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Phylogenetic analysis of the tribe Bovini (Mammalia: Artiodactyla)

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A matrix of 57 (mainly cranial) characters and 32 taxa of fossil and Recent Bovini (buffaloes, bison and cattle) has been analysed using the parsimony program HENNIG86. Among the best established results are the exclusion of *Parabos*, polyphyly of *Leptobos*, monophyly of the *Bos sensu lato* + buffaloes group (a clade including all Recent Bovini), probable monophyly of the Bubalina and Syncerina, and the close relationship between bison and yak. Some other interesting questions raised include the apparent absence of a close link between Pliocene African bovines (except "*Leptobos*" *syrticus*) and later African buffaloes, and the possible monophyly of *Pelorovis oldowayensis* + *Bos sensu lato*.

KEY WORDS:—Mammalia – Artiodactyla – Bovidae – cladistics – systematics.

CONTENTS

INTRODUCTION

The tribe Bovini today includes the largest Bovidae—oxen, bison, yak and buffaloes. Its living members are as follows:

Bos taurus Linnaeus, 1758, the ox, domestic form of the extinct wild auroch, *Bos primigenius* Bojanus, 1827;

Bibos javanicus (d'Alton, 1823), the banteng of the Sundanese Islands;

Bibos gaurus (Smith, 1827), the gaur of India, of which *B. frontalis* is the domestic form; both *B. javanicus* and *B. gaurus* are known as fossils in the Pleistocene of south-east Asia;

Bibos sauveli Urbain, 1937 the kouprey of Cambodia; these first four species are often united under *Bos sensu lato*;

Bison spp., the bison of America and Eurasia. American and European fossil forms are closely related (even though they have sometimes been given distinct

generic names) and will not be treated separately, but a supposed early representative from China will be discussed below;

Poephagus mutus (Przewalski, 1823), the Tibetan yak;

Bubalus arnee Kerr, 1792, the water buffalo of India;

Anoa depressicornis (Smith, 1827), the smaller buffalo of Sulawesi;

Syncerus caffer (Sparrman, 1779), the African buffalo, with its smaller subspecies *S. caffer nanus*.

Most of the evolution of the tribe occurred in the Old World. The earliest bovine known is from the Mio-Pliocene of Lukeino (Thomas, 1980) and there are several genera in the Pliocene of Africa and Eurasia which are supposed to have arisen from Boselaphini. Thus, the tribe appears slightly later than Reduncini and Tragelaphini, but earlier than the Alcelaphini *sensu stricto* (Hill *et al.*, 1985). Most of the significant fossil members of the tribe are discussed below. However, some very imperfectly known taxa are excluded, as are those that are so similar to other species that they require no detailed analysis.

In the Pliocene of Africa the following taxa are known:

Simatherium kohllarseni Dietrich, 1942 from the Middle Pliocene of Laetoli in Tanzania (Dietrich, 1942; Gentry, 1987);

S. demissum Gentry, 1980 from the Lower Pliocene of Langebaanweg in South Africa;

Leptobos syrticus Petrocchi, 1956, from Sahabi in Libya, of unknown age. Most of the fossils recently collected at this locality are of latest Miocene age, but there is a strong possibility that some previously collected material is of later age (Geraads, 1989);

Ugandax gautieri Cooke & Coryndon, 1970, from Kaiso in Uganda, probably of Pliocene age; a later species, from Hadar, still undescribed, referred to the same genus by Gentry (1981), will not be considered here;

Brabovus nanincisus Gentry, 1987, from Laetoli.

In the Pleistocene of Africa:

Pelorovis oldowayensis Reck, 1925, from Olduvai (Gentry, 1967), other sites in East Africa (Geraads, 1979) and also at 'Ubeidiya, Israel (Geraads, 1986). A short-horned species, presumably of the same genus, from the same area (Geraads, 1979; Harris *et al.*, 1989) is too poorly known to be considered here;

"Bubalus" antiquus (Duvernoy, 1851), referred to *Pelorovis* by Gentry (1978) and Gentry & Gentry (1978), includes most of the long-horned buffaloes of the Middle and Late Pleistocene of Africa. One of them, however, is treated separately—the skull from Bizerte in Tunisia referred by Solignac (1924) to *Bubalus palaeindicus*, a Middle Pleistocene buffalo from India very similar to *B. arnee*;

Homoioceras singae Bate, 1949, whose holotype has unfortunately lost its horn-cores, from the upper Pleistocene of Sudan (Bate, 1951).

In the Pliocene and Pleistocene of Eurasia there are:

Parabos cordieri de Christol, 1832, from the Lower Pliocene of southern France, which may not belong to the Bovini (Gromolard & Guérin, 1980);

Alephis lyrix Gromolard, 1980 (a species formerly known as *Parabos boodon*) from slightly later deposits in the same area;

Leptobos falconeri Rütimeyer, 1878, type-species of the genus, from the Pinjor of the upper Siwaliks;

Leptobos stenometopon (Rütimeyer, 1865) from the middle Villafranchian of Europe; according to Duvernois (1990), this species should be called *L. elatus*, but since the type of this latter species is a fragment of mandible, the synonymy is hard to demonstrate. I have used the well-preserved material from Saint-Vallier;

Leptobos etruscus (Falconer, 1859) from the upper Villafranchian of Europe, type-species of the subgenus *Smertiobos* Duvernois, 1990. I have used the material from Senèze;

Leptobos vallisarni Merla, 1949 from the lower Pleistocene of the upper Valdarno;

