FOSSIL MAMMALS OF AFRICA
No. 22

PELOROVIS OLDOWAYENSIS RECK,
AN EXTINCT BOVID FROM EAST AFRICA

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SYNOPSIS

New material of *Pelorovis oldowayensis* Reck from the upper part of Bed II at Olduvai shows that this animal is not a member of the Caprinae, but belongs instead to the Bovini and is related to the African buffalo *Syncerus* Hodgson. Material used to describe *Bularchus arok* Hopwood in 1936 is found to be assignable to *Pelorovis oldowayensis*. There is possible evidence for a second Bovine species in Bed II.

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I INTRODUCTION

IN 1952 and in several subsequent years Dr. & Mrs. L. S. B. Leakey excavated at site BK II in Olduvai Gorge, a site which they had first located in 1935 and which is now known to lie near the top of Bed II. It consisted of a former land surface covered with sands and with extensive clay deposits above the sand, the land surface being littered with large numbers of splintered bones, as well as with stone tools and waste flakes of an evolved Oldowan culture. Adjoining the former land surface was a clay-filled gully in which more completely preserved animal remains including some articulated limb bones were found. Leakey (1954) believes that the men who used the land surface drove their prey into the mire of the gully and then dragged them out to be eaten, but that occasionally the larger animals had to be left behind.

From BK II were excavated a complete skull and many skull fragments of the large Bovid *Pelorovis*, also many limb bones and vertebrae among which the best preserved set of limb bones was known to have come from the same individual as the complete skull.

Remains of *Pelorovis* had first been recovered from Olduvai by the German expedition of 1913, and described as the single species *P. oldowayensis* by Reck (1925, 1928).

The holotype in Berlin is somewhat weathered and consists of the back part of a skull with its horn cores ; since the front of the skull is missing no teeth were available for Reck to work on. In his 1928 article, kindly translated for me by Mr. & Mrs. G. J. Warren, Reck noted that possible similarities to previously described fossils were few, but on the basis of horn core characters he made comparisons with various Caprines, and only briefly considered the possibility of relationship with other Bovidae such as the African buffalo *Syncerus*, or the Alcelaphini. He finally chose the sheep as being least far phylogenetically from *Pelorovis*, but was aware that the East African animal could have evolved its horn shape in isolation from other known living or fossil sheep. In fact we can now be certain, with more complete material and particularly from features of the teeth, that *Pelorovis* is not any kind of Caprine.

In the following diagnosis and expanded definition the skull is imagined as having its tooth row horizontal.

Genus *PELOROVIS* Reck

TYPE SPECIES. *Pelorovis oldowayensis* Reck, 1928.
GENERIC CHARACTERS. As for the species.

Pelorovis oldowayensis Reck

1928   *Pelorovis oldowayensis* Reck : 57, pls. 1, 2, text-fig. 1.
1936   *Bularchus arok* Hopwood : 639.

HOLOTYPE. Back part of a skull with horn cores, in the Institut für Paläontologie und Museum der Math.-Naturwissenschaftlichen Fakultät der Humboldt-Universität, Berlin.

REFERRED MATERIAL. A complete skull numbered Pel 1 ; horn cores and skull pieces numbered Pel 2 to Pel 23 ; an unnumbered frontlet and a left horn core ; teeth, limb bones and vertebrae as listed at various places in the text. This material is in the National Museum of Tanzania, Dar es Salaam, and a cast of the complete skull is in the British Museum (Natural History), London. Also in the British Museum (Natural History) is a frontlet with horn cores M.14947, a frontlet with left horn core M.14948, a horn core tip M.14949, and paired mandibular rami M.15856 ; all this material had been assigned to *Bularchus arok*. Also in London are teeth numbered M.25676–81, M.25688 and M.25692.

HORIZON. The holotype is of unknown provenance within Olduvai Gorge ; most of the remains in Dar es Salaam are from site BK II, but there are also some from SHK and other sites in the upper part of Bed II. M.14947–48 were originally supposed to have come from Bed IV, but they are now believed to have come from Bed II (see p. 290). M.15856, M.25676–81, M.25688 and M.25692 are from Kanjera, a site which has usually been taken to be equivalent to Bed IV at Olduvai.

AGE. Middle Pleistocene.

DIAGNOSIS. A large Bovid with long curved horn cores without keels, horn cores inserted close together and so far posteriorly on the skull that they overhang the occipital surface. The face is long, the tooth row is placed anteriorly, and the median

indentation at the back of the palate has its anterior edge further forwards than the lateral ones.   Teeth moderately hypsodont, but have only small basal pillars, and their occlusal pattern is not advanced.   The anterior part of P_4 has a medial wall.

DEFINITION.   The preceding diagnosis selected the most noticeable characters of the skull ; in this expanded definition are listed all those characters which I have found useful in comparing *P. oldowayensis* with some other Bovidae.

A large Bovid with a long and low skull.   Its massive horn cores are slightly compressed dorso-ventrally (with the skull in a horizontal position) and without keels or transverse ridges ; they arise close together, well behind the orbits and partly behind the occipital surface as well, then they pass successively backwards and outwards, then outwards and perhaps slightly downwards, then forwards and slightly or markedly upwards as well.   When it is at all evident, the spiralization is therefore clockwise in the right horn from the base upwards.   The horn cores taper gently from base to tip, sometimes a deep longitudinal groove runs along their back outside curve.   Females have shorter and more sharply curved horns than the males.   The horn cores and frontals are hollowed.

The skull is about as wide at the orbits as across the occipital surface ; the frontals curve slightly downwards in lateral view as they pass forwards over the orbits.   The orbits are small (probably an allometric effect) and the orbital rims project only slightly.   Supraorbital foramina are found above the back part of the orbits or a short distance behind them in longitudinally extended supraorbital pits.   Behind the orbits is a long temporal fossa to house the coronoid process of the lower jaw and its attached musculature.   The nasals are rather domed transversely, and they are widest just behind the point where their front part loses contact with the maxillae ; their central anterior flanges are pronounced and there are no lateral anterior flanges. The back of the nasals probably lies above the front half of the orbits.   There is no ethmoidal fissure nor a localized preorbital fossa.   The anterior part of the lower edge of the zygomatic arch passes forwards well below the orbits.   The infraorbital foramen lies above or in front of P^2.   The palatal fissures of the premaxillae appear to have been rather small ; the premaxillae become narrower as they rise, and have little or no contact with the nasals.   The tooth row is set rather anteriorly, and the median indentation at the back of the palate passes further forwards than the lateral ones.   The vomer is not fused with the back of the palate.   At the top of the occipital surface is a deep inverted triangular depression, the mastoid exposure of the periotic is entirely on the occipital surface, and the occipital condyles are wide. The top edge of the foramen magnum is not so posterior relative to the condyles as in *Oryx*.   The anterior tuberosities of the basioccipital are sufficiently close together to give the bone a triangular shape ; they are large and have poor longitudinal ridges extending behind them ; there is a poor longitudinal groove along the centre of the basioccipital ; and the bone is not transversely constricted across its middle.   The foramina ovales are small and situated just in front of the level of the anterior tuberosities.   There is an indentation in the sides of the squamosal shelf immediately in front of the mastoid.   The auditory bulla is a little compressed from side to side and appears to be but little inflated.   The tips of the paraoccipital processes are not noticeably turned forwards.

The teeth are moderately hypsodont ; their enamel surfaces, having many tiny longitudinal striations, may be described as rugose. The upper molars have wide and quadrate occlusal surfaces ; basal pillars are present but not strongly developed ; the walls of the central cavities of the teeth do not have a complex outline ; the styles are not strongly developed ; the outward bowings of the walls between the styles are neither localized nor strongly developed ; and cement is present. The mandible is deep below the teeth ; the anterior edge of the coronoid process is only slightly curved backwards (this is correlated with the relatively anterior position of the upper tooth row) ; and the anterior part of P_4 has a medial wall, thereby closing off a central valley on the tooth.

The great trochanter of the femur is tall with a slanted antero-dorsal edge ; there is a slight indentation between the great trochanter and the articular head in anterior view and the top edge of the articular head is a little slanted in anterior view ; the articular head is not very narrowed in its lateral part in dorsal view ; distally the lateral condyle is not sharply pointed anteriorly ; and the patellar fossa is wide. On the tibia there is no middle patellar groove at the top of the cnemial crest ; the lateral facet on the top articular surface is without an upturned lateral edge ; and distally the medial malleolus exceeds the central anterior flange in length. On the astragalus there is a deeply incised facet at the back of the medial side for the naviculo-cuboid ; the ridge for the astragalo-metatarsal ligament on the medial side is present ; this ridge is at the same level or slightly lower than the ridge for articulation with the medial malleolus of the tibia ; the top of the back of the medial side of the astragalus does not project behind or away from the main mass of the bone. The naviculo-cuboid is not deep ; and the back edge of its medial wall is fairly straight. The metapodials are not antero-posteriorly compressed ; and they possess distal anterior and posterior foramina. The articular facets at the top of the metatarsal are almost flat.

On the scapula the tuber scapulae is set above the anterior edge of the glenoid facet ; the lateral side of the glenoid facet in ventral view is slightly indented ; and the area for the origin of the teres minor extends forwards to the base of the spine. The lateral tuberosity of the humerus is low ; its posterior eminence is small and not antero-posteriorly long ; the infraspinatus insertion is longer than it is deep ; the front of the infraspinatus insertion is level with the front edge of the lateral side of the bone ; the bicipital groove is wide ; distally there is a coronoid fossa ; and the medial condyle is tall. The radius is rather long relative to the humerus for a Bovid the size of *Pelorovis*. On the ulna the area for the origin of the flexor carpi ulnaris extends near to the top of the bone, i.e. the roughened area at the top of the olecranon is smaller. On the radius the medial edge of the medial facet on the top articular surface does not project as a rim ; the postero-medial part of the medial facet is not greatly expanded ; the lateral facet is antero-posteriorly long ; the lateral tubercle is moderately sized ; the axis is not swollen at its distal end in lateral view ; and the ridge between the posterior surfaces of the scaphoid and lunate facets is slanted and not sharply marked. The carpal bones are antero-posteriorly long and not tall. The tubercle towards the front of the upper facet of the scaphoid is little pronounced ; and the lower edge of the scaphoid is little indented in medial

view. Because of the length of the lunate its ventral projection where it passes behind the unciform is rather forwardly sited ; the back edge is not very pointed in medial view ; and the more posterior lower parts of the lateral side project little in dorsal view.

The cervical vertebrae are transversely wide and antero-posteriorly short ; with neural spines not slanted forwards. The hollows on the ventral surface of the atlas are deep. The vertebrarterial foramina on the axis are small. The anterior and posterior openings of the foramen transversarium on the third cervical are close to the front and back ends of the centrum ; and the transverse processes of this vertebra are already separated from their ventral flanges.

REMARKS. It is clear that *Pelorovis* cannot belong to the Caprinae, as can be seen from the skull characters alone. Its skull is relatively lower in side view than in Caprinae, its horn cores are set far behind the orbits and there is a temporal fossa, the premaxillae are not reduced as in some Caprine tribes, the anterior tuberosities of the basioccipital are not set very widely apart, its upper molar teeth are wide, they have basal pillars, they have no tendency towards exaggerated styles on the lateral walls, and there is not a pronounced reduction in length of the premolar row. The purpose of this paper is to suggest an alternative relationship for *Pelorovis*.

II DESCRIPTION OF NEW MATERIAL OF *PELOROVIS*

Skulls and horn cores

The complete skull

The complete skull of *Pelorovis oldowayensis* (Pls. 1, 2, 6) has been distorted in various ways—the tips of the premaxillae have been thrust upwards close to the nasals, the bones on the left side of the face have become separated, and the right P^2 and most of the left premolar row are missing. Enough of the skull has been preserved to suggest that drawings of how it might have appeared in life would be feasible, and the three resulting reconstructions are shown as Text-figs. 1–3.

Most of the characters mentioned in the definition can be seen on the complete skull. Its horn cores are not large in relation to the size of the skull ; the length of the right one along its back edge is only 116 cm. which may be compared with 153 cm. for the two 1957 horn cores numbered Pel 7 and Pel 8. The short length and the sharp radius of curvature which reduces the span of these horn cores suggest that the animal was a female. The sharpness of the curvature of the horn cores precludes the possibility of them later growing to a size comparable with that of Pel 7, and the teeth show that the animal was already fully adult. Another pair of horn cores numbered Pel 18 and Pel 19 are a little smaller than those of the complete skull, otherwise the known horn cores are intermediate in size between those of the complete skull and Pel 7, without sign of a sharp distinction of males from females. In so far as the curvature of the horn cores in three planes involves spiralization, the direction of the spiralization is clockwise from the base of the right horn core. Nothing of interest concerning the horn cores can be added to Reck's (1928) detailed description of the Berlin specimen.
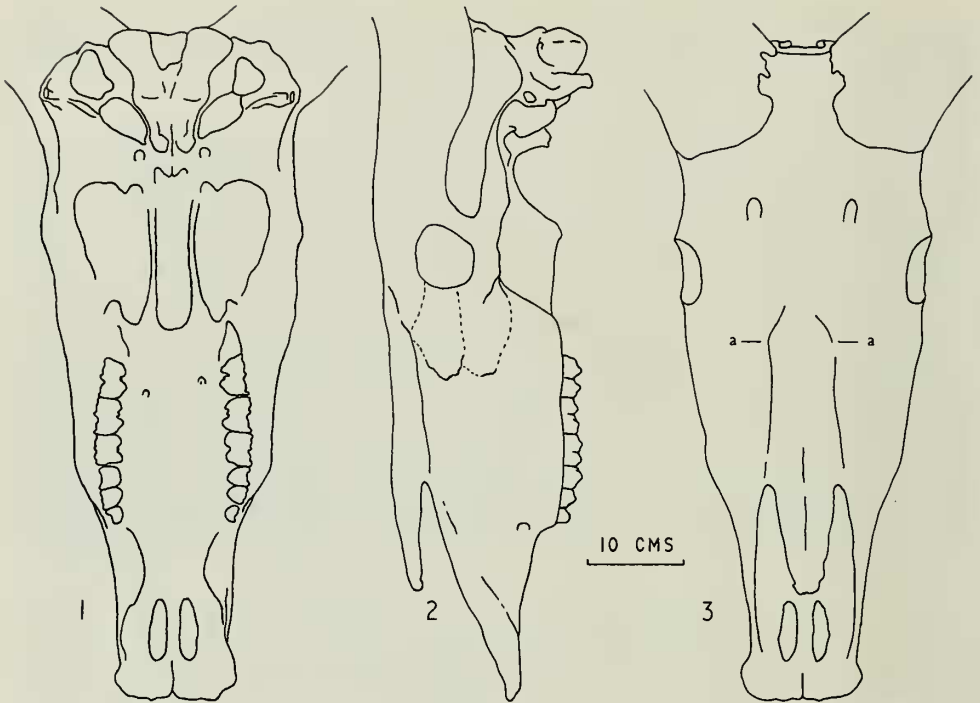
FIGS. 1–3. Reconstructions of skull of *Pelorovis oldowayensis*. The reconstructions are based on the complete skull Pel 1 for the pre-orbital regions, and on specimen Pel 2 in conjunction with Pel 1 for the post-orbital regions. 1, ventral view ; 2, lateral view showing sutures of lachrymal and jugal ; 3, dorsal view.

The supraorbital foramina cannot easily be seen on the skull ; they lie above the level of the back edge of the orbits or very slightly behind them, and are not widely separated from one another. On the left side there is a very small foramen just in front of the position of the main supraorbital foramen. A narrow and shallow longitudinal furrow runs along the bone surface in front of the supraorbital foramina on both sides almost as far as the level of the back of the nasals. The anterior parts of the nasals are transversely domed, and the downflanged lateral parts of the nasals anteriorly are fused with the maxilla as often happens in large Bovidae. Although there is no localized preorbital fossa, the whole region of the face in front of the orbits and on either side of the nasals has a hollowed surface. Towards the back of the left nasal a piece of what is presumably the lachrymal rises up and shows the beginning of the posterior narrowing of the nasal ; the back of the nasals is not otherwise indicated. On the left side of the face part of the suture marking the maxilla-lachrymal boundary can be seen, and lower down a more doubtful indication which, if it is a suture at all, marks part of the maxilla-jugal boundary ; there is nothing worthy of comment in the position of these sutures, and they are shown in Text-fig. 2.

The lower part of the occipital surface is at an angle of 90° to the plane of the top of the skull, and two low rounded ridges run up the occipital to reach the sides of the inverted triangular depression. The paraoccipital processes have been broken off. The basioccipital has both its anterior tuberosities complete. A small basal pillar can be seen on the left M^2 and somewhat larger ones on both M^3s ; a good deal of cement remains around the basal pillars.

The lower jaws of this animal (Pl. 6), which were found in position on the underlying skull, are undistorted. All teeth are present except the right P_2, but the left P_2 has been worn very low. The basal pillars on M_1 and M_2 have been nearly worn away, but that on M_3 is still present. The front cavity on M_1 has almost disappeared.

Remains of other skulls and horn cores

All but one of the other specimens of *Pelorovis* are of posterior parts only. The most useful of these is numbered Pel 2, and possesses the proximal parts of both horn cores with a complete but fractured occipital surface between them (Pl. 3). The left side of the top of the skull is missing, presumably because the men broke into it to get out the brain ; this had not happened to the complete skull which was found in the clay filled gully. A feature to be noted is the deep groove running along the back outside curve of the horn cores. On the right upper side of the skull is a lengthened supraorbital pit containing two foramina, the front one of which lies over the back of the orbit. The posterior upper part of the right orbit has been preserved although the rim is nowhere complete. The top of the occipital surface is evenly curved and marked by a small but sharp ridge even along those parts of its course which are overhung by the horn cores' bases ; this ridge has a more constant radius of curvature from the foramen magnum than it does in *Syncerus*. An inverted triangular depression is again seen at the top of the occipital surface. The basioccipital is present but without its anterior tuberosities ; one foramen ovale and the larger foramen rotundum can be seen, also the deep and long temporal fossae beneath the bases of the horn cores. Parts of the squamosal shelf for articulation with the condyle of the mandible are present on both sides, and the thickened base of the right paraoccipital process is present.

An unnumbered complete pair of horn cores with part of the frontals and still less of the occipital surface is shown in Pl. 2. The length of the outwardly directed part of the horn cores is greater than in the complete skull and their upward curvature is less marked.

Pel 5 is a distorted pair of horn cores with the occipital, the condyles and the basioccipital still surviving. The radius of curvature of the horn cores is quite small, and both of them have a moderately sized shallow longitudinal groove running along their back curve. The anterior tuberosities of the basioccipital are missing.

Pel 3 is a less complete skull piece than Pel 2, but it has an almost complete and undistorted temporal fossa and part of the orbital rim on the left side. The specimen thus shows well the transverse constriction of the skull behind the orbits, a feature which recalls *Bos* (in which the orbital rims are more projecting and the horn cores more widely set than in *Pelorovis*). The gap between the bases of the horn cores

along the top of the frontals is narrow and appears as a deep longitudinal incision ; the inference from this is that the horns of Pel 3 would have been larger and longer than those of the two skulls described above. The lack of the horn cores above their bases and of most of the right frontal allows the hollowing in the bone above the brain to be seen. The horn core cavity extends to within 4 cm. of the level of the back of the orbits, and the frontals are hollowed in front of this point, but without connection to the horn core cavity. The level to which the skull is preserved along the frontals is about the same as that to which it is preserved in Pel 2 and in the type specimen in Berlin. On the ventral surface the anterior tuberosities of the basioccipital and the paraoccipital processes are again missing. The foramina ovales are in the horizontal plane and slightly in front of the anterior tuberosities.

The skull Pel 4 has retained part of its right horn core, the occipital surface, a small part of its ventral surface and part of the temporal fossa; the anterior tuberosities of the basioccipital are missing. The triangular depression at the top of the occipital surface is less pronounced than in Pel 2.

