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10. *A Critical Revision of the Quaternary Perissodactyla of Southern Africa* *.—By H. B. S. Cooke, M.A., D.Sc., F.G.S., F.R.Met.S., F.R.S.S.Afr.

(With 30 Text-figures.)

Introduction.

The study of fossil mammals in Southern Africa has been far from systematic and, with a few rare exceptions, writers have been more concerned with placing new species on record than with studying the fauna and revising our knowledge in the light of later discoveries. The first fossil mammal known to have been found in this region is the giant "*Bubalus*" *bainii*, whose horns and damaged skull were recovered in 1839 by the remarkable civil engineer and naturalist Andrew Geddes Bain from alluvial deposits of the Modder River, Orange Free State. The material was described only in 1891 by the British palaeontologist Seeley, and the next record of a fossil mammal appeared in 1906 when Dr. R. Beck described a mastodon tooth from the gravels of the Vaal River. In the following year another German scientist, Professor E. Fraas, gave a further account of this tooth and commented on other remains from the gravels. Also in 1907, the celebrated American palaeontologist Professor W. B. Scott described a collection of fossil mammals from the coast of Zululand. Two years later Dr. Robert Broom made the first of his long series of contributions to mammalian palaeontology in South Africa with his descriptions of a new antelope from alluvial deposits at Caledon and of a new giant horse from a limestone fragment washed up on the beach near Maitland, in the south-western Cape. In 1913 Broom described an assemblage of mammalian fossils from the thermal springs at Floris Bad, and in later years he described several new mammals from the Vaal River gravels and various open sites.

In the past twenty-five years the initiative in the description of South African material has passed from the hands of outside experts like Seeley, Scott and Fraas to those of local workers such as Broom,

* Manuscript submitted in January 1946. Appendix added in October 1950.

Haughton, Dart, van Hoepen, Middleton Shaw and others. During this period a considerable body of material has been collected, but much of it has remained largely unstudied and undescribed unless something obviously new was noticed by the individuals through whose hands it passed. Even then it has been for the most part only the new genera and species which were described, and the fauna as a whole has received little attention. Van Hoepen has large collections from his site at Cornelia which still await description, the South African Museum at Cape Town and the McGregor Museum at Kimberley have hundreds of specimens collected over a long period, and other museums have smaller quantities of undescribed material. Since its inception in 1931 the Archaeological Survey of the Union has acquired notable collections as a result of the activities of several collectors, and little of this material has been described or considered as a whole.

During the years 1935–36 a joint survey of the Vaal River basin was carried out by Messrs. P. G. Söhnge and D. J. L. Visser of the Union Geological Survey, and Professor C. van Riet Lowe, Director of the Archaeological Survey, and during the survey much fossil material was recovered from various horizons in the deposits. The results of the geological and archaeological investigations were published in 1937, under the title "The Geology and Archaeology of the Vaal River Basin", as Memoir No. 35 of the Union Geological Survey, and it was intimated in the letter of transmittal of this Memoir that the fossil material collected would be described at a later date. Through the courtesy of the Director of the Geological Survey all this material was placed in the hands of the present writer for examination and report.*

It soon became apparent that a description merely of the material comprising this collection would be of little value, since it would not include all the species recorded from the deposits, and also because there occur in Pleistocene deposits other than those of the Vaal River basin many species which are likely at any time to be found within this area. For example, a tooth found at Christiana by a student and brought to the writer while this account was in course of preparation has been identified as belonging to a species hitherto recorded only at Cornelia in the Orange Free State. It was also only too obvious that the study of our fossil mammals had been far from systematic and that, with the notable exceptions of Haughton and Shaw, writers had been concerned more with placing new fossils on record than with comparative studies and revision of our knowledge in the light of

* See Appendix.

further discoveries. There exists a very considerable confusion of nomenclature and a multiplicity of specific names which renders the task of description of additional material virtually impossible unless it is accompanied by an amount of concurrent specific revision which would obscure the value of any account of the faunal assemblages. Indeed, it appears that until the material already described has been reviewed and new assessments made of the described species, it is of little value to proceed with the many other problems which our fauna presents.