Proamphibos kashmiricus Pilgrim, 1939, from the Pliocene of the Tatrot of the Siwaliks, and *P. lachrymans* Pilgrim, 1939, probably from the same level;

Hemibos triquetricornis (Rütimeyer, 1867) and *H. acuticornis* (Falconer & Cautley, 1868) from the Pinjor of the Siwaliks and perhaps the middle Pleistocene of the Near East (Pilgrim, 1939, 1941);

Bubalus murrensis (Berckhemer, 1927), a short-horned Middle Pleistocene species from Germany (von Koenigswald, 1986);

Epileptobos groeneveldtii (Dubois, 1908) from the Lower (?) Pleistocene of Java (Hooijer, 1958);

Bison palaeosinensis Teilhard & Piveteau, 1930, from the Lower Pleistocene of Nihowan, China. I have used the material housed in the Paris Museum, the hornless skull in Tientsin being perhaps different.

No formal phylogeny of the whole tribe can be found in the literature, though many authors have emphasized some supposed phyletic relationships. Among these lineages or 'sections' are (Duvernois, 1990):

Leptobos — Bibos — Bos
Proamphibos — Hemibos — Bubalus + Anoa
P. cordieri — A. lyrix
African buffaloes, and especially *Simatherium–Pelorovis* (Gentry, 1978, 1980, 1987).

METHOD

There are few characters that have been put forward to support these groupings, for example fusion of the vomer with palatine in the Asiatic buffaloes, and the closure of the anterior valley of P_4 in most African buffaloes. However, instead of selecting a few, supposedly significant, features, I have chosen to list many characters (Appendix 1), and have performed a parsimonious cladistic analysis upon them.

Since there are many fossil taxa, I have used mainly cranial characters, plus one from the post-cranial skeleton. Other features such as the development of dewlap, colour of legs, or number of ribs (Groves, 1981) are not observable in fossil species and have not been used. Some other characters mentioned by Groves (1981) have been ignored because of intra-specific variability or imprecision of measurement; these include the shape of the lachrymo-maxillary or naso-frontal sutures and shape and orientation of the lower flange of the tympanic.

A few characters are purely qualitative, and their state in each taxon is unambiguous (e.g. sexual dimorphism in the presence of horns, or palato-vomer fusion); others are subject to intra-specific variability (e.g. contacts between bones), but most vary continuously, the character states being then described either morphologically (e.g. '0 = very small', '1 = small', '2 = large') or metrically, the range of values (index or angle) being then split into classes, whose limits are largely arbitrary since we do not know which values correspond to evolutionary events. Limits between classes have been placed where there are gaps in the range of mean values, but this method depends critically upon the completeness of the fossil record. However, quantified characters are to be preferred, whenever possible, to seemingly qualitative ones, such as 'occiput rounded' or 'orbit low', estimation of which is subjective (Chappill, 1989).

Most of the morphological observations and measurements were taken from actual specimens, or from the literature, or, in a few cases, estimated from illustrations. These latter methods introduce biases because of the differences in measurement techniques and of the imperfect fidelity of illustrations, but I do not believe that the correction of these likely errors for a few species would significantly alter the results.

The matrix (Appendix 2) gives the states of 57 characters for the 32 taxa listed above, to which have been added as outgroups *Tragelaphus scriptus* and *Boselaphus tragocamelus*, members of the two tribes, Tragelaphini and Boselaphini, which compose, together with the Bovini, the sub-family Bovinae.

This matrix has been processed using HENNIG86, a program designed by S. Farris for parsimonious phylogenetic analysis. Two different analyses were performed: first with no weighting of characters, secondly by weighting them in order to compensate the effect of the differences in the number of states of the various characters (Chappill, 1989). Thus, characters with only two possible states, i.e. only one possible step, are given weight 12; with three states, weight 6; with four states, weight 4; with five states, which is the maximum, weight 3. All characters were treated as additive (i.e. two steps are needed, for instance, to change from state 1 to state 3).

In order to evaluate the impact of the inclusion of fossils in the phylogenetic analysis, I have also run the program on the Recent species alone, using the same characters, for which all states but one (the angle of the parieto-frontal suture in the rare *Bibos sauveli*) are known.

RESULTS

All taxa

There are 2 shortest unweighted trees, with a length (number of steps) of 496, a consistency index of 25 and a retention index of 55. The consistency index (c.i.) is the minimum number of changes for all characters divided by the total number of steps, while the retention index (r.i.) expresses the amount of possible synapomorphy really present in the tree (see Farris, 1989). These trees differ mainly in the relative positions of *Simatherium/Proamphibos* and in the branching orders in the *Bos sensu lato* group and among later *Leptobos*. The consensus tree (Fig. 1) displays therefore low resolution at these levels.