A number of *Pelorovis* horn cores have been taken from BK and other sites in Bed II at Olduvai. One of the largest is Pel 7, a left horn core excavated in 1957 from BK, which is 153 cm. long. About 12 cm. from its base there begins a deep groove which runs along the back edge as far as about 32 cm. from the tip. A small part of the occipital surface is preserved at the horn core's base. Towards its tip the horn core is turned well upwards, and thus comes to possess detectable spiralization.

Pel 8 is a right horn core from BK II which is again 153 cm. long and with about the same degree of spiralization as Pel 7 ; however it may belong to a different individual from Pel 7 because of its lack of a deep longitudinal groove and because the patterning of the bony surface of the frontals at the base of the horn core seems to be different. Part of the temporal fossa and a small part of the brain cavity are also preserved.

Pel 9 is a right horn core with the excavation number 1957, BK II, 1344. Spiralization is slightly less than in Pel 7 and 8, i.e. the tip is not quite so upwardly turned and remains directed mainly forwards. A rather wide, shallow, longitudinal groove exists in its more distal parts in a position slightly dorsal to that occupied by the much longer and deeper groove mentioned in Pel 7.

A left horn core, Pel 10, of which only about 40 cm. exists, may be the partner of the complete horn core Pel 9. A further piece of this left horn core may be preserved as the tip numbered Pel 11 which has a similar shallow longitudinal groove.

Pel 12 is a right horn core which is a little smaller than those mentioned previously and is less upwardly curved towards its tip. There is no longitudinal groove along the back surface. A very small part of the frontal and of the occipital surface has survived.

Pel 13 is a left horn core without its tip ; it is more sharply curved than Pel 12, and a wide shallow, longitudinal groove exists for a short distance in its more distal parts.

Pel 14 is an incomplete right horn core, rather little compressed and with some degree of spiralization. Since the core is broken off about 60 cm. above its base,

the degree of spiralization is only reliably indicated by the course of the longitudinal grooving and ridging on the lower part of the core. A wide and marked but rather shallow longitudinal groove begins on the back outside curve of the horn core about 15 cm. from the base. A fragmentary right horn core, Pel 17, could come from the same individual as Pel 14.

Pel 15 is a left horn core with part of the frontal, occipital and basicranial surfaces attached, and the brain cavity itself has survived practically complete. The anterior tuberosities of the basioccipital are missing and the left foramen rotundum can be seen. The base of the right horn core is also present. The left horn core overhangs the top of the occipital as in other *Pelorovis* specimens.

Pel 16 is a much damaged fragment of a left horn core with part of the frontal remaining at the horn base.

Pel 22 is a right horn core which exists in two unconnected pieces, and shows much spiralization. Its span would have been about 69 cm., and compares with about 41 cm. for the female horn core Pel 18 (see below) and about 93 cm. for the large Pel 7.

Pel 6 is a very crushed and incomplete right horn core about 70 cm. long. It comes from site SHK II about 26 feet lower than BK II.

Except for Pel 1, all the horn cores and skull remains hitherto considered may be regarded as being either of males or of indeterminate sex. Two further horn cores agree with Pel 1 in appearing to belong to female animals, these have been numbered Pel 18 and Pel 19. They are evenly tapered along their entire length, but considerably shorter and more sharply curved than the other horn cores ; the tips are more upwardly curved than in males of comparable size. The right horn core, Pel 18, has attached to it a part of the frontal, the back of the orbit and the roof of the temporal fossa. The temporal fossa is less deeply excavated than in either of the skull pieces numbered Pel 2 and Pel 3, and this is presumably linked with the smallness of its horns. Pel 19 is very probably the same individual as Pel 18.

There are also many other fragments of distal ends or the more distal parts of horn cores assignable to *Pelorovis* ; from these broken pieces we can see that the horn cores had thickened outer shells, inside which was a central cavity becoming narrower towards the tips. At any one level of cross section the thickness of the outer shell varies, but I did not find any of the internal struts which Reck (1928) refers to and illustrates.

A well preserved basicranial piece, Pel 20, shows several interesting features. The occipital condyles, being complete and undistorted, are wide as in other *Pelorovis* remains ; the basioccipital has its anterior tuberosities with slight longitudinal ridges behind them ; the bases of the auditory bullae show them to have been rather compressed and presumably poorly inflated. Both external auditory meati can be seen. This specimen is the only one to retain complete paraoccipital processes, they are short and squat and their tips are not at all forwardly directed. Parts of the occipital surface and of both temporal fossae are also preserved, but they give no information not already available from other specimens.

There is an occipital fragment, Pel 21, possessing both condyles and part of the right temporal fossa.

Tooth remains

From a badly crushed skull, Pel 23, there have been preserved parts of both maxillae and premaxillae (Pl. 3) and of the tooth rows. The premaxilla is wide at its base but narrows rapidly as it rises ; at its top it joins the maxilla in a sutural contact with the nasals, as often happens in large Bovids. Its teeth are a little smaller than others assigned to *Pelorovis*.

A good number of fossil maxillary and mandibular pieces and isolated teeth belonging to large Bovids are present in the collections from Olduvai. Many of them have morphological characters appropriate for very large Alcelaphini, but the largest among them are clearly not Alcelaphine and must belong to *Pelorovis*. Examples of its upper teeth are distinguished from those of Alcelaphini by the fact that the whole tooth row is more or less straight and not set in an arc, by the presence of rather weakly developed basal pillars, and the relatively simple course of the enamel walls of the central cavities. They appear to be less hypsodont than the Alcelaphine teeth, although this is an awkward feature to assess except with unworn examples of both groups for comparison. Finally, the upper teeth of *Pelorovis* are wider than those of Alcelaphini. Many examples of both upper and lower *Pelorovis* teeth show rugosity of the enamel, a characteristic which is perhaps of use in binding the surrounding cement to the tooth. The largest lower teeth of Bovidae in the Olduvai collections differ from those of Alcelaphini by the presence of basal pillars. It is apparent from looking at the mandibles and lower teeth that the size of a basal pillar will change with the stage of development of its tooth. In little worn teeth the level of the top of the basal pillar may not have been reached, later the level of maximum cross section is reached, finally in much worn teeth the level of the bottom of the basal pillar is passed, and it becomes joined to the body of the tooth.

1957, SHK II, 232 (Pl. 3) is an adult right maxilla with P^4 to M^3. Its teeth are comparatively little worn, and they show the relatively simple occlusal surfaces of the teeth of even younger *Pelorovis*.

A number of isolated upper molars are mostly smaller than the M^2s in the complete skull ; they all have traces of infoldings into the central cavities but these are never very pronounced. The outline of the occlusal surfaces becomes more squared medially as the teeth are worn down.

A few pieces of large Bovid mandibular ascending rami belonging to *Pelorovis* are known : 1953, BK II, area C, 91?, can be identified by the relative lack of curvature on the anterior edge of its coronoid process. Its mandibular foramen is situated about half way between the front and the back edges. Two other condyle fragments are a right and left pair with the excavation numbers 1955, BK II, 5 and 6. The top of a left ascending ramus, 1952, BK II, 123, differs from the other mandibular remains of *Pelorovis* by the lowness of its coronoid process above the condyle ; it could perhaps have come from a younger and smaller animal.

A number of specimens of lower teeth give information additional to that available from the more worn teeth of the mandible belonging to the complete skull.

1952, BK II, 117 (Pl. 3) is a left mandibular fragment containing all of the teeth from P_4 backwards except that M_3 is without its posterior lobe. The top of the

jaw is rather more concave than in older specimens. The P_4 has not been long erupted and the anterior part of its medial wall is only just closed at the top. The tops of the medial edges of the lobes on the molars rise high above the level of the tops of the intervening styles. The basal pillar is small on M_1, was probably bigger on M_2, but is not yet visible on M_3. The anterior end of the comparatively little worn M_3 has a sharply medially turned flange, but this would have become less pronounced with increasing age. Each molar has little contact with the molar immediately in front.

1952, BK II, 118 is another fragment of a left mandible, but here M_3 is the only tooth to have survived, P_3 to M_2 being broken off at their necks. M_3 has been about as much worn down as in the mandible of the complete skull. A great amount of cement has been preserved between the first and second lobes of M_3, and the first lobe has been excessively worn down on its medial side.

1952, BK II, 119 (Pl. 3) is another left mandible fragment, this time preserving at least parts of all its teeth. The adult premolar row is newly erupted, P_4 has a closed anterior part of its medial wall, there is only narrow contact between M_3 and M_2, and there is again a strong medially turned flange at the front of M_3. The front of M_2 has been pushed into the back of M_1, and since the underlying part of the jaw bone is complete and undistorted this appears to have occurred in the living individual. In addition the plane of the occlusal surface of the front of M_1 shows that 119 is a second example of an animal with a tooth deformity. This jaw comes from a younger animal than 117 and since the incomplete but little worn M_3 is exposed to its roots, one can get an impression of the hypsodonty of the species. The ramus looks as if it is less deep than the one belonging to the complete skull. The medial sides of the lobes do not rise so high in comparison with the styles as in 117, but this probably has no taxonomic significance. The level of the top of the basal pillar has not been reached by the occlusal surface of M_3, the pillar is quite large on M_2, and its condition in M_1 cannot be clearly seen.

1957, BK II, 1032 is a left mandibular fragment which has M_2 and M_3 in an early state of wear, hence they are not very wide at their occlusal surfaces. The last lobe of M_3 has not been worn at all, and the central cavities of its first and second lobes are still open medially at their posterior ends. Basal pillars are not visible on either tooth, perhaps because the pillar of M_2 is hidden under cement while that of M_3 has not yet been reached.

1952, BK II, 127 is a left mandibular fragment with M_1 to M_3, the central cavity of the front lobe of M_1 having been worn away. An unnumbered specimen consists mainly of plaster around a left M_1 to M_3 in which much cement is present and the front central cavity of M_1 is again missing. 1953, BK II Extension, 79 is a right mandibular fragment with M_3 and most of M_2 in about the same state of wear as the last two pieces. An unnumbered fragment from MRC II is a piece of a left mandible with M_3, M_2 and the roots of M_1.

There are a good number of isolated lower teeth among which some show points of interest. Thus 1957, SHK II, 165 is a little worn right M_3 which shows anteriorly a medial flange becoming less prominent towards the base of the tooth; a basal pillar is present all the way down. 1952, BK II, 129 (Text-fig. 4) is a little worn right

M_1 or M_2 which shows well the height of these animals' teeth and in addition preserves one of its roots complete.

A lower left molar, 1953, BK II Extension, 355 (Text-fig. 5) is likely to have belonged to a *Pelorovis* yet differs from other lower molars in having less pronounced and more localized outbowings of the medial walls between the styles.
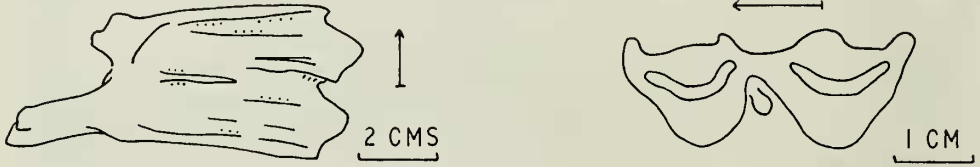
4   1952 BK II 129

5   1953 BK II EXT. 355

FIGS. 4, 5.   Medial view of right lower molar 1952, BK II, 129, and occlusal view of left lower molar 1953, BK II Extension, 355.   The arrows point anteriorly.

Measurements of skulls and teeth

On the complete skull—Pel 1—the following measurements, all expressed in centimetres, were taken:

Skull length from the front of the premaxilla to the back of the occipital condyles, estimated before distortion at . . . . 68·8
Skull width across the posterior side of the orbits . . . . 27·4
Distance from the front of the premaxilla to the nearest point on the orbital rim . . 42·4
Length of horn core along its back edge 116
Dorso-ventral diameter of horn core at a distance from its base along the back edge equal to half the maximum diameter at its base . . . . 9·7
Diameter of the horn core at 90° to above measurement . . . . . . 12·4
Width between the supraorbital foramina, taken between the central points of their lateral walls . . . . 11·6
Length of nasals, estimated at . . . . 31·8
Width of nasals, taken across level **a** in Text fig. 1 . . . . 6·8
Distance from the front of premaxilla to rearmost point of occlusal surface of M^3, estimated before distortion at . . . . 34·9
Distance from the rearmost point of occlusal surface of M^3 to back of occipital condyles, estimated before distortion at . . . . 34·0
Occipital height from the top of foramen magnum to top of occipital crest . . . 11·1
Skull width across mastoids immediately behind external auditory meati . . . 27·3
Width across anterior tuberosities of basioccipital . . . . 4·9
Width across posterior tuberosities of basioccipital . . . . 8·5
Occlusal length M^1 to M^3 . . . . 11·1
Occlusal length of M^2 . . . . 3·75
Occlusal width of M^2 . . . . 3·3
Occlusal length M_1 to M_3 . . . . 11·8
Occlusal length M_2 . . . . 3·5
Occlusal width M_2 . . . . 2·1
Occlusal length P_2 to P_4 . . . . 6·0
Occlusal length of the heavily worn P_2 . . . . 1·5

Measurements on other skull pieces of *Pelorovis* were:

	Pel 2	Pel 3	Pel 4	Pel 20
Skull width at orbits . . .	—	28·2	—	—
Width between supraorbital foramina	13·4	15·0	—	––
Occipital height . . .	9·9	9·7	13·2	—
Skull width at mastoids .	26·8	27·3	23·8	26·7
Width across ant. tubs. of basioccipital . . .	4·2	4·5	4·1	5·0
Width across post. tubs. of basioccipital . . .	7·8	7·7	8·3	8·7

Measurements of width of anterior and posterior tuberosities on other basioccipitals were: Pel 5, 4·3 and 8·3 ; Pel 15, 4·1 and 7·25.

Horn core dimensions, taken as indicated above, were:

	Dorso-ventral diameter	Diameter at 90° to the last	Length
Pel 2	9·2	13·1	—
Pel 7	11·6	13·8	153*
Pel 9	10·5	14·0	142*
Pel 12	10·6	13·6	149
Pel 18	9·6	12·6	102
Pel 5	10·4	14·1	—
Pel 6	11·1	13·3	125
Pel 4	11·3	13·9	––
Pel 14	11·7	14·3	—
Pel 15	11·0	15·4	—
Pel 22	11·1	14·0	—

* The tips of these horn cores are of plaster.

The span between the tips of Pel 6 horn cores was 184, and of Pel 7 and Pel 8 together 205.

Pel 23 had the following tooth measurements : length M^1–M^3 9·95 ; length M^2 3·1 ; width M^2 2·7 ; length P^2–P^4 6·05 ; length P^2 1·9.
The right maxilla 1957 SHK II 232 has length M^1–M^3 10·2 ; length M^2 3·5 ; width M^2 2·7.
The mandible 1952 BK II 117 has an M_2 3·9 long × 1·8 wide.
The mandible 1952 BK II 119 has length P_2–P_4 6·75 ; length P_2 1·8 ; height of M_3 from its neck to the valley on the medial side between the first and second lobes 5·9.
1957 BK II no number has an M_2 3·7 long.
The unnumbered left mandible with much plaster has an M_2 measuring 3·6 long × 2·0 wide.
A left mandible fragment 1952 BK II 127 has length M_1–M_3 11·1 and M_2 3·4 long × 2·0 wide.
    A list of isolated upper molars follows, for most of which length and breadth are given :
1941 surface of Bed I F.107 3·4 × 2·45 ; 1952 BK II 124 3·9 long ; 1952 BK II 140 3·7 × 2·4 ; 1952 BK II 141 is probably the same individual as 140 ; 1952 BK II 132?, 292 and 293 are heavily worn ; 1953 BK II Extension 57 3·6 × 2·1 ; 1953 BK II Ext. 90 ; 1953 BK II Ext. 107 3·3 × 3·1 ; 1953 BK II Ext. 299 3·65 × 2·4 ; 1953 BK II Ext. 302 is probably from the same individual as 299 ; 1953 BK II Ext. 352 3·55 × 2·1 ; 1955 BK II 97 3·8 long ; 1955 BK II 116 3·7 long ; 1955 BK II 224 two left upper molars measuring 3·7 × 2·7 and 3·3 × 2·6 ; 1955 BK II 322 3·5 × 2·6 ; 1957 BK II 694 a fragmentary upper molar ; 1957 BK II 880 3·4 × 2·6 ; 1957 BK II illegible number is probably the same individual as 880 ; 1957 SHK II 179 ; no number 3·6 × 2·5.

Isolated lower molars are : 1952 SHK II 668 fragmentary ; 1953 BK II area C no number M_1 or M_2 3·3 × 1·9 ; 1953 BK II Extension 58 M_1 or M_2 3·6 × 1·3 ; 1957 BK II 974 a much worn M_1 or M_2 ; 1957 SHK II 1129 M_1 or M_2 ; 1953 BK II Ext. 79 M_3 4·9 × 1·8 ; 1955 BK II 282 M_3 ; 1957 SHK II 165 M_3 4·5 long. 1952 BK II 129 (Text-fig. 4) is a right M_1 or M_2 measuring 3·75 × 1·5 ; since it is scarcely worn its height may be measured as was that of M_3 on the mandible 1952 BK II 119—the distance is 5·3. The left M_1 or M_2 1953 BK II Extension 355 is 3·6 long.

Many isolated upper premolars are assigned to *Pelorovis* : 1952 BK II 134, 142, 143, 144, 145 and 146 ; 1953 BK II Extension 86, 300 and 301 (probably from the same individual as molar 299), and 361 ; 1957 BK II 653, 692, 977, 1077, 1361? and 1461. Isolated lower premolars are 1953 BK II Extension 87 ; 1955 BK II 143 and 144.

Finally there are numbers of large incisors which probably belong to *Pelorovis*, and an unnumbered fragment of a mandible with a premolar which is not sufficiently brachyodont for a giraffid, and which is small in comparison with the size of the mandible.

Limb bones

There is from site BK II an almost complete limb bone skeleton belonging to the same individual as the complete skull of *Pelorovis* ; this skeleton can be used as a basis for description of the characters and proportions, while other fragmentary limb bones sometimes supplement this information. The largest Bovid limb bones from BK II and other Bed II sites are taken to be from *Pelorovis* because they showed no substantial morphological differences from the associated *Pelorovis* skeleton. The characters of the limb bones have already been listed in the definition of *P. oldowayensis*, and there follow here points of lesser interest. Occasional comparisons are made with the African buffalo *Syncerus caffer* because this is the largest living Bovid in Africa and because a skeleton of it was available in Nairobi.

Femur

The paired *Pelorovis* femora, 1952, BK II, 267 and 268 (Pl. 4 ; Text-figs. 12–14) from the associated skeleton are very slightly longer than the buffalo, and are at least as thin. Other femoral fossils are : 1952, BK II, 187—a right proximal end, and 1953, BK II Extension, no number—a right proximal end which is slightly smaller than those from the complete skeleton.

Tibia

The tibiae of *Pelorovis* are longer and proportionately more slender than in the buffalo. Tibial remains assigned to *Pelorovis* are:

1952, BK II, 269,	right complete, from the associated skeleton (Pl. 4)
1952, BK II, 270,	left complete, from the associated skeleton
1952, BK II, 189,	left distal end
1952, BK II, 190,	right distal end
1952, BK II, 881,	right distal end
1953, BK II Extension, 179,	right distal end
1953, BK II Extension, 421,	left distal end and part of shaft

Calcaneum

Only two calcanea, 1952, BK II, 195 (right) and an unnumbered left one, are referable to *Pelorovis*. They are longer bones than in the buffalo, as is shown in measurements. The height of the top of the astragalus facet above the base of the bone was 5·7 cm. in both the fossil 195 and the Recent buffalo specimen, but the length of the buffalo calcaneum was 11·1 and of the fossil 11·9 cm.

