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Systematic relationships in the Bovini (Artiodactyla, Bovidae)

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Introduction

The interrelationships of the species and supraspecific groups of the Bovini have been studied by a number of authors this century (PILGRIM 1939; SOKOLOV 1959; BOHLKEN 1958; GENTRY 1978), but a few gaps remain, in particular:

1. Are the African and Asian Buffaloes, nowadays universally placed in separate genera (*Syncerus* and *Bubalus* respectively), actually related to one other, or is one or the other more closely allied to *Bos*?
2. Is the genus or subgenus *Bibos* (defined mostly by characters interpreted PILGRIM [1939] as primitive with respect to *Bos*) monophyletic, or are some of the species assigned to it closer to *Bos s. s.* than others?
3. Does the Yak occupy a place between the Bison and true cattle, as PILGRIM (1939) inferred, or is it the closest living relative of *Bos s. s.*, as suggested by SOKOLOV (1959) and BOHLKEN (1958)?
4. Is the Bison itself a separate lineage from *Bos s. l.*, or just a highly specialised member of it?

The method here adopted is that of cladistic analysis (see below). Previous investigators have in the main worked from the fossil record; while this method can, if the record is complete enough, trace the broad outlines of a group's evolution, a detailed study of the living forms should by itself reveal the pattern of lineage branching, and such fossils as exist can then be slotted in.

BOHLKEN (1958) adopts the following classification of the Bovini:

1. Buffalo group
   a. Genus *Bubalus* with two species: *B. arnee* (Indian buffalo) and *B. depressicornis* (Anoa).
   b. Genus *Syncerus* with one species: *S. caffer* (African buffalo).
2. Cattle group
   a. Genus *Bibos* with two species: *B. javanicus* (Banteng) and *B. gaurus* (Gaur).
   b. Genus *Bos* with two subgenera: *Bos* for *B. primigenius* (Aurochs), the wild ancestor of most domestic cattle; and *Poephagus* for *B. mutus* (Yak).
   c. Genus *Bison* with one species: *B. bison* (Bison).

In this system, *Bubalus mindorensis* (the Tamaraw) was united with *B. arnee* and *Bison bonasus* (European Bison) with *B. bison;* while *Bibos sauveli* (the Kouprey) was interpreted as a hybrid between *Bibos javanicus* and domestic varieties of *Bos primigenius*. GROVES (1969) disputed the sinking of *Bubalus mindorensis*, and raised *Bubalus quarlesi* (Mountain Anoa) to species rank, separate from *B. depressicornis*. BOHLKEN himself later (1961) reversed his opinion about *Bibos sauveli* and recognised it as a valid species, and used its intermediate status as a reason to reduce *Bibos* to subgeneric rank under *Bos*. The Bison question – whether *B. bonasus* is a valid species or not – remains purely a matter of convenience.

It should be noted that four of the names used by BOHLKEN (and followed here) given to wild populations would be different were strict priority followed as their domesticated varieties were named first: *Bubalus arnee* would be *B. bubalis, Bibos* (or *Bos*) *gaurus* would be *B. frontalis; Bos primigenius* would be *B. taurus;* and *Bos mutus* would be *B. grunniens*. The matter of the nomenclature of domestic animals is at present under consideration by the International Commission on Zoological Nomenclature (see GROVES 1979 and references therein; VAN GELDER 1979). It must be noted, of course, that BOHLKEN was well aware of the nomenclatorial difficulties involved, and was perhaps more than anyone else instrumental in bringing them into prominence (BOHLKEN 1961).

Material and methods

The skulls of Bovini and Boselaphini were examined visually at the British Museum; when the salient characters had been listed and checked for cogency and consistency, photographs were taken for illustration and further study All species were represented except *B. sauveli*; four skulls of this taxon were studied in the Paris museum.

There is no dispute that the closest living relatives of the Bovini are the Boselaphini (the Nilgai, *Boselaphus*, and Four-horned Antelope, *Tetracerus*): SOKOLOV (1959) actually includes these two genera in the Bovini, but they are much more primitive. GENTRY (1978) defines the progressive characters of the true Bovini; these concern mainly the horns and brain case.

The cladistic method in the present case seeks to find characters in common between one or more species of the Bovini and one or both of the Boselaphini; such characters are, as a working hypothesis, assumed to be symplesiomorph, i. e. retained from the most recent common ancestor of both groups. The other states of the character are therefore interpreted as apomorph, or derived; two or more species both showing the derived state of that character may have acquired it by common ancestry (Synapomorph) or independently (parallel or convergent). As each character in turn is examined on this basis, if the initial hypothesis is correct a consistent pattern will emerge: otherwise a different hypothesis must be sought. The resulting picture may then be compared with the fossil record: although actual ancestors need not be expected, a predominance of the alleged primitive character states should appear further and further back in time, and perhaps dates can be tentatively assigned to the branching points. This method of analysis, illustrated for example by DELSON (1977), is based on the theoretical advances of HENNIG (1966).

Results

The 30 skull characters sample can be grouped into five regions: Postcornual, Frontal, Basal, Rostral and Tympanic.

A. Postcornual region

Characteristic of the Bovini, and distinguishing them from the Boselaphini, is the extreme shortening and flexion of the postcornual part of the skull compared to the precornual; both the degree to which this has happened, and the manner in which it has occurred, varies from species to species.

1. An intercornual ridge is absent in *Bubalus* and *Syncerus*, but occurs in all other Bovini; in Bison and Yak the ridge is flattened and craniocaudally expanded in the midline. As no ridge is found in the Boselaphini, it seems likely that its presence is a derived character, and that Bison and Yak are still further modified.

