

Rediscovery of fossil antelope holotypes (Mammalia, Bovidae) collected from Olduvai Gorge, Tanzania, in 1913

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With 3 Text-figures

Abstract

On a study visit to the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, in the summer of 1992, the first author discovered that the holotypes of *Megalotragus kattwinkeli* and *Rhynotragus semiticus* (Mammalia, Bovidae, Alcelaphini) and of *Taurotragus oryx pachyceros* (Bovidae, Tragelaphini) from Olduvai Gorge, Tanzania, had escaped destruction by Allied bombing during the Second World War, contrary to previous belief. On a further study visit in the autumn of 1994, the second author made a discovery about the refound holotype of *Rhynotragus semiticus* which corroborates its synonymy with *Megalotragus kattwinkeli*. It is now known that the name *Rhynotragus semiticus* is available from 1925, and not 1935 as thought previously, and it therefore becomes the senior synonym for the commonly used *Megalotragus kattwinkeli*. The consequences of these discoveries for taxonomy and nomenclature are discussed. *Taurotragus oryx pachyceros* is not conspecific with *T. arkei* L.S.B. LEAKEY 1965.

Zusammenfassung

Anlässlich eines Studienaufenthaltes im Sommer 1992 an der Bayerischen Staatssammlung für Paläontologie und historische Geologie in München entdeckte hier der erstgenannte Autor die als vermisst gegoltenen Holotypen von *Megalotragus kattwinkeli* und *Rhynotragus semiticus* (Mammalia, Bovidae, Alcephalini) sowie von *Taurotragus oryx pachyceros* (Bovidae, Tragelaphini) aus der Olduvai-Schlucht in Tansania. Angeblich waren die Stücke einem alliierten Bombenangriff während des Zweiten Weltkrieges zum Opfer gefallen. Bei einem weiteren Studienaufenthalt im Herbst 1994 fand die zweitgenannte Autorin am Holotyp von *Rhynotragus semiticus* deutliche Argumente für seine Synonymie mit *Megalotragus kattwinkeli*. Der Name *Rhynotragus semiticus* erwies sich, nicht wie angenommen erst seit 1935, sondern bereits seit 1925 verfügbar und somit als älteres Synonym von *Megalotragus*

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kattwinkeli. Die Konsequenzen dieser Beobachtungen bezüglich Taxonomie und Nomenklatur werden diskutiert. *Taurotragus oryx pachyceros* ist nicht konspezifisch mit *T. arkelli* L. S. B. LEAKEY 1965.

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Introduction

Olduvai Gorge, also formerly known as Oldoway or Duwai Gorge, is one of the foremost sites in the world for the remains of early man. It lies in the Serengeti Plains of northern Tanzania at 2°59' S 35°21' E, slightly west of the eastern Rift Valley. The earliest European traveller in this part of East Africa was Dr. Oscar BAUMANN in March 1892, who used the name Duvai for a small hill about 15 km south-east of Lake Elgarja or Lgarya, also called Lake Ndutu. The name Duvai is from the Masai word for the sisal plant which grows in the area. The nearby gorge runs eastwards from the lake and cuts into Pleistocene and Pliocene beds. After about 37 km it is joined by a side gorge from the south and after another 9 km drains into the Balbal depression at the foot of the Ngorongoro-Olmoti highlands.

The discovery of Olduvai Gorge has always been attributed to Professor WILHELM KATTWINKEL in 1911, although Frau MARTHA KATTWINKEL was also present at the time (BRANCA 1914: 1171). To later generations of paleontologists and anthropologists involved with Olduvai Gorge the name of KATTWINKEL became known as that of a butterfly collector who had stumbled by accident on the Gorge, and knowledge of his Christian name vanished altogether (COLE 1975: 80). GLOWATZKI (1979) resuscitated KATTWINKEL's reputation by publishing some information on his medical career, of which fuller details are given in the Allgemeine Deutsche Biographie, and by stressing that the 1911 journey arose from his professional interest in sleeping sickness and was a scientific expedition. RECK (1933: 25), however, had pointed out that the 1911 trip was partly for hunting, and to that extent recreational.

