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REVISED CLASSIFICATION FOR *MAKAPANIA BROOMI* WELLS AND COOKE (BOVIDAE, MAMMALIA)

by

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ABSTRACT

Details of skull morphology, particularly of the basioccipital, show that *Makapania broomi* from the Makapansgat Limeworks Quarry, Transvaal belongs to the tribe Ovibovini, and is very like *Megalovis latifrons* Schaub, best known from the later Villafranchian of Senèze, France. The Ovibovini have only two living species, but in the Pliocene and early Pleistocene they must have been more widespread than hitherto suspected. *Makapania broomi* is the first clear record from Africa south of the Sahara of a fossil member of the Eurasian and North American subfamily Caprinae.

Wells & Cooke (1956: 26-33, Figs. 13-16) described an extinct antelope genus and species *Makapania broomi* from the Limeworks Quarry, Makapansgat, Potgietersrus, South Africa. It was plentifully preserved, and there were associations between horn cores, upper teeth and lower teeth. Wells and Cooke noted the main characters of medium to large size, horn cores inserted just behind the orbits and passing almost directly outwards from the side of the skull, teeth hypsodont, and rather V-shaped lobes medially on the upper molars and laterally on the lowers. They considered that *Makapania* belonged to the tribe Alcelaphini, although clearly a rather unusual member of that tribe.

Having seen more material of *Makapania broomi* than was available at the time Wells and Cooke were working, I believe it to be an ovibovine. The tribe Ovibovini, hitherto known only from Eurasia and North America, contains two living species, the muskox *Ovibos moschatus* (Zimmermann) and the takin *Budorcas taxicolor* Hodgson. It also contains their fossil relatives among which the Chinese *Boopsis sinensis* Teilhard de Chardin (1936) and *Lyrocerus satan* Teilhard de Chardin and Trassaert (1938) are probably early stages in the evolution of the muskox and takin respectively. *Megalovis latifrons* Schaub (1923: 292, Fig. 5; 1943: 281, Figs. 5 & 6) from the Villafranchian of Senèze, France is related to later ovibovines, but perhaps not ancestral to them. There are two Pliocene groups of fossil ovibovines. One contains *Urmiatherium* Rodler from Maragha (northern Iran) and China, the small *Parurmiatherium* Sickenberg from Samos, *Plesiaddax* Schlosser from China and *Tsaidamotherium* Bohlin from China, all with more specialized horn cores than the Pleistocene and living species. A second extinct group contains only *Criotherium* Major from Samos and, as I believe, *Palaeoreas* Gaudry from Samos and Pikermi and Veles in Greece, both with spiralled horn cores but otherwise not very advanced.

The Villafranchian *Megalovis latifrons* is the form with which *Makapania broomi* most closely agrees. Schaub (1923) believed that *Megalovis* was related to sheep. However, it also agrees with Ovibovini in its large size, horn cores inserted behind the orbits, short braincase, not very complicated mid-frontals suture, small supraorbital pits, infraorbital foramen placed posteriorly over the back of P^3, small auditory bulla, absence of basal pillars on molar teeth, upper molars rather long relative to width, with fairly pronounced styles and rounded medial lobes, P^2 remaining large, mandible not markedly deep below the molars, and paraconid of P_4 fused to metaconid. It further agrees well with *Ovibos moschatus* and *Budorcas taxicolor* in the very wide divergence of its horn cores, a ridge from the base of the horn core to the top back of the orbit, fairly well projecting orbital rims, supraorbital pits set widely apart, and an indication of concavities postero-laterally to the anterior tuberosities on the basioccipital. In addition the dorso-ventral compression of the horn cores is like *Ovibos*, and on the basioccipital the quite sharp upstanding ridges on the posterior tuberosities and the central longitudinal groove constricted between the anterior tuberosities are like *Budorcas*. In my opinion any similarities of *Megalovis* to sheep arise from Ovibovini being related to sheep within the Caprinae of Simpsons's (1945) classification of mammals.

