

An Ovibovine (Mammalia, Bovidae) from the Neogene of Stratzing, Austria

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(With 5 text-figures)

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Abstract

A frontlet with horn cores and cranial roof from Stratzing, Austria, is identified as a member of the Ovibovini (Bovidae) belonging to the extinct genus *Pliotragus* KRETZOI, 1941. Hitherto *Pliotragus* has been known from the Late Pliocene and Early Pleistocene of Europe, but the main mammal fauna from Stratzing is thought to have a Late Miocene date. The most likely explanation for this discrepancy would be for the frontlet to have a different lithostratigraphic position from the main mammal fauna.

Zusammenfassung

Ein Schädelrest von Stratzing (Österreich), bestehend aus Frontalia mit Hornzapfen und Parietalia, konnte der fossilen Gattung *Pliotragus* KRETZOI, 1941 zugeordnet und damit als Vertreter der Ovibovini (Bovidae) identifiziert werden. *Pliotragus* wurde bisher vom späten Pliozän bis frühen Pleistozän Europas nachgewiesen, der Großteil der Säugetierfauna von die Fundstelle Stratzing wird jedoch in das Obermiozän eingestuft. Die Altersunterschiede aus verschiedenen lithostratigraphischen Positionen resultieren.

Introduction

During a study visit to the Natural History Museum, Vienna, in spring 1995, the author was requested by the late Professor Helmuth ZAPFE to prepare a report for publication on a puzzling partial skull of a bovid from Stratzing (Naturhistorisches Museum Wien, 1999z0080/0000). The skull part consists of right and left horn cores, much of the cranial roof and the topmost part of the occipital. Nothing of the orbits survives.

The fossil comes from Stratzing about six kilometres north of Krems a.d. Donau in the molasse zone of Lower Austria. Lithostratigraphically the sediments belong to the Hollabrunn-Mistelbach-Formation, which is characterised by sands and gravels of fluvial origin. This unit extends from the "Wachau" in WSW - ENE direction to the "Weinviertel" and the time of deposition ranges from the Early to the Late Pannonian. But, rare local occurrences of loess-deposits even point to a Pliocene age (ROETZEL, MANDIC & STEININGER 1999: 44, 50-51). THENIUS (1972) described a skull of the pig *Microstonyx antiquus* (KAUP, 1833) from the same locality and gave a discussion of the stratigraphy

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and age of the deposits. They consist of remnants of river gravels which are more extensive to the east in the vicinity of Hollabrunn. Identifications of ostracods, molluscs and several mammals allow a Late Miocene age to be assigned. FORTELIUS & al. (1996: 377) used the name *Hippopotamodon major* (GERVAIS, 1853) for the pig and referred Stratzing to the zone "MN10?". No evidence has been preserved concerning the original lithostratigraphic position of the *Pliotragus* skull within the gravels at Stratzing, and it is difficult to accept that it could be time-equivalent with the main mammal fauna. Thus, it probably comes from a higher stratigraphical level.

