collected immediately after death. For reference purposes the two extremes of markings found in these four animals are illustrated on Plate 10 (1, 2, 3 and 4).

2. *Results*

(*a*) *Chromosome number and karyotype*

The results of the chromosome counts are listed in Table 11. The diploid chromosome number of 44 was found for this subspecies.

Table 11

Chromosome counts of *Equus burchelli burchelli.*

Animal number	*Sex*	*Age*	*Time of collection*	*2n chromosome number* 42	43	44	45	46	*Total No. of spreads counted*
E.b.b. 1	♂	± 5 years	9.00 a.m.	2	8	37	2	1	50
E.b.b. 2	♂	± 9 years	10.00 a.m.	3	5	39	4	0	51
E.b.b. 3	♀	± 8 years	8.00 a.m.	No mitoses found.					
E.b.b. 4	♀	± 8 years	9.15 a.m.	2	5	22	3	1	33
Total				7	18	98	9	2	134

As shown in the karyograms, Plate 11 (3 and 4), chromosomes can be classified into two groups:
Group A chromosomes 1–18: meta-submetacentric (Nos. 1–4, 7, 10, 11, 13, 14 and 17 have approximately submedian centromeres, whereas 5, 6, 8, 9, 12, 15, 16 and 18 have median ones).
Group B chromosomes 19–21: all, one large and two smaller pairs are acrocentric.

Both the X- and the small Y-chromosome are metacentric. The X-chromosome resembles that of the horse very closely.

(*b*) *Polymorphic sexing*

The results of the counts of nuclear appendages of the polymorphonuclear neutrophil leukocytes are given in Table 12. As before, the sex difference is distinct.

Table 12

Polymorphic sexing of *Equus burchelli burchelli.*

Animal number	*Sex*	*No. of cells without appendages*	*No. of appendages* *Type A*	*Type B*	*Type C*	*Type D*	*Total No. of cells counted*	$\frac{A+B}{C}$
E.b.b. 1	♂	500	0	0	0	0	500	0
E.b.b. 2	♂	497	1	0	2	1	500	0.5
E.b.b. 3	♀	480	16	3	1	0	500	19.0
E.b.b. 4	♀	479	16	3	1	1	500	19.0