In the course of his investigations on the cave deposits, Broom has to a certain extent reviewed and revised the Primates, Insectivora, Rodentia and Carnivora. Furthermore, these orders furnish the bulk of the cave fauna, and are virtually unrepresented in the material from open sites. Most of the fossils recovered from the Vaal River basin, surface deposits and other open sites belong to the Perissodactyla, Proboscidea and Artiodactyla. It has accordingly been decided that before the undescribed material can profitably be dealt with, the described species of each of these three important orders of mammals in Southern Africa must be critically reviewed. The present paper considers the first, and perhaps the most important, of these orders.*

As much as possible of the material from the Vaal River basin and elsewhere in the possession of the various museums in Southern Africa has been obtained on loan and examined in addition to the large collection in the Archaeological Survey. Dr. Broom has also been kind enough to make his material available to the writer. With the exception of those specimens which are in other countries, the type specimens of every species have been studied and are figured in the present account. Many of these figures have been drawn by the writer from the original specimens where the published figures are considered inadequate or unsuitable; others are reproductions of the original figures. As far as is possible new fossil material has deliberately not been introduced in this paper, as the purpose is to revise the specific descriptions from type material or from such other specimens as can with reasonable certainty be identified with the types. These descriptions are for the most part new, and are based on a fresh assessment of the original specimens interpreted in relation to the wider assortment of material now available and considered against a background of comparative researches upon the characteristics and variability of related living forms. It is hoped that this revision and

* See Appendix.

ORDER PERISSODACTYLA.

The Rhinoceroses.

Amongst the fossil mammalia, the rhinoceroses are only very scantily represented in Southern Africa. Two supposedly extinct forms have been mentioned, each only from a single site, but petrified specimens indistinguishable from the two living species have been recovered from various superficial deposits. These latter specimens are probably not of any very great antiquity, but rhinoceros species are in any case not subject to rapid changes.

The two living forms belong to different genera, and both their skulls and their teeth are quite distinct. The square-lipped or white rhinoceros is quite considerably larger than the hook-lipped or black rhinoceros, as can be seen from the drawings of their respective skulls (fig. 1). The lower jaws are sharply distinguished, that of the black rhinoceros having a deep compressed symphysis as compared with the depressed and rather spatulate symphysial region of the mandible in the white rhinoceros. The horns have been found isolated and again differ widely in form. Incisor and canine teeth are rudimentary or absent in both species.

The cheek teeth in the rhinoceroses comprise four premolars and three molars arranged in a continuous series and having essentially the same structure, though the first premolar is considerably more simplified and is shed early. The lower third molar is also simple, and does not possess the third lobe so characteristic of the horses and most artiodactyls. The premolars are somewhat smaller than the true molars, the second premolar and first premolar particularly being smaller than the more uniform succeeding teeth. Structurally the teeth differ from those of the horse in being rather low crowned and in possessing strong, distinct roots, but their essential composition is similar to that of the equine cheek teeth. The normal order of eruption of the permanent dentition appears to be M^1, Pm^1, Pm^2, M^2, Pm^3, Pm^4, and lastly M^3, and is thus somewhat different from that of the horses.

The cheek teeth of the rhinoceroses are lophodont in form, *i.e.* the rows of cusps tend to become fused into ridges. In the upper teeth the two main outer cusps form a ridge known as the *ectoloph*, two anterior cusps form the *protoloph* and two posterior ones the *metaloph*. In the lower teeth three triangularly arranged cusps unite to form a crescentic *metalophid*, and posterior to this two cusps form an arcuate

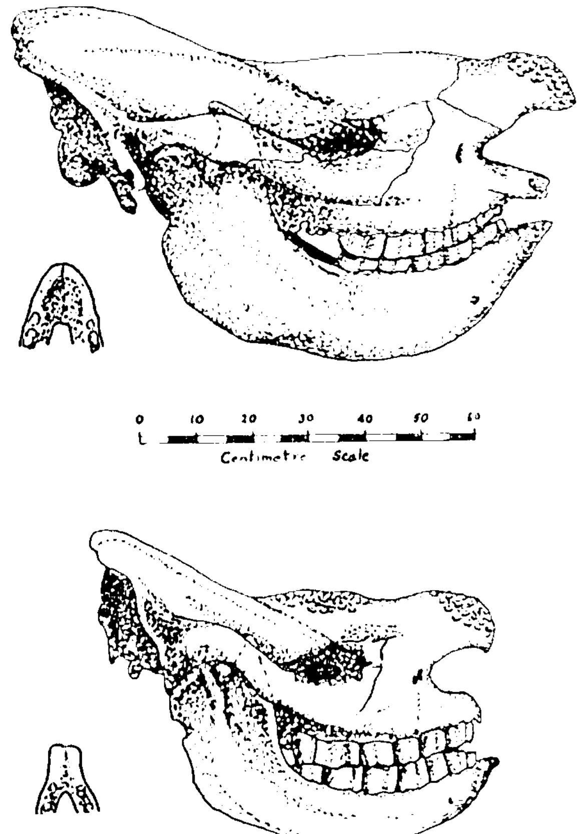

Fig. 1.

