in a male *E. burchelli böhmi* x female *E. asinus* hybrid, and possible physiological disturbance before the meiotic prophase in male *E. grevyi* x female *E. caballus* hybrids.

The fertility of the hybrid between *E. przewalskii* and *E. caballus* announced by Koulischer and Frechkop (1966) forms an exception to the rule. This horse, as mentioned in the article, "may not be a pure Prjewalski's horse". It may also have a closer relationship to *E. caballus* than exists between *E. caballus* and *E. asinus*.

On account of the relatively common fertility of the hybrids between *Vulpes fulvus* and *Vulpes vulpes*, Gustavsson and Sundt (1967) do not consider them as distinct species, but rather as subspecies.

Where polymorphism occurs, the so-called "hybrids" between males having a specific chromosome number and females of the same species having a different chromosome number seem to be fertile. In other words, it is not a simple matter of difference in chromosome numbers which must be held responsible for meiotic failure.

C.   *Karyotypes*

Levan *et al.* (1964) stated that it is important to identify chromosomes and to try to recognize homologies between those from one species and another. In this way it may be possible to find a "standard" karyotype for a particular taxon. When considering the various karyotypes as constructed for the Perissodactyla, it does not seem possible to postulate a hypothetical standard. The morphological relationship between the autosomes seem to have a certain evolutionary significance, which is discussed under the appropriate heading below. On the other hand there is a similarity in appearance of the sex-chromosomes throughout the order.

1.   *Sex-chromosomes*

(*a*)   *Sex chromosomes of the Rhinocerotidae (see also Fig. 1)*
The relationship between Rhinocerotidae and the Equidae is revealed in their sex chromosomes, since the rhinoceroses have sex chromosomes very much similar to those of the horse (see next subsection).

It would be most interesting to compare the karyotype of the Tapiridae with those of the above families.

(*b*)   *Sex chromosomes of the Equidae (see also Fig. 1)*
Previous studies (Mutton *et al.*, 1964; Benirschke *et al.*, 1963; Benirschke and Malouf, 1967; Heinichen, 1967 and Heinichen, in press) and the present results have revealed that the three zebra species: *E. grevyi*, *E. zebra* and *E. burchelli* have X-chromosomes ranging from meta- to submetacentric. According to Mutton *et al.* (1964), Trujillo *et al.* (1962) and Benirschke and Malouf (1967), the X-chromosome of the donkey differs in structure from that of the other Equidae in being the most submetacentric, in fact almost subtelocentric. In *E. przewalskii*, *E. hemionus* and *E. zebra* the position of the centromere of the X-chromosome resembles more closely that of the donkey, whereas in *E. grevyi* and *E. burchelli* it is

