 1982). Hybrids between the Sulawesi forms have been produced in zoos (Chiarelli, 1973; Bernstein & Gordon, 1980; also reported on several occasions in the *Yearbook* lists of animals bred in captivity (e.g. Volumes 11, 18 and 26)). Groves (1980) found inter-specific (or inter-subspecific) hybrids at some, but not all, boundaries between geographic ranges.

Breeding *M. tonkeana* at Brookfield Zoo began in 1977 with one wild-caught

pair. Another ♀ identified as *M. tonkeana* was acquired in 1980 but upon her arrival at Brookfield it was determined on the basis of morphological features that she was more probably a hybrid, perhaps between *M. hecki* and *M. tonkeana*. She was therefore surgically sterilised. Two additional ♂ Tonkean macaques were obtained in 1984. Altogether between 1977 and 1987 the breeding group produced six progeny. In 1984 a group of 13 macaques described as *M. tonkeana* were purchased by the zoo but remained at a primate breeding facility in Florida until November 1985 when they were brought to Brookfield with the intention of forming several breeding groups of unrelated Tonkean macaques.

When the Florida animals arrived the Primate Department staff noted that several differed markedly in appearance from the Tonkean macaques bred previously at the zoo. The possibility that some of the newly received macaques had been misclassified was considered. Dr Jack Fooden of the Field Museum of Natural History in Chicago examined the animals visually in January 1986 and offered the opinion that several of them appeared to be *M. ochreata* while others seemed to be *M. tonkeana*.

To help determine the taxonomic identities of all the Sulawesi macaques at Brookfield starch gel electrophoresis was used to examine genetic variation between the original breeding group and the 13 new arrivals (for methods, see Selander *et al.*, 1971; Lacy, 1982, 1983). Whole blood samples were collected in heparinised tubes and stored at −85°C until analysis. Samples were run on 10·5% starch gels and stained for 27 protein systems, encoded by 30 presumptive genetic loci. No variability among the animals tested was shown by 23 of the loci (albumin, alcohol dehydrogenase, aspartate amino transferase, creatine kinase, esterase-1, fructose-1-6-diphosphatase, fumarase, glucose-6-phosphate dehydrogenase, glycerophosphate dehydrogenase, isocitrate dehydrogenase, lactate dehydrogenase-B, leucine amino peptidase, malate dehydrogenase, malic enzyme, mannose phosphate isomerase, octanol dehydrogenase, leu-met peptidase, phe-ala peptidase-1, phe-pro peptidase, phosphoglucose isomerase, sorbitol dehydrogenase, superoxide dismutase and xanthine dehydrogenase). Several proteins (phe-ala peptidase-2, phosphogluconate dehydrogenase, phosphoglucomutase and retinol dehydrogenase) were apparently variable but did not form sufficiently sharp bands on the gels to permit reliable scoring of the variants. Three of the proteins (haemoglobin, lactate dehydrogenase-A and esterase-2) were suitably variable and reliably scorable to be useful for taxonomic and pedigree analysis.

Unexpectedly, the electrophoretic analysis of blood proteins revealed that the pedigree of the second shipment of macaques was incorrect. The pedigree, as received in 1985, is shown in Fig. 1 together with indications of the genotypes for the haemoglobin (Hb), lactate dehydrogenase-A (LDH) and esterase-2 (Est) loci (three animals were not tested and one, an offspring of 'Eleanor', has been omitted; the other two, 'M1500' and 'F1504', are both dead but have been included because they formed part of the founder group). In our allele designations a common variant is arbitrarily designated *c*, more slowly migrating variants are sequentially labelled *b* and *a*, with the faster variants being denoted *d, e* etc. The genetic data show that 'Jack' and 'Jeff' could not have been sired by ♂ 'Gumby', as had been indicated on the pedigree, because they are homozygous for a variant of Hb that is absent from Gumby. Moreover, although M1500 is dead and so could not be analysed electrophoretically it is likely that he was not the sire of 'Isac' as had been claimed. 'Pokey', 'Mutt' and 'Miney', all presumed offspring of M1500, must each have received a *d* allele at the Est locus from their sire(s). Since Jack and Jeff were obviously not the offspring of Gumby