Above: Lateral view of skull of *Ceratotherium simum** (Burchell) and plan view of spatulate symphysial region of the lower jaw. (After Sclater.)

Below: Lateral view of skull of *Diceros bicornis** (Linnaeus) and plan view of the compressed symphysial region of the lower jaw. (After Owen.)

hypolophid ridge. With wear the enamel is rapidly removed from the top of these ridges and an area of dentine surrounded by enamel is exposed. This can be clearly seen in fig. 2, in which typical upper and

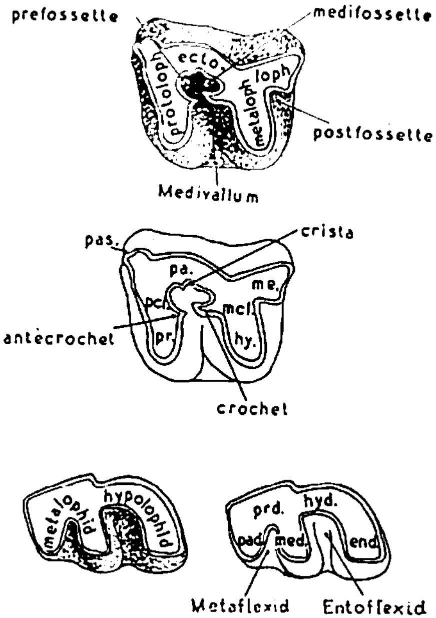

FIG. 2.—Molar elements (following Osborn) of the upper and lower cheek teeth of the Rhinoceros group.

Abbreviations.

Upper teeth: *pas*, parastyle; *pa*, paracone; *me*, metacone; *hy*, hypocone; *pr*, protocone; *pcl*, protoconule; *mcl*, metaconule.

Lower teeth: *prd*, protoconid; *hyd*, hypoconid; *pad*, parastylid; *med*, metaconid; *end*, entaconid. (Original.)

lower first molars are shown indicating the nomenclature used for the cusps, folds and ridges (following Osborn). The valley between the protoloph and metaloph appears to have received no name, and is here termed the medivallum by analogy with the corresponding valley in horse teeth. For the two inlets in the lower teeth the terms "metaflexid" and "entoflexid" are here suggested for convenience

in description, as the same terms have been proposed by Stirton (1941) in the lower teeth of the horses.

Owing largely to a lack of sufficient material, it has unfortunately not been possible to gain any reliable idea as to the constancy or variability of the tooth characters within the series in the rhinoceroses. From the limited material examined, however, it does appear that while the essential structures are reasonably constant, the effect of attrition alters the pattern of the grinding surface to such a degree that identification may be made most difficult. As wear proceeds, the ridges widen and obliterate the intervening valleys, at first fairly slowly, but afterwards very rapidly, until ultimately a uniform tract of dentine may be produced. The crochet, antecrochet and crista which project into the medivallum are generally more prominent in early wear, and are reduced in size as this valley is narrowed. In some species the crochet and crista may unite and isolate the medifossette as an accessory valley, leaving the prefossette as the terminal portion of the medivallum. The postfossette may also become isolated by closure of the posterior enamel border. In the lower teeth the chief effect of attrition is to reduce the size of the two flexids, the metaflexid in particular tending to disappear with wear. Fusion of the metaconid and entaconid may also lead to the complete isolation of the entoflexid as an accessory valley.

FAMILY RHINOCEROTIDAE.

Genus DICEROS Gray 1821.

Genotype: *Rhinoceros bicornis** Linnaeus.

*Diceros bicornis** (Linnaeus).

*Rhinoceros bicornis** Linnaeus 1758. Syst. Nat. Ed. (10), i, p. 56.
Opsiceros simplicidens (pars) Scott 1907. 3rd Rep. Geol. Surv. Natal and Zululand, pp. 258–259, pl. xvii, figs. 4, 5.
Diceros whitei (pars) Chubb 1907. Geol. Mag., V, vol. iv, pp. 447–448.