Description

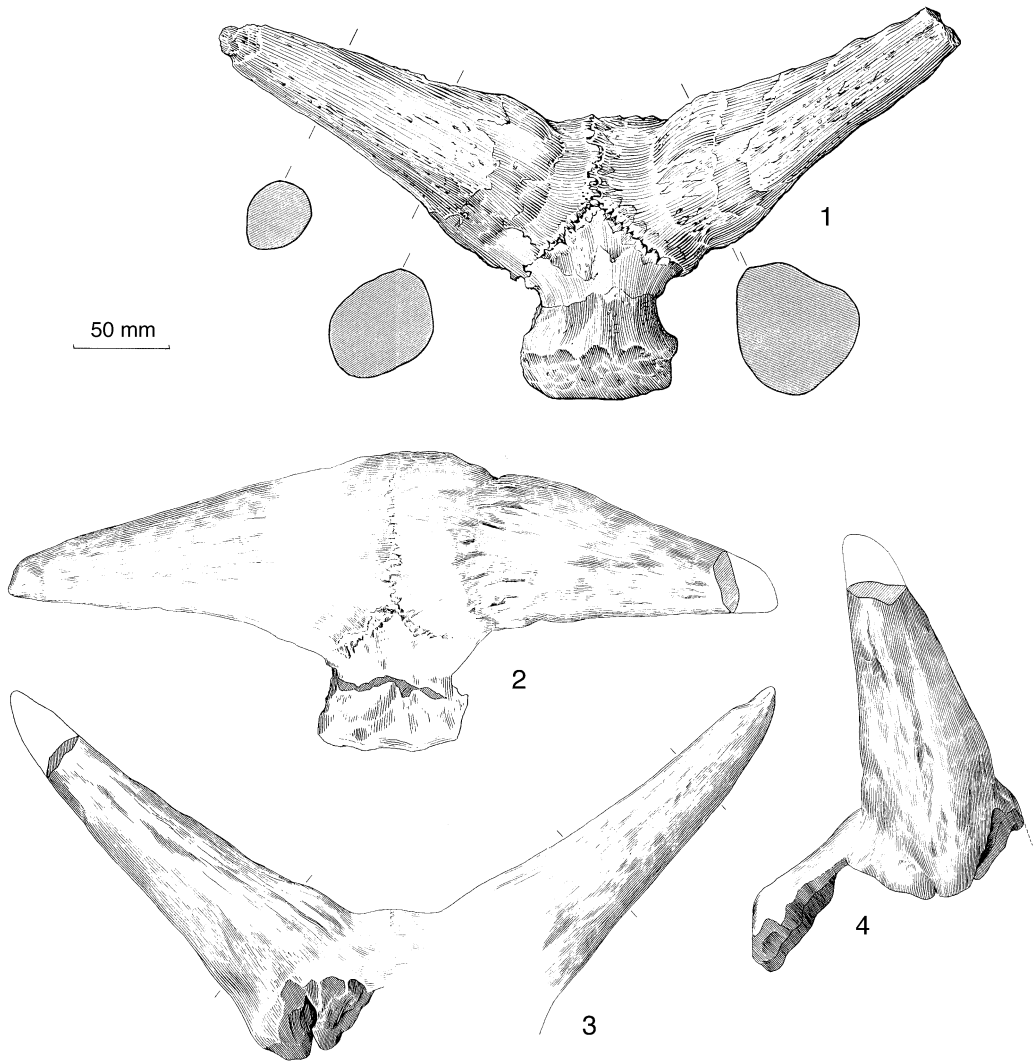
Some restoration in plaster has been carried out on both horn cores of the fossil bovid, but there is no reason to believe that their morphology has been altered thereby. The middle of the parietal has a band of plaster across part of its dorsal surface, but in ventral view the join between anterior and posterior parts is good. None of the original posterior surface of the occipital appears to have been preserved.

The fossil (Figs. 1-4) belongs to a fairly large-sized species with horn cores of short to moderate length. The horn cores are not compressed. In their proximal parts they have an almost triangular cross-section with an anterodorsal corner and with indistinct anterior, posterodorsal and posteroventral surfaces. Distally the triangularity becomes less pronounced and there is an approach to anterior and posterior keels. The insertions of the horn cores are wide apart. The horn cores emerge transversely in dorsal view and slightly upwards in anterior view. In dorsal view the front edge is slightly convex and the back edge slightly concave, but the course of the horn core as a whole is essentially straight. In anterior view the divergence does not alter distally. The horn cores thus lack forward, backward, upward or downward curvature. Sinuses exist within the frontals, the mid-frontals suture is moderately complicated and placed upon a slight longitudinal ridge, and the parietofrontals suture is forwardly indented in its centre. The braincase roof is short and considerably sloped.

The anteroposterior and dorsoventral diameters at the base of the horn core are 70.0 and 64.0 mm, the complete length along the dorsal surface would have been circa 200 mm, and the distance across the frontals between the mediodorsal bases of the horn cores is circa 56.0 mm.

Comparisons

Traditionally the tribe Ovibovini of the subfamily Caprinae has been held to contain two relict living species: 1) the muskox *Ovibos moschatus* (ZIMMERMANN, 1780) now confined to the far north of North America but with a wide Pleistocene and earlier Holocene distribution across northern Eurasia (CREGUT-BONNOURE 1984, STUART 1991); 2) the takin *Budorcas taxicolor* HODGSON, 1850 of Tibet and China. However the two species differ in many characters, suggesting at least a long evolutionary history independent of one another (GENTRY 1992) or even that *Budorcas* should be excluded from the Ovibovini (BOUVRAIN & BONIS 1984). There are few fossil species related to *Budorcas* (GENTRY, 1996), but many related to *Ovibos* BLAINVILLE, 1816, most of them from the later Pliocene and Pleistocene.



Figs. 1-4: Frontlet and cranial roof of *Pliotragus* sp. from Stratzing – NHMWien 1999z0080/0000: (1) in posterodorsal view, (2) dorsal view, (3) anterior view and (4) right lateral view.