While camped at Olduvai, KATTWINKEL and his wife discovered mammalian fossils at more than one locality in the Gorge. They carried a selection back to Munich. These were identified as being from a proboscidean, a hipparionine horse, hippopotamus and a sivathere. As a result, the beds at Olduvai were explored more thoroughly in October to December 1913 by an expedition under Dr. Hans RECK of the Institut für Geologie und Paläontologie der Friedrich-Wilhelm-Universität, Berlin (RECK 1914). Further expeditions were abandoned because of the outbreak of the First World War in 1914, but a series of faunal reports was initiated (DIETRICH 1916) and from 1925 onwards the series entitled Wissenschaftliche Ergebnisse der Oldoway-Expedition 1913. The bones collected by the 1913 Expedition were divided between the Friedrich-Wilhelm-Universität (now the Zentralinstitut Museum für Naturkunde der Humboldt-Universität), Berlin and the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.

The 1913 Expedition found no artifacts, but excavated a human skeleton which became the subject of a long controversy before being accepted in 1935 (the year of KATTWINKEL's death) as an intrusive burial of *Homo sapiens*. M.D. LEAKEY (1971: 225) gives a summary and further references on this aspect of the early studies at Olduvai Gorge. Notwithstanding the ultimate verdict on the skeleton, it helped to maintain interest in the Gorge in the years after the First World War. In the late 1920s L.S.B. LEAKEY wished to correlate his own human and faunal finds in Kenya with those at Olduvai. Accordingly he twice visited RECK in Berlin and eventually RECK joined the Third East African Archaeological Expedition of 1931–32 which worked at Olduvai (the Second Olduvai Expedition). RECK died in 1937 but both L.S.B. and M.D. LEAKEY did much more work at Olduvai in later years. On 17 July 1959 came the discovery of the famous australopithecine skull named *Zinjanthropus boisei* by L.S.B. LEAKEY (1959). Thereafter financial support was obtained for more intensive studies of the geology and fauna of the Gorge. It became clear that most Olduvai fossils come from Beds I–IV of uppermost Pliocene and Lower Pleistocene age (HAY 1976). The top of the Olduvai normal palaeomagnetic event in the Matuyama reversed epoch, now dated to 1.76 Ma (CANDE & KENT 1992), lies within the lower 75 cm or at the base of the Lemuta Member, itself at the top of the lower part of Bed I (HAY 1976: 39,64). The date of this palaeomagnetic change is close to that of the Pliocene to Pleistocene stratigraphic boundary at 1.795 Ma (PASINI & COLALONGO 1994).

Studies of Olduvai Bovidae up to 1937

The family Bovidae is the most abundantly fossilized mammal group at Olduvai Gorge. More than half the bones of tetrapods listed by M.D. LEAKEY (1971: 257, table 4 [excluding insectivores, chiropterans and rodents]) belong to this family. Early studies on material collected by the 1913 Expedition, culminating in the monograph by SCHWARZ (1937), resulted in the following new names for extinct bovids:

Species	Holotype
Tribe Tragelaphini:	
<i>Tragelaphus spekei stromeri</i> SCHWARZ 1932	Skull in Munich; not illustrated.
<i>Taurotragus oryx pachyceros</i> SCHWARZ 1937	Cranium in Munich; not illustrated.
Tribe Bovini:	
<i>Pelorovis oldowayensis</i> RECK 1925	Cranium in Berlin; (RECK 1925; 1928, text-fig.1, pls.1,2).
Tribe Reduncini:	
(See GENTRY & GENTRY 1978: 339)	
<i>Thaleroceus radiciformis</i> RECK 1925	Frontlet in Munich; (RECK 1925; 1935, fig.2; 1937, pl.8).
Tribe Alcelaphini:	
<i>Megalotragus kattwinkeli</i> (SCHWARZ 1932)	Right horn core in Munich; not illustrated.
<i>Parmularius angusticornis</i> (SCHWARZ 1937)	Crushed cranium in Munich; not illustrated.