Astragalus

The astragali of *Pelorovis* are slightly taller and less squat than in the buffalo. Assigned specimens are:

1952, BK II, 191,	left
1952, BK II, 196,	right ; this is the largest one.
1957, BK II, 625,	right
1957, BK II, 1413,	left (Text-figs. 16–18)
1953, BK II Extension, 324,	left
1953, BK II Extension, 325,	left
1957, SHK II, 1164,	right
1959, KK II, 211,	right

An unnumbered astragalus is about the same size as these but is more squat. It is illustrated in Text-fig. 19. I think that its proportions are too different for it to belong to *P. oldowayensis*. Measurements (in cm.) of the length and breadth of the astragali in the above list are : 191, 8·5 × 5·6 ; 196, 9·2 × 5·8 ; 625, 8·5 × 5·6 ; 1413, 7·9 × 5·2 ; 324, 8·3 × 5·6 ; 211, 7·4 × 5·1 cm. The mean of the ratios of breadth as a percentage of length is 66·2, while the squat astragalus measures 7·9 × 6·2 and has a ratio of 78·5. Two astragali numbered M.12802 are in the Felix Oswald Collection at the British Museum (Natural History) ; they come from Homa Mountain and agree with *Pelorovis* in size and proportions. One would need other bones for a positive identification.

Naviculo-cuboid

Naviculo-cuboids belonging to *Pelorovis* are :

1952, BK II, 192,	right
1952, BK II, 209,	left
1955, BK II, 282,	left
1952, BK II, no number	fragmentary right
No numbers	two left (Text-figs. 22, 23)

The smaller of the two unnumbered naviculo-cuboids (Text-fig. 23) has a nearly vertical back edge of the medial wall.

Metatarsal

The metatarsal of *Pelorovis* is considerably longer than in the buffalo and proportionately more slender. A number of distal ends exist and can be identified as left

or right by the slight asymmetry of the condyles—the medial side is a little smaller than the lateral side and its lowest point a little higher than the corresponding point on the lateral half.   Also the lateral tendon insertion at the distal end is usually noticeably deeper than the medial one.   Bones assigned to *Pelorovis* are :

1952, BK II, 275,	left complete, from the associated skeleton (Pl. 5 ; Text-figs. 24, 26)
1952, BK II, 197,	right proximal end
1953, BK II Extension, 415,	right proximal end
1957, BK II, 630,	left proximal end
1952, BK II, 220,	left distal end
1953, BK II Extension, 316,	right distal end
1953, BK II Extension, 413,	right distal end
1953, BK II Extension, 414,	left distal end
MRC II, no number,	right distal end

Scapula

The two bones assigned to *Pelorovis* are :

1952, BK II, 183,	a left stem (Text-figs. 27, 28)
1953, BK II Extension, 122,	another left stem

122 is larger and has a more pronounced muscle insertion at the back of the medial side of the stem, a character which is seen in some large Bovinae.

Humerus

Humerus specimens assigned to *Pelorovis* are :

1952, BK II, 271,	left complete, from the associated skeleton (Pl. 4)
1952, BK II, 272,	right complete, from the associated skeleton
1952, BK II, 184A,	right proximal end
1952, BK II, 185,	right proximal end
1957, BK II, 1847,	left articular head
1955, BK II, no number,	left shaft
1941, S.2, F.929,	left distal end
1952, BK II, 186,	right distal end
1952, BK II, 352,	left distal end
1953, BK II Extension, 44,	right distal end
1953, BK II Extension, 317,	right distal end
1953, BK II, no number,	right distal end

The proximal end 184A has the front of its articular head more ventrally sited than in the other specimens, but this is probably not an indicator of specific difference.

Radius

Radii assigned to *Pelorovis* are :

1952, BK II, 273,	left complete, from the associated skeleton (Pl. 4 ; Text-figs. 31, 32)
1952, BK II, 274,	right complete, from the associated skeleton
1955, BK II, 294	left, almost complete (Text-figs. 33, 35)
1952, BK II, 353,	right proximal end
1953, BK II Extension, 425,	right proximal end (Text-fig. 34)
1952, BK II, 188,	right distal end
1955, BK II, 242,	left distal end
1953, BK II Area C, no number,	right distal end, water rolled
SHK II, 25,	right distal epiphysis

SHK II, 25, for which the year of excavation is unknown, and a fragment of an axis vertebra 1957, BK II, 889 are the only known juvenile pieces of *Pelorovis*. 1955, BK II, 294 is smaller than the other radii and more swollen at its distal end in side view ; it could be a different species from *Pelorovis oldowayensis*.

Carpal bones

Only one poorly preserved right unnumbered scaphoid of *Pelorovis* is available. It is less tall and slightly longer than in the African buffalo ; such proportions are seen in all the carpal bones. There are two lunates of *Pelorovis*, one left and one right, and both of them unnumbered. A left and a right cuneiform are both unnumbered. A left and right magnum-trapezoid are both unnumbered ; the better preserved left one is antero-posteriorly longer and also broader than in the buffalo, the other one is smaller and has proportions more like *Syncerus*. There are an unnumbered left unciform and a right one numbered 1957, BK II, 1255.

Metacarpal

Metacarpals belonging to *Pelorovis* are :

1952, BK II, 277,	left complete, from the associated skeleton (Pl. 5)
1957, BK II, 1037,	left proximal and distal ends of the same bone (Text-fig. 36)
1955, BK II, 295,	left, almost complete
1955, BK II, 82,	right proximal end
No number,	poorly preserved right proximal and distal ends
1952, BK II, 199,	distal end
1952, BK II, 354,	distal end
1953, BK II, no number,	distal end
1953, BK II Extension, 52,	distal end
1953, BK II Extension, 138,	distal end
1953, BK II Extension, 170,	distal end
1955, BK II, 147,	distal end
1957, BK II, 19,	distal end
1957, BK II, 863,	distal end
1957, BK II, 1188,	distal end
1957, FC S, 367	distal end

It is not possible with metacarpal distal ends to distinguish left from right as was done with the distal ends of metatarsals. The complete metacarpal is longer than in the buffalo and rather thinner. 1957, BK II, 1037 is a larger bone than the complete metacarpal, but it cannot belong to the giraffid *Sivatherium* because the medial facet is not sufficiently flat and because of the existence of a small ridge between the medial and lateral facets. 1955, BK II, 295 is rather small and presumably came from the same individual as the radius 1955, BK II, 294.

Phalanges

Five fossil first phalanges are without numbers, one of them being from MRC II, others are numbered 1952, BK II, 202, 203 and 208, and 1941, S.1, F.837. Five second phalanges are without numbers, one of them again being from MRC II, the others are 1952, BK II, 201 and 204, 1955, BK II, 231 and 1941, S.1, F. 326. 1952, BK II, 239 and 321 are smaller bones but probably within the range of variation of the species. The length of combined first and second phalanges was greater in *Pelorovis* than in the buffalo ; for short (front) phalanges *Pelorovis* measured 11·6 cm. and two buffaloes 11·0 and 11·1, while for longer (back) ones *Pelorovis* measured 12·0 against 11·5 and 11·6 for the buffaloes.

There are six third phalanges without excavation numbers, plus 1952, BK II, 200 and 205, 1953, BK II Extension, 402, and a somewhat smaller bone 1952, BK II, 238 evidently matching the second phalanx 239.

Measurements of limb bones

Measurements of length (in cm.) were taken on the long limb bones of the associated skeleton of *Pelorovis* :

Length of femur from the lateral end of the articular head to the ventralmost level of the medial condyle . . . . 43·3

Length of tibia from the ventralmost point of the top medial facet to the tip of the bone behind the medial malleolus . . . . 43·1

Length of metatarsal from the highest point of the bone behind the medial part of the ectocuneiform facet to the articular surface on the medial side of the most projecting part of the medial condyle distally . . . . 27·5

Length of humerus from the top of the lateral tuberosity to the ventralmost point of the medial side distally . . . . 35·1

Length of radius from the medialmost point of the medial facet to the most distal point of the ridge bounding the scaphoid facet medially . . . . . . 35·5

Length of metacarpal from the anterior edge of the articular facet at the extensor carpi radialis insertion to the articular surface on the median side of the most projecting part of the medial condyle distally . . . . 23·8

Least thicknesses of these bones were : femur, 5·23 ; tibia, 5·72 ; metatarsal, 3·90 ; humerus, 5·01 ; radius 5·44 ; metacarpal, 4·88. The left radius 1955, BK II, 294 was c.32·7 long and had a least thickness of 4·81.

Vertebrae

A great many vertebrae belonging to large Bovidae are known from BK II.

Atlas

The best preserved atlas (Text-fig. 6) belongs to a complete row of cervical vertebrae which may have belonged to the same individual as the skull to be described on p. 291. It is a wide and very short bone with large transverse processes which do not extend very far posteriorly. The sides of the bone are straight or very slightly convex.
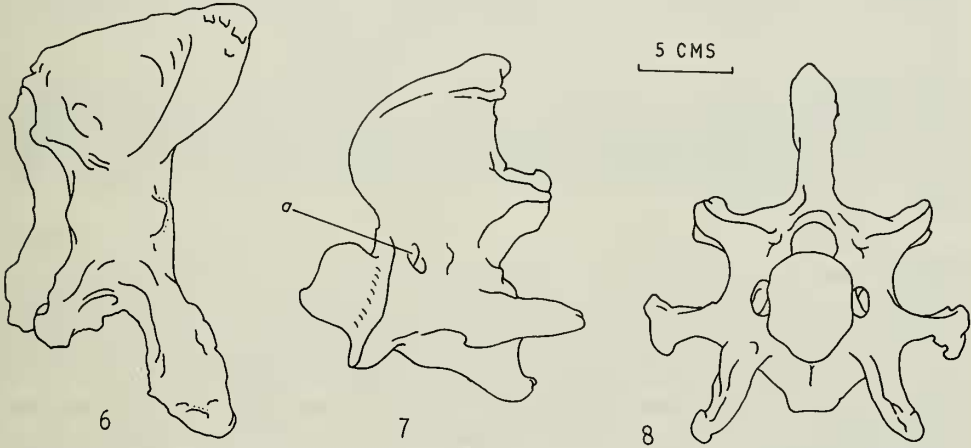
FIGS. 6–8. Three vertebrae from a complete set of cervicals. 6, atlas in ventral view ; 7, axis, in lateral view ; 8, fifth cervical in anterior view. *a* = vertebrarterial foramen.

A second and less complete atlas is similar to the first but more indented at the front of the dorsal side.

A third atlas has its transverse processes projecting less backwards, and more prominent ridges behind the ventral hollows, which may be correlated characters. Its front articular facets are less wide than in the first two atlases mentioned, and its dorsal side slightly more hollowed.

A fourth atlas has still more pronounced ridges at the back of the ventral surface than in the last one, and its front articular facets are as narrow as in that specimen. The dorsal hollowing is intermediate between that of the first two and the third atlases mentioned above. The indent at the front of the dorsal surface is as deep as in the second atlas, and the openings for the vertebrarterial and alar foramina are well separated in an elongated common fossa. It is conceivable that this atlas belongs to a different species from the others.

The articular facets of the first and second atlases fit the skull to be described on page 291 better than they do the complete skull of *Pelorovis oldowayensis* on account of the former's smaller occipital condyles. The first atlas fits Pel 5 and Pel 21, but does not fit Pel 2, Pel 4 or Pel 24 any better than the complete skull. If the first three atlases are conspecific with the skull remains of *P. oldowayensis*, the problem exists of why the largest one fits only two out of the six available occipital condyles, and not even these two very well.

Axis

The most complete axis (Text-fig. 7) belongs to the same set of cervical vertebrae as the first atlas described above, and has preserved its transverse processes. A larger fossil axis has lost its transverse processes and most of its neural spine. The base of the neural spine is longer and the postzygapophyses more slanted in posterior view than in the first axis. This second axis is too large to articulate with any of the atlases but seems to belong with a second row of very large cervical vertebrae. A ventral fragment of an axis vertebra is numbered 1957 BK II 889, and by the condition of the rear of its centrum is from a young animal.

The position so far is that we have one atlas and one axis from the same complete set of cervicals, possibly belonging to a skull to be described later, and an axis from a larger set of cervicals complete except for the atlas and fifth cervical. There are three other atlases, one of which may come from another species, and an axis fragment, possibly juvenile.

Cervical vertebrae

The third cervical vertebra from the complete set is short. It has a tall neural spine and a deep posterior indentation in the neural arch—this is correlated with the shortness of the bone which brings the neural spines of adjacent vertebrae close together. The third cervical from the larger and less complete set is a longer bone and has a proportionately less deep indent posteriorly.

Measurements of the lengths of the two cervical rows were taken while they were supported in approximately their natural positions in a sandbath. The length of the complete set was 46·1 cm. from the mid-ventral point of the front of the atlas to the mid-ventral point of the back of the centrum of the 7th cervical. The length of the less complete row from the mid-ventral point of the articular rim behind the odontoid facet of the axis to the 7th cervical, allowing for the missing 5th, is 44·6 cm. So far as could be seen from mounted specimens in the British Museum (Natural History), these lengths are about the same as in Bovini.

Two other cervicals from BK II probably belong to *Pelorovis*, so too an unnumbered 7th cervical from HWK II.

Thoracic vertebrae

A well preserved but unnumbered series of thoracic vertebrae runs from about number four to number eleven. There are also parts of eighteen other thoracic vertebrae, fifteen unnumbered and the other three a series—1953, BK II Extension, 25, 26 and 27. 25–27 and an unnumbered pair are transitional to lumbars, i.e. from the back of the thoracic series. Two fragmentary first thoracics are recognizable by their very widely spaced prezygapophyses, and one of them may articulate with the seventh of the most completely preserved set of cervicals. The prezygapophyses on the first thoracic vertebra are concave. On this vertebra the foramen behind the transverse process is not closed posteriorly, but in two other anterior thoracics it is. In the most complete and best preserved set of thoracic vertebrae this foramen becomes progressively larger in the more posterior parts of the row, as is the general

rule in Bovidae. There are fairly deep median indentations between the prezy-gapophyses. The postzygapophyses are nearer to the bases of the neural spines than in smaller Bovidae which is a difference which is better seen in anterior members of the series. The neural spines of the most complete set are tall, and the length of the tallest from the mid-dorsal point of the anterior end of the centrum to the top of the spine is 43 cm. This seems to be about usual for Bovini. The best preserved set of thoracics is not certainly from the same individual as the most complete set of cervicals.

Lumbar vertebrae

No long series of lumbars are present, but there are remains of six, all without numbers. The foramina at the side of the neural arches are small, and towards the end of the lumbar series their posterior edges are no longer closed.

Sacrum and tail

There is a fragment of a sacrum which is unnumbered, and twelve caudal vertebrae numbered 1952, BK II, 255 to 266.

III THE SYSTEMATIC POSITION OF *PELOROVIS*

It has already been noted that *Pelorovis* does not belong to the Caprinae. A far better choice for relationship is the Boselaphine-Bovine stock, but there are also a number of resemblances to *Oryx* Blainville in the tribe Hippotragini. These include the low wide skull, the horn insertions being in the same plane as the face, the absence of projecting orbital rims, the long nasals, the anterior position of the tooth rows and the characters of the teeth. The dorsal view of the *Pelorovis* skull (Pl. 1, fig. 2 ; Text-fig. 3) reminds me of *Oryx*, and the occlusal views of the molar teeth (Text-fig. 11) are similar. I shall conclude that such resemblances exist because *Oryx* has some similarities to the Bovini as a whole and not because *Pelorovis* belongs to the Hippotragini. None the less it seems desirable to include the Hippotragini with the Bovini in a detailed character comparison with *Pelorovis*. There are two living Hippotragine genera other than *Oryx*—*Hippotragus* Sundevall and *Addax* Rafinesque; the latter is similar to *Oryx* in most skull characters and need not be considered separately.

In this part of the paper bones of the living species of *Oryx* and *Hippotragus* and the Bovine genera *Bubalus* H. Smith, *Bos* Linnaeus, and *Syncerus* Hodgson will be compared to see which of them most resembles *Pelorovis*. The genus *Bos* is taken to include *Bibos* Hodgson (with the Asian species *Bos javanicus* D'Alton and *B. gaurus* H. Smith), *Bison* H. Smith, and *Poëphagus* Gray, as well as oxen in the narrow sense. The word *Bubalus* will refer only to *Bubalus bubalis* (Linnaeus) ; the small anoa, *B. depressicornis* (H. Smith), will be referred to by its full Latin name or as the anoa. The word *Syncerus* will refer only to *Syncerus caffer caffer* (Sparrman) and not to the West African bush buffalo, *S. c. nanus* (Boddaert), which will be specified separately. The English word " buffalo " will also refer only to *S. c. caffer*. Measurements, and the ratios derived from them, will be used where they are helpful ;

the methods of taking measurements have already been given. Skull measurements were taken on adult male animals, or on animals of unknown sex which could not be reliably distinguished from males, in the collections of the British Museum (Natural History). Measurements on *Syncerus* were confined to animals from East and Central Africa, these being larger than West African bush buffaloes ; measurements on Hippotragini were separated according to species.

Fossil genera are considered wherever they are a source of relevant information. Among Hippotragini, fossils of *Hippotragus* are known from the Tatrot and Pinjor (Villafranchian) of India, and from South Africa (Cooke 1947). A number of early species, probably ancestral to later *Oryx* and *Hippotragus*, are known from Pikermi and other Lower Pliocene sites of Europe and Asia. Also of Lower Pliocene age are the Chinese genera *Prosinotragus* and *Sinotragus* (Bohlin 1935), which represent a group not related to later African species. *Aeotragus garussi* is a name given by Dietrich (1950) to fossil Hippotragine teeth from the Laetolil area of East Africa.

Among Bovine fossils are the extinct large and long-horned buffaloes of the African Upper Pleistocene, recognized by Bate (1951) to be closer to *Syncerus* than to *Bubalus*, and given by her the generic name *Homoioceras*.[1] I have seen the cast of the Sudanese *H. singae* Bate in London ; a cranium with partial horn cores, another horn core and a few limb bones of the North African *H. antiquus* (Duvernoy) in Paris ; and the skeleton of *H. nilssoni* (Lönnberg) from Malewa near Naivasha, Kenya and now in Stockholm. I agree with Miss Bate about the resemblance of these animals to *Syncerus*, indeed there is at least a possibility that they might include the ancestors of the living species which can be regarded as specialized in its skull proportions and small horn cores.

Simatherium kohllarseni is a name given by Dietrich (1942) to a buffalo-sized Bovine from the beds in the Laetolil area, which are thought to be slightly older than Bed I at Olduvai.

Leptobos Rütimeyer is the Villafranchian ox of Europe and India, differing from the closely related *Bos* by having less posteriorly inserted horn cores, and by other characters associated with this. The earliest examples of *Bos* are contemporary with *Leptobos* ; they are the large and long-horned *B. acutifrons* Lydekker from the Indian Pinjor, and *B. sivalensis* (Lydekker) and *B. palaeosinensis* (Teilhard de Chardin & Piveteau) which are two bison from the Pinjor and from Nihowan in China. Later in the Pleistocene comes the great extinct Palaearctic ox *Bos primigenius* Bojanus, with its Indian subspecies *B. primigenius namadicus* (Falconer) which had somewhat longer horns with a posterior keel towards their base.

Hemibos Falconer is an extinct Villafranchian genus from India and Palestine (Pilgrim 1941) related to *Bubalus* ; it differs from *Leptobos* by having keeled horn cores, longitudinally convex frontals between the horn bases, and a braincase more bent down on the facial axis.