Fig.1. Graphic representation of decreasing acrocentric chromosome pairs accompanied by a decrease in chromosome number.
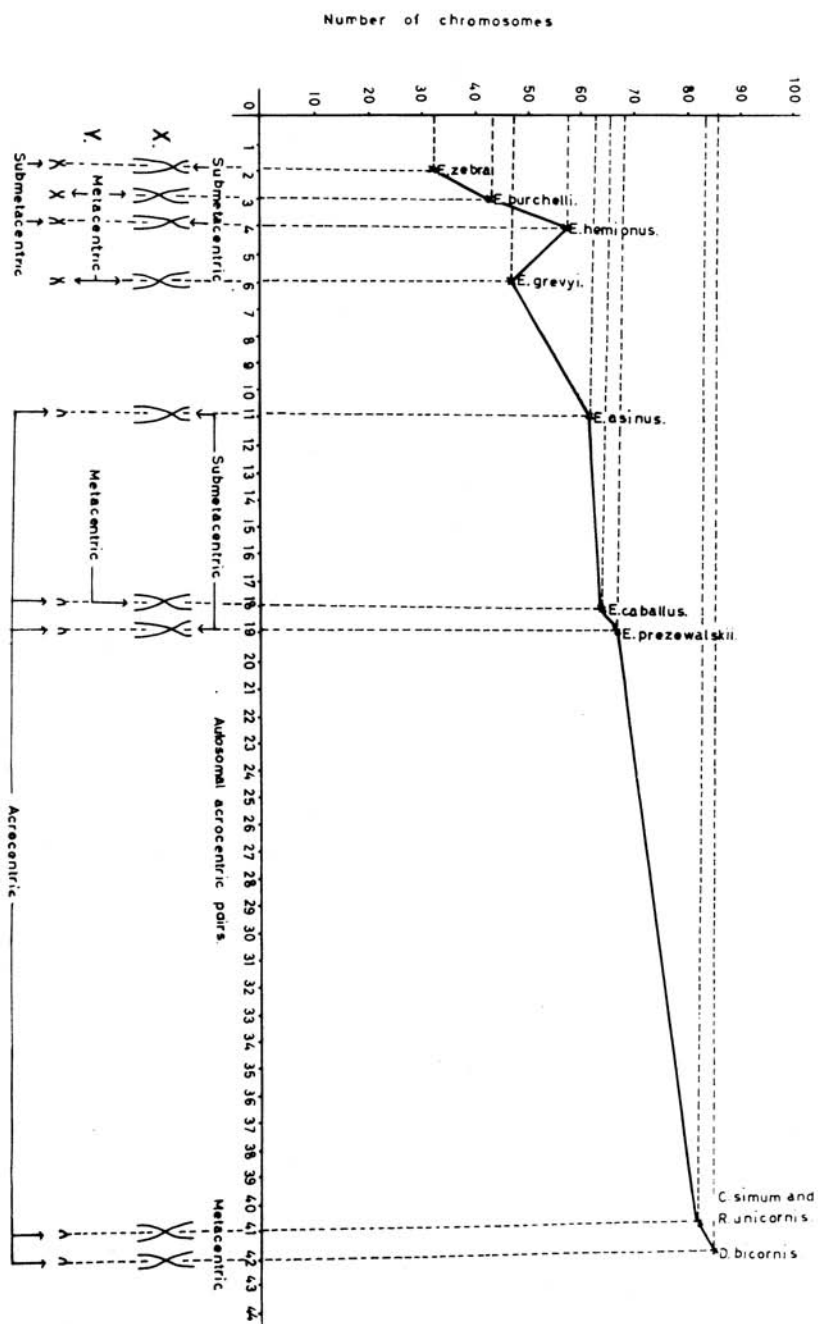
situated in a more median position, similar to the X-chromosome of the horse. Bourdelle (1941) describes *E. zebra* as having more asinine features (especially the ears and tail), while the other zebras are more horse-like. At this stage one can do no more than point out that a relationship exists between the external features and the position of the centromere on the X-chromosomes amongst some members of this order, a relationship which probably is purely coincidental.

Differences in centrometric position in Y-chromosomes also exist. As revealed in Fig. 1, three species have an acrocentric Y-chromosome (Hsu and Benirschke, 1967). Although Mutton *et al.* (1964) described *E. grevyi* as having a metacentric Y-chromosome and *E. burchelli* an acrocentric Y-chromosome, Benirschke *et al.* (1963) list the Y-chromosome in both these species as a small metacentric element. In these studies, the Y-chromosome of *E. zebra* was classified as submetacetric, whereas all members of *E. burchelli* had a metacentric Y-chromosome.

2. *Karyotype evolution in the Perissodactyla*

Of special interest is the fact that the known diploid chromosome numbers for the Perissodactyla range from 32 to 84. Decrease of chromosome number often appears to be accompanied by a decrease in number of acro-subtelocentrics and an increase in number of meta-submetacentric chromosomes, as illustrated in Table 18 and Fig. 1.

