

**THE MAMMALS
OF AFRICA**

**AN IDENTIFICATION
MANUAL**

Editors

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Introduction

The idea of undertaking this work originated in discussions held during a colloquium on African rodents held in Brussels during October, 1964, as guests of the Institut Royal des Sciences Naturelles de Belgique. Subsequently, in early 1965, Dr. Francois Bourlière, one of the participants in the colloquium, persuaded Dr. S. Dillon Ripley, Secretary of the Smithsonian Institution, to sponsor the project as a United States contribution to the International Biological Programme. One of us (J.M.) was asked to edit the work, which was to be written by a panel of experts on the mammal groups concerned. During 1966 the status of the project was changed to that of a joint United States/South African contribution to I.B.P.

The purpose of the project, and therefore of this work, is twofold: in the first place, as its title suggests, it is intended to serve as an identification manual, for use by non-taxonomists. In recent years, partly as a consequence of the I.B.P., there has been a tremendous upsurge of interest in African mammals, particularly on the part of ecologists and conservationists. Their work has, however, been hampered by the unsatisfactory state of African mammal taxonomy. The most recent pan-African treatment is that of Allen (1939), which is now 31 years old. Since then a number of good regional studies (e.g. Ellerman et al. 1953; Schouteden, 1944-6; Swynnerton & Hayman, 1951; Smithers, 1968) as well as equally good studies of particular groups (e.g. Rosevear, 1965, 1969; Hill, 1963) have appeared, but no attempt has been made to put these into a pan-African perspective. At the same time many new species and subspecies, and even new genera (e.g. *Paracroctidura* Heim de Balsac, 1956; *Liberiotis* Hayman, 1958; *Delanymys* Hayman, 1962; and *Dendroprionomys* Petter, 1966) have been described, so that the non-taxonomist has been faced not only with the need to choose between often widely-divergent treatments of known groups, but also with a proliferation of new names that sometimes have been difficult to place in an acceptable context. Needless to say, some confusion has resulted. This work, by taking into account the progress that has been made during the past 31 years, and bringing it into the context of previous knowledge on a pan-African basis, is intended to reduce the confusion as far as possible at this stage.

It was accepted from the start, however, that it would be impossible to eliminate the confusion altogether. Much remains to be learnt about African mammal taxonomy, and much collecting and study will be required before a definitive treatment of this subject can be hoped for. From the point of view of the taxonomist, therefore, it was felt that an assessment of the state of knowledge, and of the most important problems we are faced with, would be of some value. From this arose the second purpose of this work: to identify the remaining problems most urgently in need of solution, and to assemble whatever evidence is available concerning them.

This dual task has been undertaken in two stages: the first stage was represented by the "Smithsonian Institution Preliminary Identification Manual for African Mammals" (edited by J.M.), and consisted of draft revisions by specialists on the groups concerned, which were circulated in parts by courtesy of the United States National Academy of Sciences, in serial form, to a limited number of colleagues with an interest in African mammal taxonomy. The comments and criticisms received were taken into account in the preparation of revised drafts, which constitute the subject matter of the present work.

This work will also appear in parts which will be published as they are completed, not necessarily in taxonomic order. However, each order will be published as a unit, although it may be composed of parts written by several people. All these parts will be numbered so that, when placed in numerical sequence, they will follow roughly the organization used by Simpson (1945). The different parts, and their authors, are listed on p vii

Where possible uniformity has been strived for in this work. However, complete uniformity has not been achieved, and neither do we regard it as desirable. For one thing, not all groups are equally well known, and some are vastly more complex taxonomically than others. So, while it has been possible to provide workable keys to species level in most cases, in others (such as the Soricidae and some of the Anthropoidea) this has not been possible.

Besides this, not all the authors involved in this identification manual have had the same aim in mind, nor have they used exactly the same approach. Some have been concerned mainly with providing the non-taxonomist with workable keys; others have emphasised more the needs of the taxonomist. Some have, of necessity, placed their reliance on diagnostic characters of the skull; others have, again of necessity, relied more on external features. All factors taken into account, the departures from uniformity in the various treatments are less surprising than is the degree of uniformity actually achieved.

Geographically, this manual covers roughly the area dealt with in Allen's (1939) checklist, i.e. the African continent up to the Suez Canal, and sometimes the Sinai peninsula; Madagascar; and other off-shore islands. Geographic names present a problem. As a byproduct of the political changes which have taken place in Africa during recent years, many place names have been changed, and are continuing to do so. To keep up with these name changes, particularly in a publication appearing in sections over a considerable period of time, would be impossible. Accordingly, December 31st, 1967, has been regarded as a deadline; and while we have attempted to take into account all geographic name changes until that date, subsequent changes have been ignored. The names here used are, with minor changes, those given by Ansell (1968) in his draft revision of the Artiodactyla for the Preliminary Identification Manual. The map reproduced on p v.... taken, with modification, from the same source.

This work involved the active co-operation of a number of persons and organizations, and it is a most pleasant duty to express our indebtedness to them. First of all, our warmest thanks must go to the contributors to this manual whose names and contributions are listed on p. vii. Without their knowledge and hard work this project could quite literally not have been undertaken. Our thanks go further to Dr. S. Dillon Ripley, Secretary of the Smithsonian Institution for initiating this project, and for his active support and encouragement thereof; to Dr. Richard S. Cowan, Director of the Museum of Natural History, Smithsonian Institution, for his encouragement, confidence and patient support while it has been under way; and to Mr. Anders Richter and the Smithsonian Institution Editorial staff, for copying and duplicating the Preliminary Identification Manual, as well as for their assistance in planning and executing this final version of the manual. Sincere thanks are due also to Col. Harvey E. Sheppard and the U.S. National Academy of Sciences for circulating the Preliminary Identification Manual to an ever-growing host of recipients; and to the U.S. National Committee of the International Biological Programme for generous financial support.

The South African National Committee of the I.B.P. deserves thanks for kindly granting further financial support. So does the Institute for Information and Research Services, South African Council for Scientific and Industrial Research, particularly Messrs. P.J. v.d. Westhuizen and J.F. Herbst and Dr. W.O. Everest, for their active co-operation, particularly in proof-reading and typing the revised text.

Mrs. Loma R. Whitehead kindly placed at our disposal the meticulous notes prepared by her late husband, Mr. G.H. Swynnerton, for an unpublished revision of Allen's (1939) checklist. These notes were invaluable in the preparation of this Manual, and it is a pleasure to express to her our sincere thanks for them.