Species	Holotype
Tribe not determined: <i>Rhynotragus semiticus</i> RECK 1925	Partial skull in Munich; (RECK 1925; 1933: 166, fig. 28; 1935, fig.1).
Tribe Antilopini: <i>Gazella gazella praecursor</i> SCHWARZ 1937	Horn core in Munich; not illustrated.
<i>Antidorcas recki</i> (SCHWARZ 1932)	Skull in Munich; (SCHWARZ 1932, pls.1-2; 1937, pl.1 fig.1).

Hitherto the name *Pelorovis oldowayensis* has been dated from RECK (1928) and the names *Thaleroceros radiciformis* and *Rhynotragus semiticus* from RECK (1935). RECK wrote his 1935 paper specifically to provide diagnoses for the two latter taxa which he had described in two earlier publications (RECK 1925, 1933). We have been able to see RECK's article in the weekly *Illustrierte Zeitung*, Leipzig, for 19 March 1925. The descriptive remarks in the text, together with the illustrations with these names in their captions, are sufficient to render all three names available from this publication.

Olduvai Bovidae since the Second World War

After the Second World War no Olduvai bovids survived in Berlin other than the *Pelorovis oldowayensis* holotype. Late in 1967 and again in July 1969 A.W. and A. GENTRY were assured by Professor Dr. RICHARD DEHM and Dr. FRIEDLINDE OBERGFELL that nearly all Olduvai material in the Munich collection had been destroyed by Allied bombing of that city in 1944. Only the *Thaleroceros radiciformis* holotype and a few primates had survived.

Hence GENTRY & GENTRY (1978) in their lengthy treatment of Olduvai Bovidae were able to use the names *Pelorovis oldowayensis* and *Thaleroceros radiciformis* without difficulty. Type specimens, illustrations and adequate descriptions were all available. *Antidorcas recki* also presented no problems because there was a cast of the holotype in the Natural History Museum in London, BM(NH) M21460 (now duplicated in the National Museum of Kenya, Nairobi). For *Parmularius angusticornis*, SCHWARZ had specified a paratype, an incomplete right horn core in London, BM(NH) M14553, which still exists and which was illustrated by L.S.B. LEAKEY (1965: pl. 63). In all these cases there was no difficulty about understanding or identifying in later collections the species to which the older names had been applied. However GENTRY & GENTRY (1978) abandoned use of the three names founded by SCHWARZ as subspecies of living antelopes: *Tragelaphus spekei stromeri*, *Taurotragus oryx pachyceros* and *Gazella gazella praecursor*. The only illustrated pieces were a tibia and cervical vertebra of the gazelle and the descriptions were insufficient to allow comparisons.

For *Megalotragus kattwinkeli* the position was more complicated. The holotype had been a right horn core with frontal, VI-1099 from an unknown horizon which SCHWARZ (1932: 4, no picture) designated as type of his new species *Alcelaphus kattwinkeli*. The subsequent illustration of a cranial piece of this species in SCHWARZ (1937: pl.1 fig.3) showed a frontal region with horn bases, which the caption alleged to be VII-468. However in SCHWARZ's own list (1937: 56) of specimens, VII-468 was the number of a lower jaw. Further, the skull part shown in pl.1, fig.3 did not fit the description of the holotype as a right horn core with frontal.

GENTRY & GENTRY (1978: 356) surmised that the figured specimen could be VI-487, another listed skull part. Since the original holotype had been destroyed and never figured, they designated a neotype (International Code of Zoological Nomenclature, Article 75). This was a damaged skull BM(NH) M21447, lacking nasals and previously used as the holotype of *Xenocephalus robustus* L.S.B.LEAKEY (1965: 62, pls.81-82), a name regarded by GENTRY & GENTRY as a junior synonym of *Megalotragus kattwinkeli*.