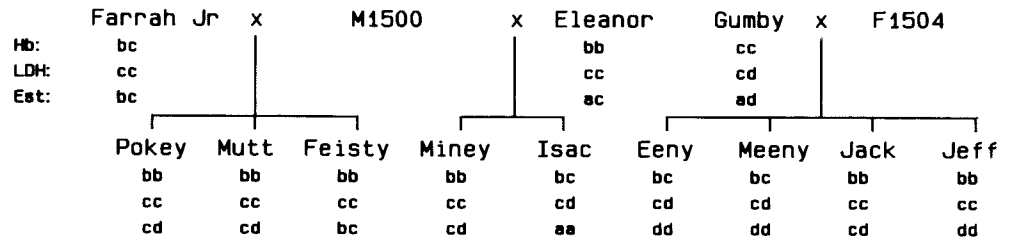

Fig. 1. Pedigree of a group of Sulawesi macaques *Macaca* sp as received with the animals at Brookfield Zoo in 1985. The genotypes, as determined by electrophoresis, of the haemoglobin, LDH-A and Est-2 loci, are given below each individual. 'M1500' and 'F1504' are dead and were not tested.

they must have been sired by the only other adult ♂ in the group, M1500. Jeff must have received the Est *d* allele from this ♂ and Jack either the *c* or *d* allele. 'Feisty', another presumed offspring of M1500, must have received either the *b* or the *c* allele at Est from her sire. Therefore, M1500 must have been either *bd* or *cd* for the Est locus and could not have sired Isac who is *aa*. Furthermore, it is highly unlikely (probability = 0·00098 that a heterozygote for two loci passes the same allele to each of six offspring at each locus) that M1500 would have passed the *b* Hb allele and the *c* LDH allele to six offspring (Pokey, Mutt, Feisty, Miney, Jack and Jeff), but the *c* Hb allele and the *d* LDH allele to Isac as would have been the case if he had been Isac's sire. Genetically, Gumby could have sired Isac and is presumed to have done so. The modified pedigree of all these animals, based on our electrophoretic data, is given in Fig. 2. The pedigree of the original Brookfield breeding group, shown in Fig. 3, is entirely consistent with the genotypes deduced for those animals by electrophoresis.

The identification of species cannot be determined unequivocally by electrophoresis if there are no reference samples from animals of known taxa. For the Sulawesi macaques at Brookfield, however, there are suggestions in the data of taxonomic identities which correlate well with the assessment of external features by Dr Fooden. The original breeding group, which had been identified as *M. tonkeana* and which have the physical characteristics of that species, are polymorphic for Hb with alleles *b* and *c* in the group, are monomorphic for LDH (allele *c*) and are polymorphic for Est with alleles *b*, *c* and *d* present. Of the macaques which arrived in 1985, 'Farrah Jr', her offspring (Pokey, Mutt and Feisty) and Jack and Jeff (all identified as *M. tonkeana* by Dr Fooden) show the same alleles at these three loci as do the *M. tonkeana* of the original Brookfield group. If Jack and Jeff are *M. tonkeana* then so must their deceased parents, M1500 and F1504, have been. The two older animals, Gumby and Eleanor, identified by Dr Fooden as *M. ochreata* are polymorphic for Hb with alleles *b* and *c*, are polymorphic for LDH with alleles *c* and *d* and are polymorphic for Est with alleles *a*, *c*, and *d*. This is also the case for their presumed offspring Isac. The tentative species identifications of the animals are shown in Fig. 2.

On the basis of this very limited sample we suspect that *M. tonkeana* and *M. ochreata* share a polymorphism of the *b* and *c* alleles of Hb, that the LDH *d* allele and the Est *a* of *M. ochreata* may be absent from *M. tonkeana*, and that the Est *b* allele of *M. tonkeana* may be absent from *M. ochreata*. The possible *tonkeana* × *hecki* hybrid ('Florence') has a *d* variant of Hb that was not seen in any of the other animals. Kawamoto, Takenaka & Brotoisworo (1982) reported a two-allele beta-haemoglobin polymorphism in *M. tonkeana* (the one *M.*