2. The braincase slopes backward and downward in Buffaloes, downward in the Banteng, and downward and forward in all others – most sharply forward in true *Bos*. This is a quasi-

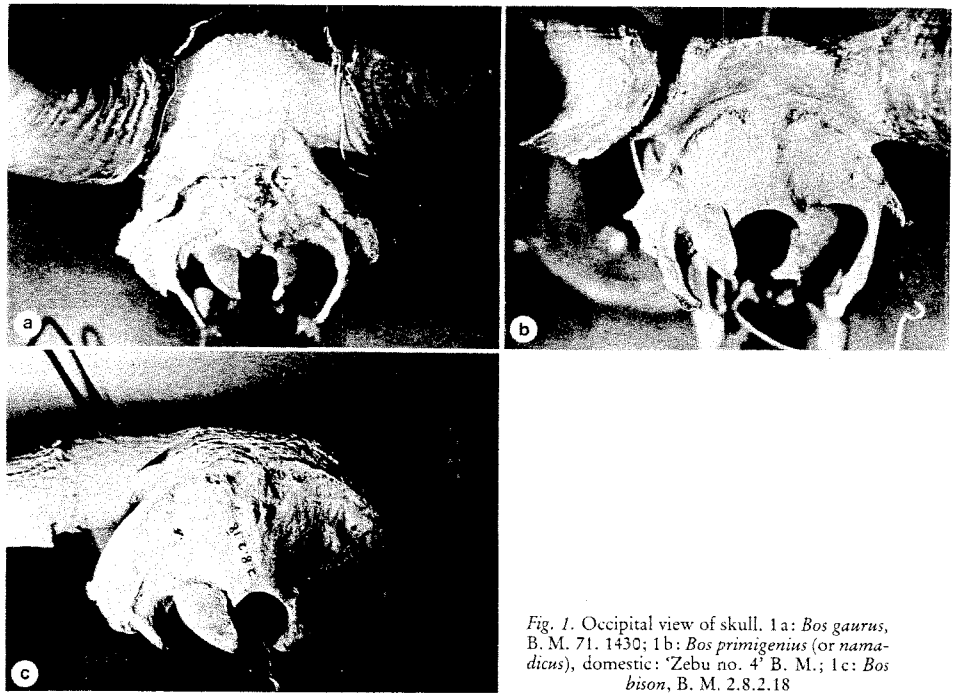

Fig. 1. Occipital view of skull. 1a: *Bos gaurus*, B. M. 71. 1430; 1b: *Bos primigenius* (or *namadicus*), domestic: 'Zebu no. 4' B. M.; 1c: *Bos bison*, B. M. 2.8.2.18

evolutionary sequence illustrating the progressive "tucking under" of the postcornual part.

3. The postcornual constriction, between the occipital and parietal segments (see HOOIJER 1958, who shows that PILGRIM's identification of the supraoccipital was in error), is very marked in Buffaloes and in *Bibos*, though among the latter less so in *B. sauveli* than in *B. javanicus* and in *B. gaurus* (Fig. 1a); it is less marked in the Yak (about the same as the Kouprey) and poorly marked in true *Bos* (Fig. 1b) and *Bison* (Fig. 1c). As the braincase is shortened the occiput is pushed upwards, progressively crowding out the constriction.

4. Connected with the previous character, but not entirely coincident with it, is the suppression of the nuchal ridge. This is strongly developed in Buffaloes and Gaur (Fig. 1a), as in Boselaphines; it is weaker in Bison (Fig. 1c), Banteng, Kouprey and Yak, and hardly developed at all in true *Bos* (Fig. 1b).

5. As the occiput is pushed upwards, the parietal/interparietal region is shortened and telescoped into it. So the relation between the lengths of these two parts of the postcornual region, from being 1:2 or more in the Boselaphini, becomes 1:1 in *Syncerus* and *Bibos gaurus*, about 1.5:1 in *Bubalus*, *Bibos javanicus* and *B. sauveli*, and 2–3:1 in *Bison*, *Bos mutus* and *B. primigenius*. HODGSON (1841) expressed this and the previous two characters as far as the Nepal forms were concerned by describing the posterior skull surface in "the common bull of Nepal" as a trapezium entirely occupied by nuchal insertions; in the Yak, as an equilateral triangle divided into two parts, occipital and "parieto-frontal"; and in the "Gowri Gao" (= Gaur) as sphenoidal, deeply indented at the centre by the temporal fossae.

6. The lateral corners of the nuchal crest swing forward in the Boselaphini, as they do in *Bubalus* and in *Bos primigenius*; somewhat backward if at all in *Bos mutus*, and distinctly backward in all other forms.

7. Primitively, the braincase is roofed over largely by the parietals (and interparietal, where present), and some parietal share is retained in most Bovini; but in *Bos primigenius* and its domestic derivatives none remains. The fronto-parietal suture closes early in life in all forms, but prenatally in these true cattle.

8. As a final index of parietal reduction, related especially to the elimination of the postcornual constriction, is the position of the nuchal ridge relative to the horn-cores. In the Buffaloes, Gaur and Banteng the ridge is well below the lower edges of the horn- cores; in the Kouprey and Yak it is pushed somewhat above, and in Bison and true cattle well above.

In the characters of the postcornual region, therefore, the Buffaloes would appear to be the least advanced of the Bovini, with the Bison and the true cattle most derived; the other species are variably intermediate.

B. Frontal region

Unlike the characters of Group A which all form a functional-evolutionary group, the characters of Group B are more disparate, though they obviously affect each other to some degree.