Proamphibos Pilgrim from the Dhok Pathan and Tatrot (Pliocene and earliest Pleistocene) of India is smaller than *Hemibos*, and could be its ancestor. A contemporary genus from Europe is *Parabos* Arambourg and Piveteau. A cranium of *P. cordieri* (Christol) from Montpellier and a skull and cranium of *P. boodon* (Gervais)

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[1] The name *Homoioceras* actually dates from 1949 (see Bate 1951).

from Perpignan are available in Paris, together with more fragmentary pieces.   The teeth of these animals are slightly less advanced than in *Proamphibos*.   It is not necessary to continue the list of fossils ; all that need be said is that there is little doubt that later Pliocene Europe and India were inhabited by a variety of Boselaphine or Bovine species, not all of which need have phyletic connections with later Bovini. Teeth in the palaeontological collections at Uppsala show that similar animals inhabited later Pliocene China.   It is an as yet unanswered question whether the ancestry of *Syncerus*, like that of *Bubalus* and *Bos*, lies among these animals, or whether its progenitors were by then already living in Africa, having separated from the Eurasian stock at an earlier date.

I.   It may be noted at the outset that the large size of *Pelorovis* is a good reason for thinking it to be Bovine ; Hippotragini are medium to large Bovidae, and although there are small Bovini such as the anoa, the progress of evolution through Boselaphini to Bovini has usually been accompanied by increasing size.   According to measurements of skull length and length of upper molar row (Text-fig. 9) *Pelorovis* is large among Bovini ; in orbital width as a measure of size it is easily exceeded by *Bos primigenius* ; while its femur length is less than in *Homoioceras nilssoni, Bubalus,* or *Bos primigenius*.   The largeness of Bovini hinders comparison with other Bovid
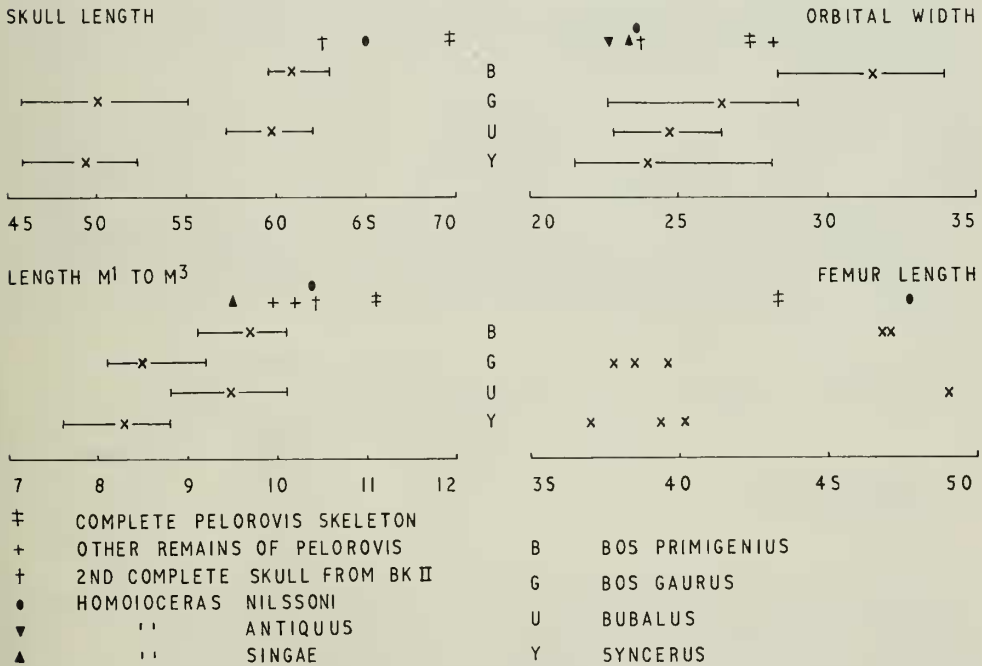

FIG. 9. Four diagrams to show the size of *Pelorovis oldowayensis* in relation to some Bovini. Individual readings are shown for African fossils and for the femur lengths of all animals ; in other cases the mean value and observed range are shown. Measurements in cms.

tribes because I am so often unsure about the extent of allometric influence on the characters.

2. A comparison of general skull proportions shows that *Syncerus* has a wide skull with a shortened facial region ; that *Bubalus* has a narrower skull with a longer face ; and that *Bos* is very wide across the frontals, with oxen having a long face and bison a shortened face. In *Hippotragus* the skull is high and narrow and although *Oryx* does have a broader and lower skull than *Hippotragus*, this is not carried so far as in the larger Bovine genera, for which allometry must be largely the deciding factor. *Pelorovis* is closest to *Bubalus* in these proportions, but if the supposed allometry is taken into account it could equally be considered to be like *Oryx*.

The two ratios of length from the premaxilla tip to the front of the orbit as a percentage of skull length and orbital width as a percentage of skull length give quantitative indications of skull shape. Readings for the first ratio in Bovini were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	18	7	9	4
Mean value . .	53·3	59·9	56·5	63·4
Range . . .	49·7–56·4	57·4–61·9	54·3–58·2	62·4–63·7

The face of *Syncerus* is shorter than in the two *Bos* species or *Bubalus*, although this effect might be less pronounced in females and the smaller West African bush buffaloes which have not such large basal bosses to their horn cores. The reading for *Homoioceras nilssoni* was 52·8—close to that for *Syncerus*, and for the complete skull of *Pelorovis* 61·6—close to *Bos primigenius*. Hippotragini have values from 59·6 (mean of three *Addax*) to 63·8 (mean of five *Oryx beisa*), i.e. their faces are as long as in *Bubalus*, *Bos primigenius* and *Pelorovis*. However in *Hippotragus niger* the component of length of face in this ratio has been increased by the bending of the braincase on the facial axis. *Hippotragus equinus* has a slightly longer braincase ; its appearance of having a very long braincase is caused partly by the height and narrowness of its skull and partly by the uprightness of its horn insertions.

Readings for the ratio orbital width as a percentage of skull length were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	18	7	9	4
Mean value . .	48·7	41·2	52·3	55·1
Range . . .	44·8–53·7	39·0–44·0	48·0–56·0	47·5–64·5

Bos is very wide at the orbits, due to expansion of the frontals, while *Bubalus* is rather narrow, and *Syncerus* is intermediate. The value for the complete skull of *Pelorovis* is 39·8, which is narrower than the mean for *Bubalus*, but in male animals with bigger horns the orbital width would probably have been greater. In *Homoioceras nilssoni* the value was c. 36·3, the orbits of this specimen being probably closer together than in either the *H. antiquus* or *H. singae* specimens. Hippotragini have

values from 38·1 (mean of six *Hippotragus niger*) to 44·2 (mean of three *Addax*). Length of face also affects the dimensions of the nasals and the position of the tooth row, both of which will be considered later.

3. Among living forms horn cores are long in Hippotragini, long in *Bubalus*, intermediate or short in most *Bos*, and short in *Syncerus*. The African *Homoioceras* had very long horns, and so too did the Indian *Bos acutifrons* which is older than *Pelorovis*. This character is obviously not useful in determining the affinity of *Pelorovis*.

4. The horn cores are straighter in *Oryx*, except in *O. algazel*, than in the other genera considered here, and *Oryx* is also unlike *Pelorovis*. The torsion of the horn cores of *Pelorovis*, in so far as it exists, is clockwise from the base upwards in the right horn core, which is the same as in *Leptobos*, *Bos* and *Syncerus*. The difference between weakly clockwise and weakly anticlockwise torsion is slight, so even were *Pelorovis* different from the Bovines, it would count for little. However the actual course of the curvature as opposed to the torsion of the horns of *Pelorovis*, as seen in Pl. 1, fig. 2, consists first of a backwards swing, then of one to the front, whereas in *Homoioceras* the swing is at first forwards then backwards ; i.e. the horns of *Homoioceras* are on a different arc of a clockwise circle. The curvature of *Pelorovis* horns is like that of long-horned species of *Bos*.

5. At the present time dorso-ventral compression of the horn cores is more pronounced in *Syncerus* than in *Bos*, with *Bubalus* being intermediate. Measure-
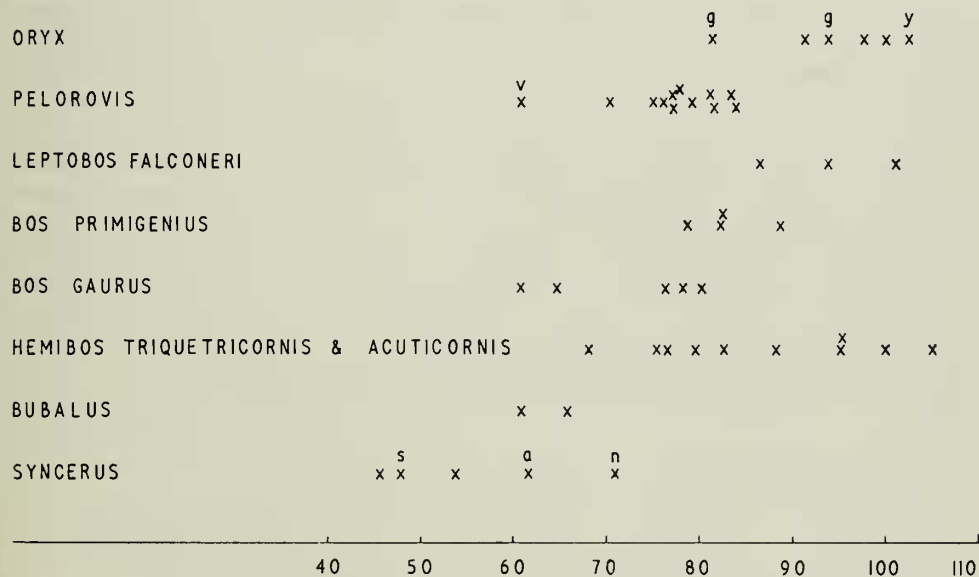

Fig. 10. Histogram of dorso-ventral diameter of horn cores as a percentage of transverse diameter. g = *Oryx gazella*, y = *O. algazel* ; the remaining three *Oryx* belong to *O. beisa*. v = the second complete skull from Olduvai BK II, s = *Homoioceras singae*, a = *H. antiquus*, n = *H. nilssoni*. One specimen of *Hemibos* had a ratio of 126.8.

ments are difficult to take, but it does seem (Text-fig. 10) that the horn cores of *Leptobos* are less compressed than in *Bos*, *Hemibos* than in *Bubalus*, and *Homoioceras* possibly less than in *Syncerus*.   Therefore it is not possible to say that *Pelorovis*, with its slight compression, resembles one Bovine group rather than the others. *Oryx* has almost rounded horn cores (although there are probably valid differences among the species for this), but *Hippotragus* has transverse compression.

6.   Keels on the horn cores are absent in *Pelorovis*, in living and most fossil Hippotragini, in *Bos* except for the Indian *B. acutifrons* and *B. primigenius namadicus*, and in *Leptobos*.   They are present in *Bubalus*, *Hemibos* and *Proamphibos*, and in West African bush buffaloes.   Those in larger *Syncerus* and in *Homoioceras antiquus* appear to be a result of the compression of the horn cores, and they are less marked in the less compressed horn cores of *H. nilssoni*.   All that emerges with certainty from this character is that *Pelorovis* is unlike the *Bubalus* group.

7.   Among Bovini the earlier species have more nearly uprightly inserted horn cores in lateral view, but later in evolution their basal parts come to be more nearly in the plane of the face.   The horn cores of *Hippotragus* are more uprightly inserted than in any other genus considered here ;   however, those of *Oryx* are in the plane of the face as in later Bovini, and this state was acquired earlier in the *Oryx* stock than in Bovini as witnessed by the Lower Pliocene *Palaeoryx*.   This character is therefore of little use in helping to decide the tribal affinity of *Pelorovis*, since the Bovini lie between the two Hippotragine extremes.

8.   The horn cores of Bovini arise behind the orbits.   In larger *Syncerus* their front edges are more anterior than in comparably sized *Bubalus*.   Some *Bos* species have very posteriorly-sited horn cores, so much so that they may overhang the occipital surface of the skull, and for this character *Bos* most resembles *Pelorovis*. Horn cores are inserted behind the orbits in *Oryx* but not in *Hippotragus*, the difference here being linked with the angle of insertion of the horns.

9.   In larger *Syncerus* the great basal bosses bring the horn cores closer together than in the larger *Bubalus*, while *Bos* has horn cores set far apart on its wide frontals. Hippotragini have closer insertions than Bovini, and within the Hippotragini *Hippotragus* has closer insertions than *Oryx*.   The question of how widely apart horn cores are inserted is not always easy to decide since increasing size of horn cores in evolution may bring their bases close together, and also because backward migration of the horn cores must sometimes allow them to become more widely inserted ; this last factor is perhaps responsible for their greater separation in *Oryx* than in *Hippotragus*.   In *Pelorovis* there is no doubt that the horn cores are set close together. This may be appreciated by comparing the Indian *Bos acutifrons* (Lydekker 1878, pls. 12, 13), which appears to have horn cores of about the same size and with a similar curvature to *Pelorovis*, with Pl. 1, fig. 2 and Pl. 2, fig. 3 in this paper.   The contrast between *Pelorovis* and any species of *Bos* for this character suggests that both genera have evolved their posterior horn insertions independently.

10.   Both sexes have horns in even the earliest known Hippotragini ;   in the Bovini all Recent species except the anoa have horned females, but the fossil genera *Hemibos*, *Proamphibos*, *Leptobos* and the skull which Pilgrim (1913, 1939) called *Proleptobos* all have, or are, hornless females.   The fact that I interpret *Pelorovis*

to have horned females is of no consequence, since it occurs late enough to have evolved from ancestors with or without horned females.

11. In Bovini the parieto-frontals' suture has a forwardly pointed indentation between the horn bases, although it is usually invisible in adults. In living Hippotragini it is transversely directed without anterior indentation between the horns, but early Chinese and European Hippotragini had such an indentation like Bovini. One might expect some correlation between shape of the suture and antero-posterior position of the horn cores ; however in such earlier Bovine genera as *Leptobos*, *Hemibos* and *Proamphibos* the suture does lie behind the level of the horn cores, but is none the less anteriorly indented in the centre of its course across the top of the skull. This character is not useful in relation to *Pelorovis*, since its horn cores are so posterior that the suture would be bound to be indented, even were it visible in a single specimen. The suture is straight in living *Boselaphus* Blainville, but this animal is probably remote from Bovine lineages.

12. Temporal fossae are present behind the orbits in *Pelorovis* and in Bovini, but their presence is at least partly correlated with the massiveness of the horn bases, and thus with the size of the animal, and also with the generally posterior position of the horn insertions in Bovini. They are absent in Hippotragini.

The character of temporal crests behind the horns ought to be mentioned here. Their presence or absence is said by Pilgrim (1939 : 148–149) to be correlated with the degree of bending down of the facial on the basicranial axes. The axes are at an angle to one another in Hippotragini, and temporal crests are not found. Originally the axes were little bent on one another in Bovini and their ancestors, hence temporal crests are found in *Proamphibos* and *Leptobos*. However *Hemibos* has developed a greater angle between the axes (the longitudinal convexity of the frontals between the horn bases is probably linked with this), and *Bos* has moved its horn cores to a more posterior position, thereby doing away with the need or possibility of temporal crests. The horns are so large in *Bubalus* and have such large bosses in *Syncerus* that there is no room for temporal crests, but it is not easy to say whether the facial axis is more bent on the basicranial axis than in *Leptobos* and *Proamphibos*, and whether the convexity of the frontals in the small bush buffaloes and small examples of *Bubalus bubalis* are comparable with that in *Hemibos*. It is apparent that *Pelorovis*, having horn insertions as far back as in *Bos*, could not have temporal crests.

13. The supraorbital pits are relatively closer together in Hippotragini than in Bovini. Readings for the distance between the supraorbital pits as a percentage of orbital width in Bovini were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured	21	8	10	4
Mean value	51·1	58·1	56·6	57·6
Range	42·2–59·5	55·1–61·9	43·2–72·2	55·2–62·2

The closeness of the supraorbital pits in *Syncerus* could be interpreted by supposing that the growth in size of their basal horn bosses, particularly in males, must have caused an increase in orbital width. *Bubalus* and *Bos* have supraorbital pits which

are wider apart than in *Syncerus*. The values for *Homoioceras singae, H. antiquus* and *H. nilssoni* were 50·4, *c.* 49·3 and *c.* 65·2, the last value probably reflecting that specimen's narrowness across its orbits. The value for the complete *Pelorovis* skull was 42·3 and for Pel 3 53·2. In Hippotragini the values for this ratio extend from 42·3 (a single *Oryx leucoryx*) to 47·3 (the mean of five *O. beisa*), thus supraorbital pits are closer together than in Bovini.

A point to be remembered is that the antero-posterior position of the supraorbital pits may influence their transverse separation from one another. They are more anteriorly sited in *Syncerus* (and some bison) than in *Bubalus* or *Bos* (other than bison), so that they have less space in which to be wide apart. This factor would, however, have little effect on the difference between *Bos* (other than bison) and *Syncerus* compared with the effects of the wider frontals of *Bos*. This factor does not seem to apply to *Pelorovis*, which has supraorbital pits set more posteriorly than in *Syncerus* or *Bubalus*, but none the less close together.

14. The orbital rims are strongly projecting in *Bos* (especially in bison species), less so in *Bubalus*, while in *Syncerus* such tubularity occurs only in few individuals. The orbits usually protrude little in Hippotragini except in *Hippotragus equinus*. The small bush buffaloes of West Africa have horn cores which are close to the orbits, and, being directed diagonally backwards at their bases, prohibit the development of tubularity in the orbits, but this explanation does not apply to the absence of tubularity in most larger *Syncerus*. The orbits of *Pelorovis* do not project very strongly, thus making it most like Hippotragini or *Syncerus*.

15. The nasals of *Oryx* are flatter across their upper surface than in the other genera considered here.

16. The nasals are wide in *Bos*, slightly less so in *Syncerus*, and narrow in *Bubalus*. This character can be assessed quantitatively by taking nasals' breadth as a percentage of nasals' length, and nasals' length as a percentage of skull length. The readings for the first ratio in the Bovini were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	14	5	9	2
Mean value . .	33·2	26·2	36·6	35·5
Range . . .	25·7–40·1	22·0–30·6	31·3–39·8	35·2 & c. 35·8

Width of nasals is a variable dimension.

Readings for nasals' length as a percentage of skull length were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	16	5	8	2
Mean value . .	39·8	42·4	43·8	43·0
Range . . .	34·1–43·8	40·3–45·8	39·9–48·0	42·4 & c. 43·6

Homoioceras singae had a value of *c.* 37·6 for the first ratio, but *H. nilssoni* could not be measured.

Despite its very long and narrow nasals according to the first ratio, *Bubalus* has nasals no longer relative to skull length than in the *Bos* species. The complete skull

of *Pelorovis* has a value of *c.* 21·4 for the first ratio and *c.* 46·2 for the second ; these could be taken as showing great length of the nasals (presumably linked with the long face) rather than narrowness, especially as the nasals are wider in their front half than in their back half (Text-fig. 3). Hippotragine readings for the first ratio ranged from 18·75 (mean of six *Hippotragus niger*) through 21·3 (mean of nine *H. equinus*) to 30·9 (mean of five *Oryx beisa*), and for the second from 36·2 (one *O. leucoryx*) to 42·5 (mean of three *O. gazella*). Thus *Pelorovis* is nearest to *Bubalus*, *Oryx* and possibly *Hippotragus equinus* for the first ratio, while for the second it is near the extreme for either tribe.

17. Lateral flanges at the anterior end of the nasals are pronounced in *Bubalus*, *Bos javanicus* and some *B. gaurus*, and practically absent in other *Bos* species, *Syncerus* and *Homoioceras*. They are present in *Hemibos* if the skull 23109 at the British Museum (Natural History) is indeed of *Hemibos*, although Pilgrim (1937, fig. 47c) has drawn the genus without them. They are absent in Hippotragini. In the complete skull of *Pelorovis* they are clearly absent.

18. A transverse expansion at the back of the nasals is present in *Bubalus* and *Hemibos* and in some *Syncerus*, and absent in *Bos*, Hippotragini and *Pelorovis*.