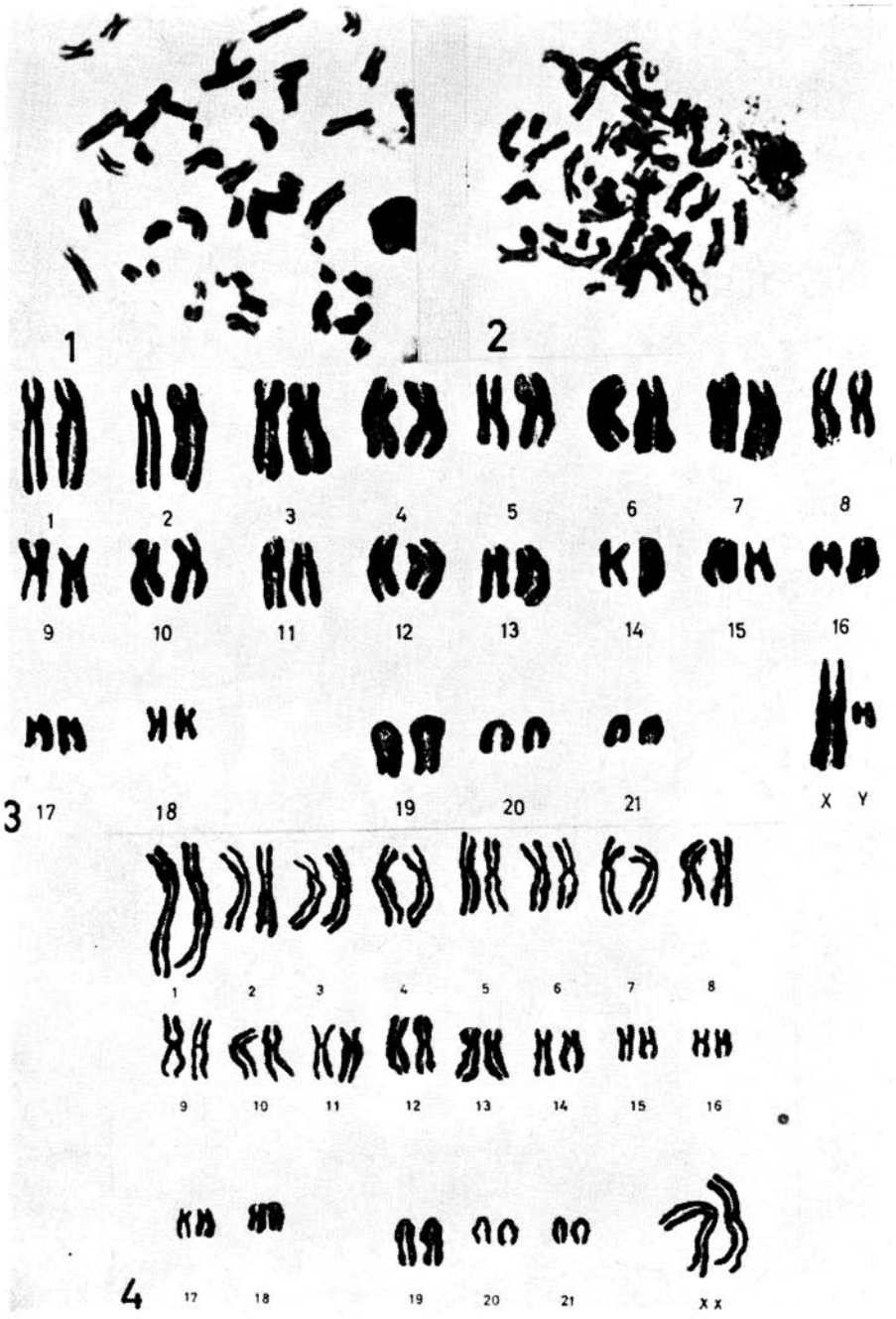

Plate 11. Mitotic chromosomes of *Equus burchelli burchelli.*

(1) Male (No. *E.b.b.* 1), and (2) female (No. *E.b.b.* 4), metaphase spread, ± × 1,200.

(3) Male karyogram, ± × 1,600 and

(4) female karyogram, ± × 1,600.

F. *Equus burchelli antiquorum* H. Smith, 1841.

Plate 10 (5).

1. *Material*

During an expedition to the Kruger National Park in April 1967, bone marrow biopsies were done on a colt and three stallions (Nos. *E.b.a.* 1, 2, 3 and 4, respectively) and two fillies and one mare (Nos. *E.b.a.* 5, 6 and 7, respectively). Blood smears were collected from Nos. *E.b.a.* 1, 3, 4, 6 and 7. As stated earlier, the three foals had been tied down, stallion No. *E.b.a.* 2 had been chemically immobilized, while stallions Nos. *E.b.a.* 3 and 4 and the mare No. *E.b.a.* 7, had been shot during operations for the artificial reduction of the overcrowded zebra population.

2. *Results*

(*a*) *Chromosome number and karyotype*

The chromosome number was found to be 2n = 44 (Table 13). It is noteworthy that the chromosomes from the three foals were smaller than those of the adult animals. The same also applies to the marrow cells in general.

Table 13

Chromosome number of *Equus burchelli antiquorum*.

Animal number	*Sex*	*Age*	*Time of collection*	*2n chromosome number* 42	43	44	45	46	*Total No. of spreads counted*
E.b.a. 1	♂	Foal	9.45 a.m.	1	1	42	4	2	50
E.b.a. 2	♂	2 years	11.00 a.m.	1	6	39	4	1	51
E.b.a. 3	♂	5 years	6.00 a.m.	1	5	57	4	1	68
E.b.a. 4	♂	4 years	6.30 a.m.	3	6	32	1	0	45
E.b.a. 5	♀	Foal	10.45 a.m.	2	2	41	5	0	50
E.b.a. 6	♀	Foal	11.15 a.m.	2	5	38	3	0	48
E.b.a. 7	♀	2 years	10.30 a.m.	2	6	42	2	1	53
Total				12	31	291	23	5	365

These chromosomes were found to be morphologically indistinguishable from those of the other subspecies, *Equus burchelli burchelli*, as will be noted on comparing the microphotographs of the two spreads and the two karyograms illustrated in Plate 11 (1, 2, 3 and 4) with those of Plate 12 (1, 2, 3 and 4).

(*b*) *Polymorphic sexing*

The results of sex determination, according to counts of nuclear appendages, are shown in Table 14. As before, there was a distinct sex difference.