9. The forehead is primitively short in Bovids, with the horn pedicels arising not far behind the orbits. It remains short in Buffaloes and Bison, but is considerably lengthened in all other species. PILGRIM (1939) measured frontal and parietal lengths, giving the relation between them as 2:1 in living Boselaphines, 2–3:1 in *Bubalus*, and 4–6:1 in *Bos* and *Bibos*, the latter tending to be lower than the former. This ratio is somewhat inefficient, depending on parietal shortening as well as frontal lengthening. A rather better ratio would be that between breadth (between orbits) and length, which in PILGRIM's material is 1:1 in *Bubalus*, much less than this in *Bos* and *Bibos*, and more than this in *Bison*; but even this is influenced additionally by orbital tubularity and the position of nasion (characters 14 and 23 below).

10. The supraorbital foramina, in dorsal view, are level with the middle of the orbits in most Bovids (with their anterior rims in *Tetracerus*). In Buffaloes (Figs. 2a, b) they are level with the upper margins of the orbits; in Bison (Fig. 2c), somewhat above; in other species (Figs. 2d–f), well above. It appears that the foramina are carried upwards as the forehead is lengthened.

11. In shape, the foramina are primitively broad in Buffaloes (Fig. 3a) and Bison, but elongated and narrow in the other species (Fig. 3b).

12. The channels descending from the supraorbital foramina are broad and short, as in Bovids generally, in Buffaloes and Bison; they are actually absent in Boselaphines. They are elongated and narrow in the other forms and lead upward towards the horn-pedicels as well as downwards; and in these forms the channels tend to be groove-like and may be partially roofed over; however, in Yak and true cattle the grooves (though just as narrow) may be nearly obsolete.

13. Accessory supraorbital foramina are rare in Bovidae, and appear not to occur in Boselaphini; they do not occur in Buffaloes, but are the usual condition in other Bovini, Bison included. HOOIJER (1958) notes the variability in number, even on two sides of the same skull, of these accessory foramina in the Banteng.

14. The orbits are flush with the cranial surfaces in most Bovids, as in Boselaphines, *Syncerus* (Fig. 2a), Banteng (Fig. 2d), Kouprey, and most true cattle (Fig. 2b); but slightly tubular in *Bubalus* (Fig. 2b), Gaur and Yak (Fig. 2c), and strongly so in Bison (Fig. 2c). GRIGSON (in press, pers. comm.) notes an allometric influence on tubularity in western breeds of true cattle and the European aurochs. GUTHRIE (1966) correlates orbital tubularity in Bison with the development of the facial mat of hair: this explanation would also hold for the Yak but clearly will not do in other cases.

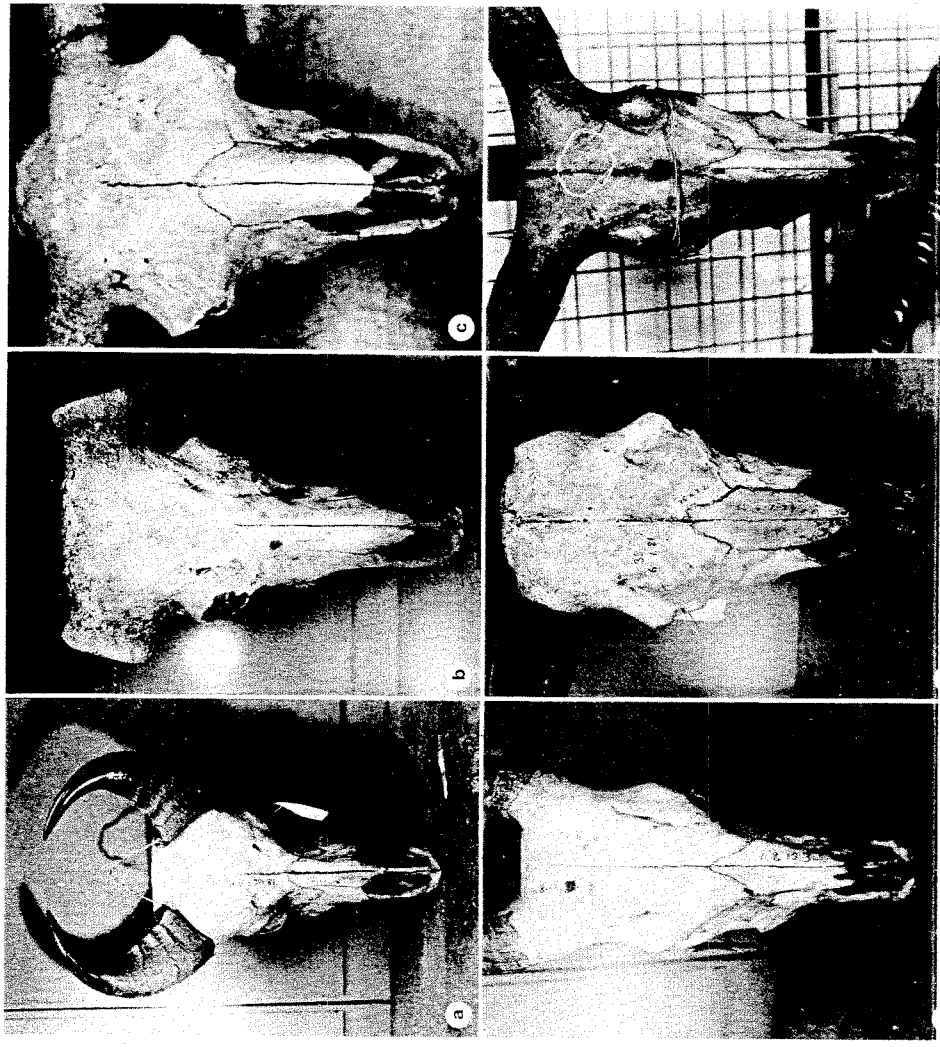

Fig. 2. Skull in *N. dorsalis*. a: *Syncerus caffer nanus*, B. M. 58. 106. Note that the postcornual portion is largely caudally oriented, and the most posterior part of the cranium is the nuchal ridge; b: *Bubalus arnee*, B. M. 30.10.5.1; c: *Bos bison*, B. M. 2.8.2.18; d: *Bos javanicus lowi*, (female) B. M. 1.8.15.3; e: *Bos mutus*, B. M. 35.6.1.21. Note, in this and the previous (subadult specimens), the interparietal is visible from the front; f: *Bos primigenius* (or *namadicus*), B. M. 'Zebu, no history'