To the University of Pretoria, and particularly the Chairman of the Department of Zoology, Prof. F.C. Eloff and his staff, our sincere thanks for permission to undertake this task, and for willingly suffering the inevitable consequence of reduced productivity by J.M. in other directions.

Originally we intended to thank individually all those who responded to our request for comments and criticism on the original draft revisions of the Preliminary Identification Manual. Some of these have indeed been thanked by the authors of drafts on which they have commented. However, it soon became clear that there were far too many to thank personally. At the same time, and for this very reason, their contribution has been invaluable, and in extending our warmest thanks to all of them we wish to assure them that their contributions are no less sincerely appreciated for not being individually specified.

Finally, nowhere more than in taxonomy is progress dependent on previous work. We would be remiss, therefore, if we did not thank the many men and women, scientists and amateurs, alive or long dead, on whose contributions, large and small, this work is based.

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Political subdivisions of Africa

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LIST OF PARTS AND CONTRIBUTORS

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ORDER PERISSODACTYLA

INTRODUCTION

As a group the odd-toed ungulates have long passed their zenith. They are today represented only by a few species in three families, of which two rhinoceroses and four equids (plus one which became extinct during the last century) occur in Africa. Several of these have been reduced in range and numbers, but recently conservation measures have, at least for some of them, been effective in halting, and to some extent reversing, the downward trend. The general considerations given in the introduction to Part 15 of this work (Artiodactyla), including the zoogeographical zones, apply *mutatis mutandis* to the Perissodactyla. I have taken into account all data and references available to me up to May 1971.

- | | | |
|----|---|----------------|
| 1. | Build heavy; skin very thick; three digits on each foot; two "horns" on the nose* | RHINOCEROTIDAE |
| | Build lighter; skin comparatively thin; one digit on each foot; no nasal "horns" | EQUIDAE |

Family RHINOCEROTIDAE

- | | | |
|----|---|----------------------|
| 1. | Larger; upper lip square; pronounced nuchal hump visible when head is raised; skull longer and narrower, with occipital part produced backwards behind condyles | <i>Ceratotherium</i> |
| | Smaller; upper lip pointed and prehensile; no such nuchal hump; skull shorter and broader, with occipital part not produced backwards behind condyles | <i>Diceros</i> |

Note: Ellerman, Morrison-Scott & Hayman (1953: 163) regarded *Ceratotherium* as only a subgenus of *Diceros*, but Cave (1962) listed many differences and considered them separate genera. The skull and teeth of each are well illustrated by Rode (1944, Figs 127 to 133). Each has only one living species. Blancou (1954; 1958a: 313) reported claims of a form of rhinoceros in parts of the Lowland Forest zone, but as no specimen or other evidence has been produced it cannot be discussed further.

Genus *Ceratotherium* Gray, 1867

Ceratotherium simum (Burchell, 1817) Square-lipped rhinoceros

Original distribution: Strikingly discontinuous. Between the Zambezi and Orange rivers, and again west of the Nile from northwestern Uganda to southern Chad.

The original southern range was widespread between the Zambezi and Orange rivers, though the exact westward limits are uncertain. Shortridge (1934: 427) cited specimens from Omaruru and Ugab rivers in South West Africa, also linguistic indication of former occurrence in the Gobabis and Grootfontein districts, and (Great) Namaqualand. Gaerdes (unpubl. Ms) accepts that it formerly occurred in the Kaokoveld. It occurred in southeastern Angola. Though unproven, it may also have been found between the Zambezi and Mashi rivers in southwestern Zambia (Ansell, 1959). In Mozambique Vaughan-Kirby did not find the animal itself (Bigalke, 1963: 12), but in 1904 found two skulls near the southern bank of the Zambezi above the Shiré confluence

* In the African species--two of the three Asiatic species have only one horn.

(Vaughan-Kirby, 1920: 224). This distribution covers part of the Southern Savanna and part of the South West Arid zone and, as stated by Player & Feely (1960: 3), available evidence points to an original range in southern Africa corresponding to the "Bushveld" of Acocks (1953) and Wellington (1956), which would include Mozambique south of the Zambezi, but (*pace* Shortridge, 1934: 427) not Namaqualand. The map in Bigalke (1963: 10-11) omits the northwestern part of South West Africa, and Mozambique north of the Limpopo, but includes all the Transvaal, though this author cited no actual record from those areas of the Transvaal omitted by Player & Feely (*loc. cit.*). He mentioned, however, a skull found near Kroonstad, and a semi-fossilized one from Fauresmith, both localities in the Orange Free State, slightly south of the present-day Bushveld limit.

The original northern range comprised northwestern Uganda and the southern Sudan west of the River Nile; the northeastern Congo (K.); the eastern part of the Central African Republic; and southern Chad. The exact northwestern limits are somewhat uncertain, but it may have ranged as far west as Lake Chad itself (Schomber, 1966, Fig. 4), whence two horns were said to have come (Lydekker, 1908: 37). Harper (1945: 408) pointed out that the northern range corresponded approximately with the eastern part of the Ubangi-Uele Savanna District of Chapin (1932: 90), or the Ubangi Savanna District of Bowen (1933: 256, 258). L. S. B. Leakey (*in litt.*) states that specimens have been found in Iron Age material from Kenya, but there appears to be no good evidence that it survived later in this area, and in more recent times the River Nile has evidently been its eastern limit. I accept the opinion of Heller (1913: 34) that early reports from Kenya by Speke, Grant and others must really have referred to *Diceros bicornis*.

Present distribution: The southern, nominate, subspecies was virtually exterminated shortly after the end of the 19th Century, except in Zululand. Reports of possible survival in Rhodesia (Fleming, *in litt.*, *cit.* Shortridge, 1934: 426; Fraser, 1958: 470) and in southeastern Angola (Guggisberg, 1966: 80) were never confirmed; nor was a sight record from the Kaokoveld (Barnard, 1952: 76, which Bigalke, *in litt.*, finds unconvincing). However, it evidently did survive until at least as late as 1935 in the Gorongosa area of Mozambique, though believed no longer to occur there (Sidney, 1965: 61).