19. The posterior end of the nasals is in front of or barely level with the front of the orbits in Hippotragini, but lies slightly more posteriorly in Bovini, except that some individuals of *Bos* may overlap *Hippotragus* individuals. This character is unlikely to be caused by allometry because in the anoa the back of the nasals is level with the front half of the orbits and in the large Caprine *Ovibos* Blainville they start in front of the orbits. The position of the suture is not certain in *Pelorovis*, but it appears to be level with the front half of the orbits.

20. The nasals of *Syncerus* are often more nearly parallel to the tooth row in profile than in *Bubalus* ; *Bos* appears to be nearer to *Bubalus* than to *Syncerus*, and the Hippotragini are like *Bubalus*. This is not a useful character in *Pelorovis*. The reconstruction of its skull in lateral view (Text-fig. 2) does show the nasals in a position similar to *Syncerus*, and the drawing was made before I was aware of the *Syncerus* character, but one would need the preservation of an undistorted skull before accepting this character.

21. The absence of an ethmoidal fissure in the complete skull of *Pelorovis* makes it unlike *Oryx* and also unlike *Hippotragus* in which the existing fissure has become blocked by underlying bone. It is less unlike early Hippotragini in which the fissure is often small or difficult to see. Among Bovini it is more like *Syncerus* and *Bubalus* than *Leptobos* or *Bos* in which the fissure can often be seen at least until the early part of adult life.

22. The preorbital fossa is absent or only faintly indicated in Bovini, and is shallow in early Hippotragini (but deep in *Sinotragus*) and absent in later ones ; thus its absence in *Pelorovis* gives no indication of possible tribal relationship.

23. The deep zygomatic bar of *Pelorovis* is a character seen in the Alcelaphines *Damaliscus* and *Alcelaphus*, and also in the skull of *Homoioceras nilssoni*. I think that its appearance is connected with the mechanics of supporting the horn cores.

24. The position of the infraorbital foramen is a distinguishing character between Hippotragini and Bovini. It is found in *Oryx* relatively high above the tooth row

and relatively posteriorly sited, whereas in *Bubalus* and *Syncerus* it is lower and further forwards, perhaps in front of P². *Bos* and *Hippotragus* may not always be distinguishable, but their foramina are often near to the positions occupied in their respective tribes. The foramen of *Pelorovis* is undoubtedly in a Bovine position.

25. The size of the palatal fissures between maxillae and premaxillae varies among the genera considered here. They are large, chiefly noticeable in their great length, in *Hippotragus*, but much smaller in *Oryx*. In Bovini they are smaller in *Bubalus* and *Syncerus* than in *Bos* but not as small as in *Oryx*. In *Pelorovis* only the front parts of the fissures are present, but I would judge them to lie between *Oryx* and *Syncerus* in size.

26. In the Hippotragini the premaxillae make or just avoid making a short contact with the nasals ; this character is less constant within Bovine genera, but *Syncerus* appears to be nearest to the Hippotragine condition. In *Bos* the premaxilla often falls well short of a contact with the nasals, but in *Bubalus* it invariably has a long contact. The premaxilla of *Pelorovis* is closest to the condition of *Syncerus* and Hippotragini.

27. The tooth row is set more anteriorly in some *Bos*, e.g. *B. grunniens* (the yak) and *B. primigenius*, than in other Bovini, and in *Oryx* and *Hippotragus niger* than in *H. equinus*. This character can be linked with the more posteriorly sited orbits of the *Bos* species, *Oryx*, and *Hippotragus niger*, and can be quantitatively expressed by the length from the premaxilla tip to M³ expressed as a percentage of the length from the premaxilla to the nearest point of the orbit :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	19	8	10	3
Mean value . .	108·8	101·0	108·8	89·1
Range . . .	102·8–114·8	97·3–103·5	106·3–111·5	88·1–90·1

Readings for Hippotragini pass from 91·1 (mean of five *Oryx beisa*) to 98·8 (mean of ten *Hippotragus equinus*). The reading for the complete skull of *Pelorovis* is 82·3, which is most nearly approached by *Bos primigenius* in the above table. In *Homoioceras nilssoni* the reading is 97·4 ; this is most interesting because this animal has as short a face as in *Syncerus*, as was seen on page 268 above. It is thus less remote from *Pelorovis* for this proportion than are the *Syncerus* in this sample.

This is perhaps a good place to sum up the differences in skull shape revealed by the last ratio and those under characters 2 and 13 above. *Syncerus* has a very short face as shown by the anterior position of its orbits, although this effect is likely to be exaggerated in males. In *Homoioceras nilssoni* too the face is short, but the skull is narrower across the orbits, and the tooth row is situated more anteriorly. *Bubalus* has a longer face and a less posteriorly placed tooth row, presumably correlated features. It is narrow across the orbits but less narrow than in *Homoioceras nilssoni*, and its supraorbital pits are not so anterior or so close as in *Syncerus* and the three *Homoioceras* species. *Bos* is characterized by a wide frontals region, and agrees with *Bubalus* in having supraorbital pits set widely apart and posteriorly. Some *Bos* may have long faces and tooth rows set far forwards as do *B. primigenius* and *B.*

grunniens.   *Pelorovis* has a long face, is narrow across the orbits, and has a markedly anterior tooth row.   It differs from *Syncerus* in all these features, and from *Homoioceras nilssoni* in its long face and to a lesser extent in the position of its tooth row. It differs from *Bubalus* in its more anterior tooth row, and from *Bos* in its narrow width across the orbits and very slightly in the position of its tooth row.   The Hippotragini have longer faces than some Bovini, are narrow across the orbits, and their supraorbital pits are more anterior and closer together.

28.   The level of the median indentation at the back of the palate is a good distinguishing character between Hippotragini and Bovini.   In Hippotragini it is level with the lateral ones or slightly anterior or posterior.   *Bubalus* is the Bovine most remote from the Hippotragini, by having a long backwards extension of the median part of the palate taking the indentation well posterior to the lateral ones. This also occurred in *Hemibos* and *Proamphibos*.   Many individuals of *Syncerus* are less remote from the Hippotragine condition, while *Bos* lies between *Syncerus* or *Bubalus*.   In *Pelorovis* the median indentation is anterior to the lateral ones, more so than in many Hippotragini, and if *Pelorovis* is a Bovine this character is no longer distinctive for the two tribes.

29.   The vomer is fused with the back of the palate in *Bubalus bubalis, B. depressicornis* and *Hemibos*, but not in *Pelorovis* or any other genus considered here. Pilgrim (1939 : 274) states that fusion probably occurred in *Proamphibos*.

30.   The occipital surface of the skull is low and wide in *Bos gaurus* and *Syncerus*, but higher in *Bubalus* and *Bos primigenius* ; it is also lower in *Oryx* than in *Hippotragus* especially *H. niger*.   Readings for the height of the occiput as a percentage of its width were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	18	5	9	4
Mean value . .	31·9	37·5	32·0	36·3
Range . . .	28·8–36·5	34·4–39·8	29·4–35·3	32·7–40·1

The reading for *Homoioceras singae* was 31·7, for *H. antiquus* 32·3, and for *H. nilssoni* 31·9, which agree very well with *Syncerus*.   The readings for Hippotragini range from 35·6 (one *Oryx leucoryx*) to 52·0 (mean of six *Hippotragus niger*), readings which are rather higher than in Bovini.   Three values for *Pelorovis* are 40·7, 36·9 and 35·5, making it unlike *Syncerus* and *Homoioceras*, but more like *Bubalus, Bos primigenius* or *Oryx*.   The difference between the size of horns in male and female cattle was found by Howard *in* Mourant & Zeuner (1963 : 96) to affect this ratio, male animals having a lower occiput.

31.   The mastoid exposure of the periotic is entirely on the occipital surface in Bovini, including the anoa, and in *Oryx*, but in *Hippotragus* it is visible in lateral view as well.   In *Pelorovis* it is on the occipital surface.

32.   The top edge of the foramen magnum is more posterior relative to the occipital condyles in *Oryx* than in *Hippotragus* in which the paraoccipital processes are markedly anterior relative to the condyles.   *Pelorovis*, Bovine genera and Lower Pliocene Hippotragini are intermediate for this character.

33. The distance across the anterior tuberosities of the basioccipital is a variable dimension ; it is narrow in *Syncerus*—perhaps because the main mass of the horn cores is concentrated in their basal bosses, wider in *Bos* and *Bubalus*, and wider still in Hippotragini. Often in *Syncerus* there is a transverse narrowing immediately in front of the posterior tuberosity which gives the bone a more quadrangular appearance than would be expected from its measurements. Readings for the width across the anterior tuberosities as a percentage of the width across the posterior ones were :

	Syncerus	Bubalus	Bos gaurus	Bos primigenius
Number measured .	19	7	9	3
Mean value . .	45·9	53·7	55·2	49·3
Range . . .	36·6–55·9	47·7–59·4	46·2–65·0	46·2–53·4

The reading for *Homoioceras singae* was 50·0, for *H. antiquus* 45·0, and for *H. nilssoni* 54·7 ; probably these animals had wider tuberosities than living *Syncerus*. The three available readings for *Pelorovis* were 53·8, 57·6 and 58·4—all rather wide compared with the readings in the above table. But there can be no doubt that for this character *Pelorovis* shows Bovine affinities ; the living Hippotragini range from 73·3 (mean of three *Oryx gazella*) to 107·7 (one *O. leucoryx*). Early fossil Hippotragini are scarcely less different, as the four following readings on fossils from Pikermi in the British Museum (Natural History) show :

M.10832,	*Palaeoryx woodwardi*	80·0
M.11415, M.10839,	*Protoryx carolinae*	71·8 and 72·5
M.10833,	*Microtragus parvidens*	83·7

Hippotragus has anterior tuberosities which have grown large and have expanded to some extent laterally. In the course of expansion a longitudinal ridge has tended to build up behind each tuberosity, leaving a deep groove running along the centre of the bone. In *Oryx* the anterior tuberosities are smaller and more localized, without the development of longitudinal ridges. In Bovini the anterior tuberosities are not so localized as in *Oryx*, nor are they so expanded as in *Hippotragus*. *Pelorovis* could be said to be like *Oryx* or Bovini in this.

34. The foramina ovales are large in living Hippotragini, especially in *Oryx*, but even in *Hippotragus* they are larger than is usual in Bovini, although there is a good deal of overlap. They are smaller in some lower Pliocene Hippotragini. The foramina are sufficiently small in *Pelorovis* for it to resemble the Bovini (or early Hippotragini) for this character.

35. An indentation in the squamosal shelf immediately in front of the mastoid occurs in *Oryx*, Bovini and *Pelorovis*, and can be seen in ventral view (Pl. 2).

36. The size of the auditory bulla is probably not a good distinguishing character unless one is dealing with undoubtedly closely related forms, so it is here of doubtful validity. It is less inflated in *Bos* and *Bubalus* than in *Syncerus* and Hippotragini. In *Pelorovis* it is within the range of *Syncerus* and Hippotragini.

37. The upper molar teeth are wide in *Hippotragus* and Bovini, but not in *Oryx*. Within any one genus the width of the molars is a variable dimension, but during their evolution the Bovini have undoubtedly widened their molars. The widening is partly connected with increasing size, but large Bovidae such as *Taurotragus* Wagner and *Ovibos* do not have noticeably wider upper molars than their smaller relatives. *Pelorovis* has molars as wide as in *Hippotragus* and Bovini. This character, and others of the teeth, are illustrated in Text-fig. 11.
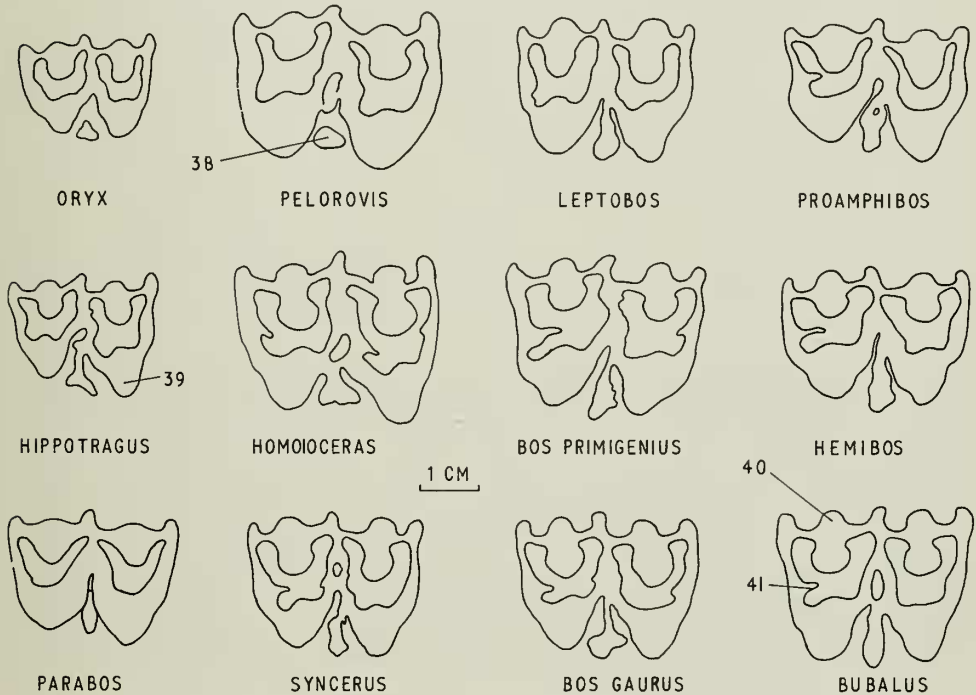

ORYX   PELOROVIS   LEPTOBOS   PROAMPHIBOS

HIPPOTRAGUS   HOMOIOCERAS   BOS PRIMIGENIUS   HEMIBOS

1 CM

PARABOS   SYNCERUS   BOS GAURUS   BUBALUS

FIG. 11. Occlusal views of right M^2 in some Bovid genera. The anterior side is towards the right side of the page. The numbers are those by which characters are referred to in the text.

38. Basal pillars on the molar teeth are small in *Oryx*, but large and complicated in *Hippotragus*; they are also large and complicated in Bovini. Within the Bovini this character is affected by allometry since *Syncerus* and smaller *Bos* have smaller basal pillars than *Homoioceras*, *Bubalus* and larger *Bos*. However those of *Pelorovis* are small despite the large size of its teeth.

39. The medial lobes of the upper molars are less narrowed in *Oryx* than in *Hippotragus*. Neither *Pelorovis* nor the Bovine genera being considered here have lobes as narrow as in *Hippotragus*.

40. Localized outbowings on the lateral walls of the molars are well marked in *Bubalus* and some *Bos*, but less so in *Syncerus* and smaller *Bos*; this is again likely

to be influenced by allometry. They are better marked in *Hippotragus* than in *Oryx*, as can be seen in Text-fig. 11. They are hardly present in *Pelorovis*.

41.   *Syncerus* and some *Bos* have a slightly less complicated course of the enamel borders of the central cavities of the upper molars than in *Homoioceras, Bubalus* or larger *Bos*, which is probably allometric although *Oryx* certainly shows less complication than the equally sized *Hippotragus*. *Pelorovis* agrees with *Oryx*.

42.   The front edge of the coronoid process of the lower jaw is strongly curved to fit the temporal fossa in Bovini other than *Homoioceras nilssoni* and some *Bos* such as *B. grunniens* and *B. primigenius*. In *Pelorovis* (Pl. 6) and *Oryx* there is little curvature as in the *Homoioceras* and two *Bos* species, while in *Hippotragus* the curvature is not much stronger. It may be noted that the lack of strong curvature in *Pelorovis, Homoioceras nilssoni* and some *Bos* is connected with the anterior position of the tooth row, in *Hippotragus* the absence of a temporal fossa has an effect, and in *Oryx* both factors may have acted.

43.   The horizontal ramus of the lower jaw is deep in the Hippotragini and in *Pelorovis* (Pl. 6).

44.   The lower molars of *Oryx* have weaker goat folds than in *Hippotragus*. They are absent in the Bovini and in *Pelorovis*. Goat folds are transverse expansions of the most anterior part of the lower molars separate from the main mass of the anterior lobes.

45.   The central cavity of the anterior part of P_4 is open medially to the outside of the tooth in Hippotragini, *Bubalus* and *Bos*. It is enclosed by a medial wall in *Syncerus* (except that in 62·219 at the British Museum (Natural History) it is open on the left and closed on the right). It is also open in *Homoioceras nilssoni*, but the medial wall has only just failed to close. It is closed or almost closed in all *Pelorovis* (Pl. 3, fig. 2 ; Pl. 6, fig. 3) except in the lower jaws (M.15856) from Kanjera. This character is useful for differentiating African from Eurasian Bovini.

Colbert & Hooijer (1953 : 119–20) found that *Bubalus* never has a small accessory column between the hypoconid and talonid as is seen in some *Bos gaurus*, and that it has a greater tendency to have the posterior medial valley of older P_3s and P_4s forming an isolated fossette.

46.   The length of the premolar row may be quantitatively expressed as a percentage of the length of the molar row, but the results are not very useful because only small numbers of animals could be measured. In Pel 23, an old animal, the ratio for the upper dentition is 60·8. This is low compared with the Bovine range from 60·9 for one *Syncerus* to 70·6 which was the mean for two *Bos gaurus*. Eleven *Syncerus* had a mean value of 65·5, *Homoioceras nilssoni* had a reading of *c*. 63·5, four *Bubalus* a mean of 68·8, and one *Bos primigenius* a reading of 64·4. In the Hippotragini *Hippotragus equinus* has a very long premolar row with a mean value of 74·8 and a range from 70·7 to 79·4 for ten specimens, *H. niger* has a shorter row with a mean of 67·4 and a range from 65·8 to 69·2 for five specimens, and *Oryx* species have readings mostly below 60 except that the mean for five *Oryx beisa* rises to 60·9. These differences presumably indicate differences in Hippotragine feeding habits.

In lower jaws two values for *Pelorovis* at 50·9 and 58·5 have a mean less noticeably different from Bovini than was the value for the upper jaw. The mean of five

Syncerus was 58·7, of two *Bubalus* 59·0, and seven *Bos gaurus* 57·5. It is obvious from discrepancies between upper and lower dentitions that larger samples are needed to clarify the facts, but one may tentatively conclude that *Pelorovis* had rather shorter premolar rows than in living Bovini.

47. For the ratio of length of P^2 or P_2 in relation to the length of the total premolar row, *Pelorovis* seems to lie at about the centre of both Bovine and Hippotragine ranges. It is not possible to find trustworthy differences without more specimens to measure.

To sum up the tooth characters, while the teeth of *Oryx* are not greatly advanced other than in their hypsodonty, the course of morphological evolution has some similarities in Bovini and *Hippotragus*, i.e. increasing width of the upper molars, increasing size of the basal pillars, stronger and more localized outbowings of the lateral walls of the upper molars, and a more complicated outline of the enamel borders to the central cavities. However *Hippotragus* differs from Bovini in other details : basal pillars are often Y-shaped in section and are extremely large for the size of the teeth, lateral outbowings of the upper molars are smaller, borders of the central cavities are less complicated, and there are goat folds on its lower molars. *Pelorovis* therefore resembles *Oryx* in possessing a moderate development of hypsodonty without a very advanced pattern of the occlusal surfaces. It is also like Boselaphini and early Bovini in its occlusal pattern, differing from a form like *Parabos* only in being more hypsodont and having wider upper molars, so that if *Pelorovis* is a Bovine genus, then it is one with primitive teeth. The influence of body size on tooth characters is great, and it is possible that a *Parabos*, growing to a size equivalent to that of *Pelorovis*, would acquire wider and more hypsodont molars. It is also true that while the living Bovini have more advanced teeth than *Pelorovis*, it is the larger species which differ more. *Syncerus* has less advanced teeth than *Bubalus* in several characters mentioned above, but *Syncerus* is a smaller animal ; the upper molars of the closely related, larger *Homoioceras nilssoni* (Lönnberg 1933, pl. 1, fig. 4) are no less advanced than those of *Bubalus*. Within *Bos* too it is the larger animals which have the closest resemblance to *Bubalus*.

