ANTELOPES IN THE PLEISTOCENE OF SOUTHERN AFRICA

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This survey is based both on previously published data and on as yet unpublished studies of material from the Orange Free State and from the south-western Cape Province preserved respectively in the National Museum, Bloemfontein, and the South African Museum, Cape Town.

Four faunal stages have provisionally been recognised in the Pleistocene of southern Africa (Wells 1962). These are, in ascending order, the Sterkfontein, Swartkrans, Cornelia and Florisbad stages. Radiocarbon age-estimates for the Florisbad stage (van Zinderen Bakker 1957) indicate that it covers the period 40,000–20,000 years B.P., with some undetermined further extension outside of these limits, and is thus definitely Upper Pleistocene; the preceding Cornelia stage is therefore either Upper Mid-Pleistocene or at latest Early Upper Pleistocene. At the other extreme the Sterkfontein stage has been considered at latest Cromerian and very possibly Late Villafranchian in age; however, correlation of this stage with Central and Northern Africa and Eurasia can only be tentative at present, owing to the drastic changes in interpretation which have become necessary particularly in East Africa.

Comprehensive assemblages of antelope material are available from the Sterkfontein stage (Makapansgat Limeworks), Cornelia stage (Cornelia, O.F.S.; Vaal River "Younger Gravels"; Hopefield, Cape), and Florisbad stage (Florisbad, O.F.S., and a number of other O.F.S. and Transvaal sites). The genera, extinct as well as surviving, represented in these assemblages can be provisionally distributed in seven groups, which are ranked, following Simpson (1945), as tribes rather than subfamilies.

Strepsicerotini. In the Sterkfontein stage this group is represented by forms comparable with the eland, kudu, and nyala respectively, but not certainly identical with the existing species. A form comparable with the bushbuck appears first in a Transvaal breccia deposit of either the Swartkrans or the Cornelia stage. The existing eland and kudu are identified in the Cornelia stage. In and after the Florisbad stage these two species, and apparently also the nyala and bushbuck, had approximately their historic distribution.

Reduncini. Two species of *Redunca* are recorded in the Sterkfontein stage: an extinct form (*R. darti* Wells and Cooke 1957) in some respects intermediate between the existing reedbuck *R. arundinum* and puku *Kobus vardoni*, and a smaller form provisionally identified with the existing mountain reedbuck *R. fulvorufula*. *R. arundinum* is widely distributed in the Cornelia stage and thereafter. A larger reduncine antelope (*Kobus venterae* Broom 1913), from riverine and pan sites of both the Cornelia and the Florisbad stages, appears to be related to the existing lechwe. The true waterbuck is recorded only in very late contexts, with approximately its historic distribution. It may be noted that "*Kobus altidens*" (Cooke 1949) is a myth, the type specimen being not reduncine but bovine.

Hippotragini. Two forms from the Sterkfontein stage are assigned to this group, one ("*Hippotragoides*" *broomi* Cooke 1946) comparable in size with the roan antelope but with distinctively specialised lower molar teeth, the other with relatively simple molars larger than those of the existing roan and gemsbok. The latter was initially identified as *Oryx*, but more recent evidence suggests that it may be identical with a *Hippotragus* more robustly built than the existing roan, present at Hopefield in the Cornelia stage. "*Hippotragus problematicus*" (Cooke 1946), also found at Hopefield, is almost certainly to be identified with the historic bloubok *H. leucophaeus*. Remains not distinguished from the existing roan occur in the Orange Free State during both the Cornelia and Florisbad stages.

Cephalophini. At Makapansgat in the Sterkfontein stage a large forest-duiker *Cephalophus pricei* has been recorded together with a smaller form provisionally identified with the existing blue duiker *C. caerulus*. The latter may prove to be the same as the supposedly extinct small species from Taung (*C. parvus* Broom 1934). In the Cornelia stage the existing gray bush-duiker *Sylvicapra grimmia* has been provisionally identified at Cornelia and in the Vaal River deposits, but not at Hopefield; it recurs in the O.F.S. during the Florisbad stage.

Neotragini. In the Sterkfontein stage a large extinct klipspringer (*Oreotragus major* Wells 1951) is recorded from Makapansgat. A supposedly extinct genus from Taung, *Palaeotragiscus* (Broom 1934), is also assigned to this group. The possibility that it is related to the existing vaal-ribbok *Pelea* and that this last may be an aberrant Neotragine needs to be further examined. A form provisionally identified with the existing steenbok is present at Hopefield in the Cornelia stage. Cooke (1962) reports the existing klipspringer, and possibly both the steenbok and the oribi, as well as the vaalribbok, in the Florisbad stage at Makapansgat; these forms have not as yet been identified in the O.F.S. during either the Cornelia or the Florisbad stage.