However, with adequate protection the southern subspecies has eventually increased so much that it has been removed from the list of endangered mammals (Red Data Book, 1966), and has been re-introduced to the Kruger National Park, and on a smaller scale elsewhere, including other parts of South Africa, Botswana, Rhodesia, Mozambique and Swaziland (Anon., 1965a; Anon., 1965b; Bigalke, 1963: 13; Condy & Davison, 1964; Player, 1967; Rochat & Steele, 1968; Roth, 1967: 228-229; Pienaar, 1970). In the Kruger Park the species may be considered safely re-established (I. Player, *in litt.*), and in Rhodesia too the re-introduction has probably been successful (J. Vincent, *in litt.*). Outside the natural range it has been imported to other parts of South Africa; into Zambia (Attwell, 1964: 9-10) where the three survivors of the original four, plus three calves born there, are now kept in semi-captivity in Livingstone (Bainbridge, 1965: 11, and subsequent data); and into Kenya where six were being kept in semi-captivity in the Meru Game Reserve (Anon., 1966; Ansell, 1966). Totals exported from Zululand, including those sent to zoological gardens overseas, were summarized in Anon. (1968) and Vincent (1969, 1970a, 1970b, 1971).

The status and distribution of the northern subspecies, *cottoni*, is not as favourable. It was discussed in detail by Schomber (1966) but his estimate of numbers in the Congo (K.) is now out of date, and probably also that for the Sudan. The great reduction in total range is shown in his Fig. 4. It is believed extinct in Chad; reduced to a few survivors in the Central African Republic; and there has been a drastic decline in recent years in Uganda and the Congo (K.) (Red Data Book, 1967: 2; Cave, 1963; Curry-Lindahl, 1966). In view of disturbed political conditions in the Sudan it seems likely that a comparable reduction has also taken place there, so Schomber's (1966: 225) optimistic figure of 2000 may be well in excess of present numbers. The northern form is listed by the Red Data Book as apparently endangered, but further study is needed of its exact status.

In Uganda Savidge (1965) recorded that by 1964 twelve had been transferred from west of the River Nile and released in the Murchison Falls National Park, which is outside the natural range.

C.s. simum (Burchell, 1817). Southern square-lipped rhinoceros.* The southern range of the species (Player & Feely, 1960, Map 1; Bigalke, 1963: 10-11). (Including *canus* Griffith, 1827; *burchelli* Lesson, 1827; *oswelli* Gray, 1854; and *crossi* Gray, 1854.)

C.s. cottoni (Lydekker, 1908). Northern square-lipped rhinoceros. The northern range of the species.

Genus *Diceros* Gray, 1821

Diceros bicornis (Linnaeus, 1758)

Black rhinoceros

Original distribution: South of the Zambezi it occurred virtually throughout the South West Cape and Southern Savanna zones. It was also widespread, and in places common, in the South West Arid zone until at least the late 18th Century. For example Vedder (1938: 35-40) recorded that 65 were killed in 1792 between the present-day Karrasberg and Rehoboth, and a certain Pienaar saw many in the lower Swakop area near Walvis Bay around 1793; while Sargent (1954: 41) cited several place names deriving from the species in the

* The older name "white rhinoceros" is better discontinued. It is not a suitable name, and its origin has never been satisfactorily explained.

northern Cape Province and southern South West Africa.

Northwards the distribution did not exactly coincide with the main biotic zones. In Angola restricted to the south, exact limits uncertain (da Silva, 1952). In Zambia virtually throughout except the extreme west and northwest (Ansell, 1969). In the Congo (K.) only in the southeast (Schouteden, 1927: 24, rejected a second-hand report that it was formerly present in the northeastern Uele until wiped out by rinderpest*). Eastern Rwanda (Sidney, 1965: 78), though not mentioned by Frechkop (1944) even as formerly occurring there; and eastern Burundi (Schouteden, 1945: Fig. 287). Widespread in Mozambique, Tanzania and Kenya. Somalia, except the extreme northeast, from which there is no record. In Uganda the north, centre and east, but not the west or south (Sidney, 1965: 77). Eastern, southern and western Ethiopia, and as far north as the Anseba River, 16° N, 38° E. In the Sudan widespread from about El Damar, c. 17° 35' N, along the Atbara River, and thence between the Nile and the Ethiopian border south to the Kenya and Uganda borders; west of the Nile recorded only from 40 miles south of Lake Keilak, 10° N, 29° E, and north and west of Wau, 07° 43' N, 28° E (Mackenzie, 1954: 20; Sidney, 1965: 78). It is not clear whether the species had been reduced to remnant populations in the Sudan west of the Nile by human agency, or whether such isolation was of long standing. Groves (1967) assigned specimens from the Bahr-el-Ghazal area to the subspecies *brucei*, the form occurring in the northeastern Sudan, thereby implying a continuous distribution in the not too distant past, and Guggisberg (1966: 52-53) seemed inclined to accept a former wide distribution west of the Nile. Blancou (in litt.) considers that up to the beginning of the present century the range could have extended continuously between the present-day Central African Republic and the southwestern Sudan. It is, however, worth noting that *Ceratotherium simum* in this same area had, at the time of its discovery there, not suffered comparable reduction, although no less vulnerable to human predation.

Farther west *D. bicornis* once ranged through the central areas of the Central African Republic, west of about 23° E; southern Chad; northern Cameroun; northeastern Nigeria; and the vicinity of N'guigmi on the northwestern side of Lake Chad, just within the boundary of the present Niger Republic.

It seems likely that *D. bicornis* may have survived between Lake Chad and the upper Niger (about Niamey and Tillaberi, 13° - 14° N, 01° - 02° E) until fairly recent times, judging from reports quoted by Johnston (1906: 712-713)** and Bigourdan & Prunier (1937: 284-285).**

The latter also quoted a report of the species near Bouna, 09° N, 02° W, as late as 1905, but Roure (1962: 57, 174) did not mention it as ever having occurred there. Johnston (loc. cit.) mentioned reports from northern Liberia (which would be in the southern part of present-day Guinea—Kuhn, 1965: 322). While even the most western of the foregoing old records could be correct, no locality west of northeastern Nigeria has ever been confirmed by a collected specimen.

Present distribution: The species, although still covering a wide total range, has everywhere become localized, and in many places mere remnant populations or none at all remain. However, where protection is adequate good populations remain. Sidney (1965: 61-81) reviewed the more recent distribution in detail, which may be supplemented by the following more up-to-date information.