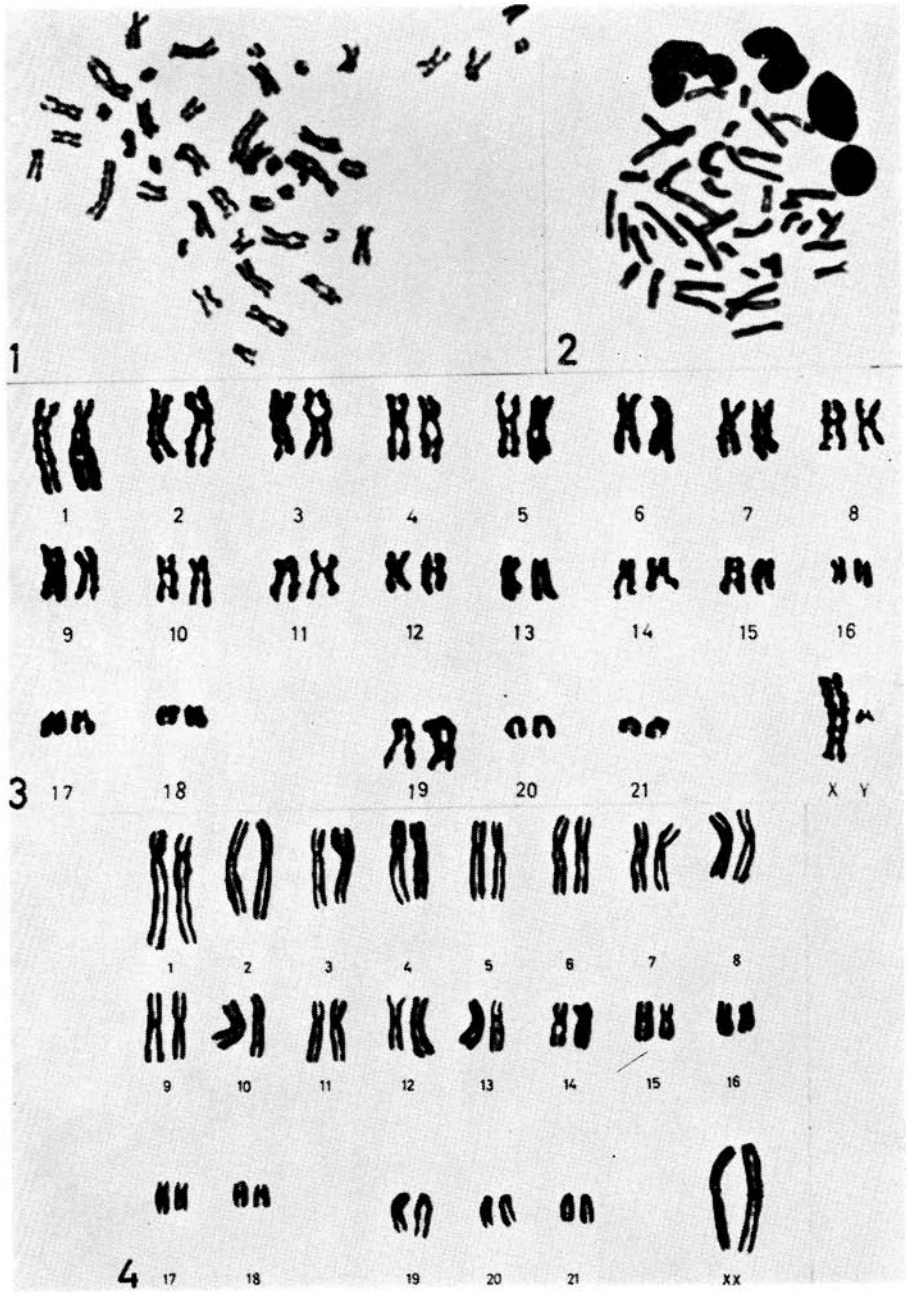

Plate 12. Mitotic chromosomes of *Equus burchelli antiquorum*.

(1) Male (No. *E.b.a.* 2), and (2) female (No. *E.b.a.* 7), metaphase spread, ± × 1,200.

(3) Male karyogram, ± × 2,000, and (4) female karyogram, ± × 2,000.