The horns of the black rhinoceros are almost invariably two in number, but exceptionally as many as five have been recorded. The anterior horn has a height of about forty-five to sixty centimetres on the average and has a basal diameter fifteen to twenty-five centimetres. The rear horn is about one-third to one-half the length of the anterior one and has a diameter only a little less than its height. The record horn lengths are about double the average figures. Both horns are rather blunt and curve very slightly posteriorly.

In the upper jaw the first premolar is very small and exhibits no structures which can be said to be recognisable as persistent. The third molar is triangular in form, the metaloph, being reduced to a small posterior prominence only, and this tooth is very variable in pattern in wear and is of little value for specific identification. The remaining three premolar and two molar teeth are generally more consistent, and are essentially similar in structure, though the premolars differ slightly from the molars. In the premolars the anterior wall of the protoloph is fairly straight and makes an angle of about 75° with the ectoloph, whereas in the molars the protoloph initially makes almost a right angle with the ectoloph, and then curves somewhat posteriorly. The protoloph and metaloph are roughly parallel or slightly divergent and with the ectoloph give the appearance of the Greek letter π. The ectoloph itself is not straight, but has an outer wall incurved or grooved between the paracone and metacone and also has a shallow groove behind the parastyle. The parastyle itself is commonly anteriorly grooved and projects very little in front of the protoloph. The antecrochet is apparently absent, and the crista is very small and disappears rapidly with attrition. A crochet is always present in the earlier stages of wear, and in the normal dentition increases progressively in size from the second premolar to the second molar. It tends to become rounded with increased wear, and may disappear completely before the medivallum is obscured. In no case has isolation of the medifossette been observed in this species except in the third molar. The postfossette is somewhat obliquely V-shaped, tending to be U-shaped with wear as a result of the expansion of the hypocone lobe of the metaloph, and then becomes isolated as an oval valley. The dimensions vary considerably with wear, the breadth across the grinding surface increasing as attrition proceeds. The height above the basal cingulum increases progressively with the successive teeth, and a typical second molar in early wear has a height of about 50–55 mm. The breadth at the base of the second molar is about 60 mm., but in normal wear the grinding surface measures only some 45 mm. transversely. The size and characters can be seen from the scale drawings in fig. 3. Two typical upper dentitions are shown, one in fairly early wear, the other well worn and lacking the first premolar.

The lower teeth have little to distinguish them from the very generalised form of most rhinoceros teeth. The first premolar is greatly simplified in form, but the remaining teeth, including the third molar, are similar in structure. The anterior and antero-external walls of the metalophid are markedly flattened, and make an

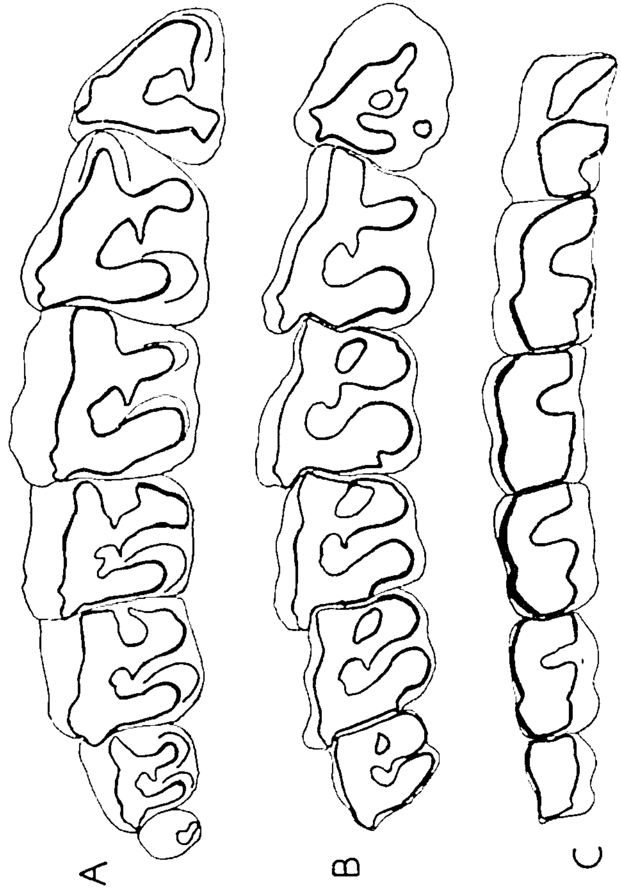

FIG. 3.—Two left upper dentitions (A and B) of *Diceros bicornis** (Linnaeus) and a right lower dentition (C) of the individual B. One-half natural size. (Original.)