The unique specimen of *Rhynotragus semiticus* came from Bed IV (DIETRICH 1933: 301) and was an odd-looking skull fragment with a strongly arched or updomed profile of the nasals. Unless the fossil was deformed, the animal must have had an extremely specialised morphology. Not surprisingly, RECK came to no conclusion about its tribal affiliation. SCHWARZ (1937: 60,85) supposed that the fossil was distorted and used the name *semiticus* as a subspecies of the extant alcelaphine *Connochaetes taurinus*, the blue wildebeest (for which he used the generic synonym *Gorgon* GRAY 1850). He assigned much other material in RECK's collection to the same subspecies. GENTRY & GENTRY (1978: 370) considered that the holotype could not belong to a *Connochaetes* because of the lack of a sharply-outlined temporal fossa along the side of the braincase between the horn core base and the back of the orbit, and because of the rather steep inclination of the braincase. But they could offer no alternative suggestion for its identity, so the animal remained mysterious.

The first step towards the solution of the problem came almost 60 years after the first publication of *Rhynotragus semiticus*. PICKFORD & THOMAS (1984) described what they called „an extraordinary bovid....probably of the Tribe Alcelaphini“ from late Pleistocene to Holocene strata on Rusinga Island, Lake Victoria, Kenya, as a new genus and species *Rusingoryx atopocranium*. Their fig.2a of the holotype in lateral view shows a partial skull lacking the face anterior to the caudal part of the nasals. If the occipital profile be positioned vertically, then the back of the top edge of the face would be rising steeply. This unusual condition is very like *Rhynotragus semiticus*, although the authors did not mention the similarity. In our view *Rusingoryx* can be taken as a junior subjective synonym of *Rhynotragus*.

HARRIS (1991) then showed the connection of *Rhynotragus* with *Megalotragus*. He described some Upper Pliocene and Lower Pleistocene *Megalotragus* remains from the Upper Burgi, KBS and Okote Members of the Koobi Fora Formation, Kenya, as a new species *M. isaaci*, believing them to be distinguishable from the Olduvai *M. kattwinkeli*. The illustrated paratype of this species (HARRIS 1991: fig.5.47) shows the same updomed nasals as in *Rhynotragus semiticus*. HARRIS described the face as narrow and the updomed nasals as forming a parallel-sided crest. There can be no doubt that both *R. semiticus* and *Rusingoryx atopocranium* are congeneric with the species of *Megalotragus*. *Megalotragus* VAN HOEPEN 1932 is a Pliocene and Pleistocene genus of alcelaphine antelopes, some of which, like the South African type species *M. priscus* (BROOM 1909), reached a very large size. On the evidence of the Rusinga and some South African finds (KLEIN 1972, KLEIN & CRUZ-URIBE 1991), it only became extinct close to the end of the Pleistocene. No evidence of its facial structure has been published from South Africa, but it is likely that the updomed nasals would characterise all species of the genus. The neotype skull of *M. kattwinkeli* was said by GENTRY & GENTRY (1978: 358) to be rather poorly preserved, but in the light of the Koobi Fora discoveries, it does not seem that it is much distorted. With the frontals positioned far above the tooth row, updomed nasals of the same shape as in *Rhynotragus semiticus* could easily have been accommodated.

The time span of *M. isaaci* at Koobi Fora largely precedes that of *M. kattwinkeli* at Olduvai. If the holotype of *Rhynotragus semiticus* did indeed come from Bed IV, then it would almost certainly not be conspecific with the earlier *M. isaaci*.

Study visits to Munich, 1992 and 1994

In July 1992, during a return visit to the Bayerische Staatssammlung für Paläontologie und historische Geologie in connection with Miocene ruminants, A.W. GENTRY noticed that a cupboard in the storeroom for mammals was labelled as containing the RECK collection. At his request the cupboard was unlocked, and within there lay a great many bovid fossils of the 1913 Olduvai expedition. Among them were three specimens of outstanding interest, the lost holotypes of *Megalotragus kattwinkeli*, *Rhynotragus semiticus* and *Taurotragus oryx pachyceros*. There was also a piece of mandible labelled as paratype of *Gazella gazella praecursor*. Even in the pages of a scientific journal it may be permitted to an author to remark what a moving and strange experience it was on a tranquil, midsummer Friday afternoon, to see and handle historic fossils which he knew, until a few minutes previously, did not exist.