It has been postulated that a decrease in acro-subtelocentrics could be due to the so-called Robertsonian fusion or centric fusion as well as tandem fusion (Bender and Chu, 1963; Gustavsson and Sundt, 1967; Chiarelli, 1968). A study of the karyotype of *E. przewalskii* and *E. zebra* (both with 26 meta-submetacentric chromosomes) proves that the decrease of acro-subtelocentrics is not necessarily accompanied by an equivalent increase of meta-submetacentrics. Some of the smaller chromosomes could possibly have been lost during the evolution of the Equidae since their origin in the Eocene of Europe and North America (Thenius, 1966). Higher organisms, however, are very sensitive to chromosome loss, hence a more acceptable explanation could be that translocations had occurred with subsequent loss of heterochromatic centromeres. Such translocations need not necessarily lead to the formation of meta-submetacentric chromosomes: such chromosomes may revert to acro-subtelocentric ones especially as a result of pericentric inversion. The black and white rhinoceroses could well serve as an example of such reversion: the black rhinoceros has 84 chromosomes and the white rhinoceros 82, yet the black rhinoceros has four pairs of meta-submetacentric chromosomes and the white rhinoceros none.

The graph in Fig. 1 follows a direction parallel to the evolution of the Perissodactyla, from rhinoceroses (and tapirs?), being the most primitive, with the highest chromosome number and acro-subtelocentric chromosomes, to the Equidae, with the lowest chromosome number and acro-subtelocentric chromosome pairs (Table 18). The zebras, with the lowest

chromosome count and number of acro-subtelocentric chromosomes, are the most specialized as Thenius (1966), regards them.

The suggestion, that the more highly specialized animals have a smaller chromosome count and few acro-subtelocentric chromosomes, has also been made for a number of animal groups among the primates (Bender and Chu, 1963).

Specialization of animals does not necessarily mean that they are more intelligent. In fact a horse seems more intelligent to us than a zebra. The horse with a higher chromosome number, may have more chromosome material (and possibly more genes) with a greater chance of variation. Even if the zebras have the same number of genes, they will be present in fewer linkage groups, that is, a greater number of them will be linked, with the result that a smaller chance exists for recombination by independent assortment and therefore also a decrease in variation of genetic characteristics could be expected. During diplotene of meiosis, chiasmata (the cytological expression of genetical crossing over) are formed (Swanson, 1960). Length of the chromosome determines to a certain extent the number of crossovers that can occur. It is a well-known fact that one crossover inhibits the occurrence of another in its immediate vicinity. This phenomenon is known as chiasma-interference. In *Drosophila* this interference is complete for 10 map units (Swanson, 1960). It is clear then, that if the distance between two genes increases, the chances of crossing over occurring increases. One would expect that if zebras have the same number of genes on fewer chromosomes than horses and donkeys, the crossover percentage of zebra chromosomes will be lower than that of horses and donkeys.

The zebras, with a smaller chromosome count, inhabit only small parts of the African continent. Today, mainly through the action of man, their distribution area is still decreasing. This applies especially to the mountain zebras inhabiting only a very small part of South Africa and here being restricted to the mountainous regions (Bigalke, 1952). The chance of their becoming extinct through just a slight change in their "evolutionary niche" is certainly much greater than for horses and donkeys. The latter two species, however, owe their present wide distribution to a great extent to the fact that they have become domesticated. In fact, the horse has been re-introduced to the American continent where it previously had become extinct. Here it has also been able to propagate itself in the feral state.

The Rhinocerotidae, with a *high* chromosome count are also threatened with extinction. Cooke (1950) regards them as very primitive and not subject to rapid changes. Their chromosome complement, most autosomal chromosomes being acro-subtelocentric, also bears this out. They have undergone little adaptive change, in fact these animals do not seem to have changed at all since their origin in the Eocene (Thenius, 1966). Reasons for their threatened extinction in modern times must rather be sought in the fact that they have a long generation time and in man's

superstitious belief in the medicinal value of rhino horn.