The actual fossil of *Makapania broomi* which first suggested a relationship to Ovibovini was M.2793 in the Bernard Price Institute for Palaeontological Research, Johannesburg. This is a skull fragment consisting of part of the frontals, part of the left side of the braincase, and the basioccipital. The basioccipital (Fig. 1) is short, with raised areas close together anteriorly, hollows postero-laterally to these raised areas, and quite bulky posterior tuberosities with a hollow between them which widens towards the rear. The raised areas are in part of the position occupied by the larger and

better defined anterior tuberosities of other bovid basioccipitals, and I shall here call them anterior tuberosities. The basioccipital of M.2793 differs from that of *Megalovis latifrons* in its closer anterior tuberosities, lack of a central longitudinal groove between them, and less upstanding ridged posterior tuberosities. But this is all extremely similar to the basioccipital of *Ovibos* (Fig. 2), and such a pattern can be found in no other bovid. M.2793 differs from Alcelaphini by the triangular rather than quadrangular shape of the basioccipital, and in having no central groove running forwards for the whole length of the bone; in fact, forward of the posterior tuberosities, the centre of the bone is raised between the paired hollows.

Other *Makapania broomi* pieces with basioccipitals, M.555 and M.2935, have less obvious hollows behind the anterior raised areas, but they do show the posteriorly widening valley between the posterior tuberosities and a tendency to high central parts.

M.2793 and M.555 both show a ridge running from the lowest point of the horn base to the nearest part of the orbital rim (Fig. 3); such a ridge is also seen in *Megalovis latifrons* (Schaub 1923, Fig. 5).

M.1024 is the base of a right horn core and the orbit of *Makapania broomi*. The anterior part of the zygomatic arch beneath the orbit is not deepened as it is in Alcelaphini.

When I was able to see the examples of *Megalovis latifrons* in Basle and Paris, I found other impressive similarities to *Makapania broomi*: the wide insertions of the horn cores just behind the orbits, their transverse emergence, the gentle ascent towards the tips, absence of transverse ridges on the horn cores, the short braincase well angled on the facial axis, the extent of the projection of the dorsal parts of the orbital rims, the small localized preorbital fossae, fairly hypsodont teeth, absence of basal pillars, poor to moderate development of styles and ribs between the styles, indentations into the walls of the central cavities of the upper molars, fused paraconid and metaconid on P_4 closing the anterior part of the medial wall, and the mandible not markedly deep below the molar row. Some of these resemblances of *Makapania broomi* to *Megalovis latifrons* are also found in the Alcelaphini, and one might even draw strained parallels with *Connochaetes*. However, such distinctive alcelaphine characters as the rounding of the medial lobes of the upper molars and the lateral lobes of the lowers, the curvature of the entire upper tooth row, and the deep mandibles are absent. Also the median indentation at the back of the palate in *Makapania broomi* is behind the level of the lateral ones, quite unlike Alcelaphini and like *Budorcas* and *Ovibos* although the state of this character is not known in *Megalovis latifrons*.

Differences of *Makapania broomi* from *Megalovis latifrons* are few: longer horn cores, frontals raised between the horn bases, horn cores positioned with their greatest diameter dorso-ventrally in side view instead of antero-posterior, and more of a V shape to the medial lobes of their upper molars and to the lateral lobes of their lowers. Moreover, the raising of the frontals between the horn bases and the position of the longest diameter of the horn bases are similar to the condition found in *Budorcas*.

These morphological similarities of their skulls and dentitions show that *Makapania broomi*, *Megalovis latifrons*, and the living takin and muskox can be taken as quite a neatly defined group of Ovibovini. I shall not here make a prolonged investigation of whether their existing Linnaean names are the best for expressing their relationships; I note only that *Megalovis latifrons* is the closest to *Makapania broomi*.

Megalovis latifrons occurs at European Villafranchian sites other than Senèze, and its nomenclature is tangled like most other mammalian species. The cranium of *Deperetia ardea* from Senèze (Schaub 1923, Fig. 3) is very probably conspecific with the *Megalovis latifrons* fossils from the same site. The skull of *Pliotragus ardeus* from Olténie in Romania (Bolomey 1965, Figs. 1-3) is probably also conspecific. (Kretzoi 1941: 349 had changed the generic name *Deperetia* to *Pliotragus*). It is even possible that this same species includes the original maxilla of *Antilope ardea* Depéret (1884: 252, pl. 8, Fig. 3) from Etouaires, France, in which case a name change might be needed. I shall continue to use *Megalovis latifrons* here. *Hesperoceras merlae* Villalta and Crusafont Pairo (1955: 431, Figs. 1-3) must be at least a closely related form, if not actually conspecific. Finally *Soergelia elizabethae* Schaub (1951: 376, pls. 11, 12) which occurs later in the middle Pleistocene of Süssenborn, Germany, could be a species descended from *Megalovis latifrons*.