The comparisons of limb bones and vertebrae were based on material in the Osteology Room at the British Museum (Natural History) : five skeletons of Chillingham and Chartley cattle, three *Bos gaurus*, one *Bos grunniens*, one *Bubalus bubalis*, three *Syncerus caffer*, three *Hippotragus niger*, two *H. equinus* and two *Oryx beisa*. The *Bubalus* skeleton and two of the three *Syncerus* were mounted so that not all characters were accessible. In addition to these specimens, some *Bos primigenius* limb bones from Ilford were seen, one *Syncerus* had previously been available in Nairobi for direct comparison with the bones of *Pelorovis*, and a mounted *Syncerus* skeleton was seen in Stockholm. The limb bones of the mounted skeleton of *Homoioceras nilssoni* were also seen in Stockholm ; characters 48, 51, 55, 62, 63, 69, 70, 77, 78, 82, 83 and 84 were not visible, and I have assumed that the animal resembles other Bovini in characters 48, 51, 63 and 78.

48. In *Hippotragus* (but to a lesser extent in *Oryx*) the great trochanter of the femur has a horizontal top edge and a tendency to antero-posterior lengthening,

which can be seen in lateral view. In Bovini the trochanter appears taller, and is without a tendency to antero-posterior lengthening ; it either has a slanted antero-dorsal edge descending to an anterior point or its whole front edge is evenly rounded. *Pelorovis* resembles Bovini (see Text-fig. 13).
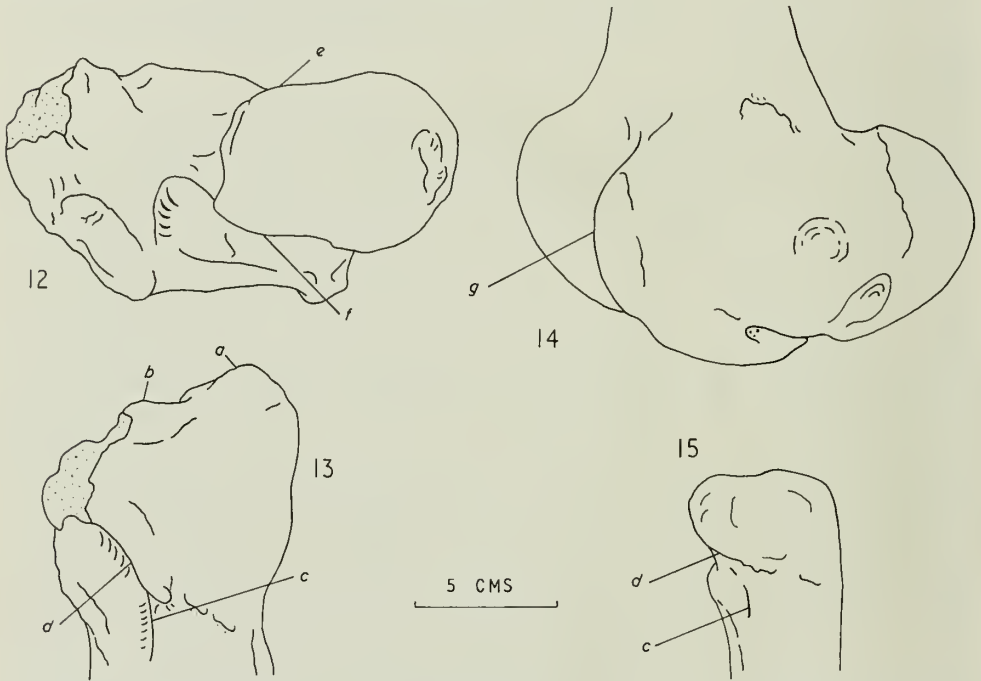
FIGS. 12–15. 12, dorsal view of top of left femur 1952, BK II, 268 with anterior side towards top of the page ; 13, lateral view of great trochanter of same femur ; 14, lateral view of distal end of same femur ; 15, lateral view of great trochanter of a left femur of *Hippotragus*. *a* = high back of great trochanter, *a–b* = its slanted antero-dorsal edge, *c* = gluteus accessorius crest, *d* = vastus lateralis crest ; all these points are mentioned in character 48. *e–f* = wide lateral parts of articular head mentioned in character 50, *g* = front edge of lateral condyle mentioned in character 51.

In Hippotragini the ridge for the insertion of the gluteus accessorius is often at an angle to the lower part of the crest for the vastus lateralis which may continue horizontally behind it. In Bovini the gluteus crest often appears to continue the line of the vastus crest, and *Pelorovis* resembles them (Text-fig. 13). The condition in the Hippotragini is linked with the antero-posterior lengthening of the trochanter mentioned in the last paragraph.

49. A deeper hollowing is present in anterior view between the articular head and the great trochanter in Hippotragini, *Syncerus*, the one *Bubalus* and probably *Homoioceras nilssoni* than in *Bos*. Linked with this character is the fact that *Bos* tends to have a steeper slope on the top edge of the articular head in anterior view

than the other genera, although this feature is not distinguishable in every bone. *Pelorovis* is unlike *Bos*, and like the other genera for this character (Pl. 4).

50.   The articular head of the femur is less narrowed in its lateral parts in dorsal view in Hippotragini than in *Bos* and the single *Bubalus*.   *Syncerus* and *Homoioceras nilssoni* have a condition intermediate between Hippotragini and the other Bovini, and *Pelorovis* agrees with *Syncerus* (Text-fig. 12).

51.   The distal lateral condyle of the femur is more sharply pointed anteriorly in *Oryx* than in *Hippotragus*, Bovini or *Pelorovis* (Text-fig. 14).

52.   The patellar fossa on the femur is wider in Hippotragini than in Bovini ; within the Bovini some individuals of *Bos* may have it still narrower.   It is wide in *Pelorovis* as in Hippotragini (Pl. 4).
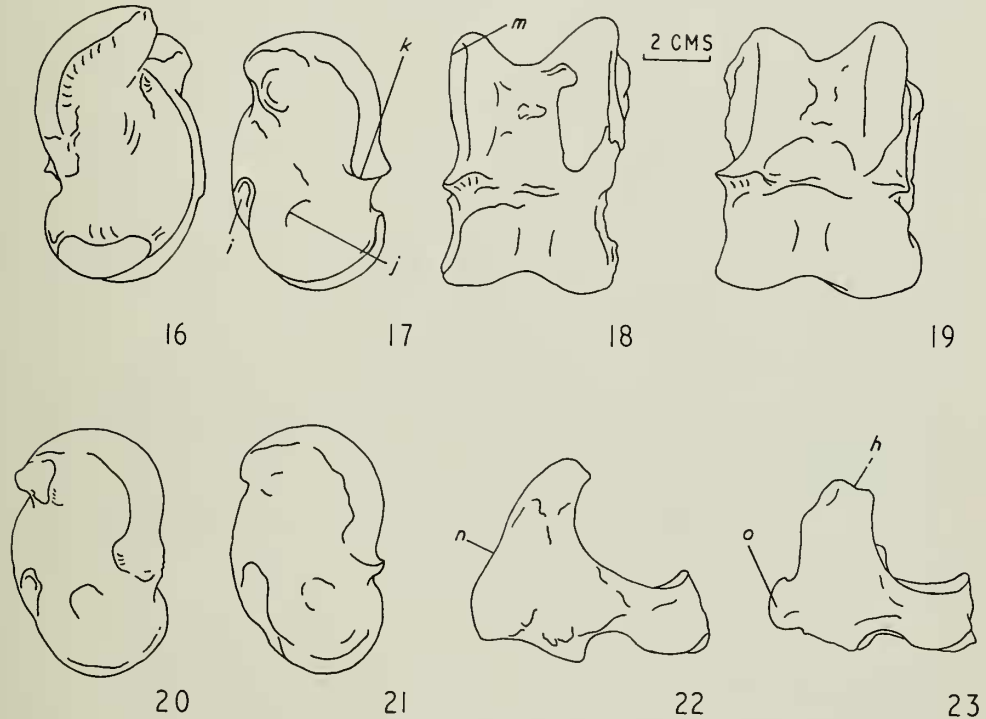
FIGS. 16–23.   16–18, lateral, medial and anterior views of left astragalus 1957, BK II, 1413 ; 19, anterior view of a fossil astragalus with different proportions from those of *P. oldowayensis* astragali ; 20, medial view of astragalus of *Bos gaurus* ; 21, medial view of astragalus of *Syncerus*.   22, medial view of a naviculo-cuboid of *P. oldowayensis* ; 23, medial view of a naviculo-cuboid rather smaller than others belonging to *P. oldowayensis*. i = incision for naviculo-cuboid as mentioned in character 56, j = ridge for astragalo-metatarsal ligament mentioned in character 57, k = ridge for medial malleolus of tibia mentioned in character 58, m = position of projection mentioned in character 59. n = back edge of the naviculo-cuboid, o = localized projection at its base, h = top edge separate from back edge ; all these points are mentioned in character 60.

53.   A middle patellar groove is present at the top of the cnemial crest of the tibia in Hippotragini, but less markedly or not at all in Bovini or *Pelorovis* (Pl. 4).

54.   The lateral articular facet at the top of the tibia has an upturned lateral edge in *Oryx* but not in the other genera being considered or in *Pelorovis* (Pl. 4).

55.   The medial malleolus of the tibia is shorter in *Syncerus* than in the other genera or *Pelorovis* (Pl. 4).

56.   There is a deep incision for the naviculo-cuboid at the back edge of the medial side of the astragalus in Bovini and *Pelorovis* but not in the Hippotragini (Text-fig. 17).

57.   The ridge for the astragalo-metatarsal ligament on the medial side of the astragalus is weaker in *Syncerus* than in the other genera or *Pelorovis* (Text-fig. 17).

58.   This ridge is level with the ridge for the base of the medial malleolus of the tibia in Hippotragini.   In *Syncerus* and the *Bubalus* individual it may be lower, but in *Bos* the ridge for the malleolus is also low, and so the two ridges are at the same level.   *Pelorovis* is most like Hippotragini, *Syncerus* and the *Bubalus* (Text-fig. 17). This character must be linked with 55 above, and one can say that the tibial-astragalus articulation of *Syncerus* differs from that of *Pelorovis* by having a shorter medial malleolus of the tibia, and *Bos* differs from *Pelorovis* by having a lower astragalar facet for the tibia's medial malleolus.

59.   The back part of the top of the medial side of the astragalus projects slightly away from the main mass of the bone in *Oryx* in anterior view.   This does not occur in any other genus or in *Pelorovis* (Text-fig. 18).   The astragalus of *Homoioceras nilssoni* has a backwardly-directed extension in this position.

60.   The naviculo-cuboid is a relatively deeper bone in Hippotragini than in Bovini or *Pelorovis*.   This is most noticeable in lateral view.

61.   The back edge of the medial side of the naviculo-cuboid is slightly or much curved in Hippotragini ; it tends to be straighter in Bovini and sometimes has a localized backwards projection at its lower end, and a top edge separate from its back edge.   *Pelorovis* agrees with the Bovini (Text-figs. 22, 23).

62.   Both front and back metapodials of *Syncerus* and the metacarpals of *Bos primigenius* are more antero-posteriorly compressed than in the other genera considered here or *Pelorovis*.

63.   The back part of the naviculo-cuboid facet on the metatarsal rises high above the level of the immediately adjacent ectocuneiform facet in Hippotragini, and therefore has a strongly curved outline in medial view.   This is not seen in Bovini or *Pelorovis* (Text-figs. 24, 25).

64.   In medial view the ectocuneiform facet of Hippotragini is upcurved ; this is not seen in Bovini or *Pelorovis* (Text-figs. 24, 25).

65.   In *Hippotragus* the foramen at the top of the posterior surface is situated on the medial side of the midline.   This is less obvious in *Oryx* while in Bovini and *Pelorovis* the foramen is situated centrally (Text-fig. 26).

66.   The distal anterior and posterior foramina of the metapodials are absent in *Syncerus*, or disappear earlier in adult life than in the other genera and *Pelorovis* (Pl. 5).

67.   The tuber scapulae is low and strongly projecting in Hippotragini, i.e. its
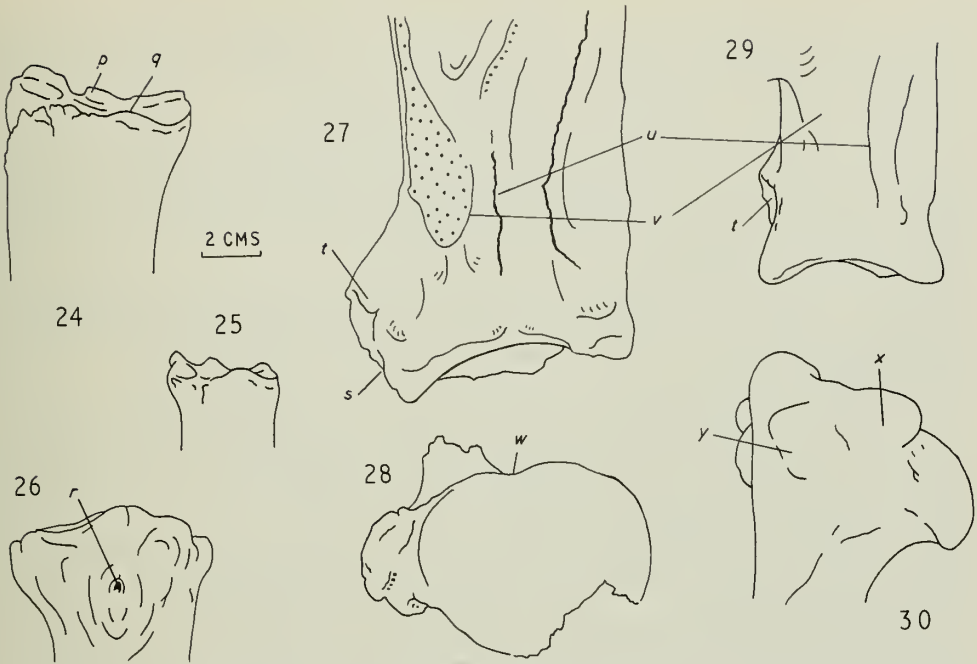
FIGS. 24–30.   24, medial view of top of left metatarsal 1952, BK II, 275 ; 25, medial view
of top of left metatarsal of *Hippotragus* ; 26, posterior view of top of left metatarsal 1952,
BK II, 275 ; 27, lateral view of left scapula stem 1952, BK II, 183 ; 28, ventral view of
glenoid facet of 1952, BK II, 183 ; 29, lateral view of left scapula stem of *Bos gaurus* ;
30, lateral view of proximal end of left humerus of *Hippotragus*. p = back of naviculo-
cuboid facet mentioned in character 63, q = edge of ectocuneiform facet mentioned in
character 64, r = foramen at top of posterior side of metatarsal mentioned in character 65.
t = tuber scapulae, s = height of base of tuber scapulae above rim of glenoid facet
mentioned in character 67, w = indent in lateral side of glenoid facet mentioned in
character 68, v = base of spine of scapula, u = front of teres minor hollow mentioned in
character 69. x = posterior eminence of lateral tuberosity of humerus mentioned in
character 71, y = infraspinatus insertion mentioned in character 72.

ventral edge in lateral view rises from the rim of the glenoid facet and passes far
in front of the facet.   The tuber is higher in Bovini, but generally projects as far
or almost as far as in the Hippotragini.   In *Bos gaurus* it has an excavation on its
antero-lateral side.   *Pelorovis* most resembles Bovini other than *B. gaurus*.   (Text-
figs. 27, 29).

68.   The lateral side of the glenoid facet on the scapula is indented in Bovini and
Pelorovis, but not in Hippotragini (Text-fig. 28).

69.   In Bovini there is a tendency for the teres minor cavity on the scapula not
to pass so far forwards as the base of the spine ; this is less clear in *Syncerus* than in
Bos and the single *Bubalus*, although it is not possible to tell *Syncerus* from every
specimen of *Bos*.   *Pelorovis* is like the Hippotragini or *Syncerus* (Text-figs. 27, 29).

70.   The lateral tuberosity of the humerus is low in Hippotragini, i.e. it does not rise far above the bicipital groove in anterior view.   It is higher in Bovini, except that two out of the five available *Syncerus* were intermediate between other Bovini and Hippotragini.   In *Pelorovis* the tuberosity is low (Pl. 4).

71.   *Syncerus* and *Homoioceras nilssoni* have a smaller posterior eminence behind the lateral tuberosity of the humerus than in *Bos* or the *Bubalus* individual.   In the Hippotragini the eminence is perhaps still smaller but is antero-posteriorly lengthened and sometimes approaches having a posteriorly directed point.   *Pelorovis* resembles *Syncerus* (Pl. 4 ; Text-fig. 30).

72.   The front of the infraspinatus insertion is level with the front edge of the humerus in lateral view in *Bos*, the *Bubalus* individual and *Homoioceras nilssoni*, but lies slightly behind the front edge in *Syncerus* and Hippotragini.   *Pelorovis* agrees with *Bos*, *Bubalus* and the *Homoioceras*.   (Pl. 4 ; Text-fig. 30).

73.   The bicipital groove at the top of the humerus is more frequently narrowed in anterior view in *Bos* than in the other genera or *Pelorovis* (Pl. 4).

74.   The coronoid fossa at the distal end of the humerus is more shallow in Hippotragini than in Bovini or *Pelorovis* (Pl. 4).

75.   The medial condyle at the distal end of the humerus is tall in *Hippotragus* and perhaps in *Homoioceras nilssoni*, but lower in other Bovini and *Oryx*.   *Pelorovis* is like *Hippotragus* (Pl. 4).

76.   The medial side of the medial articular facet at the top of the radius projects as a rim in anterior view in *Bos* and *Homoioceras nilssoni* but not in the other genera or *Pelorovis* (Pl. 4).

77.   The postero-medial part of the medial facet has a greater area in *Bos* than in Hippotragini.   Two out of four *Syncerus*, the one *Bubalus* and *Pelorovis* are like Hippotragini.

78.   The lateral facet at the top of the radius is antero-posteriorly long in *Oryx* and some *Hippotragus*, but often short in the other genera being considered.   *Pelorovis* (Text-fig. 34) agrees with Hippotragini, but is not convincingly different trom Bovini.

79.   The lateral tubercle at the top of the radius is larger in *Oryx* than in *Hippotragus*, and intermediate in the Bovini and *Pelorovis* (Text-fig. 34).

80.   The distal ends of radii of Bovini and *Hippotragus* appear swollen in lateral view, but this is not so for *Pelorovis* except in specimen 1955, BK II, 294 which is smaller than the other fossils and may therefore be a separate species (Pl. 4 ; Text-fig. 33).

81.   The ridge between the posterior surfaces of the scaphoid and lunate facets at the distal end of the radius tends to be more slanted or less marked in *Syncerus*, the single *Bubalus* and *Homoioceras nilssoni* than in *Bos* or Hippotragini.   *Pelorovis* is like the former group (Text-fig. 32).

82.   The tubercle towards the front of the dorsal facet of the scaphoid is more sharply marked in *Bos* than in other genera or *Pelorovis*.