South of the Limpopo and Save rivers it is now found only in Zululand***, apart from a few re-introduced to the Addo National Park (Bigalke & Bateman, 1962: 92. The National Parks Board, in litt., confirms that they were from Kenya). In Rhodesia good numbers still occur in the middle Zambezi valley, and a few survive in one or two other places in the northeast and east; while it has been re-introduced in the Wankie National Park (Roth, 1967). In Botswana now restricted to a few in the north and northeast (Smithers, 1968: 96-97). In Zambia much reduced in range, but common in the Luangwa Valley, and viable populations remain in several other areas (Ansell, 1969). Scarce in Malawi (Sweeney, 1959: 57), but may still occur in the Wwaza Marsh (Ansell, 1969: 187). According to recent Malawi tourist literature, a few remain in the Kasungu Game Reserve in the Central Province. In the Congo (K.) believed extinct since about 1957 (K. Curry-Lindahl, in litt.). Six were re-introduced to Kagera National Park, Rwanda, from Tanzania (Haezaert, 1959). In Tanzania and Kenya the species still occurs in good numbers in many places. In Somalia it survives in the south, although almost extinct (Funaioli & Simonetta, 1966: 296). In Ethiopia the only definitely known survival areas are between the lower Omo Valley (05°30' - 06°30' N) and the Sudan border (09° - 10° N), between the Dabus River and the Sudan border, and at about 04° - 05° N in the Daua Parma Valley near the Kenya border (J. H. Blower, in litt.). In Uganda still common in the north (Bere, 1958: 419). In the Sudan no longer found in the northeast between the Nile and the Ethiopian border, and scarce elsewhere (Sidney, 1965: 78; Mackenzie, 1954: 20; Schomber, 1963: 32-33). Still found in the Central African Republic, Chad, and northern Cameroun. In Nigeria considered extinct (Petrides, 1965: 7), and must be completely absent west of Nigeria, whatever its former distribution there (see above under original distribution).

D. bicornis (Linn., 1758). Western Cape Province, and north at least to middle South West Africa. Extinct. (Including *africanus*, Blumenbach, 1803; *keitloa* A. Smith, 1836; *gordoni* Lesson, 1842; *niger* Schinz, 1845; *camperi* Schinz, 1845; and *capensis* Trouessart, 1898.)

D. b. chobiensis Zukowsky, 1964. Konsumbia, parent streams of the Loma, tributary of the Cuando,

* Rinderpest is a bovine disease and is not known to affect rhinoceros.

** These authors simply referred to "rhinoceros", but this can doubtless be taken as *D. bicornis*.

*** Guggisberg (1966: 48, footnote) stated that four were transferred from Umfolozi to the Kruger National Park in 1961, but this was not mentioned by Pienaar (1963).

Angola. Known only from southeastern Angola, where it appears to be isolated, with *minor* west as well as east of it.

D.b.minor (Drummond, 1876). Transkei (where now extinct), and northern South West Africa, northeastwards to Lake Victoria and northeastern Tanzania. It is not clear whether this would be the Botswana form, or whether the latter might be closer to *chobiensis* (see Groves, 1967: Fig. 2). (Including *major* Drummond, 1876; *keitloa* Drummond, 1876, *nec* A. Smith, 1836; *holmwoodi* Sclater, 1893; *occidentalis* Zukowsky, 1922; *punyana* Potter, 1947: 385; *angolensis* Zukowsky, 1964: 73; *nyasae* Zukowsky, 1964: 93; and *rowwmae* Zukowsky, 1964: 94. Mertens, 1966, pointed out that the last two names are invalid.)

D.b.michaeli Zukowsky, 1964. Between Engaruka and Serengeti. Kenya east of the Rift Valley, and extreme northern Tanzania. (Including *rendilis* Zukowsky, 1964: 122.)

D.b.brucii (Lesson, 1842). Northern Somalia and Ogaden to Sennaar and Bahr-el-Ghazal district. (Including *keitloa* Blanford, 1870, *nec* A. Smith, 1836; *somaliensis* Potocki, 1897; *palustris* Benzon, 1947: 529; and *atbarensis* Zukowsky, 1964: 141.)

D.b.ladoensis Groves, 1967. Shambe, upper Nile, near Lado. Shambe and Gondokoro to Baringo district, thence to Lake Naivasha. (Including *somaliensis* J. Allen, 1914, *nec* Potocki, 1897; and *ladoensis* Zukowsky, 1964: 124, invalid--see Mertens, 1966.)

D.b.longipes Zukowsky, 1949. Described from Mogrum, Chad. Extends over the species range from Chad and the Central African Republic westwards.

Note: The works of Hopwood (1939) and Zukowsky (1964) have been superseded by Groves (1967), whose classification is followed here. Hollister (1924: 136) considered *brucii* (Lesson, 1842) a nomen nudum, but Groves accepted it as valid. *D.b.ladoensis* must date from Groves, 1967, Zukowsky's proposal of the name being invalid (Mertens, 1966). Groves omitted mention of *Rhinoceros cucullatus* Wagner, 1835, which was regarded by Hollister (loc. cit.) as unidentifiable, perhaps even referring to an Asiatic species. Joubert (1970), who did not cite Zukowsky (1964) or Groves (1967), considered the form in northern South West Africa inseparable from that of Natal. But he had not examined specimens from southern South West Africa or the western Cape Province and so used the name *D.bicornis bicornis*, which Groves (op. cit.) restricted to the form in these southwestern areas. Apart from this Joubert's conclusion supports that of Groves.

Family EQUIDAE

Genus *Equus* Linnaeus, 1758

I follow Ellerman & Morrison-Scott (1951: 341), Ellerman et al. (1953: 164), and Azzaroli (1966) in regarding *Equus* as the only valid genus for the living species of the family with *Asinus*, *Dolichohippus* and *Hippotigris* (including as synonyms *Quagga* and *Pseudoquagga**) as subgenera. The close affinity of the various species is evident from the readiness with which they interbreed in captivity (Gray, 1954: 45-59), though the hybrids are sterile.

Frechkop (1967) noted that in the family the chromosome numbers decrease from north to south. Chromosome numbers of the African species (King, Short, Mutton & Hamerton, 1966: 516, modified for *E. zebra* and *E.z. hartmannae* by Heinichen, 1967, 1969, 1970) are:

<i>E.africanus</i>	2n = 62
<i>E.grevyi</i>	2n = 46
<i>E.burchelli</i>	2n = 44
<i>E.zebra</i>	2n = 32