There are two shortest weighted trees, with a length of 2678 (c.i. = 25; r.i. = 54). They are almost identical in the *Bos* group, and differ mainly in the
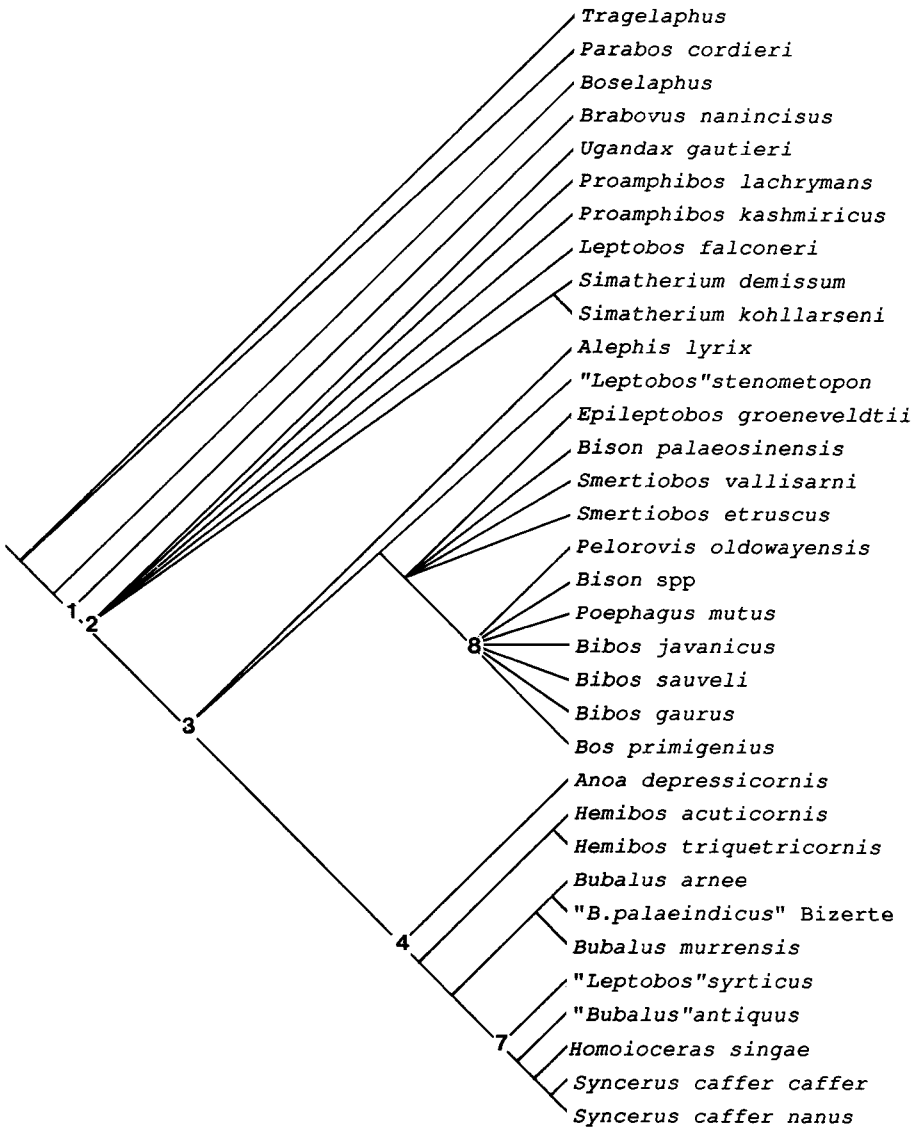
Tragelaphus
Parabos cordieri
Boselaphus
Brabovus nanincisus
Ugandax gautieri
Proamphibos lachrymans
Proamphibos kashmiricus
Leptobos falconeri
Simatherium demissum
Simatherium kohllarseni
Alephis lyrix
"Leptobos" stenometopon
Epileptobos groeneveldtii
Bison palaeosinensis
Smertiobos vallisarni
Smertiobos etruscus
Pelorovis oldowayensis
Bison spp
Poephagus mutus
Bibos javanicus
Bibos sauveli
Bibos gaurus
Bos primigenius
Anoa depressicornis
Hemibos acuticornis
Hemibos triquetricornis
Bubalus arnee
"B.palaeindicus" Bizerte
Bubalus murrensis
"Leptobos" syrticus
"Bubalus" antiquus
Homoioceras singae
Syncerus caffer caffer
Syncerus caffer nanus

Figure 1. The consensus tree of the two shortest unweighted trees. The numbered nodes are discussed in the text.

branching pattern of *Proamphibos–Hemibos–Bubalus*, which is unresolved in the consensus tree (L = 2939; c.i. = 23; r.i. = 48). A tree slightly modified (by hand) from one of the shortest weighted trees is shown on Fig. 2, and is discussed below. The low consistency indexes reflect the high level of homoplasy, but such low values are common with large matrices (cf. Platnick, 1989: table 1). The consensus tree of the six trees generated by successive weighting (applying greater weight to the most consistent characters) groups all buffaloes with *Proamphibos* and *Hemibos*, and *Simatherium* with *Bos sensu lato*.