Fig. 3. Supraorbital foramina. a: *Syncerus caffer nanus*, B. M. 91.3.26.1; b: *Bos gaurus*, B. M. 71.1430

15. The forehead is mildly concave in Boselaphines and most Bovids. It is strongly concave in *Bibos gaurus*, flat in most bovines, and broad and convex in *Syncerus* and *Bison* (as is the intercornual region) and, very occasionally, in *Bubalus*. It is difficult to determine the polarity of the changes here, except that convexity is obviously derived.

In the characters of the frontal region, the Buffaloes again appear primitive; the Bison however is less like true cattle than are Gaur, Banteng etc. One has the choice of regarding either postcornual shortening as convergent in *Bison* and *Bos*, or frontal elongation as convergent in *Bibos* and *Bos*; or in the latter case, a reversal of evolution, concomitant with frontal broadening and convexity, could have occurred in *Bison*.

C. Basal region

Under this head are combined, artificially, two characters whose functional significance is not at all obvious.

Fig. 4. Basioccipital tuberosities. a: *Bubalus arnee*, B. M. 30.10.5.1; b: *Bos gaurus*, B. M. 71.1430

16. The basioccipital tuberosities (or basilar tubercles) are flattened and inconspicuous in the Boselaphini. This is the case also in *Bubalus* (Fig. 4a), but they are somewhat more prominent in *Syncerus*, more so still in *Bison*, and prominent and ridged (especially the anterior pair) in *Bos* and *Bibos* (Fig. 4b). PILGRIM (1939) refers to this part of the basicranium, but his descriptions are not the ones that would spring to mind when confronted with actual specimens. The tuberosities are the site of insertion of *Mm. recti capitis ventrales major et minor*, which flex the head on the neck; their different development may therefore reflect differences in habitual head carriage.

17. In the midline the palatines are prolonged well behind the lateral borders of the palate (roofing over the posterior nares) in many Bovids, including Boselaphines. They are similarly prolonged, and somewhat thickened, in *Bibos*, but level with the lateral margins in most forms. The exception is *Bubalus*, where they are prolonged and thickened as in *Bibos*, and in addition firmly united to the vomer, thus completely dividing the nasal cavity. This character has long been known, and was the major one used by HOLLISTER (1911) for putting African and Asian Buffaloes in different genera; but it is not a very major step from a hypothetical *Bibos*-like condition.

D. Rostrum

Many, but not all, of these characters have to do with facial lengthening or shortening. It is likely that both processes have occurred within the Bovini.

18. The muzzle is noticeably broader in Buffaloes compared with other Bovini, with a broadened, flattened, lower surface to the premaxillae and anterior end of the maxillae. The only other form with an approach to this condition is the Yak; and it contrasts with the narrow muzzle of the Boselaphini, suggesting that this is a derived character for Buffaloes.

19. When viewed from above, the incisive foramina are long in most Bovines, and in Boselaphines, and disappear from view below the nasals; only in *Syncerus* (Fig. 2a) are they short enough to be wholly visible from above.

20. The infraorbital foramina on either side face laterally in Boselaphines and most Bovines: most markedly so in the Yak (Fig. 5a). Only in *Syncerus* (Fig. 5b) do they face forwards, perhaps (like No. 19) connected with shortening of the anterior snout.

21. The course of the lacrimo-maxillary suture in Boselaphines runs downward and forward from a very short, often point-like, naso-lacrimal suture, then turns more backward; and this occurs in the Buffaloes too. In all other Bovines, the course is evenly backward and downward, so that the anterior border of the lacrimal is more or less parallel to the posterior border, and the naso-lacrimal suture is approximately the same length as the naso-maxillary (see Fig. 5).

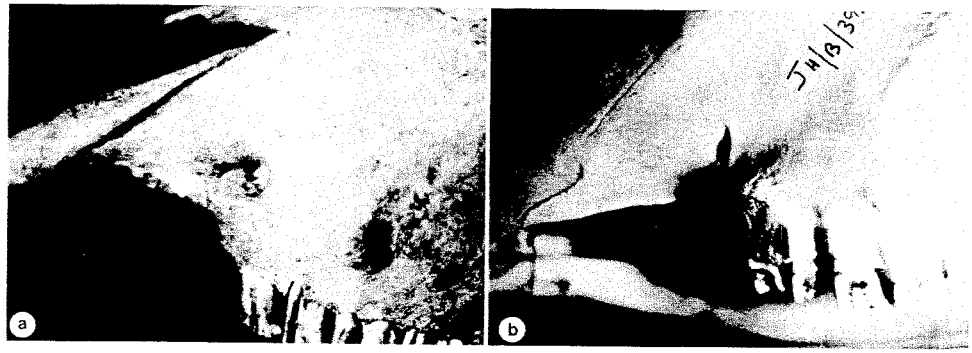

Fig. 5. Infraorbital foramen, left side. a: *Bos mutus*, B.M. 35.6.7.21; b: *Syncerus caffer caffer*, B.M. 67.1297

22. The naso-frontal suture is short, so that the nasals do not invade the frontals very far, in Buffaloes, as in Boselaphines; but the suture is long, the nasals deeply wedged in the frontals, in other Bovines (see Fig. 3).