H. MAYR had discovered the boxes containing the Olduvai bovids in the basement in Theresienstrasse 41, an outstation of the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich in 1989. The most likely explanation for their survival is that shortly before the Second World War material on loan to SCHWARZ in London had been returned and part of it was still awaiting reincorporation into the collections. Hence it was not in the collections destroyed by bombing on the night of 24-25 April 1944. Five clues favour this explanation. Firstly the RECK collection in Munich, as it now stands, contains only Bovidae, the family studied by SCHWARZ. Secondly, on the afternoon that the cupboard was opened, Dr. V. FAHLBUSCH noticed that many of the fossils carried labels of the British Museum (Natural History). These were tie-on labels as used in the Department of Zoology and not labels of the Department of Palaeontology (known as the Department of Geology until 1956). While in England from 1933-1937 as a refugee from the Nazi regime in Germany (HILL 1962), SCHWARZ had been unofficially attached to the mammal room, Department of Zoology, of the British Museum (Natural History), and therefore would have had access to labels of this pattern. Thirdly, Dr. K. HEISSIG was able to show us, in November 1994, a sheet from a London newspaper, the Daily Mail of Wednesday 2 September 1936, used as part of the wrapping of the fossils. He, along with H. MAYR and the preparator M. DROBEK, remembered that both South African and British newspapers had been among the wrappings. Fourthly it is clear from the museum archives in London (letter from SCHWARZ in Berlin to M.A.C. HINTON [Deputy Keeper of Zoology in London] dated 2 August 1933, and an internal memorandum from HINTON to W.D. LANG [Keeper of Geology] dated 11 August 1933) and from SCHWARZ's (1937:8) published acknowledgements, that he did indeed take to London Olduvai bovids of the 1913 Expedition and that their carriage was paid for by the British Museum (Natural History). Fifthly is the surviving inventory of some collections of fossils evacuated in 1941 to Oettingen Castle, Bavaria, from the Bayerische Staatssammlung in Munich. A single-line entry for cases 197 to 213 reads „Oldoway-Material, Berliner Expedition (Antilopen Schwarz)“. These cases were thus outside Munich for the rest of the war.

The move of material to Oettingen had been organised by Dr. THERESE VON OETTINGEN-SPIELBERG who became a scientific research assistant at the Institut in 1943 and, after the war, a curator. This Oettingen material was taken back to Munich in 1948. It remained at the so-called „collecting point“ for antiquities belonging to public institutions at Arcisstrasse 10 until 1950 when it was taken to the new premises of the Bayerische Staatssammlung für Paläontologie und historische Geologie in Richard-Wagner-Strasse 10. In 1969 it was moved again to an outstation in Türkenstrasse. By 1989 when H. MAYR investigated the seventeen boxes marked in red with the logo of the Shell Oil Company of South Africa, there was no knowledge of their contents. Not all the Olduvai bovids of the 1913 Expedition have been recovered from the Oettingen consignment. The holotypes of *Tragelaphus spekei stromeri*, *Parmularius*