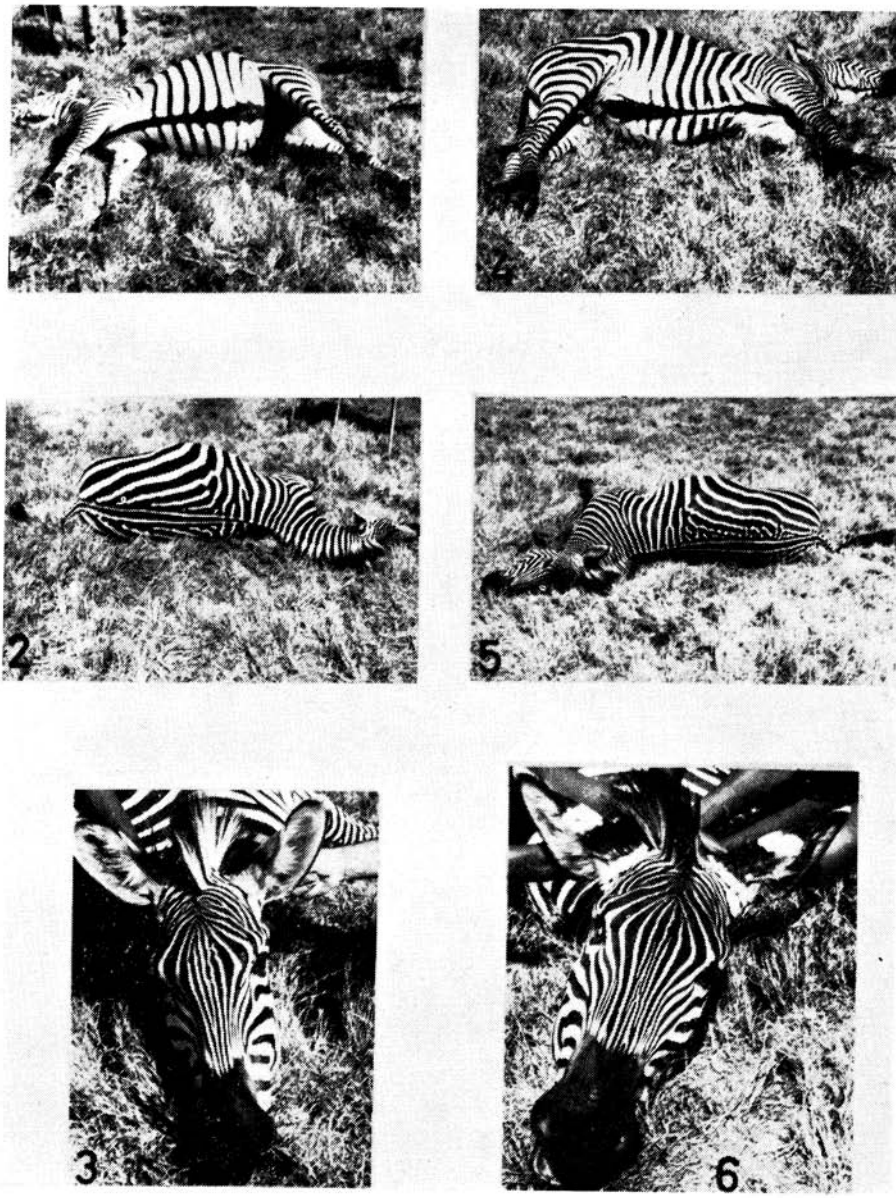

Plate 13. (1, 2 and 3).Ventral, dorsal and frontal views of *Equus burchelli crawshaii* female from Gorongosa.
(4, 5 and 6). Ventral, dorsal and frontal views of *Equus burchelli crawshaii* male from Gorongosa.

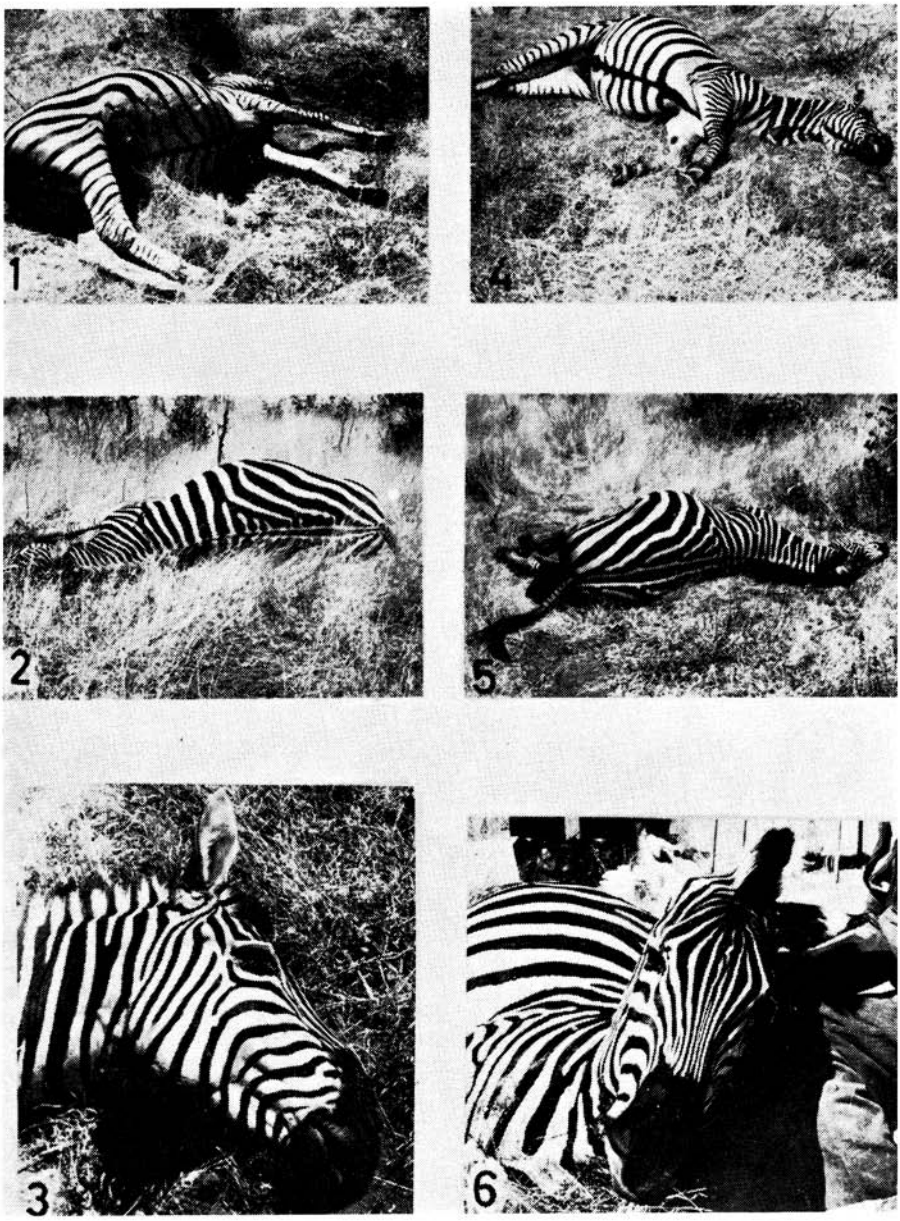

Plate 14. (1, 2 and 3). Ventral, dorsal and lateral facial views of *Equus burchelli* female from the Wankie area.
(4, 5 and 6). Ventral, dorsal and frontal views of *Equus burchelli* male from the Wankie area.

Table 14

Polymorphic sexing of *Equus burchelli antiquorum*.