Ovibos horn cores have bases which are much flattened and expand across the top of the frontals so as almost to meet in the mid-line. The horn cores turn downwards against the sides of the braincase and their anteroposterior diameter diminishes rapidly. Their tips then turn forwards and upwards. The basal flattening is less pronounced in females, and in juveniles the horn insertions are at first situated widely apart.

Fossil species related to *Ovibos* are as follows, starting with its closest relatives.

- 1) *Praeovibos priscus* STAUDINGER, 1908 and other species of this genus from Eurasia and northern North America; Early and Middle Pleistocene. *Praeovibos* STAUDINGER,

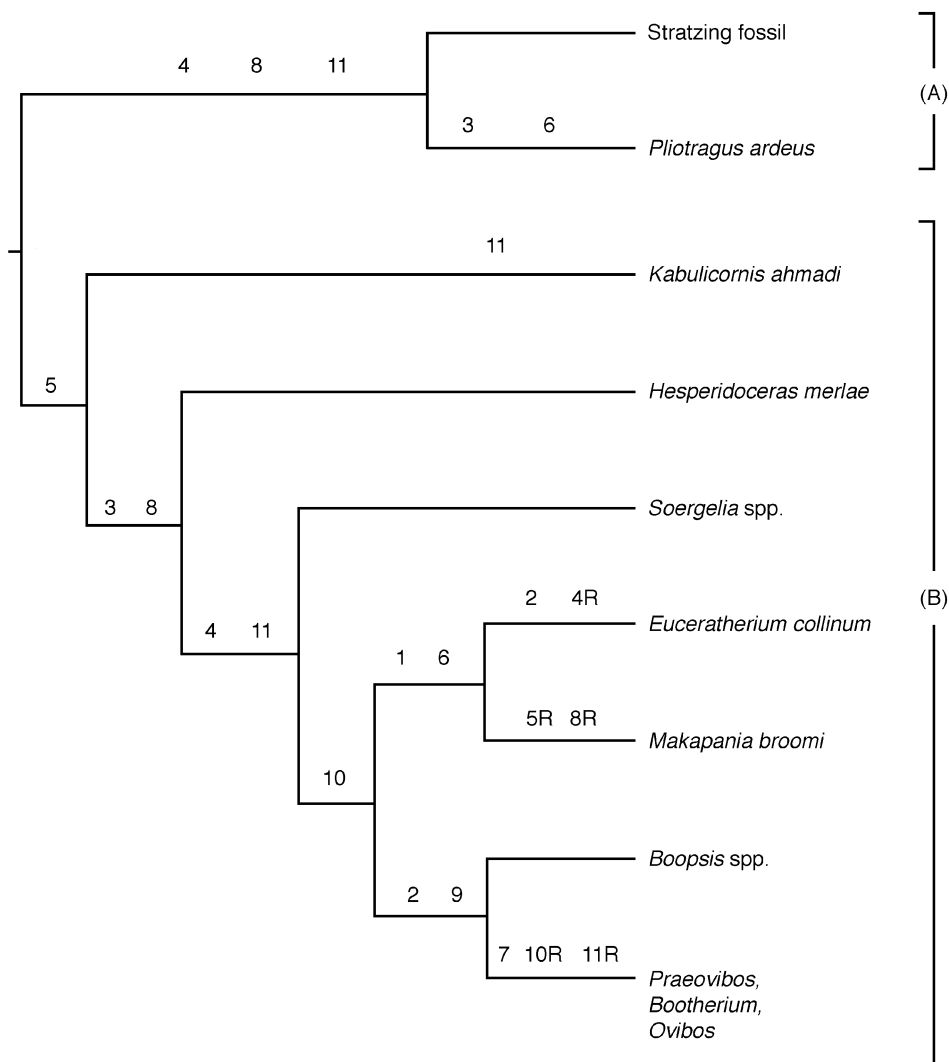


Fig. 5: Cladistic dendrogram for horn core and cranial roof characters in some Ovibovini. The numbers indicate advanced states of characters 1-11 on Table 1, R = character reversals.

1908 is very like *Ovibos* but has horn core bases less expanded and more raised above the frontals' surface than in male *O. moschatus*. Distal to their bases the horn cores are less tightly tucked in against the sides of the skull. (MCDONALD & al. 1991).