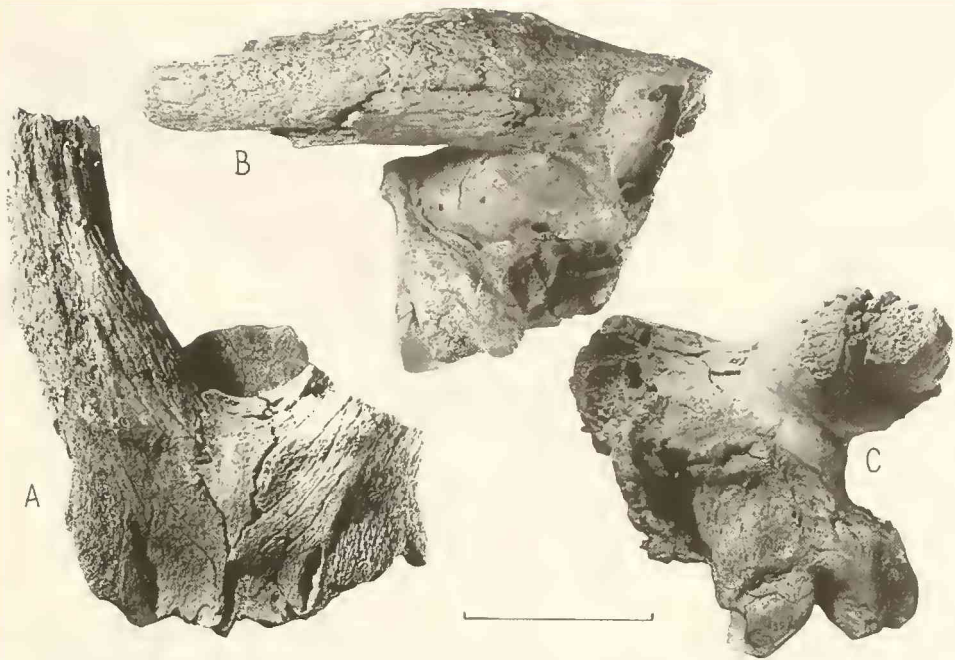


Fig. 1: Holotype cranium of *Taurotragus oryx pachyceros*, E-58, in (A) dorsal, (B) lateral and (C) occipital views. Scale = 10 cm.

angusticornis, *Gazella gazella praecursor* and *Antidorcas recki* have not made a reappearance and were presumably destroyed in 1944.

The chief interest in the rediscovered type of *Taurotragus oryx pachyceros* (Fig.1) is that the horn cores are inserted at a low inclination in side view, as in the living eland. Therefore it cannot belong to the more primitive, extinct Olduvai species *Taurotragus arkelli* L.S.B. LEAKEY 1965, and so this name is not a junior synonym of *T. pachyceros*. One would expect *T. oryx pachyceros* to have come from a younger stratigraphic horizon than *T. arkelli*, which was a surface find in Bed IV. Elsewhere in Africa, middle Pleistocene *T. oryx* is known from Broken Hill (= Kabwe), Zambia, and Elandsfontein, South Africa (GENTRY & GENTRY 1978:307). In general, the Olduvai bovids of the 1913 collection are predominantly from Bed IV, whereas those collected in later years by L.S.B. and M.D. LEAKEY are mostly from Beds I and II.

The paratype of *Gazella gazella praecursor* is a piece of a right mandible with worn P3 to M1, numbered II-40. SCHWARZ (1937) did not list it as a paratype and its status is no different from that of other fossils forming part of the hypodigm of the subspecies. It is certainly an antilopine bovid, but little more can be surmised about its identity.

The label on the holotype horn core of *Megalotragus kattwinkeli* reads „Or. No. VI. 1099 + Typus Alcelaphus kattwinkeli Schwarz Oldoway O.Afrika Reck Smmlng. 1913“. It is indeed a right horn core, as indicated by SCHWARZ (1932: 4; 1937:56), and part of the frontal with supraorbital pit and top of the orbit is also preserved (Fig.2). The anteroposterior and transverse basal diameters of the horn core are 44.4 and 66.0 mm. In our opinion it is conspecific with the skull designated as the neotype (see above). Two other frontlets of *M. kattwinkeli* are included in this collection, numbered VI-487 and VI-1088, and neither is the specimen figured by SCHWARZ (1937, pl.1 fig.3) as VII-468 (see above). We can now only suppose that the illustration must be of the fourth, unnumbered, „Frontale mit Hornwurzeln“ of SCHWARZ's list.



Fig. 2: Holotype right horn core of *Megalotragus kattwinkeli*, VI-1099, in anterior view. Scale = 5 cm.