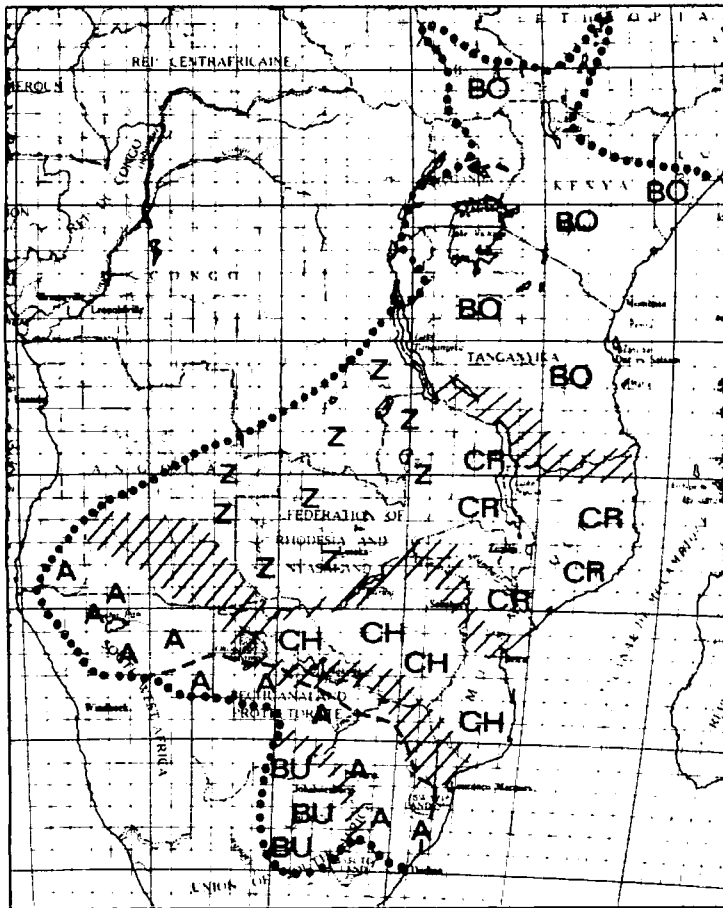
There are three living species of zebra. Skorkowski (1955) ranked both *grevyi* and *burchelli* as conspecific with *zebra* on craniometrical grounds. This is quite unacceptable, as it ignores not only their very distinct stripe patterns and other external differences, but also the different karyotypes noted above and sympatry. In South West Africa *E.burchelli* overlaps in range with *E.zebra* (Shortridge, 1934: 390; Bigalke, 1958: 487), and in the north of its range occurs alongside *E.grevyi* without hybridization (Keast, 1965).

Equus wardi Ewart, 1904 was based on a menagerie hybrid between *E.zebra* and *E.burchelli*. Similar crosses have been made several times since (Rzasnicki, 1941, 1951: 243-245).

Cabrera (1936), Lundholm (1951), Ellerman et al. (1953) and Azzaroli (1966) all accepted *E.quagga* as specifically distinct from *E.burchelli*. This is also my view.

* *Pseudoquagga* Hoffstetter, R., 1951: 690 proposed as a subgenus, type species *E. granti* de Winton, 1896.

Map 1



Distribution of *Equus burchelli* (Gray, 1824).
 Dotted line--putative original range limit;
 broken line--southern limit of present range;
 diagonal hatching--areas of probable intergrading.
 BU--*E. b. burchelli*; A--*E. b. antiquorum*;
 CH--*E. b. chapmani*; Z--*E. b. zambesiensis*;
 CR--*E. b. crawshati*; BO--*E. b. boehmi*

- | | | |
|----|---|------------------|
| 1. | Body striping limited to a dorsal line and single shoulder stripe at most; muzzle pale (subgenus <i>Asinus</i>) | <i>africanus</i> |
| | Either wholly striped, or with striping at least on head and neck; muzzle dark | 2 |
| 2. | Size larger, up to about 150 cm at withers; head and ears large in proportion; body markings with numerous vertical stripes behind shoulders, ending on haunches in a "triangle" pattern (subgenus <i>Dolichohippus</i>) | <i>grevyi</i> |
| | Size smaller; pattern not as above (subgenus <i>Hippotigris</i>) | 3 |
| 3. | Stripes on croup forming "grid-iron" pattern; dewlap present on throat | <i>zebra</i> |
| | Stripes on croup not forming "grid-iron" pattern; no dewlap | 4 |
| 4. | Striping whitish on dark ground, and usually restricted to head, neck and foreparts of body | <i>quagga</i> |
| | Striping dark on a light ground, over whole of body, and usually at least partly on legs | <i>burchelli</i> |

Note: For skull characters see Azzaroli (1966)

Equus africanus (Fitzinger, 1857)

Wild ass

Original distribution: It is extremely difficult to determine accurately the original range of the true wild ass, but it certainly seems to have been endemic to the western parts of the Saharo-Sindien zone of Ranck (1968: 54-55), although surprisingly not mentioned by that author. Sidney (1965: 7-12) noted the difficulty of distinguishing between true wild asses, feral and crossbred animals; and discussed various opinions on the status of present-day populations. The species occurred in the Atlas region until about A.D. 300 (Harper, 1945: 349, 353), but there seems to be no definite evidence of a continuous range within historical times across the northern part of the continent to the Sudan. Records during the past century indicate only a remnant distribution in parts of the Sudanese and Somali Arid zones, from the northeastern

Sudan, southeast to eastern Ethiopia and northern Somalia. It has been claimed that true wild asses occur in the Tibesti area of northern Chad (Malbrant, 1936: 27) and in the vicinity of the Hoggar massif in the central Sahara (Antonius, 1931; Dupuy, 1966: 44). But the status of these animals has not been conclusively proved, and they could well be feral, or at least crossbred, animals, as maintained by Monod (1933) in respect of those in the Hoggar area, and more recently for those of Tibesti by Ziccardi (1970: 205-206) who published a photograph of one such animal. Johnston (1906: 714) mentioned reports of alleged wild asses in the western Sahara, to which the same considerations would no doubt apply as to those in the Hoggar and Tibesti. The asses on Socotra Island (c. 300 km off the northeastern tip of Somalia) are not indigenous, but believed to be descendants of Nubian stock introduced by man many centuries ago (de Winton, Forbes & Ogilvie-Grant, 1903: 10-11). The possibility (Harper, 1945: 368) of the species having once existed in a wild state in the region of Syria and Israel has never been proved, and seems unlikely. Groves (1966: 4-5) thought it likely that a true wild ass occurred, or at least formerly occurred, in southern Arabia, but in view of the difficulty of telling whether those recently reported were truly wild or just feral he left the question open.

Present distribution: True wild asses, *E.a.somaliensis*, survive in fair numbers in the Danakil region of eastern Ethiopia, approximately 09° - 15° N; but there is no recent evidence of their continued presence in the Ogaden, farther southeast (Blower, 1968: 279, and in litt.). In Somalia a very few remained at least until 1964 in and northwest of the upper Nogal Valley (Funaioli & Simonetta, 1966: 296-297). In 1967 there were some asses living wild on the western side of the Red Sea Hills in northern Eritrea, about 16° 30' N, 37° 30' E, but it was not known whether they were of feral origin (J. H. Blower, in litt.). Those in the Sahara have been claimed to be truly wild (see above); but on balance it seems likely that *E.a.somaliensis* is the only form of really wild ass now surviving. In the Red Data Book *africanus* (1966) and *somalicus* (= *somaliensis*--1968) are both listed as critically endangered.