23. Despite their evidently primitive status in the length of the suture, the Buffaloes would seem to be strongly derived in its shape, which is strongly convex and rounded and very different from the Boselaphines in which the two halves are straight or slightly concave, converging in an acute angle. Most other Bovines have the primitive condition; in the Yak, however, the angle is wider and blunter.

24. Facial lengthening has been accompanied by a reduction in its depth below the orbits in *Bison, Bibos* and *Bos*: the malar bone occupies less than half of the distance from lower margin of orbit to alveolar margin. The Buffaloes show the apparently primitive, Boselaphine condition, in which the malar occupies more than half the facial depth.

25. An ethmoid vacuity occurs, at least in the younger stages, in *Bison, Bibos* and *Bos*, but not in Buffaloes at any age. In Buffaloes and the Boselaphines, there is an extension of the frontal bone where the vacuity would be; when the vacuity is closed, with age, in *Bos* (etc.), it is covered by a protrusion of the lacrimal. As it does not occur in Boselaphines, its presence should be the derived condition. (It would appear to have arisen independently several times within the Bovidae.)

26. In the Boselaphines, the nasals widen anteriorly, as they do in Buffaloes, Gaur and Banteng; but in Bison, Yak, Kouprey and true cattle they are parallel-sided without anterior widening (the usual condition in the latter two forms) or narrow anteriorly fairly markedly (in the first two).

27. As in very many Bovidae, including *Tetracerus* but less markedly in *Boselaphus*, the free ends of the nasal bones are strongly bifid in *Bubalus*, Banteng and true cattle, such that the accessory (lateral) prongs are often longer than the main (medium) tips; but in *Syncerus, Bison*, Gaur, Kouprey and Yak the lateral prongs are short or absent – evidently a derived condition.

E. Tympanic region

Characters of this region have not been used as taxonomic differentiators before, but quite strong differences do none the less exist.

28. The paroccipital (paramastoid) processes are directed back and down in Bison, Yak, Kouprey and true cattle, as in Boselaphines; more backwards in *Bubalus*; and even more back, at an angle of 45 in *Syncerus*; and are shorter, thicker and largely downturned in Banteng and Gaur.

29. In all forms there is a downpointing flange of the tympanic (sometimes called the Acoustic Crest), running along its undersurface slightly behind the level of the auditory meatus. In Boselaphines this is short, adherent for its whole length to the anterior face of the paroccipital process, and retains this state in *Bison* and *Bibos* (Fig. 6a); in Kouprey, Yak and especially true cattle (Fig. 6b) it is longer, and so has a long portion free from the paroccipital process; while in *Syncerus* it is very long and almost totally free. In *Bubalus* (Fig. 6c), unlike other forms, there is a long posttympanic process distinct from the paroccipital, and the flange adheres to this.

30. The upper margin of the zygomatic arch kinks upward level with the glenoid fossa in the Gaur as in Boselaphines; but it remains flat in Buffaloes; and is somewhat upraised in other forms.

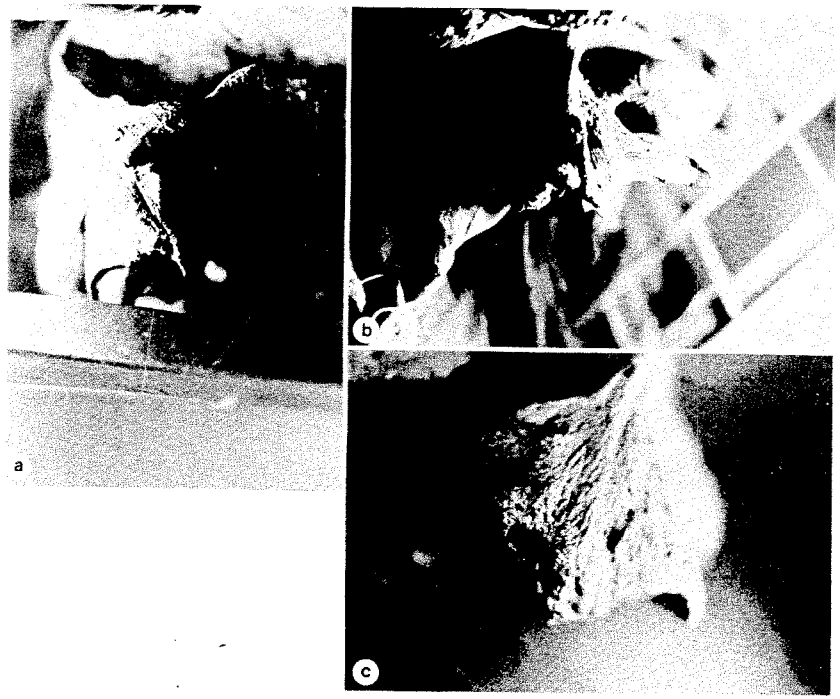

Fig. 6. Tympanic region. a: *Bos javanicus*, B. M. no history (right side). Paroccipital process is directed mainly ventrally, tympanic flange adheres to it for its whole length; b: *Bos primigenius* (or *namadicus*), B. M. 'Mysore ox' (left side). Paroccipital process is directed more posteriorly, tympanic flange has a longer free portion; c: *Bubalus arnee*, B. M. 30.10.5.1. Paroccipital process points mainly posteriorly, a bulky posttympanic process, to which tympanic flange adheres closely

Conclusions

1. Cladistic analysis

If polarity has been correctly interpreted in all cases, then out of 30 characters the number of derived character states is as follows: *Bubalus* 9, *Syncerus* 11, *Bison* 18, *Bibos gaurus* 17, *B. javanicus* 19, *B. sauveli* 24, *Bos mutus* 26, *B. primigenius* 22. Buffaloes are thus overall "primitive", and Kouprey (*contra* COOLIDGE 1940), Yak and true cattle are highly evolved.