These results may be compared with the characteristics of a tree (Fig. 3) constructed according to the currently generally accepted relationships among
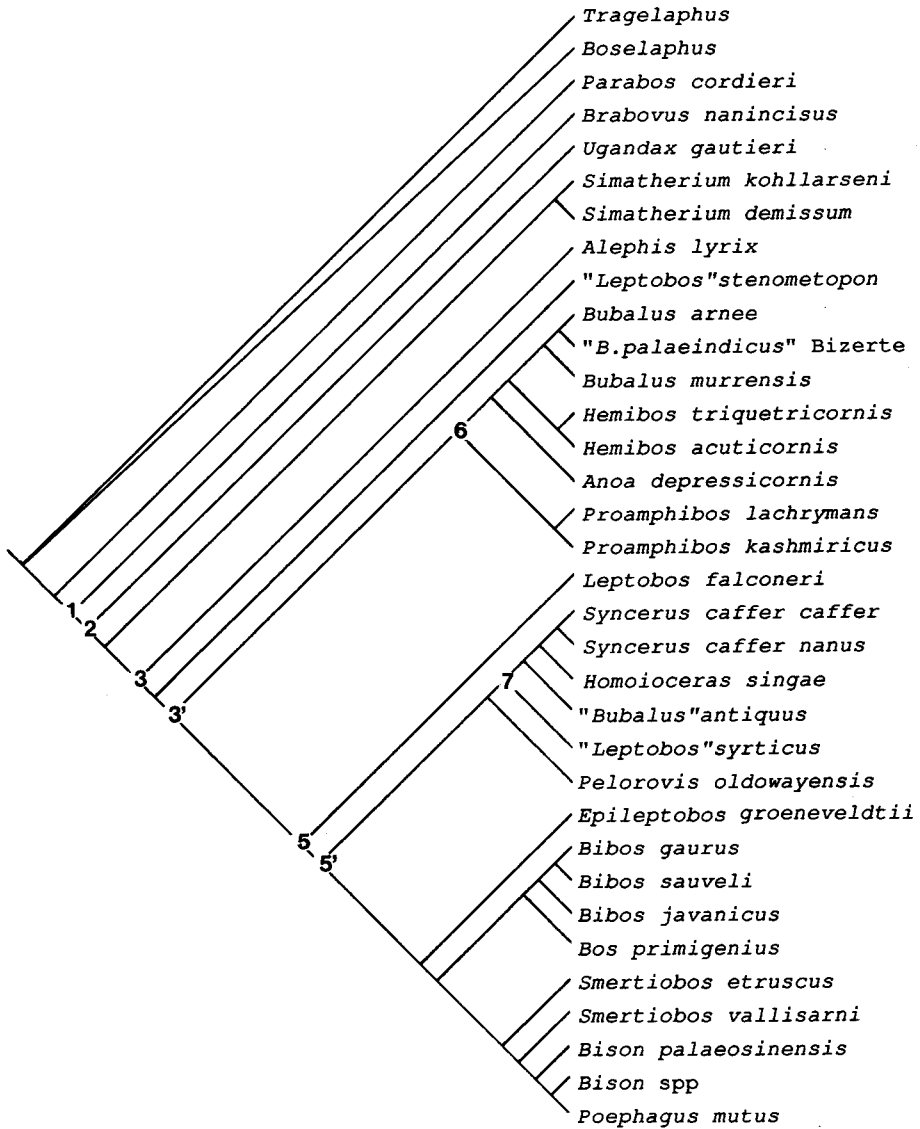
Figure 2. A tree slightly modified from one of the shortest weighted trees. It has 2702 steps. The numbered nodes are discussed in the text.

the tribe (e.g. Pilgrim, 1939; Duvernois, 1990; Gentry, 1978, 1980, 1987; Groves, 1981), and used as input in the program. Its weighted length is 3123 (c.i. = 21; r.i. = 44), and unweighted length 583 (c.i. = 21; r.i. = 44). It is therefore clear, even if the most parsimonious trees cannot be accepted in every detail, that they are much shorter than this 'classic' tree.

Recent taxa alone

The unweighted and weighted shortest trees differ only in that *Bison + Poephagus* must be added to *Bos + Bibos* to preserve monophyly in the
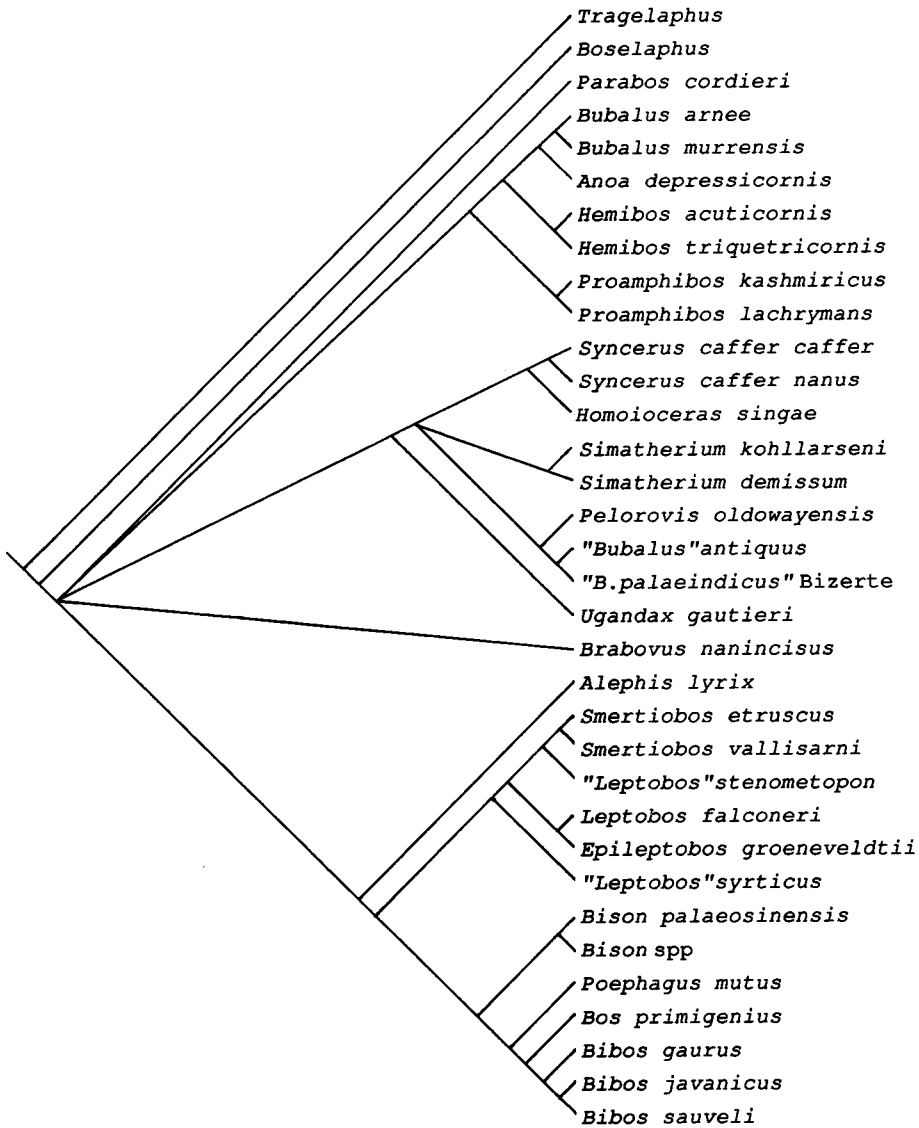
Figure 3. A tree depicting the classically admitted relationships in the tribe Bovini. It has 3123 steps.