83.   The bottom edge of the medial side of the scaphoid is less indented in *Syncerus* and *Hippotragus* than in other genera or *Pelorovis*.   Correlated with this
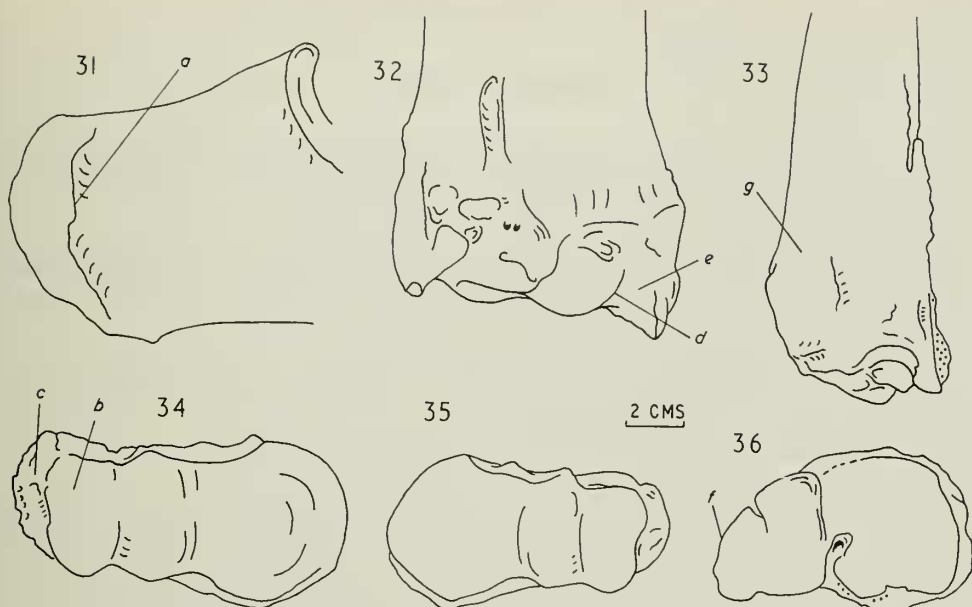
FIGS. 31–36.   31, medial view of left olecranon 1952, BK II, 273 with its front edge towards top of page ; 32, posterior view of distal end of same radius ; 33, lateral view of distal end of left radius 1955, BK II, 294 ; 34, dorsal view of top articular surface of right radius 1953, BK II Extension, 425 with the anterior edge towards bottom of page ; 35, dorsal view of left radius 1955, BK II, 294 ; 36, dorsal view of top articular surface of left metacarpal 1957, BK II, 1037 with anterior edge towards top of page. a = high origin of flexor carpi ulnaris muscle which is a peculiarity of *Pelorovis*, b = lateral facet mentioned in character 78, c = lateral tubercle mentioned in character 79, e = scaphoid facet and d = ridge between scaphoid and lunate facets mentioned in character 81, g = swollen distal end of radius mentioned in character 80, f = edge of unciform facet of metacarpal mentioned in character 85.

is the absence of a projection towards the posterior end of the upper surface of the magnum-trapezoid.

84.   The projecting back edge of the lunate is narrowly pointed in *Hippotragus* in medial view, but not in the other genera or *Pelorovis*.

85.   The unciform facet at the top of the metacarpal is angled in *Hippotragus* but not in *Pelorovis*, *Oryx* or Bovini (Text-fig. 36).

Among the limb bone characters of *Pelorovis* were three which might be valid as specific or generic characters, but which were not seen in Bovini or Hippotragini. These were the small sustentaculum on the calcaneum, the antero-posteriorly long infraspinatus insertion on the humerus (Pl. 4), and the flexor carpi ulnaris origin on the medial side of the olecranon which extended almost to the top of the bone (Text-fig. 31).

86.   Bovini have wider cervical vertebrae than Hippotragini.   This may be owing to allometry at least in part, but the long cervical vertebrae of a large form

like *Taurotragus* show that allometry need not be the only determining factor. *Pelorovis* agrees with Bovini.

87. Bovini and *Pelorovis* have deep ventral hollows on the atlas for the paraoccipital processes.

88. The vertebrarterial foramina on the axis (Text-fig. 7) are smaller in *Bubalus*, *Syncerus*, *Homoioceras nilssoni* and Hippotragini than in some *Bos*. *Pelorovis* agrees with the former group.

89. The openings of the foramina transversa are nearer to the front and back edges of the side of the centrum on the third cervical in Bovini and *Pelorovis* than in Hippotragini. This difference is not visible on the more posterior cervical vertebrae.

90. The transverse processes are separate from their ventral flanges as far forwards as on the third cervical in Bovini and *Pelorovis*. In Hippotragini the separation occurs only in the more posterior cervical vertebrae.

91. The neural spines of the 4th, 5th and 6th cervical vertebrae are not so forwardly slanted in Bovini or *Pelorovis* as in Hippotragini.