Antelopini. The gazelle group is represented in the historic fauna of southern Africa only by the springbok and, according to most authorities, the impala, though the inclusion of the latter has with some justification been questioned. During the Pleistocene this group had a much more diversified representation, including forms apparently belonging to three of the four sub-groups into which Schwarz (1937) has divided the African species of *Gazella.*

At Makapansgat in the Sterkfontein stage three species have been recognised. One of these has been provisionally identified with the existing impala. A second (*Gazella gracilior* Wells and Cooke 1957) belongs to the *G. gazella* sub-group of which the East African *G. thomsoni* is the most southerly living representative. The third is assigned to an extinct genus *Phenacotragus* (Schwarz 1937), apparently intermediate between *G. soemmeringi* and the springbok. Chronologically the Makapansgat *P. vanhoepeni* appears to be earlier than the type species *P. recki* of East Africa.

Two species of *Gazella* are widely distributed in the Cornelia stage. One of these (*G. wellsi* Cooke 1949) appears to resemble the living West African *G. dama;* the other may be related to *G. leptoceros*. A third species, apparently of the *G. gazella* type but distinct from the earlier *G. gracilior*, is so far known only from Hopefield. "*Gazella*" *helmoedi* (van Hoepen 1932) from Cornelia appears to be an alcelaphine of undetermined genus and not a gazelle at all. Remains ascribed to *Antidorcas* are also widely distributed in the Cornelia stage. Those from

Hopefield are considered specifically distinct from the existing springbok *A. marsupialis*, but this may not be true of those from Cornelia and the Vaal River. Some remains from the Vaal River deposits are considered to belong to the existing impala.

In the Florisbad stage the existing springbok is recorded in the O.F.S. and Transvaal. A smaller, probably related species with extremely high-crowned cheek teeth ("*Gazella*" *bondi* Cooke and Wells 1951) ranges from the O.F.S. northwards to Matabeleland. The impala is recorded during this stage only in the central and northern Transvaal and in northern Zululand.

Alcelaphini. This is the most highly diversified group of Pleistocene antelopes. The extinct forms can be largely fitted into the existing threefold division of damaliscines, gnus, and hartebeests, although some present transitional characters. For several reasons it is convenient to trace these divisions independently through the successive time phases.

Damaliscus is represented in the Sterkfontein stage by a type almost certainly distinct from but possibly ancestral to the existing bontebok and blesbok. A very distinctive type occurring in the O.F.S. during the Cornelia stage has medio-laterally compressed, almost untwisted and boldly recurved horns of an almost ibex-like character; this type, which might be considered remotely akin to the topi rather than to the blesbok and bontebok, persists into the Florisbad stage. A species from the Cornelia stage at Hopefield generally resembles the tsessebe but has more lyrate horns, suggesting a transition towards the herola *Beatragus*. Another type from this site possibly related to *Damaliscus* has horns with a strong axial torsion in the opposite sense to those of the bontebok and blesbok. The blesbok and bontebok are only doubtfully recorded in their respective areas during the Cornelia stage. In the Florisbad stage the blesbok is represented in the O.F.S. and the tsessebe in the Central and Northern Transvaal (Cooke 1962).

Dentitions comparable with those of the existing blue wildebeest occur in the Sterkfontein stage, but have not yet been associated with horncores. In the Cornelia stage the blue wildebeest type is present both at Cornelia and at Hopefield. The remains from the former site have been described as a distinct species (*Gorgon laticornutus* van Hoepen 1932). Some remains from the Vaal River, not certainly dating back to the Cornelia stage, are assigned to the black wildebeeste type. Wildebeest remains from O.F.S. sites of the Florisbad stage (*Connochaetes antiquus* Broom 1913) have horn bases of black wildebeest type, but the distal part of the horn is intermediate in splay and curvature between those of the blue and black wildebeests.

The extinct genus *Makapania* of the Sterkfontein stage (Wells and Cooke 1957) has elongated laterally splayed horncores resembling those of the kongoni group of hartebeests rather more than those of the blue wildebeest, but arising close to the orbits as in *Damaliscus*. It is further distinguished by the angular crown pattern of the molar teeth. A type found at Hopefield and possibly also in the O.F.S. during the Cornelia stage presents an analogous mixture of characters. Its horns resemble in their torsion those of the Cape hartebeest, but arise close to the orbits and are directed forward above the face.