The argument, that decrease in chromosome number leads to a lessening of the scope for genetic variation, would not seem to hold in the case of the rhinoceros. It is therefore clear that, despite the parallelism between karyotype evolution and animal evolution, oversimplified conclusions are not justified.

Polyploidy plays an important rôle in plant evolution, but among animals there is little evidence for its existence (White, 1945). In the family Cercopithecidae, chromosome numbers of 48, 54, 60, 66 and 72 (all multiples of 6) were found and polyploidy was suggested as an explanation for this phenomenon (White, 1945). White, however, raised several objections to this as an explanation: 1. It is difficult to understand how the sex determining mechanism of a polyploid primate would function. 2. Each species of the Cercopithecidae has one chromosome pair with a secondary constriction. If some of the species developed by polyploidy one would find several numbers of these constrictions. 3. The DNA values were measured and were found the same among all these species. If polyploidy was the reason for the differences in chromosome number, then the DNA value should also be different.

Polyploidy could never be used as an explanation for the wide range of chromosome numbers found in the Perissodactyla, as it presupposes doubling of a certain basic chromosome number with increase in evolutionary status. In this order there is a progressive decrease in number which does not occur in relative submultiples.

A better concept of karyotype evolution can only be gained once the karyotype of a much greater number of existing mammals becomes known.

D. *Taxonomy and cytogenetics*

The Cradock mountain zebra and the mountain zebra of S.W.A. seem to be conspecific: their karyotypes are morphologically and numerically identical (see Plate 7 and 8) (no relative arm lengths could be determined, due to insufficiency of spreads available for this particular purpose, nor were DNA determinations possible). Therefore the practice of regarding the one as *E. zebra zebra* and the other as *E. zebra hartmannae* is purely a subspecific (not specific) taxonomic differentiation and one on which most taxonomists agree (Ansell, 1967).

Similarly the plains zebras of southern Africa, as well as Grant's zebra (occurring north of the middle Zambezi, Luangwa and Rovuma rivers according to Ansell, 1967) appear to be conspecific judging by their karyotypes (see Plates 11, 12 and 15; Benirschke *et al.*, 1963).

In this respect the karyotypes do not assist in clarifying the taxonomic problem at subspecies level. At best, it has confirmed the existing classification at the species level.

Differences among animals with the same chromosome number are usually morphological, resulting in two subspecies or rather races, as

is seen in the zebras, where distinctions between the subspecies are based mainly on the stripe pattern of the animals (stripe pattern and colour could be the same as differences in hair- or eyecolour in man or distinctions as described by Cabrera (1936) caused by the animals' geographic distribution).

These studies can only give some support for the taxonomists and not solve their problems. All the subspecies of a particular species of zebra have an identical chromosome number, which is typical for the species to which they belong. Taxonomists can and do still place them in various subspecies mainly according to the basic pattern formed by the stripes.

As only four to seven representatives of each species were examined (examination of more animals was practically impossible) variations of the typical numbers may perhaps still be encountered, but then as examples of polymorphism only, and this at low frequency. Nevertheless, this work forms a basis from which further expansions can be made.

E. *Polymorphic sexing*

In all the animal species studied, distinct polymorphic sexing was possible, the relative frequency of drumsticks serving as the most useful guide. The highest number of this type of nuclear appendage found in the male was two and the lowest number in females was ten per 500 polymorphonuclear leukocytes. Kosenow and Scupins' formula was not useful, because of the frequent absence of nuclear appendages of the C-type, giving a value of ∞ for both males and females in these cases. The polymorphic sexing in the southern African forms of the Perissodactyla is thus simplified: only the drumsticks need to be counted.