former, while both groups are sister-taxa in the latter (Fig. 4). Both trees have c.i. = 50, r.i. = 58.

DISCUSSION OF THE TREES

Parabos cordieri *and* Brabovus

The former species always occupies a basal position, sometimes below *Boselaphus*. This confirms the view of Gromolard & Guérin (1980) that *P. cordieri* cannot be accepted as a bovine. The true Bovini (node 1 on the trees) are defined by horn-cores that are less upright, less angular in cross-section (with an especially weaker anterior keel), and a less marked sagittal crest on the occipital.
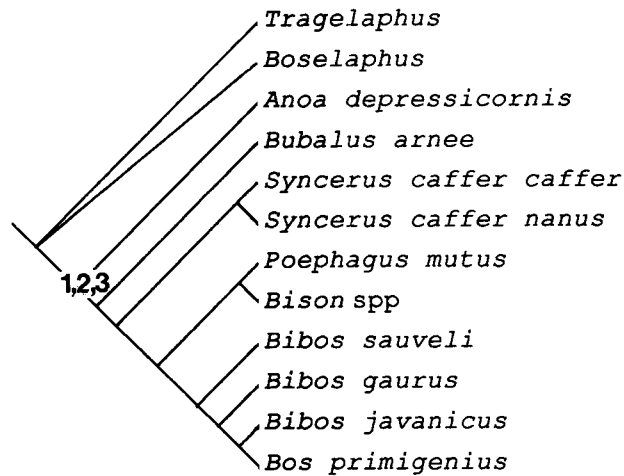
Figure 4. The shortest weighted tree of Recent taxa.

These characters lead to the inclusion of *Brabovus* within the Bovini, if it is accepted among the Bovinae (Gentry, 1987).

The remaining Bovini appear as a monophyletic group (node 2) on all cladograms. They have horn-cores that are divergent, curved (at least slightly) and closer to the back of the skull. Thus changes in horn-core morphology and orientation pre-date reorganization in the rear of the skull. Another evolutionary event possibly occurring at this level is an opening of the mesial lobe of P_4, but this might be an artefact of the choice of the outgroups.

Pliocene East and South African Bovini

These three species, *Ugandax gautieri*, *Simatherium kohllarseni* and *S. demissum* (this genus usually appears as monophyletic) are usually clustered close to *Leptobos falconeri*, but they do not seem to be particularly closely linked to later African bovines. *Alephis lyrix* and *L. stenometopon*, especially the latter, have a rather unstable position. *Leptobos* is never monophyletic.

Higher Bovini

On all cladograms a large group appears at node 3, which comprises all buffaloes, *Hemibos*, *L. syrticus*, *L. etruscus/vallisarni*, *Epileptobos*, *Bison* and *Bos sensu lato*. It may also include *L. stenometopon*, *L. falconeri*, *Proamphibos* and *Alephis*. This well-established clade has raised frontals, the parietal plane less angled on the occipital, mastoid facing more backward, horn-cores more inclined and more distant behind orbit, and more complex upper molars.

Since this group includes all living species, most of the apomorphic features of nodes 1, 2 and 3 define the Bovini as a whole on the cladogram of Recent taxa (Fig. 4), except that the horn-core section is supposed to become first more compressed, with a sharper postero-medial keel, before reverting in *Bison–Bos sensu lato*.

Asiatic buffaloes

These never appear as monophyletic in computer-generated cladograms, some of them at least being linked with the African ones. The group including all

buffaloes (node 4 in Fig. 1) is defined by its large supra-orbital foramina, wide premaxillae, basioccipital more retracted backwards, horn-cores with a more angular cross-section, but also by the fusion of palatine and vomer (peculiar to the Asiatic buffaloes) and therefore implying an unlikely reversal in the African forms. If this reversal is not accepted, African buffaloes may be the sister-group of the Asiatic ones, as biogeography would perhaps suggest. However, such an Afro-Asiatic buffalo group would be poorly defined, and increase the tree length to 2726. An alternative tree (Fig. 2), obtained by modifying one of the shortest weighted trees, is only 2702 steps long (c.i. = 25; r.i. = 54), and includes a well-defined (*Bos sensu lato* + African buffaloes) clade (node 5), which has more elevated frontals, no contact between parietal and alisphenoid, no sagittal crest on occipital, backwardly facing mastoid, nasals not bifid and with only a short contact with the premaxilla, more rounded horn-core section and more folded valleys of upper molars. Monophyly of the Asiatic buffaloes (group 6 in Fig. 2) is then supported by the palato-vomer fusion, and by the presence of anterior and posterior keels on horn-cores. Also, this branching order (Asiatic buffaloes (African buffaloes—*Bos sensu lato*)) fits the fossil record better, since *Proamphibos*, an Asiatic genus, is certainly the earliest among the group.