Remains not distinguished from the Cape hartebeest occur in the Cornelia stage at Cornelia and in the Vaal River deposits. In the Florisbad stage this form extended northwards to Matabeleland (Cooke and Wells 1951).

Teeth of alcelaphine antelopes larger than the existing wildebeest and hartebeest have

been recorded in the Sterkfontein stage. In the Cornelia stage a very large hartebeest-like form (*Megalotragus eucornutus* van Hoepen 1932) has proved to be widely distributed. A second such antelope (*Lunatoceras mirum* van Hoepen 1947) may be present as early as the Cornelia stage at Hopefield, but in the O.F.S. is not certainly recorded before the Florisbad stage. Another very large form present in the O.F.S. during the Florisbad stage is a true hartebeest (*Alcelaphus helmei* Lyle 1931), apparently belonging to the kongoni group. Other species names of doubtful validity have been attached to groups of large alcelaphine teeth. At least one of the large alcelaphines ranged northwards as far as Matabeleland in the Florisbad stage (Wells and Cooke 1955).

DISCUSSION

There is an obvious contrast between the composition of the known antelope fauna of the Sterkfontein stage and those of the considerably later Cornelia and Florisbad stages. The former consists of types either definitely extinct or only provisionally identified with existing species; in the latter, a considerable part if not the whole of the existing southern African antelope fauna was supplemented by a progressively decreasing number of extinct species.

In the Sterkfontein stage a few extinct species can be considered potentially or probably ancestral to living forms. The number of such species in this stage may well be increased as forms at present provisionally identified with existing species become better known. In later stages such a position has been claimed for only one species, *Connochaetes antiquus*. There is some evidence to suggest a gradation from this species to *C. gnou* during the Florisbad stage in the O.F.S., but it is also possible that *C. gnou* already existed in the Cornelia stage. While the emergence of new species during the later part of the Pleistocene is not impossible, it seems that most existing species are probably to be traced back at least to the middle of the Pleistocene.

The extinct species which do not have living descendants appear to be divisible broadly into two categories, either possessing or lacking living analogues further north in Africa. The first of these comprises such species as the lechwe-like *Kobus venterae*, the large forest-duiker *Cephalophus pricei*, the various species of *Gazella*, the tsessebe-like *Damaliscus* of Hopefield, and the large kongoni-like hartebeest (*A. helmei*) of Florisbad. Those extinct species which do not have such analogues, e.g. *Redunca darti*, the extinct hippotragines of Sterkfontein and Hopefield, the antilopines *Phenacotragus vanhoepeni* and "*Gazella*" *bondi*, and extinct alcelaphines such as *Makapania*, *Megalotragus*, and *Lunatoceras* may be envisaged as extending, or filling gaps in, the spectrum of variation of the existing members of their groups. It seems probable, however, that the apparently transitional forms in this category are in fact the terminal points of independent lineages, possibly preserving some features of earlier annectant forms but possibly also representing convergent modifications.

Most of the extinct antelope species so far recognised in the Pleistocene of southern Africa belong to two groups, the Antilopini and the Alcelaphini. It has previously been pointed out (Wells 1957) that the Alcelaphini, Cephalophini, and Neotragini, unlike the other groups, are not represented in the Pliocene of Eurasia, and were presumably differentiated in Africa. These groups may therefore have constituted an early stratum in the antelope fauna of Africa, to

which the Strepsicerotini, Reduncini, and Hippotragini, and possibly the Antilopini, were later accretions. The number and diversity of of Pleistocene and recent antilopines in Africa, however, suggests that this group might have belonged to the earlier stratum. While Schwarz's (1937) proposed merging of the Alcelaphini with the Antilopini is unacceptable, it is quite possible that the basic alcelaphine stock was derived from a primitive antilopine ancestry, and the possibility that the problematical *Aepyceros* is a survival of the transitional stage between these groups deserves further examination.

In the inferred early African antelope fauna, the Alcelaphini would presumably have provided most of the large forms and have become adapted to the greatest variety of ecological conditions. Its members would therefore have been to some extent competitive with similarly adapted forms in the strepsicerotine, reduncine, and hippotragine groups. These considerations would possibly explain the very great diversity achieved by the alcelaphine group in the earlier and middle Pleistocene and its later canalisation into more limited directions of specialisation. There is also, however, at least in the middle and later Pleistocene, a suggestion of direct competition between genera and species within both the alcelaphine and the antilopine groups.

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