Perhaps more important working out a family tree is to note which characters are derived in common, i. e. synapomorph. Buffaloes share few synapomorphies with any other bovine, including each other: *Bubalus* shares 7 with the Yak and *Syncerus* 8; *Syncerus* shares 6 with the Bison; no other figure is above 5. In contrast to this, there are never fewer than 13 synapomorphies between pairs within and between *Bison*, *Bibos* and *Bos*; and between Kouprey, Yak and true cattle there are 21 to 23 synapomorphies. The Bison and the Banteng each share 16–19 synapomorphies with the Kouprey-Yak-cattle group, and are about equally related to this group; the Gaur has fewer derived characters in common with them (13–16), in each case fewer than either Banteng or Bison.

This means, surprisingly, that the Gaur is likely to be less closely related to the true cattle than is the Bison. The only characters in which the gaur approaches the true cattle more than does the Bison are those of forehead elongation and the basioccipital tuberosities. It could be inferred from the position of the supraorbital foramina and the presence of accessory supraorbital foramina that frontal elongation occurred at one stage in the Bison lineage – as, unquestionably, did rostral elongation – and was partially reversed by a lowering of the horns and intercornual crest. The Bison resemble true cattle, Yak, Kouprey and Banteng in the weakening of the superior nuchal line (character 4), reduction of occipital:parietal ratio to 1.5:1 (No. 5), and perhaps flattening of forehead from a primitively concave state (No. 15), and flattening of the upper margin of the zygomatic arch (No. 30). If frontal elongation did indeed characterise Bison ancestors, then the Banteng too must be less closely related to the true cattle/Yak/Kouprey complex: Bison, but not Banteng, share with the latter the reduction of postcornual constriction (No. 3), nuchal ridge above lower margins of horn-cores (No. 8), nasal posterior broadening (Nos. 26), and form of paroccipital processes (No. 28). If the traditional view that Gaur and Banteng are closer to true cattle is maintained, all these features would have to be ascribed to convergent evolution.

There is even some doubt where the Bison should be placed with respect to the Kouprey and Yak. The Kouprey shares with Yak and Aurochs only the direction of the paroccipital processes (No. 28) and free tympanic flanges (No. 29) among derived characters which Bison do not share (excluding the frontal elongation characters); Bison shares with Yak and Aurochs an occipital:parietal ratio of more than 2:1 (Character 5), and staphylion brought forward level with lateral palatine borders (No. 17); Aurochs (true cattle) and Yak share the nuchal crest not laterally turned back (Character 6); Bison and Yak share the flat-topped intercornual ridge (No. 1) and tubular orbits (No. 14). It is at the present time not possible to resolve the interrelations between these four species by cranial features alone.

As far as the *Bos* lineage is concerned, then, the first branch to separate would seem to have been the Gaur, followed by the Banteng; the other four species are almost equally related. The whole group is characterised by the presence of an intercornual ridge; the lack of any backward slope to the braincase; the beginnings of frontal elongation with supraorbital foramina above the orbits, and multiple; a long fronto-nasal suture; presence of an ethmoid vacuity; rostral elongation, with a forward-sloping lacrimo-maxillary suture and a shallow malar bone; and prominent basioccipital tuberosities. This suite of derived characters is so clear and thoroughgoing, and the relations between the species of the lineage so close, that inclusion of the whole lineage within a single genus, *Bos*, is indicated: with no subgenera – *Bibos*, *Novibos*, *Poephagus* and *Bison* being synonyms. The alternative, to award a taxon of equal rank to each sister-group (though the usual practise in this type of analysis), would have *Bibos* Hodgson as a full genus for the Gaur alone; with all others being placed in a genus *Bos*, within which a subgenus for the Banteng (*Microbos* Heude, 1901) would have to be recognised, with other species going into a nominate subgenus *Bos*. But this scheme is too cumbersome, and divides too finely for the degrees of differentiation: in this instance, therefore, strict cladism must be tempered with practical considerations.

This leaves the Buffaloes. Although each does share some derived characters with other species, especially with the Yak, these can be seen, in the light of the homogeneity of the genus *Bos*, as parallelisms or convergences. Five synapomorphies characterise the Buffaloes as a whole: the at least incipient convexity of the forehead (character 15), though this is convergent with the Bison; muzzle broadening (No. 18); the convex, blunt-pointed naso-frontal suture (No. 23); the more backwardly-directed paroccipital processes (No. 28); and the flat upper margin of the zygomatic arch (No. 30). The concept of "buffalo" does, therefore, have some validity in monophyletic terms.

The differences between the African and Asian Buffaloes are nonetheless numerous and well-marked: they are much more distinct than are any of the species in the expanded genus *Bos*, and their universal separation as *Syncerus* and *Bubalus* respectively is justified. *Syncerus*

has backwardly-produced lateral edges to the occipital crest; staphylion level with lateral palate borders; highly convex, rugose forehead; nasal free ends hardly bifid; shortened muzzle and incisive foramina; forward-facing infraorbital foramen; long free tympanic flanges; and more prominent basioccipital processes. *Bubalus* has the occipital element enlarged compared to the parietal, convergent with some species of *Bos;* somewhat tubular orbits, also convergent on species of *Bos;* and vomer fused with palatines.

2. Other anatomical characters

The presence of a forward kink (overall S-shape) of the horns in cattle, Yak, Kouprey and Bison forms a definite link between them and distinguishes them from Gaur, Banteng and Buffaloes. The cross-section of the horns has long been used as a definitive character: triangular in the Buffaloes (but lacking keels in *Syncerus*); oval in Gaur, Banteng and Kouprey, becoming circular 10–20 cm from the base; rounded-oval in Yak and Bison; and circular, lacking keels, in Aurochs and its domesticates.