Branching patterns within the Asiatic buffaloes do not differ much from what is generally accepted. *Proamphibos* is a valid genus, and the two species which are chiefly known by their type-specimens (of which I have seen only casts) are very similar. *Hemibos* also appears as a valid genus, perhaps because of the imperfect sorting of the material belonging to the two Indian species, but its revision is beyond the scope of this paper. There is no doubt that these two genera are close to the living Asiatic buffaloes.

Anoa is the sister-taxon of all other Bovini in the cladogram of Recent species (Fig. 4), but this implies the parallel acquisition of palato-vomer fusion in both Asiatic buffaloes, and their monophyly increases the tree length only slightly (L = 236 v/ 229).

The skull of "*Bubalus palaeindicus*" from Bizerte in Tunisia, described by Solignac (1924), deserves special mention. Its geographic provenance, as well as its superficial appearance, would prompt us to unite it with the long-horned African buffaloes, but it is consistently grouped with *B. arnee* on the cladograms, even though the relations of the palatine with the vomer are unknown; indeed, Solignac's description and figures confirm beyond any doubt that this skull is a true *Bubalus*, which poses a biogeographic problem. Solignac's stratigraphic description is inconsistent (B. Keraudren, personal communication) and the geological age of the specimen cannot therefore be determined; however, it is likely to be earlier than Late Pleistocene and it could be the true ancestor of the herd of *Bubalus* which were living recently in Garaet Ichkeul near Tunis and were generally supposed to have been imported from Asia by the Romans or Carthaginians. Since no other buffalo of Asiatic type is known in Africa, we do not know whether it is of Asiatic or European origin, it may perhaps descend from a species like *B. murrensis*.

African buffaloes

Homoioceras singae, presumed by Gentry & Gentry (1978) to be a short-horned buffalo, is indeed close to *S. caffer*, with the long-horned "*Bubalus*" *antiquus* as the next closest taxon. This group of African Late Pleistocene to Recent buffaloes is

defined by the frontal rugosities, the low and wide occiput and the strongly compressed horn-cores.

Leptobos syrticus, which is certainly not closely related to the other "*Leptobos*" species, might be an early member of the African buffaloes, but is probably not older than Pliocene (Geraads, 1989). This group (node 7), when included within a large buffalo group (Fig. 1), is rather poorly defined by its posteriorly facing mastoid and loss of sagittal keel on basioccipital, but also, when African buffaloes are the sister-group of *Bos sensu lato* (Fig. 2, node 7), by its lower occiput, frontal more angled on parietal, very divergent horn-cores which are closer to the orbit (because of their larger basal diameter) and with an anterior keel.

Most unexpected at this level is the position of *Pelorovis oldowayensis*. On all computer-generated cladograms, it is grouped with bison and yak. These three taxa are united by few features, including several simplifications of upper molars, but their linkage to the *Bos–Bibos* group (node 8) is supported by a large set of apomorphies: supra-orbital foramina wider apart; less obtuse fronto-parietal suture; longer suture between nasal and lacrimal; loss of contact between parietal and alisphenoid; loss of sagittal crest on occipital; horn-cores more divergent, more inclined, more curved and more spiralled, more distant from orbit, and without anterior keel. Strict parsimony does not support the grouping of *P. oldowayensis* with African buffaloes, suggested by Gentry (1967) mainly on the basis of the lingual closure of the anterior wall of P_4. Indeed, the discovery of this species in Israel (Geraads, 1986) had already raised the possibility of its Eurasian origin. However, some of the above-mentioned synapomorphies are probably linked, and should not perhaps be computed as many different characters, and the moving of *Pelorovis* with the African buffaloes only slightly lengthens the trees. The position shown in Fig. 2 is equally parsimonious (L = 2702) as the linkage with *Bison–Poephagus*.

Cattle and bison

Leptobos vallisarni and *L. etruscus* are always very close, and Duvernois' opinion (1990) that both species are synonymous is likely. They may, at least, be included in the same sub-genus, *Smertiobos* Duvernois, 1990. They occupy a position close to *Bison palaeosinensis* and to the base of the *Bos sensu lato-Bison* group, and are probably not far from their common ancestor but, when these branchings are resolved, they are closer to the latter than to the former. However, they are never associated with *L. stenometopon* (or whatever the name of Saint-Vallier species is) or *L. falconeri*, and nothing suggests the monophyly of *Leptobos* (even when *L. syrticus* is not included). Indeed, most of the diagnostic characters of this genus (Duvernois, 1990: 20) are plesiomorphic.

The relative positions of the various species of *Bos* and *Bibos* are somewhat variable; *Bibos* appears sometimes as a valid monophyletic taxon.

Bison are often shown as the sister-taxon of yak. The monophyly of this group is supported by a broad skull, supra-orbital foramina which are wide apart, acute parieto-frontal suture, loss of ethmoidal fissure, widely inserted horn-cores, loss of contact between nasal and premaxilla, short premolar row, mesial lobe of P_4 wide open, and more simple molars. The yak is commonly held as closer to *Bos sensu stricto*, but the branching order (*Bison* (*Bos* + *Poephagus*)) lengthens the tree of recent taxa from 229 to 241.