The sites from which *Megalovis latifrons* and its synonyms have been published occur through the whole of the Villafranchian according to Heintz (1969) and Kurtén (1963). A horn core, L.7-82, which could belong to *Makapania*, was found below tuff G at Omo, southern Ethiopia in 1968, and is the only possible occurrence of the genus away from the Makapansgat Limeworks Quarry (Fig. 4). According to the dating of lower and higher tuffs in the Omo sequence, this horn core would be aged between 1,8 and 2,6 million years (Howell 1968: 569). This date, together with the time of occurrence in Europe of the genus most closely related to *Makapania*, offer slender indications of the age of Makapansgat Limeworks Quarry.

As interesting as such very tentative indications of a date for the Makapansgat Limeworks fauna is the zoogeographical question of the occurrence of Caprinae in Africa. At the present day the only caprines in Africa are *Capra (Ammotragus) lervia* (Pallas), *Capra nubiana* F. Cuvier and *Capra walie* Rüppell, but only the last in the mountains of Ethiopia is even marginally in the Ethiopian rather than the Palaearctic realm. In the

past various African fossils have been wrongly or doubtfully identified as Caprinae or Caprini, e.g. the Olduvai *Pultiphagonides* Hopwood (see Wells & Cooke 1956: 26, 33 for comment on this), and some other Olduvai fossils (see Leakey 1965: 68). It seems that whatever may ultimately be decided about such questionable fossils, there is now definite evidence of a member of the Ovibovini in subfamily Caprinae in Africa a very long way south of the Palaearctic. The evolutionary problem of how it came to be there is still not solved, but it is certain that in the Pliocene the Ovibovini were more widespread and they can now be regarded as a relict group. Accepting that Caprinae have occurred in Africa, one can question again the tribal affinity of the South African vaal rhebbok, *Pelea capreolus* (Forster), long considered a member of the Reduncini but now recognized as clearly not in that tribe (Roberts 1937: 86, Wells 1967: 100, Gentry 1970: 314). Could it be fairly closely related to goats or to the chamois, *Rupicapra rupicapra* (Linnaeus), despite its geographical isolation from them?

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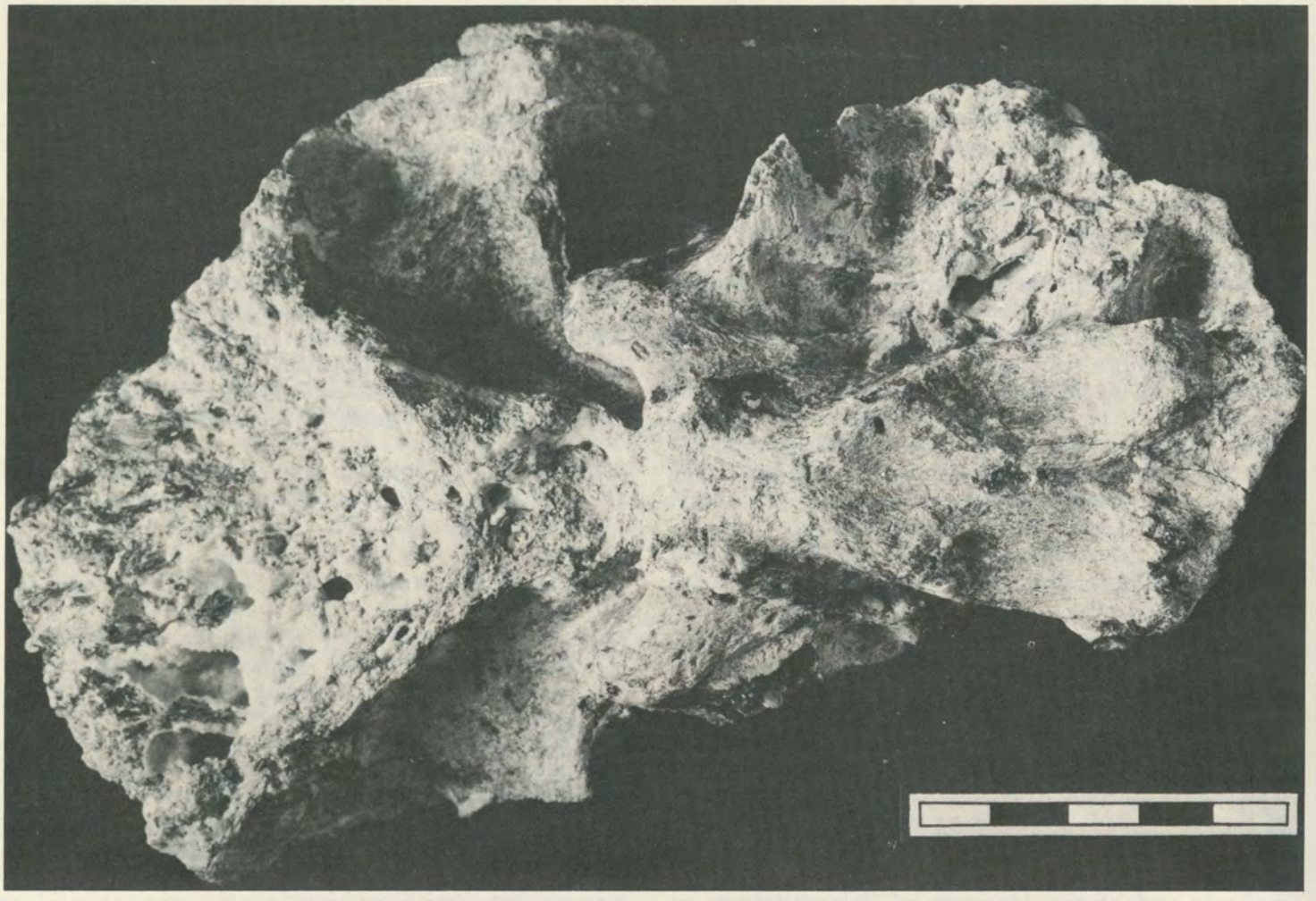