E.a.africanus (Fitzinger, 1857). Nubian wild ass. The Nubian Desert of northeastern Sudan, east of the River Nile, south to the Atbara River and, according to Sidney (1965: 9), even to about Sennaar. In northern Eritrea to about Massawa. Perhaps at one time also ranging into Egypt, though not definitely recorded there in the 19th Century (Flower, 1932: 432); and perhaps also west of the Nile to the western Sahara. It seems probable that this subspecies no longer survives in the pure state. Of surviving populations possibly that on Socotra Island, imported many centuries ago, may be the nearest to the true *africanus*. (Including *diana*e Dollman, 1935; *hippogrurus* Schomber, 1963: 121 *nec* H. Smith, 1841; and, possibly, *sahariensis* Dupuy, 1966: 44.)

E.a.somaliensis Noack, 1884. Somali wild ass. Northeastern Ethiopia in the Danakil area, south to about 06° N, and northern Somalia east to about the upper Nogal Valley. (Including *somalicus* Sclater, 1884; *taeniopus* de Beaux, 1928, *nec* Heuglin, 1861 which, according to Groves, 1966: 7, was based on a hybrid; and *aethiopicus* Denman, 1957: 116.)

E.a.atlanticus P. Thomas, 1884. Atlas wild ass. Extinct. Formerly the Atlas region of northwestern Algeria and the adjacent parts of Morocco and Tunisia, where it survived to about 300 A.D.

E.a.arabicus (Trumler, 1961: 116). As noted above, Groves (1966: 5) regarded the existence, or former existence, of a genuine wild ass in Arabia as likely, but unproven. Should it be a valid subspecies it would require a name, Trumler's being, according to Groves, a *nomen nudum*.

Note: The above synonymy follows Groves (1966), including adoption of *africanus* as the specific name, in accordance with the usage proposed by Bohlken (1958), rather than the more usual *asinus* based on the domestic donkey. Ziccardi (1970) reverted to recognition of *E.a.taeniopus* Heuglin for the Danakil ass, as separable from *somaliensis*.

Equus grevyi Oustalet, 1882

Grevy's zebra

Original distribution: Endemic to the Somali Arid zone. Widespread in northern Kenya from east of Lake Rudolf and the eastern wall of the Rift Valley, and north of Mount Kenya and the upper Tana River, its southward limit being about 01° S between the Tana and the Somalia border; but evidently not recorded from northeastern Kenya along the Ethiopian border (Stewart & Stewart, 1963: 10; see also Roosevelt & Heller, 1922, Map 39). In Ethiopia it occurs in the south and east, though scarce or absent in the Boran area north of the Kenya border. It ranges from Lake Rudolf up the east side of the Omo River to about Lake Zwai. It is found in the Awash National Park, 08° N, 39° E (Blower, 1968: 279) and in the Danakil country to the northeast (Glass, 1965: 179). In eastern Ethiopia its range included the Ogaden. In the former British Somaliland it used to occur in the west (Drake-Brockman, 1910: 105). In the former Italian Somaliland definite records are limited to the south, in the vicinity of the Juba and Webi Schebéli rivers, but it may once have occurred as far northeast as the upper Nogal Valley (Funaioli & Simonetta, 1966: 298).

Present distribution: In Ethiopia it may no longer survive in the southern Ogaden (Blower, 1968: 280); and in Somalia is now limited to a few in the vicinity of the lower Webi Schebéli. Elsewhere its range is believed substantially unaltered.

Note: Rzasnicki (1951: 242) considered the species monotypic, regarding *faurei* Matschie, 1898 and *berberensis* Pocock, 1902 as synonyms of *grevyi*.

Equus zebra Linnaeus, 1758

Mountain zebra

Original distribution: Mountainous country, mainly in coastal areas, from about 160 km north of Mossamedes in Angola, through coastal South West Africa to the southwestern and southern Cape Province, and thence as far eastwards as Cathcart Division, i.e. about 27° E. Shortridge (1934: 390) pointed out that it nowhere ranged farther inland than 100 miles (160 km) and usually less, although Antonius (1938: 562) thought that it formerly ranged more inland, noting older records from Kenhardt District (27° S, 18° E), and he also suggested that it might have occurred at one time about the upper Nosob River, which would be about 22° S, 18° E. Bigalke & Bateman (1962: 95) mentioned an old record by Burchell, which they were inclined to accept, from the vicinity of Kuruman (27° S, 23° E). This would have been considerably farther inland than the species has otherwise been recorded. Roberts (1951: 245) thought this record of Burchell mistaken, but R. Liversidge (in litt.) accepts it, pointing out that Burchell was a very careful observer who left clear descriptions of the three South African equids, and who reported *E. zebra* in just the kind of mountainous habitat where it occurred elsewhere. Dr. Liversidge has also drawn attention to an old record by Krebs of a specimen collected near Wepener in southwestern Lesotho, which seems likely to have been *E. zebra*.

Present distribution: There is no very recent information from Angola. In South West Africa the range may not extend as far inland as in the past (see above under original distribution), but has not much altered in recent times, although there has been a decline in numbers. The subspecies concerned (*hartmannae*) is currently listed as rare in the Red Data Book (1967). In South Africa the species in 1970 survived only in the Cradock Mountain Zebra National Park and a few unprotected areas outside it, apart from three specimens in the De Hoop Provincial Wildlife Farm according to Millar (1970), who pointed out that there had been a considerable increase in the protected area, but a continued decline elsewhere. Millar listed 140 known individuals, of which 98 were in the Cradock National Park.

E. z. zebra Linn., 1758. Cape Mountain zebra. The southwestern and southern Cape Province. Perhaps formerly in isolated populations around Kuruman and in southwest Lesotho. (Including *montanus* Burchell, 1822; *campestris* Gray, 1852; *indica* Trouessart, 1898; and *frederici* Trouessart, 1905.)

E. z. hartmannae Matschie, 1898. Hartmann's mountain zebra. The Angolan and South West African range of the species. Perhaps also at one time extending south of the Orange River (Shortridge, 1934: 391), if so presumably intergrading with the nominate race. (Including *penricei* Thomas, 1900; and *matschiei* Zukowsky, 1924.)