angle with each other of about 100° or a little more. A fairly marked groove separates the outer wall of the metalophid from the curved hypolophid wall. The inner walls of the metaconid and entaconid are somewhat flattened. The metaflexid is a good deal smaller than the entoflexid and is rapidly reduced to a shallow V shaped notch. The height of a normal second molar is about 50 mm. The lower teeth of a typical specimen are shown in fig. 3, and belong to the same individual as the upper dentition figured immediately above it.

Referred Material.

Apart from the petrified specimens from superficial deposits in various parts of Southern Africa which obviously belong to this species, two of the teeth from Zululand which Scott (1907) very tentatively referred to his species *Opsiceros simplicidens* do not appear to warrant distinction from the living *Diceros bicornis**. The type LM^2 of Scott's species manifestly is not that of *D. bicornis**, but the two heavily worn teeth (M^1 and Pm^4) do not differ appreciably from correspondingly worn teeth in old individuals of the living black rhinoceros. Scott himself realised the close similarity, and suggested that these two teeth did not actually belong to his new species. The specimens themselves have not been seen by the present writer, but natural size photographs kindly supplied to the writer by Professor Scott, together with the admirable description, form an adequate basis for the conclusion reached above.

Genus CERATOTHERIUM Gray 1868.

Genotype: *Rhinoceros simus** Burchell.

*Ceratotherium simum** (Burchell).

*Rhinoceros simus** Burchell 1817. Bull. Sci. Soc. Phil. Paris, F. 1, 2, p. 97.

Opsiceros simplicidens Scott 1907. 3rd Rep. Geol. Surv. Natal and Zululand, pp. 257–258, pl. xvii, fig. 3.

Rhinoceros scotti Hopwood 1926. Occ. Papers No. 2, Geol. Survey, Uganda, pp. 16–17, fig. 3.

The white rhinoceros possesses a long and rather slender anterior horn which attains a height of about ninety centimetres and, exceptionally, as much as a hundred and fifty centimetres.* The second or rear

* Southern race: 62¼ inches. Rowland Ward's Records of Big Game, 9th ed., 1928, p. 446.

horn is small and does not usually attain a height exceeding twenty-five centimetres. The anterior horn is normally more slender than that of the black rhinoceros.

In the upper jaw the first premolar is small and is shed early, but the other premolars differ notably from the molars, for in the former the medivallum becomes rapidly enclosed by fusion of the protocone and hypocone, the form of the metaloph being consequently also affected. From *Diceros bicornis** they differ most markedly in the arcuate, posteriorly curving protoloph, and in the early fusion of the well-developed crista with the crochet to form an isolated medifossette. Due to the posterior curving of both protoloph and metaloph the π-like shape of the teeth is very distorted and not nearly as noticeable as in *D. bicornis**. The form of the ectoloph is also different, being rather more undulate in *Ceratotherium simum** with a distinct outward bulge at the paracone. The parastyle is more pointed and is not apparently grooved, but there is a groove immediately behind it. The postfossette becomes isolated with wear as a result of closure of the posterior enamel. As in *D. bicornis** this isolation of the postfossette is not a constant feature and is generally less marked in the molars than in the premolars. The teeth are higher crowned than those of the black rhinoceros, a typical second molar in normal wear measuring about 75 mm. above the indistinct cingulum. Fig. 4 shows (half natural size) two upper dentitions, one in very early wear with the third molar only just erupting and the fourth premolar coming into use, the second dentition being in a more advanced state of attrition.

The lower teeth are somewhat difficult to distinguish from those of the black rhinoceros. The anterior and antero-external walls of the metalophid make an angle with each other close to 90° instead of the obtuse angle found in *D. bicornis**. The metaflexid appears to be more persistent in the white rhinoceros than in the black, and the enclosure of both metaflexid and entoflexid with advanced wear is a common feature. The height of a typical second molar above the cingulum is about 60 mm. The lower dentition of the same individual as the more worn upper dentition figured is shown in fig. 4.