2) *Bootherium bombifrons* (HARLAN, 1825), including *Symbos cavifrons* (LEIDY, 1852a,b) from North America; Middle and Late Pleistocene. *Bootherium* LEIDY, 1852 is again recognisably close to *Ovibos*. Its main differences from *Ovibos* are the median fusion of the expanded horn core bases on the top of skulls of males, and the horn cores less tucked in against the sides of the skull (MCDONALD & RAY 1989).

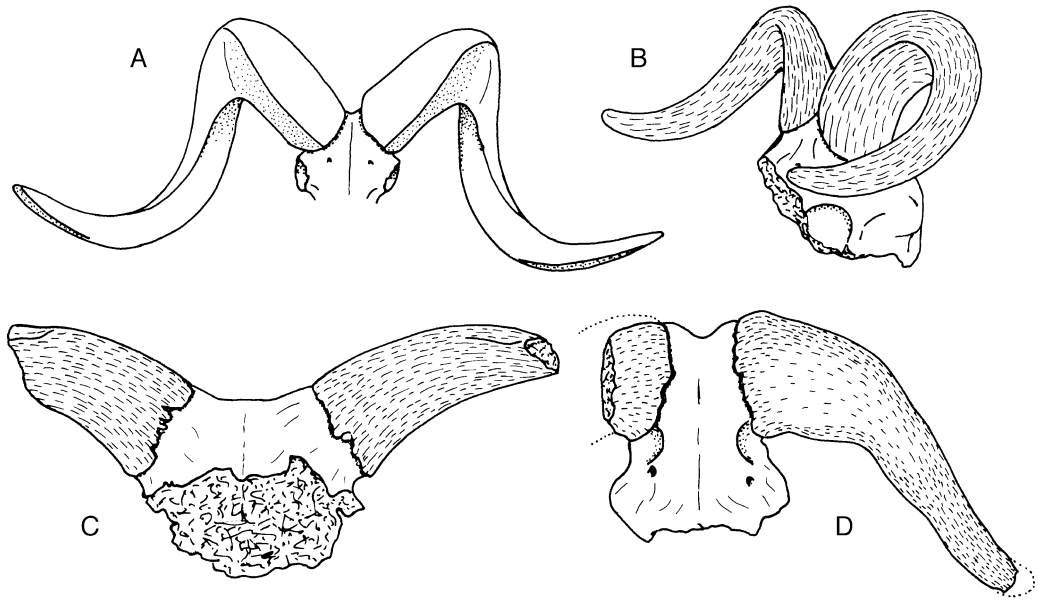


Fig. 6: Horn curvature in sheep and some extinct ovibovines: (A) extant *Ovis ammon* with sheaths on horn cores in anterodorsal view; (B) *Euceratherium collinum* in anterolateral view; (C) *Soergelia elisabethae* in anterior view; (D) *Boopsis breviceps* in dorsal view. Horns of sheep curve backwards in their basal portion, those of the ovibovines do not. Not to scale. After LYDEKKER, HIBBARD, SCHAUB and TEILHARD DE CHARDIN & TRASSAERT.

- 3) *Boopsis sinensis* TEILHARD DE CHARDIN, 1936 and *Boopsis breviceps* TEILHARD DE CHARDIN & TRASSAERT, 1938 from China; Middle Pleistocene (*B. sinensis*) and later Pliocene (*B. breviceps*), the latter from the Yushe Basin zone III – see QIU (1989: table 1). *Boopsis* TEILHARD DE CHARDIN, 1936 horn cores curve upwards and predominantly outwards from their insertions (Fig. 6D) and can be quite long. The distal parts finally curve a little forward. The horn cores thus have a similar curvature to *Praeovibos* and *Bootherium* but without any downturning.
- 4) *Euceratherium collinum* FURLONG & SINCLAIR, 1904 from North America; Pleistocene. *Euceratherium* FURLONG & SINCLAIR, 1904 horn cores are similar to *Boopsis*. They curve upwards, outwards and then forwards (Fig. 6B). They do not show any abrupt narrowing of cross-sectional diameter such as can be seen in the ovibovines listed above. They are variable in the extent to which the bases are raised on the pedicels, in the initial degree of divergence, and in the inclination of the basal part of the horn cores in side view. *Euceratherium* had a more southerly and westerly distribution in North America than did *Ovibos* or *Bootherium* (CARRANZA-CASTANEDA & MILLER 1987; KURTEN & ANDERSON 1980).
- 5) *Soergelia elisabethae* SCHAUB, 1951 and other species of this genus from Eurasia, ?North America; Early to Middle Pleistocene. *Soergelia* SCHAUB, 1951 has shorter horn cores than in *Euceratherium* but their curvature is very similar (Fig. 6C) (MOYA SOLA 1987; KURTEN & ANDERSON 1980; SHER 1987).