The holotype of *Rhynotragus semiticus*, as seen again in 1992, corresponded to RECK's (1925, 1933 and 1935) illustrations, but had suffered damage to the ventral orbital rim and side wall of the braincase. The broken pieces have been preserved. The undamaged portion bore no number or label although both RECK (1935) and SCHWARZ (1937: 60) gave its number as VII-1111.

In November 1994 the first two authors visited Munich again, so that ANTHEA GENTRY could see the rediscovered RECK collection. She noticed that a separated partial left horn core, VI-306, one of many specimens listed by SCHWARZ (1937: 61) as *Gorgon* (now *Connochaetes*) *taurinus semiticus*, could be fitted exactly to the *R. semiticus* holotype, and is unquestionably from the same individual (Fig. 3). Thus horn core VI-306 is not from a *Connochaetes taurinus*, in which the horn cores are inserted more widely apart, further behind the orbits, and show more divergence. The horn core corroborates all the evidence given above that *R. semiticus* is an alcelaphine antelope congeneric with the species of *Megalotragus*. Moreover it can at last be seen that *R. semiticus* is indeed conspecific with *M. kattwinkeli* rather than with *M. isaaci*; its horn cores are only moderately long, they have no backward curvature at their bases, and they show a slight diminution in divergence distally.

It is apparent both from the contents of the RECK cupboard and from SCHWARZ's (1937) lists of assigned material that most of the surviving Olduvai Bovidae in Munich belong to the Alcelaphini. SCHWARZ thought that there were four species among the horn cores and cranial material of this tribe. Hence it is unlikely that as much postcranial material as he claimed is really from *Connochaetes*, especially if the presence of a *Connochaetes* in addition to *Megalotragus kattwinkeli* is doubtful. It is impossible now to recover information about the associations of fossils collected in 1913, but there must be a suspicion that many of the alcelaphine postcranial elements were from a fossilised herd of *Megalotragus kattwinkeli*.

The discovery by the present authors of the availability from RECK (1925) of the name *Rhynotragus semiticus* has the unfortunate consequences that *Rhynotragus* becomes the senior generic synonym for *Megalotragus* VAN HOEPEN 1932, and *Rhynotragus semiticus* the senior specific synonym for *Megalotragus kattwinkeli* (SCHWARZ 1932). *Megalotragus* and *M. kattwinkeli* have both been much used in recent years (e.g. KLEIN 1972, GENTRY & GENTRY

1978, VRBA 1985, HARRIS 1991, KLEIN & CRUZ-URIBE 1991). Accordingly the International Commission on Zoological Nomenclature is being petitioned by A.W. & A. GENTRY to conserve the usage of the familiar names *Megalotragus* and *M. kattwinkeli*. A further decision is needed from the Commission as to whether the London neotype or the rediscovered holotype of *Megalotragus kattwinkeli* shall function as future name-bearing type of that species. The London neotype is a more complete specimen of known stratigraphic provenance. Against this the Munich holotype has a very considerable historic interest and it would be satisfying to restore its name-bearing status. Moreover, if at a future date, our assertion of the conspecificity of neotype and holotype were challenged, and if the holotype were again the name bearer, then *kattwinkeli* would continue to be the name of the species which SCHWARZ had founded.



Fig. 3: Holotype face of *Rhynotragus semiticus*, VII-1111, with left horn core VI-306 attached to it, in (A) lateral and (B) dorsal views. Scale = 10 cm.

GENTRY & GENTRY (1978: 356, 360, figs. 21, 22) stressed the large size, simple occlusal pattern of the cheek teeth, and lengthened limb bones of *Megalotragus kattwinkeli* in comparison with contemporaneous *Connochaetes*. Their assertion applied particularly to the material of *Megalotragus kattwinkeli* from middle and upper Bed II at Olduvai. It remains to be ascertained how far these *Megalotragus/Connochaetes* differences are maintained at other time periods or localities and between other species of the genera.

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