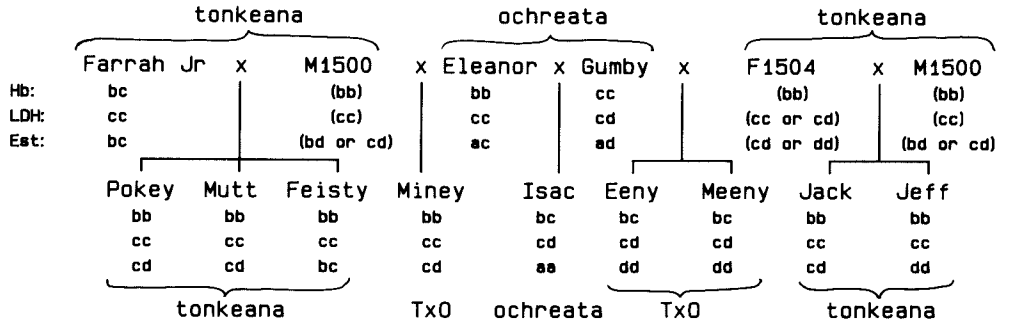

Fig. 2. Pedigree of the Sulawesi macaques in Fig. 1, modified to accord with genetic data obtained. Note that M1500 appears in two places on the pedigree. Genotypes in parentheses are inferred from relationships to other animals (see text). Species identifications are indicated (T × O = hybrid between *M. tonkeana* and *M. ochreata.*)

ochreata examined was homozygous for the slower *b* allele), and an additional faster migrating allele (probably *d*) present in their *M. hecki, M. nigrescens* and *M. nigra* samples. Kawamoto, Takenaka & Brotoisworo (1982) did not observe polymorphism among *M. tonkeana, M. ochreata* or *M. hecki* for LDH or Est. Blood samples of Sulawesi macaques from known collection localities would be needed to verify the preliminary indication of alleles unique to each species, and the species designations of the Brookfield animals.

SQUIRREL MONKEYS

The taxonomy of the genus *Saimiri* is problematic and often zoos do not know which subspecies or species they hold. Hershkovitz (1984) classified Squirrel monkeys into four species: *S. boliviensis* around Peru, Bolivia and western Brazil; *S. sciureus* in tropical South America mostly north of the Amazon River; *S. oerstedi* along the Pacific coast of Panama and Costa Rica; *S. ustus* in central Brazil south of the Amazon. Thorington (1985) considers the first three as subspecific forms of *S. sciureus* and the latter as a distinct species under the name *S. madeirae*. The two authors also differ in the number of subspecies recognised.

All Squirrel monkeys have 44 chromosomes but differ in the number which are acrocentric (V-shaped) or metacentric (X-shaped). Animals from

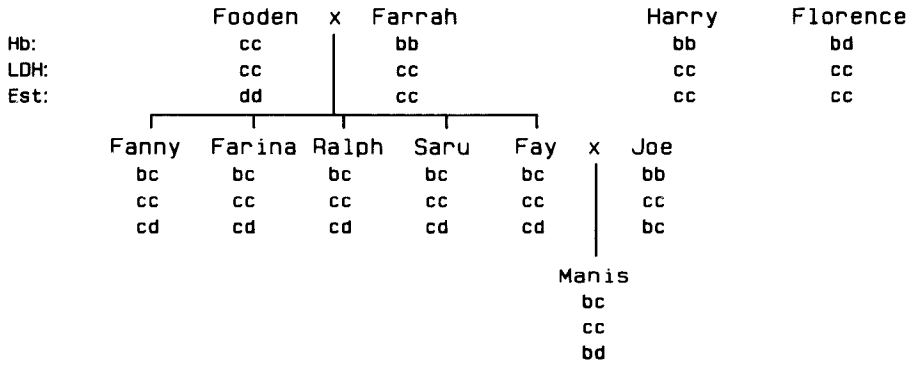

Fig. 3. Pedigree of the first group of Sulawesi macaques held at Brookfield Zoo, with genotypes indicated as in Figs 1 and 2. 'Florence' is thought to be a hybrid between *M. tonkeana* and *M. hecki;* the other animals are *M. tonkeana.*