Bison and Yak have (usually?) 14 thoracic vertebrae and 5 lumbars; all other species have 13 thoracic, 6 lumbars. This could be (and has been) used as evidence of a close relationship between Bison and Yak; but no survey has ever been made to determine whether the differences are absolute or only a matter of frequency, despite being first noticed as long ago as 1841, by HODGSON.

In the Gaur and, to a less marked degree, the Banteng the neural spines of Thoracics 3 to 5 are very elongate; there is then a gradual reduction to T. 10, followed by a sudden drop to T. 12. In cattle, Bison and Yak, the reduction from T. 3 to T. 13 is much more gradual. This, again, was first noticed by HODGSON (1841). The Kouprey resemble true cattle (COOLIDGE 1940). In Buffaloes the spinal elongation extends over the whole thoracic region but is not at all prominent.

Buffaloes, Gaur, Banteng and cattle (POCOCK 1918), and Kouprey (COOLIDGE 1940), have a large rhinarium with broad, slightly grooved philtrum. Bison and Yak have a rhinarium which is, by contrast, more overgrown with hair, leaving only a narrow bare strip around the nostrils, as well as the philtrum; in the Yak the muzzle is low and broad, and the philtrum narrows above the lip, whereas in the Bison it expands near the lip. The rhinarium is black, except in the Gaur where it is white: a peculiarity which seems to have passed unnoticed previously.

The penis of "*Bibos*" and Yak has a short urethral prolongation not found in other Bovines (POCOCK 1918).

In Gaur, Banteng, Kouprey and many *Bubalus* (wild *B. arnee*, and *B. depressicornis*) the legs are white from just above the knees and hocks down to the hoofs. The occurrence of this distinctive colour pattern in diverse members of the tribe suggests that it is primitive for the Bovini as a whole and, where it is lacking, has been lost. The pale dorsal stripe of aurochs and Kouprey may be a derived character linking these two, as may the elongated dewlap. The long hair and beard of the Yak and Bison may, equally, link these together.

The karyotypes of Bovini are very interesting. In all Buffaloes the fundamental number is 60 and the X chromosome is a large acrocentric; in *Bos* (as here defined) N. F. is 62, the X a large metacentric. Other differences in karyotype, except perhaps for a dubious difference in the (very small) Y chromosome, can be put down to simple Robertsonian changes. 2n is 60 for all *Bos* except the Gaur, in which it is 58 (WURSTER and BENIRSCHKE 1963); it is 54 in *Syncerus caffer nanus,* 52 in *S. c. caffer,* 50 or 48 in *Bubalus arnee* (different domestic breeds), 48 in *B. depressicornis* and 46 in *B. quarlesi* (KOULISCHER et al. 1972).

From a consideration of characters other than cranial, therefore, there emerges some slight support for the possibility that within the *Bos* "terminal tetrachotomy" there could be a special kinship between Bison and Yak, and between Aurochs and Kouprey.