The results of comparing length measurements of *Pelorovis* limb bones with those of two *Syncerus caffer* and three *Bos gaurus* are shown in Text-fig. 37. These Bovines were chosen for comparison because they were available and were of a similar massiveness to *Pelorovis*. One mounted *Bubalus* could only be measured for its femur (Text-fig. 9), humerus and radius, and has not been shown. It is seen that *Pelorovis* has a relatively long radius and short humerus, and also that the metapodials of *Syncerus* are noticeably short. Measurements of least thickness

```
       METATARSAL    METACARPAL
G           x   x    x            x    x   x          G
Y            x                     x                  Y
             x                     x
P              x                      x              P
    |_____|_____|_____|    |_____|_____|_____|
    15      20      25       30       15      20      25       30

                TIBIA   RADIUS
G          x x    x               xx      x         G
Y           x      x               x   x            Y
P                    x                        x     P
    |_____|_____|_____|    |_____|_____|_____|
    30      35      40       45     25      30      35       40

                FEMUR   HUMERUS
G      x x  x                 x       x  x          G
Y    x     x                   x       x            Y
P            x                    x                 P
    |_____|_____|_____|    |_____|_____|_____|
    35      40      45       50     30      35      40       45


        G= BOS  GAURUS        Y= SYNCERUS        P= PELOROVIS
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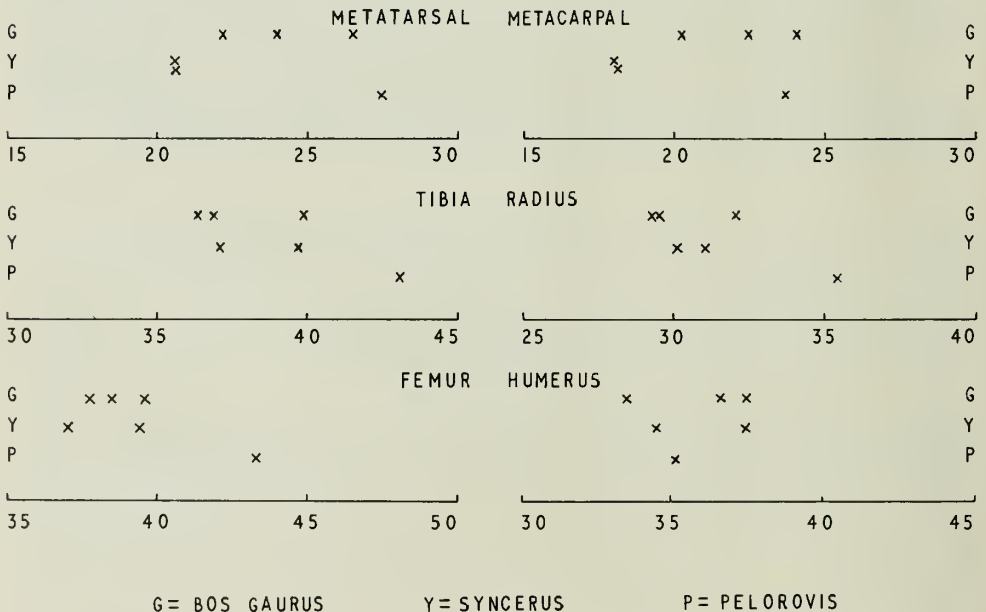
Fig. 37. Lengths of long limb bones. Measurements in cm.

of each limb bone in relation to its length failed to show reliable differences between these genera.

Colbert & Hooijer (1953 : 120) found fossil *Bubalus bubalis* to have shorter metapodials than *Bos gaurus*.

It is possible to assess numerically the differences of the other genera from *Pelorovis* in the 91 characters listed above. Character 2 was taken as the two characters face length and skull width ; character 16 was taken as the relative width of the nasals irrespective of skull length ; characters 63 and 64 were taken as one ; three characters were added to the total to represent the possibly valid limb bone characters of *Pelorovis* which were not seen in other forms ; characters 10, 22, 47 and 79 were omitted as not being sufficiently different among the forms compared ; and characters 11 and 20 were omitted as being not applicable to *Pelorovis*. This procedure left 43 skull characters and 45 limb bone and vertebrae characters for comparison, a combined total of 88. For *Bubalus* characters 62 and 82 were omitted, and this genus was assumed to be like other Bovini in characters 63, 78 and 85. Characters 82, 83 and 84 were omitted for *Bos primigenius*. Characters 16, 19, 25, 26, 28, 29, 36, 55, 62, 69, 70, 77, 82, 83 and 84 were omitted for *Homoioceras nilssoni*, it was assumed to resemble other Bovini in characters 48, 51, 63 and 78, and it was not checked for the three unique limb bone characters of *Pelorovis*.

In the following table is listed the number of differences which each form shows from *Pelorovis* ; the figures in brackets show the number of characters used in each comparison ; and the last column shows the number of differences which would be expected if 100 characters had been used in the comparisons, i.e. it is the readings of the third column converted to percentages of the corresponding figures in brackets.

	Skull characters	Limb bone and vertebrae characters	All characters	All characters out of 100
Syncerus . . .	19 (43)	13 (45)	32 (88)	36
Bubalus . . .	21 (43)	11 (43)	32 (86)	37
Bos gaurus . .	24 (43)	20 (45)	44 (88)	50
Bos primigenius .	18 (43)	19 (42)	37 (85)	44
Homoioceras nilssoni .	10 (36)	5 (34)	15 (70)	21
Oryx . . .	16 (43)	24 (45)	40 (88)	45
Hippotragus . .	26 (43)	25 (45)	51 (88)	58

The points to be noted from this table are :

1. That the Hippotragine *Oryx* appears as so little different from *Pelorovis* in its skull characters ; this is principally owing to the tooth similarities of the two genera.

2. That *Bubalus* appears as hardly more different from *Pelorovis* than *Syncerus* ; yet my opinion is that *Bubalus* is certainly much further phyletically from *Pelorovis* than is *Syncerus*.

3. That *Homoioceras* appears as the animal phenetically closest to *Pelorovis*, and as considerably closer than the living African buffalo. Even if the three unique characters of *Pelorovis* were added to the total for *Homoioceras* as differences, its final reading would still be only 25.

Conclusions

From the examination of skull characters it appears that the question of whether a fossil is assignable to the Hippotragini or Bovini may best be decided by reference to the following characters : the position and shape of the parieto-frontals suture, the level of the back of the nasals, whether the ethmoidal fissure is absent or present, the position of the infraorbital foramen, the level of the median indentation at the back of the palate, whether the basioccipital is triangular or more nearly quadrangular, and the size of the foramina ovales. The first of these characters is not applicable to *Pelorovis*, but it agrees with the Bovini in the remainder except for the level of the palatal indentation. In addition its large size and the posterior insertion of the horn cores tell for Bovine affinities. In most characters which *Pelorovis* shares with either of the Hippotragine genera—usually *Oryx*, there is also a resemblance to a Bovine genus ; the level of the palatal indent is the only firm resemblance to Hippotragini.

For the sake of completeness, three further points must be made. Firstly, the Lower Pliocene Hippotragini of Europe and China show a forwardly-indented parieto-frontals suture whenever this feature is visible, their ethmoidal fissure may be absent or very reduced, their foramina ovales are small, and *Sinotragus* has a well marked preorbital fossa.

Secondly, keels on the horn cores are present in many Bovini but not in Hippotragini apart from the early *Prosinotragus* and *Sinotragus* and possibly some others in which they may appear in connection with the transverse compression.

Thirdly, the earlier Bovine or Boselaphine genera *Selenoportax* Pilgrim, *Parabos*, *Proamphibos*, *Hemibos* and *Leptobos* all show (or all contain species showing) horn cores more divergent than in Hippotragini, and if the horn cores have any curvature in anterior or dorsal view it involves a reapproach of the tips or at least a lessening of the angle of divergence. Such a curvature is not seen in Hippotragini.

Within the Bovini, the *Hemibos-Bubalus* group has (or has retained) keels on its horn cores, and *Hemibos* already has the basicranial axis quite strongly angled on that of the face. The specialized vomer at the back of the palate may be connected with aquatic habits, and other distinctive characters such as the posterior expansion of the nasals and the lateral flanges at their anterior ends could also be connected with this.

Leptobos has preserved a basicranial axis nearly in line with the facial axis, but the closely related *Bos* has developed wide frontals and posteriorly inserted horns, and in so doing has presumably increased the bending of the basicranial axis on the face. Some *Bos* species have such posterior horn cores that they overhang the occipital surface at their bases. Keels are absent on the horn cores, or have been lost earlier than in *Hemibos* and *Bubalus*, on the other hand the ethmoidal fissure is not always absent in this stock. One learns from *Bos* that facial length is not a reliable character for use in classification above the species level, since there are striking differences of skull proportion between cattle and bison.

Homoioceras and *Syncerus* have neither wide frontals nor horn cores placed so far posteriorly as in some *Bos* species ; it seems possible that they too have evolved a bending of the basicranial on the facial axis, as in *Hemibos* and perhaps *Bubalus*

and *Bos*. They have a tendency to flattening of the horn cores and consequently may possess irregular back and front keels. P$_4$ has a closed anterior part of its medial wall.

It is the absence of wide frontals, of keels on the horn cores, of a posterior contact of the vomer with the palate, and of an ethmoidal fissure, as well as the possession of an anterior medial wall of P$_4$, which allow *Pelorovis* to be considered as related to *Syncerus* despite the markedly posterior insertion of its horn cores. The closeness of the supraorbital pits and the extent of the premaxillary contact on the nasal are also like *Syncerus*, but are less convincing resemblances. *Pelorovis* is unlike *Syncerus* in the dimensions of its occipital surface, and in the width of the anterior tuberosities of its basioccipital. The latter character is likely to be directly related to the size of the horn cores, since *Homoioceras* and *Bubalus* both have tuberosities wider than in living *Syncerus* with its short horns.

The limb bones and vertebrae of *Pelorovis* are like Bovini rather than Hippotragini in the following characters : the shape of the great trochanter at the top of the femur ; no anteriorly directed point on the lateral condyle at the distal end of the femur ; no upturned lateral edge to the lateral facet at the top of the tibia ; no middle patellar groove on the tibia ; the deep incision at the back of the medial side of the astragalus ; no projection at the top of the medial wall of the astragalus ; naviculo-cuboid not deep ; no markedly curved outlines of the naviculo-cuboid and ectocuneiform facets at the top of the metatarsal ; the central position of the top posterior foramen of the metatarsal ; the shape and position of the tuber scapulae ; the indented lateral edge of the glenoid facet on the scapula ; the shape of the posterior eminence of the lateral tuberosity on the humerus ; the level of the front of the infraspinatus insertion ; the depth of the coronoid fossa on the humerus ; the size of the lateral tubercle on the radius ; the lack of a narrow projection at the back of the lunate ; the outline of the unciform facet at the top of the metacarpal ; the wide cervical vertebrae ; the deep ventral hollows on the atlas ; the position of the foramina transversa on the third cervical ; the separation of the transverse processes from their ventral flanges as far forwards as on the third cervical ; and the neural spines of the posterior cervicals not being very forwardly slanted.

In a number of other characters *Pelorovis* is like either or both genera of Hippotragini, but is also like or approached by *Syncerus* : the indentation between the articular head and great trochanter of the femur in anterior view, the wide lateral parts of the articular head in dorsal view, the teres minor cavity on the scapula reaching as far forwards as the base of the spine, the low lateral tuberosity of the humerus, the wide bicipital groove, the smallness of the posterior eminence of the lateral tuberosity, the absence of a rim on the medial side of the medial facet of the radius, the small area of the postero-medial part of the medial facet at the top of the radius, the more slanted or less marked ridge between scaphoid and lunate facets on the back of the radius, the poorly marked tubercle at the front of the dorsal facet of the scaphoid, the little indented bottom edge of the medial side of the scaphoid, and the small vertebrarterial foramina on the axis vertebra.

Pelorovis differs from *Syncerus* in not having the short medial malleolus of the tibia, not such a weak ridge for the astragalo-metatarsal ligament on the medial side

of the astragalus, not such short or such antero-posteriorly compressed metapodials, and in having better marked foramina on the metapodials.   The only resemblances of *Pelorovis* to Hippotragine limb bones but not to Bovini are the wide patellar fossa of the femur, the length of the lateral facet at the top of the radius, and the absence of a swollen distal end of the radius in lateral view.

From these results I believe that *Pelorovis* is a genus of Bovini, and since it shows slightly more phenetic similarity to *Syncerus* than to other Bovine genera it may well be phyletically related to this genus.   The posteriorly inserted horn cores, long face, and the primitive occlusal pattern of the teeth make it very unlikely to have been the ancestor of *Syncerus*.   It may be noted that so far as skull characters go, *Homoioceras* is more like *Pelorovis* than is *Syncerus* in its larger size, long horn cores with less emphasis on basal bosses, possibly having less compressed horn cores, the strengthened front part of the zygomatic bar beneath the orbit in *H. nilssoni*, a more anteriorly sited tooth row, and the wider anterior tuberosities of the basi-occipital.   Whether *Pelorovis* separated from the *Homoioceras-Syncerus* lineage before or after they became Bovini is not known.   I take it to be Bovine rather than Boselaphine because of its large size, large posteriorly inserted horn cores, and the fairly hypsodont teeth, thus choosing to regard these characters as outweighing other more primitive tooth characters.   If *Pelorovis* is accepted as a Bovine, then a qualification must be added to the use of the level of the median indentation at the back of the palate as one of the distinguishing characters between Hippotragini and Bovini.

IV   A NOTE ON *BULARCHUS AROK* HOPWOOD

This species was described by Hopwood (1936 : 639–40) referring to material collected by the East African Archaeological Expeditions of 1931–32 and 1934–35. His generic diagnosis reads : " Bovidae of large size with massive horn cores, compressed from back to front, oval in cross section, closely approximated at their bases, curving crescent-wise upwards and downwards.   So far as is known, the horns are in the same plane as the face and are not spirally twisted ".   The specific diagnosis for *B. arok* is : " a *Bularchus* in which the span of the horn cores measures two metres, or more, from tip to tip ".   Dr. G. E. Pilgrim is quoted as suggesting that *Bularchus* may be a very advanced member of the bubaline group in which the anterior keel on the horn cores has been suppressed.   Two of the three specimens, M.14947–48, were supposed to have come from Bed IV at Olduvai and M.14949 from Bed II, but Mrs. M. D. Leakey has said (personal communication) that the matrix on the holotype, M.14947, shows that it is more likely to have come from the very top of Bed II, probably at the site now known as PLK (see also Leakey, 1965 : 106).

The holotype is a frontlet with horn cores ; it is poorly preserved compared with the finds of *Pelorovis* dating from 1952 and later years, but there can be little doubt that it is a specimen of Reck's *P. oldowayensis*.   The compression of the horn cores is to be seen only at their bases where there has been some crushing, more distally the section becomes more nearly rounded as in other *Pelorovis*.   There was possibly a longitudinal groove along the right horn core at least.   So far as can be seen, the

insertion of the horn cores overhung the occipital surface, and the angle of divergence of their bases was as in other *Pelorovis*. The ventral surface cannot be seen on the specimen as at present mounted.

The paratype, M.14948, is a frontlet with part of the left horn core. The core appears to be compressed, but part of its thickness may be missing. Taking the diameters of the horn core by the procedures described earlier gave readings of $10 \cdot 0 \times 15 \cdot 2$ cm., but an estimate for the complete horn core was $c. \ 10 \cdot 7 \times 15 \cdot 2$ cm. In the former case the index of compression would be $65 \cdot 8$ and in the latter $70 \cdot 4$— a value easily possible for *P. oldowayensis*.

M.14949 is a horn core tip which is certainly not distinguishable from *P. oldowayensis*. Also in the British Museum (Natural History) is a pair of mandibular rami from Kanjera (M.15856) referred to *Bularchus arok* (see Kent 1942). The outbowings of the medial walls of the molars are not very localized and the ramus is quite deep under M_3. Both these characters are like *Pelorovis*, but P_4 is different from the Olduvai remains by having an open valley on the anterior part of its medial wall ; I do not think that this difference is sufficient by itself to separate M.15856 from *P. oldowayensis*.

Measurements on the specimen were :

occlusal length M_1–M_3,	$11 \cdot 2$ cm.
occlusal length M_2,	3.5 cm.
occlusal width M_2,	$1 \cdot 9$ cm.
occlusal length P_2,	$1 \cdot 7$ cm.

All teeth except P_3 are present on the right side but M_1 is damaged, on the left side P_3 to M_3 are present but M_3 is damaged. Also from Kanjera are a left upper molar, M.25676, measuring $3 \cdot 35$ cm. long by $2 \cdot 35$ cm. wide, incomplete upper molars, M.25677 and M.25688, an incomplete M_3, M.25692, a lower premolar, M.25678, and three tooth fragments, M.25679–81 ; all are inseparable from *Pelorovis*. There are also some unregistered fragments of Bovine cervical vertebrae with loose centrum ends. Unfortunately it is not possible to assign these remains, nor those of some Bovine limb bones from Kanjera, to *Pelorovis*, because there is definite evidence from an upper molar fragment, M.25715, of another Bovine at Kanjera with smaller and more advanced teeth.

In the National Museum of Tanzania, Dar es Salaam, is a large Bovid skull with long horn cores which was found with the herd of *Pelorovis* in 1952 (Pls. 5, 6). It shows some differences from the other skulls and had provisionally been taken to belong to *Bularchus* (Leakey 1965 : 45). Mandibular rami were found with the skull. It has been distorted complexly but not too severely. The back of the skull is twisted on the front part, and there has also been some transverse compression causing the orbits to be slightly too close. In addition the right orbital rim lies more anteriorly than its own internal parts and the base of the right horn core has obliterated the right temporal fossa. The left temporal fossa and horn core base are missing, perhaps because the contemporary men broke into the skull for the brain ; on the other hand the skull was found in the clay of the gully and not on the land surface where the men have left their tools. The tooth rows are not in their natural positions

and all the upper premolars are missing. Only the left anterior tuberosity is preserved on the basioccipital.

The skull is from a slightly younger individual than the complete skull of *Pelorovis oldowayensis*, providing that the less worn condition of the lower premolars and M_1 indicates age and not that the animal's food plants were less abrasive. It was probably four or five centimetres shorter than the complete *P. oldowayensis* skull, and there are no signs of sutures on the face bones. Measurements (in cm.) on this skull were :

Skull length	62·6
Skull width across the orbits	23·8
Distance from premaxilla tip to nearest point on the orbit	41·3
Length of horn core	160
Span of horn cores, tip to tip	216
Dorso-ventral diameter of horn core	9·3
Diameter at 90° to preceding diameter	15·3
Width between supraorbital foramina	13·3
Length from premaxilla tip to M^3	36·0
Length from M^3 to occipital condyle	26·7
Occipital height	9·6
Skull width across mastoids	28·2
Width across anterior tuberosities of basioccipital	c. 5·2
Width across posterior tuberosities of basioccipital	8·1
Occlusal length M^1–M^3	10·4
Occlusal length M^2	3·6
Occlusal width M^2	2·8
Occlusal length M_1–M_3	11·75
Occlusal length M_2	3·5
Occlusal width M_2	1·9
Occlusal length P_2–P_4	6·9
Occlusal length P_2	1·8

The main points of difference between this skull and the other skull remains with which it was found are :

1.   Its slightly smaller size. Despite its long horn cores, the skull appears to be slightly smaller than the complete skull of *Pelorovis* which I have taken to be from a female animal.

2.   The horn cores are not so posteriorly inserted and do not overhang the occipital surface of the skull. There is no triangular depression at the top of the occipital surface.

3.   The horn cores are more dorso-ventrally compressed than in *P. oldowayensis*, with an index of 60·8 compared with a range of 70·2 to 84·1 in the other skulls (Text-figs. 10, 40). They are also more nearly in a single plane than most of the horn cores of *P. oldowayensis*, i.e. there is a little less spiralization.

4.   The width between the supraorbital pits expressed as a percentage of orbital width is 55·9 which compares with values of 42·3 and 53·2 for *Pelorovis oldowayensis*.

5.   The zygomatic arch, continuing forwards under the orbits, is still deeper than in *P. oldowayensis* (Pl. 6), and more strongly concave on its ventral surface. This could be correlated with the mechanically less favourable position of the horn cores.

6.   The tooth row is sited less anteriorly than in *P. oldowayensis*, as may be seen
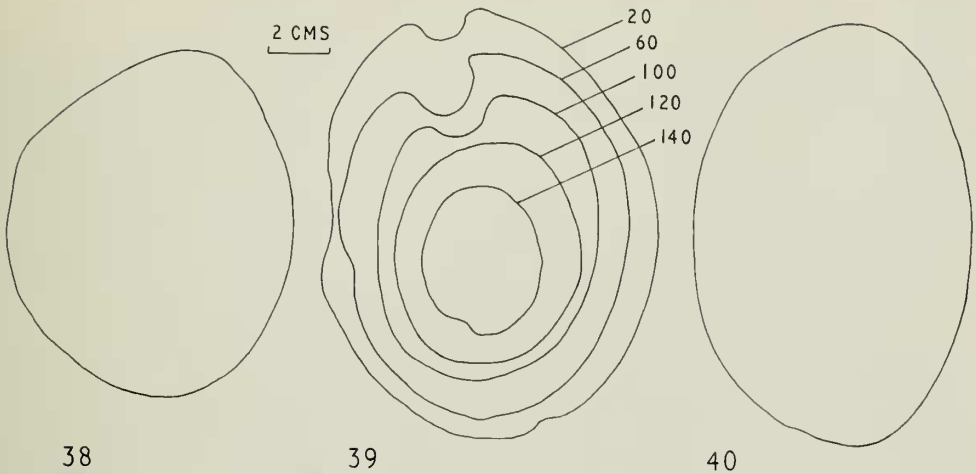
FIGS. 38–40. Horn core sections at 20 cm. above base. 38, in the complete skull of *Pelorovis* ; 39, in Pel 7 ; 40, in the second complete skull from BK II. Sections of Pel 7 are also shown at distances of 60, 100, 120 and 140 cm. above the base. If the horn cores pictured here are related to skulls with tooth rows in a horizontal position, then the ventral sides are on the right, the dorsal on the left and the anterior towards the foot of the page.

by comparing the positions of M³ and orbit on Pl. 2, fig. 1 and Pl. 6, fig. 1 (the orbit being as far back in this skull as in *P. oldowayensis*). The ratio of the length from the premaxilla tip to M³ as a percentage of that from the premaxilla tip to the nearest point on the orbit was *c*. 87·2 compared with 82·3 in *P. oldowayensis*.

7. The occipital surface of the skull has a reading of 34·0 for height as a percentage of width, which compares with readings of 40·7, 36·9 and 35·5 for *P. oldowayensis*.

8. The reading for the width between the anterior tuberosities of the basioccipital compared with the posterior ones was 64·2, which is different from the *P. oldowayensis* readings of 53·8, 57·6 and 58·4. This could be connected with the very great span of the horn cores as well as with their insertion in front of the level of the occipital surface.

9. The coronoid process of the lower jaw is slightly more sharply curved back than in *P. oldowayensis* (Pl. 6). This is correlated with character (6) above.

10. The horizontal ramus of the lower jaw is slightly more shallow beneath the molars.

11. P_4 on both sides has an open anterior part of its medial wall.

12. The anterior edge of each molar tooth in the lower jaw has a longer contact with the tooth in front than has *P. oldowayensis*.

The length of the lower premolar row as a percentage of the molar row is 58·7, which compares with values of 50·9 and 58·5 in *P. oldowayensis*.

In characters 2, 3, 6, 7, 9 and 10 this skull is more like that of *Syncerus* than is *P. oldowayensis*, but in 8 and 11 it is less similar. It is also nearer to *Homoioceras* in 2, 3, 6, 7 and 10,

One would not necessarily look for a greater amount of morphological difference between two Bovine species than exists between this skull and *P. oldowayensis*; on the other hand it is known for the Bovini to be very variable in their skull morphology (see Pilgrim 1939 : 263 on variability in *Hemibos triquetricornis* Rütimeyer), and this Olduvai skull is not at all beyond a possible range for *P. oldowayensis*. Because I cannot be certain, even with a whole skull, that this animal is specifically distinct from *P. oldowayensis*, I shall not name it. More Bovine remains diminishing the morphological gap between *Pelorovis* and buffaloes may well be found as further excavations add to faunal knowledge of the African Pleistocene.

V PHYLOGENETIC AND FUNCTIONAL CONSIDERATIONS

Some of the skull characters of *Pelorovis* may be distinguished as primitive, advanced or specialized. Primitive characters are those in which *Pelorovis* does not differ from Boselaphini or early Bovine genera such as *Pachyportax*, *Parabos* and *Proamphibos*; advanced ones are those in which it does differ from such early forms and which it shares with all or many of the later Bovine genera *Homoioceras*, *Syncerus*, *Hemibos*, *Bubalus*, *Leptobos* and *Bos*; specialized ones are those for which *Pelorovis* is distinctive although not invariably unique. This sort of assessment is not possible with all skull characters, nor with those of the limb bones and vertebrae.

Primitive characters, principally to be seen on the teeth, are: the poorly developed basal pillars, the absence of localized outbowings of the lateral walls of the upper molars, and the not very complex enamel walls of the central cavities.

The advanced characters of *Pelorovis* are : its large size and very large horns, the lack of an ethmoidal fissure, the lack of a preorbital fossa, and the fairly hypsodont teeth.

Its specialized characters are : the posterior insertion of the horn cores, anteriorly sited tooth row, and characters linked with these two.

One can suppose that with increasing size in any stock of Bovidae, the support of larger horn cores becomes a problem ; this may be appreciated by comparing the post-orbital part of a horse's skull with the more massive construction of a larger Bovid. Within the Bovini, cattle have the horn cores set widely apart and far back. Thus the weight of the horn cores is supported above instead of in front of the occipital condyles, and the strain of support is widely spread across the back of the skull. In *Bubalus* and *Homoioceras* the horn cores are large, and set closer together in front of the level of the skull's occipital surface. Hence there is noticeable enlargement of the frontals for support, and, in *Homoioceras nilssoni*, strengthening of the zygomatic arch beneath the orbits as well. The curvature of the long horns is such that these skulls are most stable in an almost horizontal position. In *Pelorovis* the horn cores are set as far back as in cattle, although not so widely apart ; their curvature carries the greater part of their weight so far behind the level of the occipital condyles that in life the animal must have counteracted by holding its head more nearly in the vertical position than do other Bovini. This is probably the reason for the strengthening of the zygomatic arch in an animal with its horn cores set so posteriorly. The complete skull from BK II at Olduvai, the identification of which is doubtful, has less posteriorly inserted horn cores than in *Pelorovis*,

and their curvature takes them less behind the level of the occipital condyles. This might mean that in life the head was held a little less nearly vertically than in *P. oldowayensis*, except that in this skull the strengthening of the zygomatic arch is immense. Unless the skull of this animal was held nearly in the vertical plane, the curvature of its horn cores would have given less stability than there is in *Bubalus* and *Homoioceras* skulls.

The skull of *Pelorovis* shows a number of parallels with *Alcelaphus*, a genus which also holds its head in a more nearly vertical plane than other Bovidae. In both, the horn cores are inserted far back and close together, the face is long, there is sub-orbital strengthening of the zygomatic arch, an anteriorly placed tooth row, the median indent at the back of the palate passes well forwards, and there are small palatal fissures between premaxillae and maxillae. The 1952 find of *Pelorovis* was of a herd, and it might be thought that these animals could have been plains-dwelling grazers like *Alcelaphus*. However this may be carrying the comparison too far, and it is awkward to accommodate with the primitive occlusal pattern of the molars. The only ecological possibility likely for a Bovid which I would eliminate for *Pelorovis* would be eye-level browsing.

There are also a number of limb bone similarities between Alcelaphini and *Pelorovis* : the hollow between the great trochanter and articular head of the femur, the wide lateral part of the articular head, the wide patellar fossa on the femur ; the small posterior eminence and low lateral tuberosity of the humerus, the wide bicipital groove and the high medial condyle distally ; and possibly the non-swollen distal end of the radius in side view.

(It is none the less quite clear that *Pelorovis* is not an Alcelaphine because it has not such distinctive characters of one or more Alcelaphine genera as an abrupt alteration in the course of the horn cores, transverse ridges on the horn cores, excessively narrow nasals, a long contact of the premaxillae on the nasals, the premaxillae narrowing very little as they rise towards the nasals, the foramina towards the back of the palate being wide apart, the curved arcade of the tooth row, a strongly developed hypsodonty, the absence of basal pillars, or a complicated course of the enamel walls of the central cavities of the molar teeth.)

It is possible that while Africa is today inhabited by only one Bovine species which varies in morphology and ecology, it has been simultaneously inhabited at various times in the past by two or more species with more restricted ecologies.

The skull described in the last section of this paper is a possible example. There may also be mentioned two left upper molars, 1953, BK II Extension, 84 and 1957, BK II, 532 which are surely Bovine but which are smaller than the molars of *Pelorovis*, have more localized outbowings of their lateral walls, and central cavities which have perhaps too complicated enamel walls. The first one is 3·65 cm. long and 2·5 wide, the second 3·8 × 2·6. M.25715 in the British Museum (Natural History) is half a Bovine upper molar from Kanjera which is certainly not from *Pelorovis*, since it is smaller and definitely more advanced ; other specimens from Kanjera which could belong to the same species are M.25683, M.25697 and M.25705. In the Natron beds (see Isaac 1965), contemporary with the upper part of Bed II at Olduvai, is a Bovine left mandible fragment, WN 64,256, MP 1, which is perhaps

a little smaller than *P. oldowayensis* and has more advanced teeth.   It has retained M_2 and M_3, and they have large basal pillars, localized outbowings of the medial walls and noticeably narrowed lateral parts of the front and back lobes.

1957, SHK II, 671 is the tip of a horn core which appears to have been much shorter than *Pelorovis* horn cores and with less curvature.   From its size it is likely to have belonged to a Bovine animal.

On the question of the ancestry of *Pelorovis, Simatherium kohllarseni* (Dietrich 1942 : 119–20, pl. 20, figs. 161, 163, 165) may be mentioned.   It is the rear part of a damaged skull from the Bird River Region, Laetolil, found in deposits thought to be a little older than Bed I at Olduvai.   So far as can be seen from the description and three photographs this animal has characters which fit it to be ancestral to *Pelorovis oldowayensis*.   It is apparently about the size of a buffalo, and hence a little smaller than *P. oldowayensis* ; the horn cores arise behind the orbits but not so far back as in *P. oldowayensis*, and are larger than in its supposed contemporaries *Hemibos* and *Leptobos* in Eurasia although they look smaller than in *P. oldowayensis*. The horn cores are stated to have some degree of flattening, they either have no keel or have only a slight one in the position found in *Bos primigenius namadicus* and *B. acutifrons*, there is a wide shallow groove on the less damaged left horn core, and this horn core also shows a curvature comparable to that in *P. oldowayensis*.   The frontals are raised between the horn bases ; in this the animal resembles *Hemibos* rather than *Leptobos*.   Excavations have yet to reveal the ancestor of *Simatherium*.

The linking of *Pelorovis* with *Syncerus* does not illuminate the evolutionary origins of the Bovini.   Previous work on Asian fossils has shown that the living *Bubalus* belongs to a group containing the extinct *Hemibos* and probably *Proamphibos* as well, and *Proamphibos* may be accepted as phyletically close to its Boselaphine contemporaries *Parabos* and *Pachyportax*.   The *Bos-Leptobos* group represents another stock of Bovini in which the horn cores have more or less evenly rounded cross sections, and the central question is the history of keels on the horn cores. Have *Leptobos* and *Bos* lost keels so that their ancestors could be *Parabos, Pachyportax* or similar forms, or have they never had keels so that ancestors without keeled horn cores must be looked for?

Pilgrim (1939 : 141) supposed that the *Leptobos-Bos* ancestors did have keels, his evidence being that the early *Bos acutifrons* of the Pinjor stage had what could be the remains of a single keel, so too did *Bos primigenius namadicus* and at least one specimen of *Leptobos falconeri* (American Museum of Natural History, no. 19816, see Pilgrim 1937 : 817).   It may also be noted that the Pleistocene bison of East Asia, discussed by Matsumoto (1918), appear from his diagrams to have had traces of keels.   Both Merla (1949 : 147) and Rütimeyer (1878 : 117, 160, 167) were convinced of the Boselaphine relationship of *Leptobos*, and since all known genera of Boselaphini have keeled horn cores, there is a supposition that the ancestors of *Leptobos* also did.

The evolution of Bovine horn cores would thus be from the original more or less circular cross section of the earliest Bovidae such as the Miocene *Eotragus* Pilgrim, perhaps through some degree of lateral compression, then through a genus like *Protragocerus* Depéret of the European Upper Miocene (according to Thenius 1956

this genus should now include *Strepsiportax* Pilgrim from the Indian Chinji) which has at least the beginnings of keels, then an increase in size to *Pachyportax* and *Parabos* or their relatives. This would have been the latest stage at which the *Leptobos-Bos* group could have separated from the *Hemibos-Bubalus* group, since *Proamphibos* seems to be already approaching the vomer specializations of the latter group.

How can *Syncerus* and *Homoioceras* be fitted into such a scheme, assuming that they do have a Boselaphine ancestry? If my opinion of a relationship of *Pelorovis* to *Syncerus* is accepted, then *Pelorovis* reinforces the views of those who have held that Asiatic and African buffaloes are not very closely related, and provides no basis for connecting *Syncerus* with the *Leptobos-Bos* group instead. There is no diminution of the phenetic distance between the African Bovini and those of Eurasia. It is not clear how far Bovine evolution has consisted of a few long-independent lineages advancing gradually and often in parallel, or how far there have been repeated radiations of similar adaptive types at successive levels of overall advance.

There are many interesting chronological and ecological questions still to be answered on Bovine evolution in Africa alone : did *Pelorovis* overlap *Homoioceras* in time? There are very slender indications (e.g. the Natron Bovine mandible) that it could have done. Was there a difference in ecological requirements between the long faced *Pelorovis* and the short faced *Homoioceras* in any way comparable to that between the long faced *Bos primigenius* and the short faced bison? What are the ecological differences between cattle and bison anyway? How did *Bos primigenius* coexist with *Homoioceras antiquus* in North Africa? What was the other Bovine at Kanjera, of which we have half a molar tooth?

VI ACKNOWLEDGMENTS

VII SUMMARY

Much Bovid material assignable to *Pelorovis oldowayensis* Reck has been excavated at Olduvai Gorge since 1952. This large species has horn cores inserted close together and so far behind the orbits that they overhang the occipital surface. The median indentation at the back of the palate comes well forwards, and the occlusal pattern of the teeth is not very advanced.

It is clear that *Pelorovis* is not a Caprine but is a member of the Bovini, and is phenetically nearest to the African genera *Syncerus* and *Homoioceras*. The reasons for this opinion are given in the conclusions to section III above. *Pelorovis* is very unlikely to have been an ancestor of *Syncerus* and *Homoioceras*, but published

photographs (Dietrich, 1942) give no indication that the Laetolil species *Simatherium kohllarseni* could not have been an ancestor of *Pelorovis*.

Material in the British Museum (Natural History) used to define *Bularchus arok* Hopwood (1936) is thought to be assignable to *Pelorovis oldowayensis*.

An almost complete Bovine skull excavated from site BK II at Olduvai in 1952 differs from *P. oldowayensis* in having horn cores less posteriorly inserted and its tooth row less anteriorly placed, rather more compressed horn cores, a wider occipital surface, wider anterior tuberosities of the basioccipital, and a shallower jaw ramus. It has a greater overall likeness to *Homoioceras* and *Syncerus*, and may be a separate species from *P. oldowayensis*.

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