Guyana *(S. s. sciureus)* have 14 acrocentrics, those from Colombia *(S. s. macrodon (sensu* Hershkovitz), *S. s. sciureus (sensu* Thorington)) have 12 and those from Peru *(S. boliviensis peruviensis* or *S. s. boliviensis)*, Panama and Costa Rica *(S. oerstedi* or *S. s. oerstedii)* have ten (Jones *et al.*, 1973; Ma *et al.*, 1974; Jones & Ma, 1975). Dr Thomas Fogle of St Mary's College in Notre Dame, Indiana, karyotyped many of the Brookfield Squirrel monkeys in 1984 and 1985. He determined that there were four chromosome types in the breeding group, distributed as follows: seven Peruvian (P, with ten acrocentrics), one Colombian (C, 12 acrocentrics), four Peruvian × Colombian hybrids (P × C, 11 acrocentrics) and one Guyanan (G, 14 acrocentrics). Analysis of the pedigrees of these animals has revealed that one of the 11-acrocentric individuals is a first-generation hybrid (P × C), while two others are progeny of a back-cross between Peruvian ♂♂ and first-generation hybrid ♀♀ (P × (P × C)); two of the ten-acrocentric animals are progeny of a second-generation back-cross between a Peruvian ♂ and a P × (P × C) ♀ (P × (P × (P × C))). Subsequent to the chromosome study the breeding group has produced additional Peruvian individuals and one back-cross; also, one karyotyped Peruvian ♂ has been purchased. Although the chromosomal differences are in the form of pericentric inversions, which often cause hybrid sterility, fertile hybrids between the Peruvian and Colombian forms are clearly possible. First-generation hybrids will have a number of acrocentric chromosomes intermediate to those of the parents and thus are often easily identifiable as hybrids (P × C will have 11 acrocentrics and C × G will have 13 acrocentrics, but P × G will have 12 which is the same as the number found in pure Colombian animals). Second and later generation hybrids, however, can have variable numbers of acrocentrics (e.g. P × (P × C) may have ten or 11; (P × C) × (P × C) may have ten, 11 or 12), making conclusive taxonomic identifications from karyotyping alone impossible.

To clarify the specific and subspecific status of the Squirrel monkeys in the Brookfield collection, and also to facilitate taxonomic assessment of groups in other collections, we are using electrophoretic analysis of blood proteins as a means of examining the genetic divergence between the chromosomal forms (subspecies or species) of Squirrel monkeys. Unique alleles would provide diagnostic loci for assessing taxonomic status of unknown individuals more quickly and at a lower cost than karyotyping, and could also reveal second and later generation hybrids. Moreover, the presence of protein variants unique to a chromosomal race would indicate that the population has been isolated from other populations for considerable evolutionary time.

We tested blood samples from 19 Squirrel monkeys held at Brookfield and nine Guyanan squirrel monkeys at Woodland Park Zoo in Seattle for each of 27 blood proteins (Alb, AK-1, catalase-1, Cat-2, Est-1, Est-2, Est-3, G6PD, glyceraldehyde-3-phosphate dehydrogenase, Hb, IDH, LDH-1, LDH-2, LAP-1, LAP-2, MDH, ME, leu-met peptidase, phe-pro peptidase, PGI-1, PGI-2, PGM, 6PGD, SDH, SOD and two probable transferrins stained with a general protein stain). The animals were invariant for all proteins except PGI-1, MDH, Est-1, Est-3 and phe-pro peptidase.

The blood protein variants (Table 1) showed strong concordance with the chromosome-race determinations given by Dr Fogle. For PGI-1 the pure Peruvian animals were all homozygous *(cc)*, the one pure Colombian individual was homozygous for a less cathodal variant *(bb)* and the Guyanan animals in both collections had the *b* and an *a* allele. Among the Peruvian × Colombian hybrids were *bc* heterozygotes and *cc* homozygotes. This pattern is consistent