Equus quagga Gmelin, 1788

Quagga

Original distribution: Penzhorn (1969) pointed out that the word "quagga" is the equivalent in Afrikaans of "zebra" in English, and that, strictly speaking, it applies to all three indigenous South African equids. Care has to be taken, therefore, in assessing old records of "quaggas" bearing on the limits of range and possible sympatry of *quagga* and *burchelli*.

E. quagga occurred virtually throughout the South West Cape zone and in part of the South West Arid and Southern Savanna zones. It was found in the southern and eastern parts of the Great Karroo, and possibly extended northwest into Great Namaqualand, where Levallant is believed to have seen it (Roberts, 1951: 246; Sargent, 1954: 41). If this is correct then the Nama Hottentot tradition mentioned by Shortridge (1934: 401) would no doubt have referred to *E. quagga* rather than to *E. burchelli*. This would accord with the believed absence of the latter species, except marginally, from the South West Arid zone (see further below under *E. burchelli*). In the Southern Savanna zone *E. quagga* did not occur east of the Kei River, and only to a very limited extent, if at all, north of the Vaal River. Bryden (1905: 85) stated that it ". . . was seldom found north of the Vaal River" and Sclater (cit. Shortridge, 1934: 41) considered that it did not occur there. Sargent (1954: 41) mapped two localities north of the Vaal on the basis of place names, but as mentioned above, care has to be taken over old records of "quaggas", so these might not be authentic. The eastern limit of the species may have been about the Orange Free State/Natal border (Grout, cit. Shortridge, 1934: 402). From the historical records of Harris (1840) and also Liebenberg (1964) the distribution of *E. quagga* and *E. burchelli* overlapped in the Orange Free State.

Present distribution: Extinct. Animals which died in European zoological gardens in 1872 (London), 1875 (Berlin) and 1883 (Amsterdam) were the last known survivors in captivity. In the wild state it may possibly have survived in the Orange Free State until as late as 1878, according to Willoughby (1966: 61). From time to time there have been claims that the species may have survived in South West Africa (see for example Foran, 1960), but these have been based on pious hope rather than anything else and remain without substantiation. One definite attempt to investigate the matter led to the conclusion that reports of quaggas may have been based on hybrids between *E. zebra* and feral donkeys (Carp, 1952: 104), which seems possible.

Note: Although several subspecies have been named material is not sufficient to distinguish between geographic and individual variation (Rzasnicki, 1951: 240; Roberts, 1951: 247). The latter author, however, considered that *isabellinus*, although without definite locality data, may have been a pale form from the vicinity of the lower Orange River. This would accord with the general pallor of mammals in the area, and, although speculative, seems not unreasonable. Unfortunately there is little chance of fresh evidence coming to light. (Synonyms of *quagga* are *quagga* Lesson, 1827; *quaccha* Griffith, 1827; *isabellinus* H. Smith, 1841, possibly valid--see above; *Lorenzi* Lydekker, 1902; *greyi* Lydekker, 1902; *danielli* Pocock, 1904; and *trouessarti* Camerano, 1908.)

Equus burchelli (Gray, 1824)

Burchell's zebra

Original distribution: See Map. Apparently the species range did not coincide very closely with the major biotic zones. In the South West Arid zone it seems to have occurred in South West Africa, southward to about the Gobabis area (Shortridge, 1934: 401); in Botswana rather more extensively than today, its former limits perhaps about coincident with the 400 mm (= c. 12 in) isohyet of mean annual rainfall (cf map in Smithers, 1968: 9); and it also ranged into the northeastern Cape Province in the Mafeking area and between the present-day Campbell and the Vaal River. The limits of the South West Arid zone seem to have encroached, during the past century or so, some way into the Southern Savanna, and when the species occurred in the foregoing areas conditions were doubtless less arid than today. However, as pointed out by R. C. Bigalke (1964), there is no reason to suppose that it ever occurred farther southwest in the drier parts of the Kalahari.* The maps in Cabrera (1936: 104) and Rzasnicki (1951: 241) are misleading in this respect. In the adjacent part of the Southern Savanna it did not occur south of the Orange River (nor, presumably, in Lesotho). It perhaps occupied most of Natal, though its exact southern limit there is uncertain. Northwards from South Africa it occurs, or once occurred, in the Southern Savanna in eastern and northern Botswana; northern South West Africa; southern and southeastern Angola; Rhodesia; Mozambique; Zambia; Malawi; southeastern Congo (K.); Tanzania; Rwanda (although apparently not Burundi, according to Schouteden, 1945, Fig. 284); southern Uganda and southwestern Kenya. In the Somali Arid zone the range is northeastern Tanzania; Kenya (except the northeastern part); northeastern Uganda; southeastern Sudan, to about as far northwest as Shambe, 07° N, 30° E; southern Somalia in the vicinity of the lower Juba River; and Ethiopia, from the extreme southwest through the Rift Valley to about Lake Zwai.

Present distribution: Though reduced or locally exterminated in many places it is only the southernmost part of the original range that has been substantially altered (see map). In Botswana, and perhaps the northeastern Cape Province, increased dessication of the country was probably the main factor; but in the Orange Free State, the Transvaal, and Natal, human predation combined with agricultural development may have been the primary cause. Eloff (1966: 199) considered that "gene pool pauperization" was the primary cause of its reduction in the southern part of its range, but he appears to have underestimated the impact of firearms and settlement which, in South Africa particularly, reduced ungulates of many other species during the past two centuries. Adverse and cumulative genetic effects may well impair the chances of survival of progressively isolated and decreasing populations, without necessarily being the cause of the initial decline. Further, there is evidence that in the related *Equus zebra* a reduced population may be capable of increasing again from a very low level if given protection within suitable habitat (Millar, 1970). Eloff's suggestion (1966: 204) that *E. burchelli* is "more vulnerable to nagana" seems likewise unjustified, as there is good evidence that tsetse do not feed on the species (Weitz & Glasgow, 1956: 603, 606-607).

As indicated on the map, the species is extinct in the Gobabis area; much of its Botswana range; the Cape Province (Bigalke & Bateman, 1962: 92); the Orange Free State; most of the Transvaal (Kettlitz, 1955: 145); Natal, except for Zululand (Vincent, 1962: 113); and in Mozambique south of 23° S (Sidney, 1965: 30). Re-introductions have, however, been made in some central areas of the Transvaal (Kettlitz, 1962: 123-124), the Orange Free State (Meester et al., 1964: Per. 2), and on some farms in Natal (J. Vincent, in litt.). It has also been introduced artificially into the Cape of Good Hope Nature Reserve (Anon 1967/68: 34), which is well outside the natural range of the species.