Animal number	*Sex*	*No. of cells without appendages*	*No. of appendages*				*Total No. of cells counted*	$\frac{A+B}{C}$
			Type A	*Type B*	*Type C*	*Type D*		
E.b.a. 1	♂	500	0	0	0	0	500	0
E.b.a. 3	♂	500	0	0	0	0	500	0
E.b.a. 4	♂	498	2	0	0	0	500	∞
E.b.a. 6	♀	459	29	9	2	1	500	19.0
E.b.a. 7	♀	481	14	4	1	0	500	18.0

G. *Equus burchelli crawshaii* de Winton, 1896.
(= *selousi* Pocock, 1897).

Plates 13 and 14 (1, 2, 3, 4, 5 and 6).

Since there is still some uncertainty about the westward limits of *E.b. crawshaii* in Rhodesia (see above), it was decided to obtain material from zebras in two different areas.

1. *Material*

Three animals (Nos. *E.b.c.* 1, 2 and 4) of the Wankie Game Reserve in Rhodesia and two zebras (Nos. *E.b.c.* 3 and 5) of the Gorongosa National Park were investigated in July 1968. Bone marrow biopsies and blood smears were collected immediately after the animals had been shot.

The striping of the zebras from Gorongosa (see Plate 13) was found to be quite different to that from the Wankie area (see Plate 14). The animals from Wankie resemble *E. burchelli antiquorum* and *E. burchelli burchelli*, while the Gorongosa type has no shadow stripes, is more black with thin white stripes and has the reddish brown colour on the face like the mountain zebras, but restricted to the lateral aspect. It is likely that the Wankie zebras represent an intermediate type between *E. burchelli antiquorum* and *E. burchelli crawshaii* (Ansell, personal communication 1968). They have been grouped here under *E. b. crawshaii* purely as a matter of convenience.

2. *Results*

(*a*) *Chromosome number and karyotype*

The results of the chromosome counts are shown in Table 15. The diploid chromosome number was also found to be 44.

Table 15

Chromosome counts of *Equus burchelli crawshaii*.

(*a*) *Counts on dividing bone marrow cells*

Animal number	*Sex*	*Age*	*Time of collection*	*2n chromosome number* 42	43	44	45	46	*Total No. of spreads counted*
E.b.c. 1*	♂	± 8 years	12.00 p.m.	2	1	16	2	0	21
E.b.c. 2*	♂	Foal	12.30 p.m.	1	1	4	1	0	7
E.b.c. 3	♂	Adult	11.30 a.m.	0	1	8	1	1	11
E.b.c. 4*	♀	Adult	12.15 p.m.	1	5	35	1	1	43
E.b.c. 5	♀	± 6 years	9.45 a.m.	4	4	33	3	0	44
Total				8	12	96	8	2	126

(*b*) *Counts on meiotic spermatocytes*

Animal number	*Sex*	*Age*	*Time of collection*	*n chromosome number* 20	21	22	23	24	*Total No. of spreads counted*
E.b.c. 1*	♂	± 8 years	12.00 p.m.	1	2	44	3	2	52
E.b.c. 3	♂	Adult	11.30 a.m.	1	2	41	4	2	50
Total				2	4	85	7	4	102

These chromosomes were found to be morphologically indistinguishable from those of the other subspecies, *Equus burchelli burchelli* and *Equus burchelli antiquorum*, as shown in the spreads and karyograms illustrated in Plate 15 (1, 2, 3 and 4), nor was there any difference in this respect between the zebras from the Wankie area and Gorongosa.

*Likely to be intermediate types, resembling *E. burchelli antiquorum*.

(*b*) *Polymorphic sexing*

The sex difference was distinct as before and the results of counts of nuclear appendages are shown in Table 16.

Table 16

Polymorphic sexing of *Equus burchelli crawshaii*.

Animal number	*Sex*	*No. of cells without appendages*	*No. of appendages* *Type A*	*Type B*	*Type C*	*Type D*	*Total No. of cells counted*	$\frac{A+B}{C}$
E.b.c. 1*	♂	496	0	0	2	2	500	0·0
E.b.c. 2*	♂	498	1	0	1	0	500	1·0
E.b.c. 3	♂	498	0	0	2	0	500	0·0
E.b.c. 4*	♀	485	10	3	0	2	500	∞
E.b.c. 5	♀	485	11	2	1	1	500	13·0

H. *The effect of excitement and physical stress.*

To test the effect of excitement and physical stress on the number of chromosome spreads obtained by bone marrow biopsy, the following

Plate 15. Mitotic chromosomes of *Equus burchelli crawshaii*.

(1) Male (No. *E.b.c.* 1*), and (2) female (No. *E.b.c.* 4*), metaphase spread, ± × 1,200.
(3) Male karyogram, ± × 2,200 and (4) female karyogram, ± × 1,600.

pilot test was undertaken. An aged stallion that had to be destroyed for other purposes, was quietly handled and placed under Fluothane inhalation anaesthesia and a sternal bone marrow biopsy performed. Three days later the animal was driven hard for 40 minutes and slaughtered immediately afterwards.