Fig. 1. Basioccipital of skull fragment M.2793 of *Makapania broomi.* The anterior side is to the left. The scale is in centimetres. Top.

Fig. 2. Basioccipital of a muskox, *Ovibos moschatus,* in the British Museum (Natural History), No. 612b. The scale represents 20 mm. Bottom.



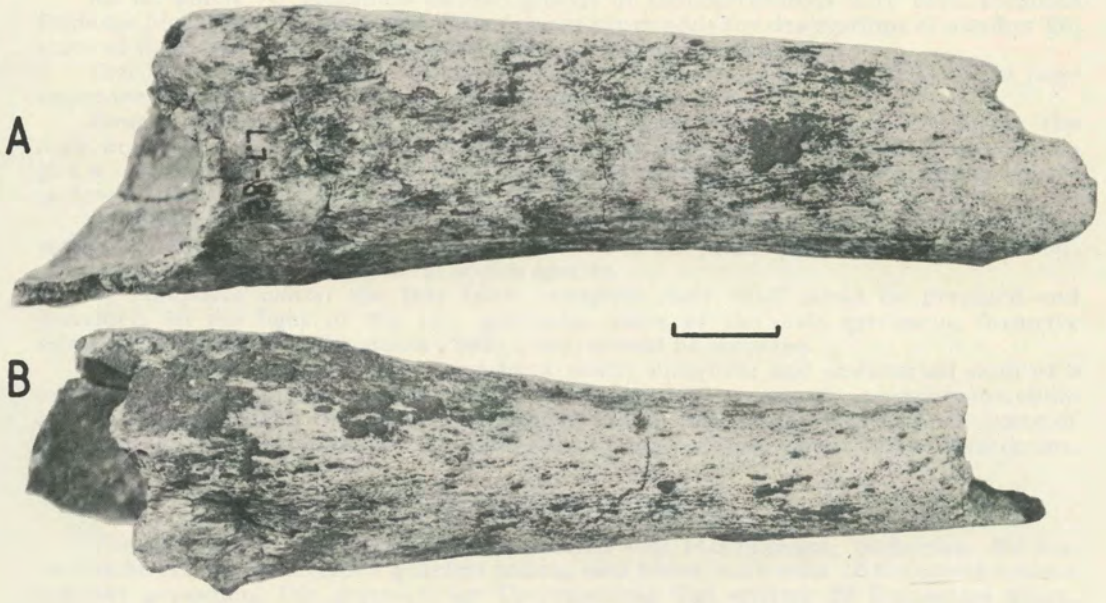


Fig. 3. Lateral view of skull fragment M.2793 of *Makapania broomi*. The anterior side is to the bottom left, and the scale in centimetres. The arrow indicates the ridge from the base of the horn core to the orbit rim.

Fig. 4. Horn core L.7-82 from below tuff G at Omo, Ethiopia. The scale represents 20 mm. The view A is probably ventral, and B is probably anterior.