Referred Material.

Petrified specimens of this species have been found in various superficial deposits in the coastal region and in the interior. A portion of an anterior horn is also recorded from a cave deposit near Kuruman, Cape Province (Malan and Cooke, 1941).

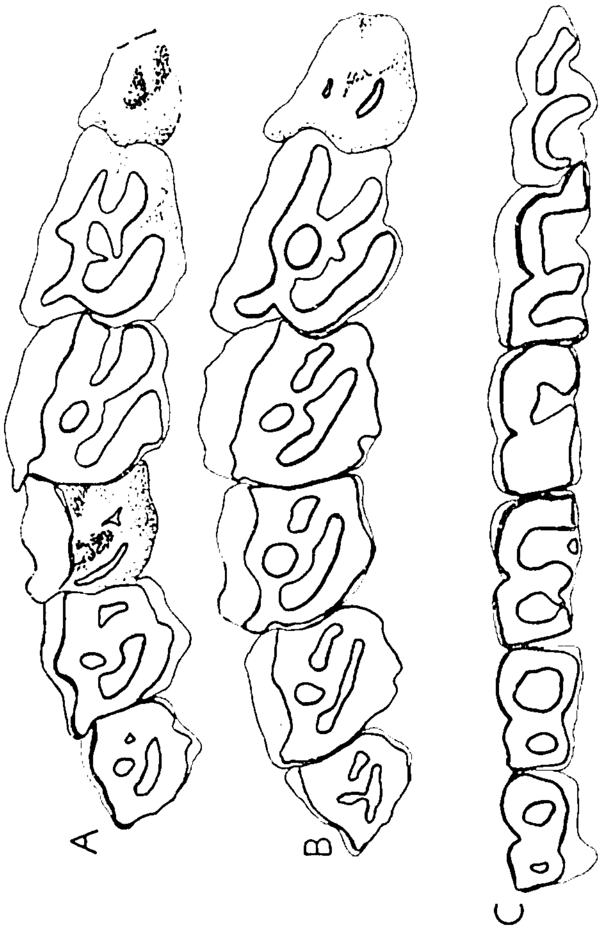

FIG. 4.—Two left upper dentitions (A and B) of *Ceratotherium simum** (Burchell) and a lower right dentition (C) of the individual B. One-half natural size. (Original.)

W. B. Scott reported in 1907 the discovery of a supposedly extinct species in fossiliferous marine clays from the Zululand coast, and he named this species *Opsiceros simplicidens*, with an unworn upper left second molar as the type. Scott compares this tooth with the corresponding one of *Diceros bicornis**, and states that the differences are "clearly of specific value". The distinctive characters are stated to lie, *inter alia*, in the much stronger recurving of the protoloph and in the much better development of the crista, which "fuses with the antecrochet so as to enclose a small and apparently shallow fossette". (Scott here used the term 'anticrochet' in error for crochet, as his figure shows, and in this follows an error previously made by Osborn in describing the Perissodactyla of White River (Scott and Osborn, 1890).) The characters which Scott used to differentiate the species from *D. bicornis** are exactly those which distinguish the white rhinoceros. A skull of the latter species in the South African Museum possesses a second molar in much the same state of development, and the dimensions and appearance of this tooth correspond very closely to the data and figure furnished by Scott. There can thus be little doubt that *Opsiceros simplicidens* is a synonym of *Ceratotherium simum**, a fact which Scott would undoubtedly have realised had comparative material of this rather rare species been available to him.

In 1926 Hopwood recorded an upper left second molar from the Kaiso beds of Uganda and assigned this specimen to Scott's species. He also pointed out that the name *R. simplicidens* was preoccupied and proposed *Rhinoceros scotti* as a substitute. There seems no doubt of the correctness of the reference of this specimen, and equally there is little doubt of its similarity to teeth of the living white rhinoceros. *Rhinoceros scotti* is thus also apparently a synonym of *Ceratotherium simum**.

DISCARDED SPECIES.

Diceros whitei Chubb.

Diceros whitei Chubb 1907. Geol. Mag., V, vol. iv, pp. 447–448.
Diceros whitei Hopwood 1928. Rhodesian Man and Associated Remains.