Without delay a second biopsy was performed. Treatment of the two specimens was identical. The incidence of mitotic figures obtained from the two biopsy specimens is compared in Table 17.

Table 17

Preparation number	*Total number of mitoses*	
	Biopsy 1 *No physical stress*	*Biopsy* 2 *After physical stress*
1	45	12
2	55	13
3	40	9
4	52	7
5	35	3
Total	227	44
Average	45.4	8.8

Although this was only a preliminary trial on one animal, the results suggest that excitement and physical stress have a depressing effect on the number of mitotic figures observed in bone marrow biopsy specimens, although, remarkably enough, more cells are noted in the preparations.

On the strength of these preliminary results, rhinoceroses Nos. *C.s.s.* 12 and 13 were only chased a short distance before being darted and rhinoceroses Nos. *D.b.b.* 1 and 2 were cautiously stalked and not chased at all.

Discussion and Conclusions

The ensuing discussion and conclusions refer to mammals only, although some statements may be applicable to other classes or phyla.

A. *Mitosis and the mitotic cycle*

The existence of a diurnal mitotic cycle is generally accepted (Bullough, 1963). Gerneke (1967 and personal communication, 1966) incidentally found some evidence for such a cycle in the bone marrow of mammals, both domestic and wild.

In the case of the white rhinoceros the small number of spreads found in Nos. *C.s.s.* 1 and 2 (Table 3) are directly referable to technical difficulties experienced in the early stages of the work. In the case of No. *C.s.s.* 3 (Table 3) bone marrow was collected at 10.00 o'clock in the morning and yielded sufficient spreads.

It is considered that other factors, which will be discussed subsequently, contributed to the poor results obtained in the case of white rhinoceroses Nos. *C.s.s.* 5 to 9 and 11. Bone marrow biopsy was performed on black rhinoceroses No. *D.b.b.* 1 at 2.15 p.m. and no mitoses were found, whereas the material from No. *D.b.b.* 2, collected at 3.15 p.m., yielded a reasonable number of spreads, suggesting the occurrence of a second mitotic wave in the afternoon (perhaps occurring only in juveniles).

No mitoses could be found in the case of No. *E.z.z.* 1 (Table 7) from which the collection was done at 1.00 p.m., whereas sufficient metaphase spreads were obtained from the other mountain zebras from which material was collected between 8.30 a.m. and 11.00 a.m. In the case of *Equus burchelli* a good yield of mitotic spreads was obtained between 9.00 a.m. and 11.15 a.m. Although in some instances reasonable preparations were obtained as late as 12.00 p.m. and 12.15 p.m. (Nos. *E.b.c.* 1 and 4), there was a tendency for more anaphase stages to appear in material taken later in the morning. Interesting enough, No. *E.b.b.* 3 yielded no mitoses at 8.00 a.m., whereas Nos. *E.b.a.* 3 and 4, collected at 6.00 a.m. and 6.30 a.m. respectively, yielded an adequate number of mitotic figures for chromosome counting, but the cycle was still at the early metaphase stage. It may be noted that the material from No. *E.b.b.* 3 was collected during winter at a longitude further west.

The impression is also gained that young animals, approximately one year of age or less, have a mitotic cycle more sharply circumscribed in terms of time than older animals.

Because he found fewer lysosomes in mitotic cells than in cells in the interphase stage, Allison (1967) believed mitotic inhibition to be released by enzymes freed by breakdown of lysosome membranes, such enzymes then acting as mitotic stimulants.

Bullough (1963) tried to find an explanation more directly linked to externally visible factors. He postulated that adrenalin, probably in combination with chalone, a tissue specific substance, acts as a mitotic inhibitor. In this way mitotic rhythm and the rhythm of the animal's activity are inversely linked.

The number of observations made and the nature of the investigation do not allow one to come to any definite conclusions, but nevertheless point to a number of external factors as having some influence on the duration of mitotic cycle and number of dividing cells formed in this cycle. Possible influences that suggest themselves are: 1. temperature, 2. daylight, 3. time of year (seasons), 4. longitude and latitude, 5. height above sea-level and 6. age of the animal. These may influence the activity of the animal, either directly or indirectly, and it would appear as if activity were the main factor. These suggestions need further experimental study, which should include observations on a number of diurnal and noctural "cycles" and the occurrence of such "cycles" in nocturnal animals.

As already indicated above there is suggestive evidence that excitement

and physical stress as well as delayed collection after immobilization, had a depressing effect on the number of mitotic figures obtained by bone marrow biopsy. It is difficult to believe that such an effect could be due to unusually rapid completion of the mitoses; it is more likely that circulatory changes in the bone marrow would affect sampling.

It was not the purpose of this work to determine which factors influence the number of mitotic figures obtained, but the possibility of there being a specific, chronological cycle, as well as stress effects, is mentioned for the benefit of others.

On death of the animal, all dividing cells complete their mitosis. Due to lack of oxygen, no new mitoses are initiated and "cell death" gradually takes place. It is therefore essential to collect bone marrow within half an hour after death, otherwise mitotic figures may be too scarce.