POPULATION	NO. ANIMALS ANALYSED	NO. ACROCENTRIC CHROMOSOMES	PGI-1	EST-1	EST-3	PHE-PRO PEP.	MDH
Peruvian	11	10	11*cc*	11*cc*	1*bb*	1*bb*	11*cc*
					4*bc*	7*bc*	
					6*cc*	3*cc*	
Colombian	1	12	*bb*	*cc*	*bc*	*bc*	*cc*
Guyanan							
Brookfield	1	14	*ab*	*bc*	*bc*	*bc*	*cc*
Woodland Pk	9	14	2*ab*	5*bb*	3*bc*	2*bc*	9*cc*
			7*bb*	4*bc*	6*cc*	7*cc*	
Hybrids							
P × C	1	11	*bc*	*cc*	*cc*	*bc*	*cd*
P × (P × C)	2	11	*bc*	*cc*	*cc*	*bc*	*cc*
		11	*cc*	*cc*	*bc*	*bc*	*cd*
P × (P × (P × C))	3	10	*cc*	*cc*	*bc*	*bc*	*cc*
		10	*bc*	*cc*	*cc*	*cc*	*cc*
		not karyotyped	*bc*	*cc*	*bc*	*bb*	*cc*

Table 1. Karyotypes and genotypes at five variable loci for captive Squirrel monkeys *Saimiri sciureus* of three subspecies and of subspecific hybrids at Brookfield and Woodland Park zoos.

with the *c* variant being unique to and therefore diagnostic of the Peruvian form, the *b* allele being present in both the Guyanan and Colombian squirrel monkeys (perhaps fixed in the Colombian form) and the *a* allele being present only in the Guyanan population. The Peruvian, Colombian and hybrid monkeys were monomorphic *(cc)* for Est-1 but the Guyanan forms were polymorphic, with the more common allele *(b)* being a variant not observed in the other two subspecies. At Est-3 and phe-pro peptidase the Peruvian, Colombian and Guyanan squirrel monkeys shared two-allele polymorphisms. All pure specimens of the three forms were homozygous for the same allele at the MDH locus but a fast-migrating MDH variant *(d)* was evident in two hybrids (a P × C ♀ and her P × (P × C) daughter) and may have been transmitted from either Colombian or Peruvian ancestors.

Although the samples are few, and some of the animals are related, the results suggest that electrophoretically detectable variants of blood enzymes may be useful in distinguishing the chromosomal forms (species or subspecies) of Squirrel monkeys. Affinities and differences between each pair of the three subspecies are seen in the patterns of shared and unique alleles and thus these preliminary data do not allow discrimination between alternative taxonomic classification schemes. As they become available we will be analysing further samples to refine our estimates of the genetic divergence among the different forms of Squirrel monkeys.

GUINEA BABOONS

A group of 58 Guinea baboons *Papio papio* was placed on an island exhibit at Brookfield Zoo in 1938. Through the subsequent three decades the population's history is uncertain, but more ♀ Guinea baboons and perhaps a few Olive *P. anubis* and Hamadryas *P. hamadryas* baboons were added in 1939–1940 and individuals, especially ♂♂, were removed as the colony increased in size. In 1964 86 (16.70) baboons were recorded on the island at which time all adult ♂♂ were apparently removed. Numbers have subsequently been maintained at between 40 and 60 animals, with about half being adults. Since 1970 the presumed maternity of infants has often been recorded but the presence of several adult

♂♂ has precluded the assignment of paternity with any degree of certainty.

In an attempt to determine which of the ♂♂ had sired offspring, whole blood samples from 45 individuals were collected in 1986 and examined for protein variation by gel electrophoresis. Of the 32 genetic loci scored, 31 were invariant in the population (Alb, ADH-1, ADH-2, AAT, Cat, Est-1, F16P, Hb, hexokinase-1, HK-2, hydroxybutyric acid dehydrogenase, IDH, LDH-A, LDH-B, LAP, MDH, ME, ODH-1, ODH-2, gly-leu, leu-met, phe-ala and phe-pro peptidase, PGM-1, PGM-2, 6PGD, PGI, SDH, SOD and two probable transferrins). Only glucose-6-phosphate dehydrogenase (G6PD), encoded by a gene on the X-chromosome, was clearly variable. The mean heterozygosity ('expected heterozygosity' averaged across loci) was 1·0%, which is substantially lower than the average heterozygosities estimated from similar data on populations of four baboon species in the wild: 3·9% for *P. papio* (Lucotte, 1979), 1·8% (Lucotte, 1979), 1·7% and 2·9% (Shotake, 1981) for *P. anubis*, 2·8% for *P. cynocephalus* (Lucotte, 1979) and 3·6%, 4·5% (Shotake, 1981) and 5·0% (Lucotte, 1979) for *P. hamadryas*.