EVOLUTIONARY TRENDS

Ordered series of transformations ($0 \to 1 \to 2 \to 3 \to 4$) are rather common in the shortest trees, and many of them can be traced in parallel along the various branches. These general tribal trends are a broader occiput, supra-orbital foramina more apart, more raised frontals and more sloping parietals, loss of contact between premaxilla and nasal (except in the Asiatic buffaloes), loss of sagittal crest on occipital and basioccipital, mastoid facing more posteriorly. Most of these changes are probably linked with changes in horn-cores, which become more divergent, less upright, more curved (except in the Asiatic buffaloes), and closer to the back of the skull. These sets of evolutionary trends are not found in the other bovid tribes.

CONCLUSIONS

Homoplasy is extensive, so that many changes can be made without greatly lengthening the most parsimonious trees. There are relatively few well established taxonomic results.

1. All Recent Bovini belong to a monophyletic clade (node 3), which may be called Eubovini. This group does not include many of the fossil taxa. Their clear distinction from other Recent Bovinae (Tragelaphini and Boselaphini) is due to a "gap" effect (Donoghue *et al.*, 1989), the Bovini which were "intermediate" now being extinct. Inclusion of fossil taxa does not greatly modify the general pattern of relationships.

2. Monophyly of the Bubalina (Asiatic buffaloes) of Pilgrim is most likely, although alternative groupings are possible; this is an Indian group, but some taxa migrated to Europe and even North Africa.

3. African buffaloes are monophyletic, and include *L. syrticus*, but the inclusion of *P. oldowayensis* within this group is disputable; they are probably closer to the following section than to the Bubalina.

4. *Bos + Bibos + Bison + Poephagus + L. etruscus–vallisarni + Epileptobos* is a mono- or paraphyletic group, the addition of *P. oldowayensis* is perhaps needed to preserve monophyly. Among Recent forms, the yak is close to the bisons.

The following tentative classification is proposed, mainly after Fig. 2:

Tribe Bovini Gray, 1821
    plesion *Brabovus* Gentry, 1987
    plesion *Ugandax gautieri* Cooke & Coryndon, 1970
    plesion *Simatherium* Dietrich, 1942
    sub-tribe **Eubovini nov.**
    incertae sedis: plesion *Alephis* Gromolard, 1980
    incertae sedis: plesion "*Leptobos*" *stenometopon* Rütimeyer, 1865
    section Bubalina
        incertae sedis: plesion *Proamphibos* Pilgrim, 1939
        Anoa Smith, 1827
        plesion *Hemibos* Rütimeyer, 1865
        Bubalus Smith, 1827
    incertae sedis: plesion *Leptobos falconeri* Rütimeyer, 1878
    section Syncerina
        plesion "*Leptobus*" *syrticus* Petrocchi, 1956

plesion *"Bubalus" antiquus* Duvernoy, 1851
plesion *Homoioceras singae* Bate, 1949
Syncerus Hodgson, 1847
incertae sedis: plesion *Pelorovis* Reck, 1925
section Bovina
   plesion *Epileptobos* Hooijer, 1956
   Bos Linnaeus, 1758
   plesion *Smertiobos* Duvernois, 1990
   Bison Smith, 1827

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APPENDIX 1

Codings of character states (all indexes are ratio × 100). There is no *a priori* assumption concerning polarity. < = less than; ≪ = much less than; # = approximately

No. of character		Code				
		0	1	2	3	4
0	Postorbital width/Length condylo-Premaxilla	< 32	34–40	42–44	> 46	
1	Occipital breadth/Length condylo-Premaxilla	< 36	39–43	45–51	> 51	
2	Width between supraorbital foramina/post-orbital width	< 47	48–50	53–58	> 60	
3	Min. width between temporal fossae/occipital width	< 33	34–45	53–56	> 65	
4	Occipital height/occipital width	< 33	35–37	> 38		
5	Length from anterior border of orbit to tip of Premaxilla/L. condylo-Pmx	< 51	53–58	> 60		
6	Occipital height/post-orbital width	< 37	38–45	> 45		
7	Up-arching of frontals: from absent to very strong	0	1	2	3	4
8	Fronto-parietal angle	> 150°	150–130	130–100	< 100°	
9	Fronto-parietal suture	> 150°	150–90°	< 90°		
10	Parieto-occipital angle	< 120°	120–150	150–170	> 170°	
11	Frontal rugosities	Nil	Weak	Strong		
12	Size of the supraorbital foramina	Very small	Small	Medium	Large	Very large
13	Protrusion of orbits	None	Weak	Medium	Strong	
14	Level of anterior border of orbit	$M^{2\ 3}$	M^3	Post M^3		
15	Ethmoidal fissure	Yes	Vestige	No		
16	Contact between Pmx and Na	Long	Short/variable	No		
17	Tip of nasals slit	No	Yes			
18	Posterior end of nasals broadened	No	Yes			
19	Suture between Nasal and Lachrymal	None	Short	Long		
20	Shape of premaxilla: 5 states, from 0 = narrow rounded to 4 = very broad					
21	Vomer between Mx and Pmx in palate	Yes	No			
22	Palatine and vomer fused	No	Yes			
23	Choanae shifted backward	No	Little	Yes		
24	Contact parietal/alisphenoid	Yes	No			
25	Sagittal crest on occipital	Yes	Weak	No		
26	Supra-occipital protuberance	No	Weak	Yes		
27	Outline of occipital: 4 states, from 0 = rounded to 3 = trapezoidal					
28	Orientation of mastoid: 4 states, from 0 = facing laterally to 4 = facing posteriorly					
29	Anterior tuberosities of basiocc.	Weak	Strong	Very strong		
30	Median sagittal crest on basiocc.	Yes	Weak	No		
31	Position of oval foramen relative to anterior tuberosities of basiocc.	Forward	Partly forward	Same level		
32	Angle between palate and basiocc.	Weak	#30°			
33	Angle basisphenoid/basioccipital	No	Weak	Strong		
34	Angle auditory duct/sagittal plane	< 70°	70–80	> 80°		
Horn-cores:						
35	Divergence in anterior view	< 30°	40–80	80–110	110–135	> 140°
36	Inclination in side view: 5 states, from 0 = upright to 4 = sloping downwards at the base					
37	Curvature: 5 states, from 0 = almost straight to 4 = strongly recurved					
38	Clockwise torsion	None	Weak	Present		
39	Anticlockwise torsion	None	Weak			
40	Distance from horn-core to orbit/diameter of orbit	≪	<	#	>	≫
41	Distance from horn-core to occiput/max. diameter of horn-core	≫	>	#	<	≪
42	Distance between internal sides of horn-cores/post-orbital width	< 90	> 90			