B. *Chromosome numbers*

1. *Rhinoceros*

In a previous article (Heinichen, 1967) *Ceratotherium simum simum* (2n = 82) was described incidentally as possessing the highest chromosome number in mammals. Since then, however, Hungerford, Chandra and Snyder (1967) reported a female *Diceros bicornis* to have 84 chromosomes. The chromosome count of the one black rhinoceros female investigated here was also found to be 2n = 84. In contrast to the findings of the authors mentioned, four instead of three meta-submetacentric chromosome pairs were observed. This difference may merely represent a difference in interpretation but indicates that further observations should be made. The Indian rhinoceros, *Rhinoceros unicornis* has been described by Benirschke (personal communication, 1967) as also possessing 82 chromosomes as the diploid number.

Two rodents, *Dipodomys merriami merriami* with a "2n = 86±" and *Geomys breviceps breviceps* with "2n = 84±", (Cross, 1931) are also amongst those with high numbers. Cross (1931), however, was uncertain and listed them as "approximately" 84 and 86. The squash techniques used in earlier days were not accurate in determining such high numbers. If these two rodents are omitted, as is the case in "An Atlas of Mammalian Chromosomes" (Hsu and Benirschke, 1967), then *Diceros bicornis* (2n = 84) has the highest known chromosome number in mammals, *C. simum simum* and *R. unicornis* (2n = 82) the second highest, and *Tarsius bancanus* (2n = 80) (Klinger, 1963) and the dog (2n = 78) third and fourth respectively.

2. *Zebra*

As a result of this study it can be definitely concluded that both *Equus zebra zebra* and *Equus zebra hartmannae* have a chromosome number 2n = 32. This confirms the figure given by Benirschke and Malouf (1967) for *E. z. hartmannae* and that of Hamerton (personal communication to Benirschke, 1966). Of the two explanations given for a diploid chromo-

some number of 48 possessed by a hybrid between an *E. asinus* stallion and a mare that was possibly *E. z. hartmannae* (see above), it is now clear that the first alternative is probably the more correct one, namely that the donkey stallion had an aberrant chromosome number.

In contrast to Benirschke's finding of 42 chromosomes for the "Damara zebra", this study has revealed that the plains zebra from South West Africa, to which Benirschke probably referred, has 44 chromosomes.

As no differences were found between *E. z. zebra* and *E. z. hartmannae* nor between *E. burchelli burchelli*, *E. burchelli antiquorum* and *E. burchelli crawshaii*, it is concluded that, at the subspecies level, chromosome numbers do not offer a means of distinction. In the case of *E. b. burchelli* and *E. b. antiquorum* it has to be remembered that the subspecies status of the South West African plains zebra is by no means resolved and the same applies to the zebras in the north-western (Wankie) region of Rhodesia (see above).

The three species of zebra namely *E. grevyi*, *E. burchelli* and *E. zebra* thus have diploid chromosome numbers of 46, 44 and 32 respectively (see Table 18).

3. *Chromosome number as a characteristic of species*

As shown in Table 18 a division at species level according to the chromosome number is possible amongst the Equidae, but not amongst the Rhinocerotidae. In the latter instance *Rhinoceros unicornis* and *Ceratotherium simum simum* both have 82 chromosomes, but the chromosomes of the one species are morphologically distinct from those of the other: the white rhinoceros possesses only eight subtelocentric autosomal chromosome pairs, whereas the Indian rhinoceros has 10 such pairs.

In view of this, one could postulate in a general way that if two animals have a different chromosome number they should be regarded as specifically distinct. An exception to this rule occurs in cases of chromosome polymorphism, which has been described in several animal species: spiny mouse (Wahrman and Zahavi, 1955); common shrew (Ford, Hamerton and Sharman, 1957); impala (Wallace and Fairrall, 1967) and silver fox (Gustavsson and Sundt, 1967). The latter authors found 35, 36 and 37 chromosomes in a study on four silver foxes. Wallace and Fairrall (1967) counted 60 chromosomes in 17 impalas, 59 in 14 individuals and 58 in three. No externally visible morphological distinction could be made between these three groups.

The converse of the above rule, namely, that if two animals have the same chromosome number, they should belong to the same species, does not hold at all. It has already been pointed out that the Indian and the white rhinoceros have the same chromosome number. On the other hand their karyotypes are morphologically distinct. Similar examples are quoted in Table 19:

Table 18

Presently known chromosome numbers of the Perissodactyla

Family	*Species*	*Subspecies*	*2n chromosomes*	*Metacentric (=meta-sub-meta-centric) chromosome pairs*	*Acrocentric (=acro-sub-telo-centric) chromosome pairs*	*References*
Equidae	*E. przewalskii* (Przewalski's horse)		66	13	19	Benirschke, Malouf and Low (1965)
	E. caballus (Domestic horse)		64	13	18	Benirschke, Brownhill and Beath (1962); Trujillo, Stenius, Christian and Ohno (1962)
	E. asinus (Donkey)		62	19	11	Trujillo *et al.* (1962); Benirschke, *et al.* (1962)
	E. hemionus (Onager)		56	23	4	Benirschke and Malouf (1967)
	E. grevyi (Grevy's zebra)		46	16	6	Mutton, King and Hamerton (1964)
	E. burchelli (Burchell's zebra)	*E. b. burchelli*	44	18	3	Heinichen (in press)
		E. b. antiquorum	44	18	3	Eloff (1966); Benirschke and Malouf (1967); Heinichen (in press)
		E. b. böhmi	44	18	3	Benirschke, Brownhill and McFeely (1963)
		E. b. crawshaii	44	18	3	Present investigation
	E. zebra (Mountain zebra)	*E. z. zebra*	32	13	2	Heinichen (1967)
		E. z. hartmannae	32	13	2	Benirschke and Malouf (1967); Heinichen (in press); Hamerton (according to Benirschke, 1966)
Rhinocerotidae	*D. bicornis* (Black rhinoceros)	*D. b. bicornis*	84	4	37	Present investigation; *Hungerford, Chandra and Snyder (1967)
	R. unicornis (Indian rhinoceros)		82	0	40	Benirschke (personal communication, 1967)
	C. simum (White rhinoceros)	*C. s. simum*	82	0	40	Heinichen (1967)

*See "Discussion and Conclusions"

Table 19

Examples of distantly related species having the same chromosome number but different karyotypes.

Order	*Family*	*Genus and species*	*Chromosome number*
Rodentia	Sciuridae	*Tamiasciurus hudsonicus streatori* (Red squirrel)	46
Rodentia	Heteromyidae	*Perognathus intermedius* (Rock pocket mouse)	46
Rodentia	Cricetidae	*Microtus pennsylvanicus pennsylvanicus* (Meadow vole)	46
Rodentia	Cricetidae	*Baiomys taylori subater* (Northern pygmy mouse)	48
Rodentia	Cricetidae	*Onychomys leucogaster* (Northern grasshopper mouse)	48
Carnivora	Procyonidae	*Bassariscus astutus* (Ringtailed cat)	38
Carnivora	Felidae	*Felis catus* (Domestic cat)	38
Primates	Callithricidae	*Callithrix jacchus* (Common marmoset)	46
Primates	Hominidae	*Homo sapiens* (Man)	46

It is even possible to have distinct species with the same chromosome number and apparently morphologically identical karyotypes (Table 16).

Table 20

Examples of closely related species having apparently morphologically identical karyotypes.

Order	*Family*	*Genus and species*	*Chromosome number*
Lagomorpha	Leporidae	*Lepus alleni alleni* (Antelope jack rabbit)	48
Lagomorpha	Leporidae	*Lepus californicus eremicus* (Black-tailed jack rabbit)	48
Carnivora	Canidae	*Canis familiaris* (Dog)	78
Carnivora	Canidae	*Canis latrans* (Coyote)	78
Carnivora	Ursidae	*Selenarctos thibetanus* (Asiatic black bear)	74
Carnivora	Ursidae	*Ursus americanus* (American black bear)	74
Artiodactyla	Cervidae	*Odocoileus hemionus* (Mule deer)	70
Artiodactyla	Cervidae	*Odocoileus virginianus* (White-tailed deer)	70

On comparing the data in Tables 19 and 20, obtained from Hsu and Benirschke (1967), it will be noted that generally species with the same chromosome number, but belonging to different families, have a different karyotype, whereas species with the same family, as a rule have apparently morphologically similar karyotypes (the word "apparently" has been used, as no detailed measurements have been made on the chromosomes). Exceptions, however, do occur, as in the case of the meadow vole and pygmy mouse (Table 19).

In the final analysis it must be 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.

4. *Hybrids*

For successful hybridization there should be: 1. mating compatibility (although this may be overcome theoretically by artificial insemination); 2. compatibility of the gametes; 3. genetic compatibility and 4. acceptability of the hybrid conceptus to the maternal uterus.

Under natural conditions the behaviour of the population is such that mating between animals from different species is not likely to occur. Hybridization is the result of artificial circumstances, as a rule man-made. Incompatibility of gametes has been postulated where an attempt at hybridization has not resulted in the development of a fertilized ovum. Attempts at crossing goats with sheep have resulted in non-viable embryos and the fourth reason quoted above has then been advanced (Berry, 1938).

Interspecific hybrids in the Equidae are well known. In this regard it is of interest to note that this occurs despite considerable difference in chromosome number in many instances. In all of these cases the diploid number of the hybrid was equal to the sum of the haploid number of both parents (Benirschke, 1966), with the exception of the donkey x *E. z. hartmannae* cross referred to previously. Even in this case it seems likely that the donkey stallion had an aberrant number of chromosomes. Clearly, genetical compatibility is not a simple matter of chromosome number or karyotype and the mechanism of the first and subsequent divisions of the zygote are not upset by the disparity between chromosomes contributed by the male and female cells. In amphimixis, the two sets of chromosomes come together and the mitotic spindle seems well able to deal with the unexpected disparity.

In meiosis, however, the disparity between maternal and paternal chromosomes causes the mechanism to break down and, as a rule, no viable gametes are formed, with the result that the hybrid is sterile. Benirschke (1966) is very sceptical about the supposed fertility of the few cases of mare mules described in the literature. King *et al.* (1966) mentions "block" in the meiotic division of the primary spermatocyte at late pachytene to diplotene stage as the cause of failure to produce gametes