In other parts of its range the species has in many places become scarce or locally extinct, but the general distribution remains largely unaltered.

E. b. burchelli (Gray, 1824). Extinct. Formerly occurred in the Orange Free State and northeastern Cape Province, extending into southern Botswana and the southwestern Transvaal. (Including *zebra* Burchell, 1822, *nec* Linn., 1758; *montanus* F. Cuvier, 1826, *nec* Burchell, 1822; *zebroides* Lesson, 1827; *festivus* Wagner, 1834; *campestris* H. Smith, 1841; *typicus* Selous, 1899; and *paucistriatus* Hilzheimer, 1912.)

E. b. antiquorum H. Smith, 1841. From southern Angola, across northern South West Africa through southern Botswana and much of the Transvaal to Natal. (Including *wahlbergi* Pocock, 1897; *transvaalensis* Ewart, 1897; *pococki* Brasil & Penner, 1909; *kaufmanni* Matschie, 1912; and *kaokensis* Zukowsky, 1924. The names *kaufmanni* and *transvaalensis* probably refer to intergrades.)

E. b. chapmani Layard, 1865. Northeastern Botswana, most of Rhodesia, and southern Mozambique. (Including *selousi* Pocock, 1896; ? *markhami* Tichomirow, 1878.)

E. b. zambeziensis Trouessart, 1898.** Zambia west of the Muchinga escarpment, eastern Angola, and southeastern Congo (K.).

E. b. crawshaii de Winton, 1896. Central and northern Mozambique, Malawi, and Zambia east of the Muchinga escarpment. (Including *tigrinus* Johnston, 1897; *foai* Prazak & Trouessart, 1898; and *annectens* Rothschild, 1906.)

* I consider that the record of former occurrence in Great Namaqualand, based on Nama Hottentot tradition (Shortridge, 1934: 401) must have referred to *Equus quagga*, as already noted under that species).

** Usually attributed to Prazak, 1898, but this work does not appear to have been validly published.

E.b.boehmi Matschie, 1892. The species range north of *zambeziensis* and *crawshaii*. (Including *granti* de Winton, 1896; *jallae* Camerano, 1902; *muansae* Matschie, 1906; *mariae* Roux, 1910*; *goldfinchi* Ridgeway, 1911; *cuninghamei* Heller, 1914; *borensis* Lönnerberg, 1921: 181; and *isabellae* Ziccardi, 1959: 296.)

Note: Despite the extensive literature the subspecies arrangement of *E.burchelli* has never been satisfactory. The pattern of striping has been the principal, and often the only, character used in bestowing a multiplicity of names although, in common with other striped or spotted animals, there is great individual variation. Kattinger (1952: 118), Morris (1965: 351) and Eloff (1966: 199) postulated a north-south cline in intensity of striping, the last-named author stating: "The Burchell zebras exhibit such a typical character gradient (Huxley cline) in decrease of striping from the Sahara southward". This is not true. The most fully striped form is undoubtedly that found in the area centred on the lower Zambezi valley, for which the prior name is *crawshaii*, and less intensively marked forms are found north, west and south of it.

Full leg striping is retained north and west of the range of *crawshaii*, but it decreases to the southwest and south where, at the extreme limits in each direction, occur some animals with virtually completely white limbs. While at least a suggestion of "shadow" striping may occur in *crawshaii*, the close pattern of the main stripes leaves little room for it, but shadow striping increases progressively to the west and south-- it is thus fairly limited in Zambia and the northern parts of Rhodesia, for example, but much in evidence in Natal and Etosha Pan zebras. Northwards of the range of *crawshaii* shadow striping is variable, although not as consistently or as well developed as in the south and southwest of the species range. Williams (1967: 200) considered that Grant's zebra and Boehm's zebra were distinct on the basis of shadow striping, but Rzasnicki (1951: 220) maintained that in East Africa this character was of no racial value. Maneless zebras occur in East Africa, *borensis* and *isabellae*, from the southern Sudan and southern Somalia respectively, having been named as maneless forms. But Mohr (1962) did not recognize them as valid, and Dittrich (1964) agreed with this. Further, maneless individuals are now known from other localities, the southernmost being Ngorongoro in northern Tanzania (Dathe, 1968; Kayser, 1970). Clearly it is not a constant geographical character whatever its nature and origin.

Occasionally very striking extreme individual variation may occur, as for example illustrated in Anon (1962) and King (1965: 115).

Important revisions of the taxonomy of *E.burchelli* have been by St. Leger (1932), Cabrera (1936), Antonius (1951) and Rzasnicki (1951). All except Cabrera regarded it as conspecific with *quagga*, which is no longer accepted.

The arrangement here adopted largely agrees with that of Rzasnicki (1951). Cabrera was wrong in synonymizing *crawshaii* with *boehmi*, as was rightly pointed out by Lawrence & Loveridge (1953: 76-77). Having examined the type of *selousi* in the British Museum (Nat. Hist.) I agree with Rzasnicki (1951: 232) that Cabrera was also incorrect in his treatment of this form which, as Rzasnicki maintains, seems better placed with *chapmani*, although it might perhaps represent an intergrade. The type locality of *chapmani* itself unfortunately seems to be in or near an area of intergrading. Rzasnicki recognized *zambeziensis*, although without giving any diagnostic character to distinguish it from *boehmi*, as keyed by Cabrera (1936: 108). Azzaroli (1966: 10-11), from two skulls in the Turin Museum, thought that *zambeziensis* might be differentiated on the basis of its elongated braincase, and has subsequently (in litt.) confirmed that this seems to hold good for four further skulls from the Kafue National Park in Zambia. Accordingly, *zambeziensis* is retained for the form in Zambia west of the Muchinga escarpment and the adjacent parts of Angola and the Congo (K.). There is no doubt of the close resemblance between the zebras of the Etosha Pan area of South West Africa and those of Zululand. This is explicable on the basis of a formerly continuous distribution of *antiquorum* from northwest to southeast, now broken by a large area where the species has become extinct. Both Rzasnicki (1951: 234-238) and Roberts (1951: 247-249) independently considered that the nominate *burchelli* survived in what I have regarded as the remaining northwestern range of *antiquorum*. It may be that *antiquorum* is, as these authors maintained, a synonym of *burchelli*, though I have adopted the more usual view that *burchelli* was even more lightly striped and is now extinct.

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* The name *mariae* is usually attributed to Prazak, 1898, but as noted under *zambeziensis* it appears not to have been published, and *mariae* must accordingly date from Roux, 1910, who applied it to a specimen from east of Lake Naivasha, which is therefore the type locality (Cabrera, 1936: 107).

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