The lack of genetic variability at all sampled loci except G6PD precluded analysis of paternities. Several adult ♂♂ of each G6PD genotype (*c*Y and *d*Y) are present in the breeding group. One case of an incorrectly assigned dam was discovered: a homozygous (*cc*) ♀ had been recorded years earlier as the dam of a ♂ that was genetically *d*Y and which therefore must have had a *cd* or *dd* dam. The low number of variable loci and the low average heterozygosity in the population was not unexpected because the group had been maintained for almost 50 years with little or no immigration of unrelated animals and must therefore be at least moderately inbred. The number of adult ♂♂ was often kept low in the colony and it is possible that in each generation one or only a few ♂♂ monopolised mating, thus further restricting the genetic diversity of the breeding stock and exacerbating inbreeding. As an approximation of the amount of inbreeding that may have taken place since the progenitors of the group were taken from the wild it may be noted that a 75% loss of variability, the difference between the Brookfield animals and the wild population studied by Lucotte (1979), would result from about five generations of mating between siblings, or between parents and their offspring.

SUMMARY

Separation and identification of blood protein variants by gel electrophoresis has been useful in clarifying pedigrees and taxonomic status in a number of primates at Brookfield Zoo. Previously unsuspected errors were found in the pedigree of some Sulawesi macaques received by the zoo. A lack of genetic variation in an inbred population of Guinea baboons prevented analysis of paternity for that colony; it is possible that such genetic homogeneity may hinder paternity assessments in other captive groups that have been maintained without immigration for many generations.

If specimens of known taxa can be analysed electrophoretically, then diagnostic enzyme variants can often be found that will allow easy taxonomic identification of animals with uncertain histories. Genetic differences between suspected *Macaca ochreata* and *M. tonkeana* at the zoo helped to confirm assessments of external morphology, but a thorough study of the molecular genetics of Sulawesi macaques would be necessary to permit species identifications to be made with confidence. The identification of potential diagnostic enzyme variants for several subspecies of Squirrel monkey could allow rapid taxonomic screening of the many

individuals held in zoos and medical research laboratories.

Accurate assessment of taxa and pedigrees of captive breeding stocks is essential if those animals are to contribute towards an understanding of the biological differences among species and towards the conservation of diversity of species in nature. Gel electrophoresis is one of a number of techniques which should be applied towards an assessment of captive populations.

ACKNOWLEDGEMENTS

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Changes in gastrointestinal morphology related to nutrition in giraffes

Giraffa camelopardalis: a comparison of wild and zoo specimens

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Ruminants have been classified into three distinct feeding types according to their choice of forage and the morpho-physiological adaptation of their digestive system (Hofmann & Stewart, 1972). Of the concentrate selectors, the giraffe *Giraffa camelopardalis* exhibits extreme selectivity in the wild where herbaceous forage is selected not according to relative availability in a given habitat but according to quality, that is, nutritional content and digestibility (Pellew, 1984). Preferred forage is young shoots of *Acacia* spp, *Grewia* spp, *Balanites*, etc., which have digestible protein contents greater than 12% and presumably a lower concentration of secondary compounds (tannins, phenols) than rapidly 'ageing' leaves which are also rich in fibre components. Like all concentrate selectors wild giraffes actively try to avoid fibrous food and primarily select plants rich in plant cell content.

This feeding behaviour is reflected in specific morphological adaptations of its entire digestive system (Hofmann, 1984) but primarily in the mucosal relief of its forestomachs (Hofmann, 1973).

When in October 1983 and February 1984 two giraffes which had been kept under zoo conditions for many years were sent for post-mortem examination to the Institute of Veterinary Pathology of the University of Giessen, the opportunity arose to compare the gastrointestinal morphology of these animals with the records available from giraffes investigated in the wild. The results raised a number of important questions related to species-specific feeding of selective ruminants in captivity.

MATERIAL AND METHODS

The gastrointestinal tracts of two ♀ Masai giraffes *G. c. tippelskirchi* were investigated: 'Azetta' (A 1) born 21