- 6) *Hesperidoceras merlae* VILLALTA & CRUSAFONT PAIRO, 1956 from Spain; Late Pliocene (Lower/Middle Villafranchian), the type locality, Villaroya, being likely to date from 2.0 - 2.5 Ma (CALVO & al. 1993: fig. 2). *Hesperidoceras* VILLALTA & CRUSAFONT PAIRO, 1956 has fairly short horn cores diverging somewhat and curving forwards mostly in one dimension. The slope of the cranial roof is not notably steep.
- 7) *Kabulicornis ahmadi* HEINTZ & THOMAS, 1981 from Afghanistan; thought to be of Early Pliocene age (BRUNET, HEINTZ & SEN 1981). *Kabulicornis* HEINTZ & THOMAS, 1981 horn cores curve upwards and forwards from insertions which are close together. The horn cores are less divergent than in *H. merlae*. The longest cross-sectional axis of the horn core bases is oriented from anteromedial to posterolateral, which is at right angles to the orientation in *H. merlae*.
- 8) *Pliotragus ardeus* (DÉPÉRET, 1884) and *Megalovis latifrons* SCHAUB, 1923 from Europe; Late Pliocene to Early Pleistocene. Both these species have straight horn cores emerging almost transversely in dorsal view. Insertions are fairly wide apart. The horn cores of *Megalovis latifrons* are more inclined and less upright in anterior view than in the earlier *Pliotragus ardeus*, but there is little other difference between them. Both show divergence lessening distally in anterior view. DUVERNOIS & GUERIN (1989) synonymise *Hesperidoceras merlae* with the senior *Pliotragus ardeus*. *Pliotragus* KRETZOI, 1941 is a replacement name for the preoccupied *Deperetia* SCHAUB, 1923. If the genera were united, *Megalovis* SCHAUB, 1923 would have to be used.
- 9) *Makapania broomi* WELLS & COOKE, 1956 from South Africa; Late Pliocene, approximately 2.5 - 2.8 Ma. *Makapania* WELLS & COOKE, 1956 differs from *Megalovis latifrons* by having longer and more divergent horn cores in which the limited degree of compression is anteroposterior rather than dorsoventral. The frontals between the horn insertions are also more elevated. The basioccipital is similar to that of *Ovibos* (GENTRY, 1970).

The morphology of the Stratzing fossil calls to mind some of the extinct Ovibovini just listed. Characters commonly but not universally found in this group are horn cores of short to moderate length, diameters diminishing rapidly from base to tip, strong divergence and wide insertions of the horn cores, forward curvature of the horn cores, postorbital horn insertions, and steeply sloping cranial roof.

A first impression of the whole group might be that the earlier species and genera show either divergent horn cores with some lessening of divergence distally (*Pliotragus*) or horn cores curving upwards and forwards (*Hesperidoceras*). Within the second subgroup *Euceratherium* developed in (or migrated to) North America, while the shorter horned *Soergelia* is a close relative in Eurasia. *Boopsis* is the first sign of transition from a *Euceratherium*-like ancestry towards the more cold-adapted northern group culminating in the various Pleistocene muskoxen and the relict living *Ovibos moschatus*. *Makapania*, far to the south in Africa, was thought to be close to *Megalovis* by GENTRY (1970), but its basioccipital is surprisingly similar to a modern muskox. *Kabulicornis* is the most doubtful of the listed genera as a candidate for ovibovine status.

Megalovis horn cores may show slightly concave front edges and slightly convex back edges (SCHAUB 1944: fig.6), but it is not certain that the later Ovibovini with forwardly curved horn cores evolved from ancestors with straight divergent horn cores. If this really

Tab. 1: Data matrix for 11 characters (rows) in 9 taxa (columns). Taxa are listed in the same order as in Fig. 5 and by the initial letters of their names. The characters used are as follows; the state described or the second alternative is considered advanced.