A supposedly new species of rhinoceros was described very briefly by E. C. Chubb in 1907 in a "List of Vertebrate Remains" from the Broken Hill Cave. It was founded on two limb bones (a right tibia and a right humerus) which had been excavated by Mr. Franklin

White and presented by him to the Rhodesian Museum. This species was also mentioned by A. T. Hopwood in the British Museum memoir on Rhodesian Man, and is there said to be "closely allied to *D. simus*". In view of the uncertainty of the generic position of the species *whitei*, the material was obtained on loan from the Rhodesian Museum, Bulawayo, and permission was obtained from Mr. Chubb to amplify his preliminary description and to figure the specimens. In his brief account Chubb remarks on the scantiness of the comparative material available to him, and this lack and the seeming association of the two bones appears to have resulted in an error in the distinction of the material. The tibia is certainly that of a rhinoceros, though comparison with recent skeletons shows no notable differences in size or in other characters from the corresponding bone in the living *Diceros bicornis**. The humerus, however, differs very considerably from both the living rhinoceroses, and it would appear that it is an artiodactyl and not a perissodactyl humerus, the differences formerly regarded by Chubb as of specific distinctness being actually too great for that possibility to be upheld. The compressed narrow olecranon fossa is a normal artiodactyl feature unlikely to occur in a rhinoceros, and the deltoid ridge and deltoid tuberosity are also much more artiodactyl than perissodactyl. With these views Mr. Chubb now expresses his agreement.

On comparison with various living artiodactyls, the closest resemblance is found between the fossil humerus and that of the living Cape Buffalo. There is no great difference in length, but the fossil bone is somewhat more massive, with the attendant minor modifications consequent upon its greater weight-supporting requirements. Otherwise, however, there is a very close agreement in every character, and it seems highly probable that the fossil humerus belongs to a member of the Buffalo group. It may possibly belong to the extinct "*Bubalus*" *bainii* Seeley, or to "*Bubalus*" *andersoni* Scott.

The species *Diceros whitei* appears, therefore, to have been founded on a humerus which is not that of a rhinoceros and on a tibia which does not warrant distinction from the living *D. bicornis**, so that *D. whitei* must be regarded as incorrectly founded.

The Horses.

There have been described at various times from Southern Africa more than twenty-five species belonging to this family, some based on upper and some on lower teeth, but of these not more than half can be

regarded as valid. The position was first reviewed by Haughton in 1931 when the twenty then existing species were reduced to eleven, and in general the present writer is in agreement with these conclusions. Haughton divided the members ascribed to the genus *Equus* into two groups, which he terms the "quagga" group and the "zebra" group on the parallelism of certain characters with those in the teeth of the two living species, the bontequagga and the mountain zebra. Unfortunately these characters in the recently extinct true quagga are very different from those in the living bontequagga and the two group terms must therefore be abandoned.

The relationships indicated by Haughton's work are of great interest and, in order the better to appreciate the definitive characters of the teeth in the extinct forms, the writer has carried out an extensive examination of skulls and teeth of the living forms and of the recently extinct true quagga. As a result of this work it is possible to distinguish on dental characters from this material three undoubted species: *Equus zebra**, the living mountain zebra, *Equus quagga**, the recently extinct true quagga, and *Equus burchellii**, the living bontequagga or Burchell's zebra. Since zoologists have been greatly at variance on the status of these forms, and since all three species occur in the fossil state, the results of the investigation have already been considered fairly fully (Cooke, 1943). These observations also throw some light on the morphological characters and variations encountered in equine species and are of great value in considering the fossil finds. To some extent they repeat and amplify the work of Gidley (1901), and in the present examination a general agreement was found with the conclusions outlined by him.

For convenience of reference the nomenclature of the important elements of the molar teeth of the Equidae (following Osborn) is given here in diagrammatic form (fig. 5). The specimens figured are upper and lower fourth premolars, and show the appearance of the cusps on the unworn crowns and the enamel patterns of the teeth in normal wear. The two enamel islands in the upper cheek teeth have long been known as the pre- and postfossettes, but the partial islands, or inlets, in the lower teeth have until recently received no name. The terms advocated by Stirton (1941) are used here. They are respectively "metaflexid" for the anterior and "entoflexid" for the posterior partial islands of the lower cheek teeth. (These terms have already been suggested for the analogous parts of the rhinoceros teeth.) It is also proposed here to call the posterior groove which lies between the hypocone and the hypostyle in the upper teeth the "hypoglyph",