The vesicular D-type appendages shown in Plate 4 (5 and 6) differ in some detail from those described by Kosenow and Scupin (1956) and have to my knowledge been described only by Gerneke (1965) in the hippopotamus. The suggestion was made there that they resemble the "paranuclear vacuoles" appearing with "cell death", studied by Bessis (1964). Possibly these structures could be similar to the degenerating vacuoles occurring near the junction of the nucleus and the cytoplasm described by Dustin (*cit.* Bessis, 1961).

Summary

A cytogenetic survey was undertaken on the southern African species and subspecies of the order Perissodactyla, taking advantage of the relatively recent improvements whereby chromosome number and karyotypes could be established with greater accuracy.

Material was obtained from male and female animals either chemically immobilized, caught or shot in various game parks or game farms in South Africa, South West Africa, Rhodesia and Mozambique. The bone marrow biopsy technique based on that of Sandberg, Crosswhite and Gordy (1960) with some adaptations (Gerneke, 1967) was employed.

Several, up to about 50, good chromosome spreads were counted and karyograms were constructed. Simultaneously blood smears were made and the nuclear appendages on 500 neutrophil polymorphonuclear leukocytes counted to determine the feasibility of polymorphic sexing.

The following results were obtained:

Species	2n Chromo-somes	Metacentric (= meta-submeta-centric) chromo-some pairs	Acrocentric (= acro-subtelo-centric) chromo-some pairs	Number of animals
Ceratotherium simum	82	0	40	5
Diceros bicornis	84	4	37	1
Equus burchelli	44	18	3	15
Equus zebra	32	13	2	8

The subspecies of *Equus burchelli*, namely *E. b. burchelli*, *E. b. antiquormu* and *E. b. crawshaii* (= *selousi*) and intermediate types between the latter two all have the same chromosome number, namely 2n = 44, and morphologically apparently identical karyograms. The same applies to the subspecies of *Equus zebra*, *E. z. zebra* and *E. z. hartmannae*, with a diploid chromosome number of 32.

The karyotypes of the different species of the Perissodactyla were compared with each other. There is a great variation in number and morphology of the karyotypes, so that no morphological relationship between the autosomes was found, although a similarity was recognized in the sex chromosomes throughout the order. The sex chromosomes of the rhinoceroses resemble those of the horse.

Karyotype evolution among the Perissodactyla was difficult to explain. Robertsonian fusion, whereby a decrease of chromosome number is accompanied by a decrease in number of acro-subtelocentric chromosomes could not be the only reason for the existence of such a wide range from 32 to 84 chromosomes in this order. Robertsonian fusion must have been accompanied by other phenomena, such as tandem fusion, translocations with subsequent loss of heterochromatic centromeres, translocations reverting to acro-subtelocentric chromosomes as a result of pericentric inversion or possibly the loss of very small chromosomes. Polyploidy could not be offered as an explanation here.

These cytogenetic studies could not assist in clarifying the taxonomic problems among the zebras at subspecies level. Nevertheless, it has confirmed the existing classification at species level, with every species of this order having its specific diploid chromosome count.

It was concluded that an identical chromosome number and an identical karyotype may not be advanced uncritically for the identity of species, neither may differences in chromosome number be accepted as proof of difference in species, unless one excludes chromosome polymorphism.

Although no chromosomes of hybrids were studied, the findings of other authors on hybrids were discussed, showing that in nearly all known hybrids of the Equidae, the diploid number of the hybrid was equal to the sum of the haploid number of both parents and that all Equidae hybrids, excluding a few exceptional mules, were sterile.

Suggestive evidence was found for the existence of a mitotic cycle with peak activity during about 9 to 11 a.m. Although not specifically investigated, indications were found that activity of the animal (and thus external factors influencing that activity) may play a rôle, yet that physical stress, excitement, and delay in collection of bone marrow after immobilization may possibly depress the number of mitotic figures obtained, presumably due to circulatory changes in the bone marrow.

Clearcut sex differences exist in all the species and subspecies examined; the female sex can be determined by counting typical "drumsticks" only.

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