1. Horn cores of short-moderate length/ long.
2. Horn cores compressed (ratio of least to greatest basal diameters less than 75%).
3. Horn cores inserted partly above/ well behind level of orbits. Sometimes this is conjectural.
4. Horn cores inserted widely apart and with strong divergence from the base. Wide insertions and strong divergence often coincide and are here taken as a single character.
5. Horn cores curved forwards. This entails the anterior edge being concave in profile.
6. Horn core divergence lessens distally. A good character for *Pliotragus* but very slight in *Makapania*.
7. Horn cores curve downwards. Characterises the latest and northernmost genera and species.
8. Plane of longest cross-sectional basal diameter of horn cores. In all but two taxa the longest diameter runs anteroposteriorly, so that if significant compression existed it would be dorso-ventral or mediolateral. This is accepted as characteristic of the group, but the validity or polarity of the character is not obvious.
9. Distal zones of horn cores with a sharp reduction in cross-sectional diameter. Linked with ultimately plate-like expansion of the horn bases across the top of the skull.
10. Frontals raised between horn core bases. Possibly a significant character.
11. Braincase roof steeply sloping. The great expansion of horn bases from *Praeovibos* onwards leads to a secondarily horizontal cranial roof. The cladogram would have only 22 steps if the apparent condition in *Hesperidoceras* (VILLALTA & CRUSAFONT PAIRO 1956, fig. 3) were treated as a reversal, but this was considered unlikely.

	SF	PA	KA	HM	SS	EC	MB	BS	PBO
1	0	0	0	0	0	1	1	0	0
2	0	0	0	0	0	1	0	1	1
3	0	1	0	1	1	1	1	1	1
4	1	1	0	0	1	0	1	1	1
5	0	0	1	1	1	1	0	1	1
6	0	1	0	0	0	1	1	0	0
7	0	0	0	0	0	0	0	0	1
8	1	1	0	1	1	1	0	1	1
9	0	0	0	0	0	0	0	1	1
10	0	0	0	0	0	1	1	1	0
11	1	1	1	0	1	1	1	1	0

has been the direction of their evolution, it would differ from that of sheep (*Ovis* or its ancestor) which separated, presumably from goats (*Capra* or its ancestor), through acquiring strongly divergent and forwardly curving horn cores from an originally backwardly curving condition. Sheep horn cores differ from the ovibovines discussed above in retaining a backward component to the curvature immediately above the base of their horn cores (Fig. 6A).

A more comprehensive analysis will not be presented here. It is only necessary to consider characters of the horn cores and cranial roof to assess as far as possible the relationships of the Stratzing fossil. A cladistic diagram may be drawn up for a restricted range of characters (Table 1, Fig. 5) using a primitive non-boselaphine bovid such as the Middle Miocene *Tethytragus* AZANZA & MORALES, 1994 as a model of a likely ancestral state.

The resulting diagram has 23 steps and a consistency index of 0.43. It shows a division between *Pliotragus ardeus* and the Stratzing fossil on the one hand (group A) and *Hesperidoceras* and its allies on the other (group B) in which the horn cores acquire a degree of forward curvature. The cladogram shows a limited concordance with what is known of the geological ages of the species. Hitherto the two earliest forms have been *Kabulicornis* and *Hesperidoceras*, and these two are indeed the most primitive members of group B. *Makapania* is placed within a clade embracing the considerably younger *Euceratherium* and *Ovibos*, but the alternative of placing it with *Pliotragus* (favoured by GENTRY 1970) would add only one more step to the cladogram. The cladogram can do no more than illustrate the possibilities for relationships among the ten taxa compared, and it would be foolish to accept it as conclusive on such a limited coverage of characters.

Conclusions

By what is known of its morphology, the Stratzing fossil can best be named as *Pliotragus* sp. Its main difference from *Pliotragus ardeus* or *Megalovis latifrons* is that the horn cores' divergence does not lessen distally. The problem remains that it would be anomalous in a Late Miocene locality by being very much older than other species to which it has any resemblance. The Turolian genera *Urmiatherium* and *Criotherium* have been regarded as Ovibovini but this seems increasingly unlikely (GENTRY & al. 1999), and, in any case, their horn cores show torsion or its remnants and the back edges of their insertions lie far posteriorly almost above the occipital surface, characters unlike *Pliotragus* sp. at Stratzing. A Vallesian genus less easily excluded from the Ovibovini is *Mesembriacerus* BOUVRAIN, 1975, fully described by BOUVRAIN & BONIS (1984), but this has long, slender horn cores showing little divergence and passing backwards at a low inclination. Its cranial roof does not slope. Once again there is no resemblance to the Stratzing *Pliotragus* sp.

Further investigations of the Stratzing locality are desirable to assess whether the postulation of a Pliocene level there can be corroborated. Otherwise we can only await an alternative interpretation of ovibovine morphology and phylogeny.

Acknowledgments

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