APPENDIX 1 *continued*

No. of character		Code				
		0	1	2	3	4
43	id.	> 30	< 30			
44	Length of horn-cores/occip. width	< 2	2–3	> 3		
45	Horn-core compression	< 61	67–74	78–90	> 90	
46	Outline of section: 4 states, from 0 = angular to 3 = rounded					
47	Postero-medial keel	None	Present	Sharp		
48	Anterior keel	Present	Weak	Absent		
49	Horns present in females	No	Yes			
Teeth:						
50	Length $P_{2\,4}$/Length $M_{1\,3}$	< 55	57–65	> 65		
51	Lingual entrance to ant. lobe of P_4	Open	Narrow	Closed		
52	Ribs and styles on outer walls of M/	Weak	Moderate	Strong		
53	Pinching of inner lobes of M/	Absent	Present			
54	Accessory columns of M/	Weak/absent	Present			
55	Outline of valleys of M/	Simple	Folded			
56	Minimum shaft diameter/length of metacarpal	< 19	> 24			

APPENDIX 2

The matrix of 57 character states and 34 taxa.

Char. numbers:	0					56
Tragelaphus	1002201000	0140001102	1100000101	0100001001	0000030000	1200000
Boselaphus	0001211000	0211110101	1001000002	0000101100	0000030000	1110000
P. cordieri	??012?0001	0010??????	????000100	0200000000	0100020001	2201000
P. lachrymans	1000212000	00111?????	??11?102?1	1?01?12100	3100121110	101110?
P. kashmiricus	100022?011	001112??01	????1?101?1	1?01113100	3100131110	1?1110?
H. triquetricornis	1120221321	1032120111	3112?11220	1001114100	2300?21211	2?1111?
H. acuticornis	1100221211	1021220?12	??12?112?0	1?01113110	2200121211	2?1111?
Anoa	1121212210	1130010111	3112010011	1002103000	2000021211	0011100
B. arnee	1122111321	2111020101	3012020000	1002244100	1210210201	0121111
B. murrensis	??111??32?	113???????	????0200??	?????33100	030001020?	???????
Brabovus	00??1?000	0?0111????	?????10??0	??02?02000	000103302?	12200??
Ugandax	??000?011?	01?0??????	??0??10100	00?0012100	020002202?	??0000?
S. demissum	??010?011?	0111??????	?????202??	1????22200	030002201?	1100000
S. kohllarseni	??010?010?	0?10??????	?????202?1	1???122200	03100?202?	??0?00?
P. oldowayensis	110312033?	2010221001	4?01?20022	2111013320	4401223021	0210001
Bizerte	12???1?32?	20?2220?01	3?????00??	??0?144100	1310211?0?	???01??
P. antiquus	1303011220	0210220002	4?01?10030	221?144200	131020111?	1121111
H. singae	330101132?	1241121???	??00?201?0	2?1?244???	1301?0101?	1?2111?
S. c. caffer	3201011321	1241122001	3000120231	2010144210	1400001211	1211101
S. c. nanus	1301010111	1140112001	3000120231	0010124100	2300001221	1211101
A. lyrix	2101121210	1010110?0?	0????112?1	2101021101	0300122111	1100100
L. etruscus	3111???211	10110?????	??0?0??0??1	0?12?24300	3410023021	?011110
L. vallisarni	3110210101	0010??0?0?	1????21011	1110143210	3310023020	1021110
L. stenometopon	2011211110	1132111?00	??010111?1	1110124210	3300?12020	1100100
L. falconeri	2100211000	0011100000	??01?112?1	1101?12200	1100133020	???101?
Epileptobos	??111?1211	001021????	??01122121	2102013310	3300123021	?12111?
L. syrticus	??011?122?	1141??????	?????20130	21??043101	030012200?	???????
Bison	3233211212	0113222002	1100111120	2110144310	2310023021	0010101
B. palaeosinensis	??212?0210	102???????	?????211?2	20?2?44420	?310033021	2?????0
Poephagus	3133221232	3111222002	3101121121	2112144220	2410122021	0010000
B. primigenius	1233222331	3012111102	3100110121	1102244320	4410023021	1121110
B. gaurus	2221111430	3131112102	2101120122	2101134320	4410012021	1121110
B. javanicus	122212331	3141111102	2101121121	1101134410	4310012021	1121110
B. sauveli	112121232?	2140102102	2101120121	1101134320	3310012121	1121110