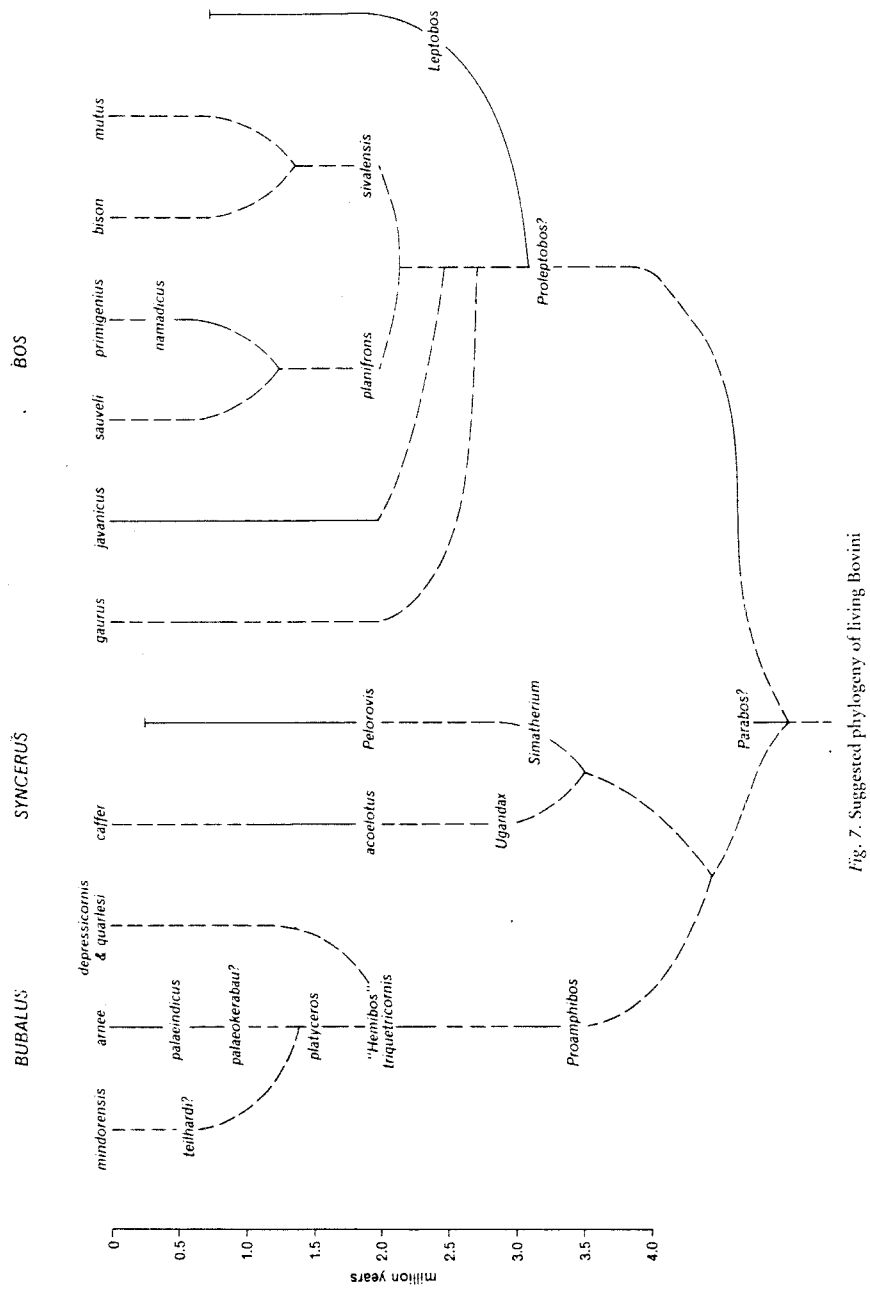

Fig. 7. Suggested phylogeny of living Bovini

3. The fossil record

The fossil record can now be used both as a testing ground for the hypothesis outlined above, and – if consistent with the hypothesis – as a means of placing absolute dates on the nodal points.

The earliest fossil to show vomer-palatine fusion is *Proamphibos* from the upper Dhokpathan Formation of the Siwaliks, India (PILGRIM 1939). Absolute dates are lacking for this area, but faunal comparisons with elsewhere suggest some 3.5 million (middle Pliocene) for the latest Dhokpathan (PILBEAM et al. 1977). It is succeeded in later deposits by *Hemibos*, which scarcely differs from *Bubalus*: especially the subgenus *Anoa* with which it could perhaps be united in synonymy.

The African buffalo lineage has recently been traced by GENTRY (1978). The earliest member would be *Ugandax*, known from Hadar (3 m. yr.) and from Kaiso (date unknown, but probably earlier). GENTRY notes its close resemblance to *Proamphibos*, and that it differs in (among other things) the reduced keels on the horn cores. The Syncerine lineage had, however, already split, with *Simatherium* (known from Laetolil, 3.5 m. yr., and Langebaanweg, probably earlier) contemporaneous with *Ugandax*, and its descendant *Pelorovis* contemporaneous, at Olduvai, with early *Syncerus*. The basic Syncerine characters of horns, nasals, occiput and facial shortening are equally well shown by *Pelorovis*.

Leptobos (Pinjor Formation, Siwaliks and Sahabi, Libya) and doubtless *Proleptobos* (from a presumed Dhokpathan equivalent, Burma) are allied with the *Bos* lineage by virtue of the presence of an ethmoid vacuity, prominent basioccipital tuberosities, and oval-sectioned horn-cores (PILGRIM 1939; GENTRY 1978). Its long parietal, forming a considerable part of the roof of the braincase, indicates its primitive status; and the anterior broadening of the nasals and their acute angulation into the frontals confirm that these characters are primitive for *Bos*. The characters of the *Bos* lineage were therefore established as early as those of the other two. BOHLKEN (1958) and SOKOLOV (1959) describe *Urmiabos* from Maragha, Iran (probably late Miocene, about 7.4 m. yr. according to BERGGREN and VAN COUVERING 1974) as having an angle between parietal and frontal, and horn cores which are oval in section and have some forward curvature, and whose lower edges are below the upper border of the occipital crest. These characters, as BOHLKEN and SOKOLOV remark, recall aurochs and Yak; they would also recall Bison and Kouprey. Without further evidence it cannot at present be substantiated that the Gaur and Banteng lines were already separate, and indeed it seems somehow implausible; yet the possibility must be borne in mind.

In the Pinjor Formation of the Siwaliks occur both "*Bison sivalensis*" with the characteristic Bison-like occiput and broad flattened intercornual region, and *Bos planifrons* (= *Bos acutifrons* of PILGRIM) with its shortened parietal, excluded from the braincase roof, and shortened median palatines. The "terminal tetrachotomy" had thereby already begun. The middle/upper Pleistocene *Bos namadicus* is, as COOLIDGE (1939) indicates, close to *Bos primigenius* but shows some (primitive) characters recalling the Kouprey: these two species had evidently, therefore, become separate.

Typical Banteng characters, except for the absence of the sexual dimorphism so characteristic of the modern species, occur in the *Bos javanicus* lineage as far back as the Pucangan Formation (about 2 m. yr.) of Java (HOOIJER 1958); a typical Gaur occurs in the Middle Pleistocene of Szechwan, China (COLBERT and HOOIJER 1952). These two lineages cannot yet be traced back any earlier.

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Summary

The craniology of the Bovini yields clear data on the interrelationships of the species of that Tribe. The characters can be arranged according to their primitive or derived state, and with a considerably degree of concordance. The results show that there are three clear-cut genera among living Bovini: *Bubalus, Syncerus* and *Bos*, the first two being somewhat closer together than either is to *Bos*. Within the latter, the most distinctive species phyletically is not the Bison, as commonly assumed, but the Gaur; the Banteng is the next most distinct, with Bison, Yak, Kouprey and Aurochs forming a cluster whose relationships, approached by considering non-craniological characters, appear to be of the pattern Bison/Yak, and Kouprey/Aurochs. Data from other sources, such as karyology and palaeontology, appear consistent with the scheme proposed.

Zusammenfassung

Systematische Beziehungen innerhalb der Bovini (Artiodactyla, Bovidae)

Eine Analyse von Schädelbesonderheiten der Bovini ermöglicht Einsichten in die phylogenetischen Beziehungen der Arten. Primitive, abgeleitete und weitgehend übereinstimmende Merkmale lassen sich unterscheiden. Nach den Befunden werden 3 Gattungen anerkannt: *Bubalus*, *Syncerus* und *Bos*. Die beiden erstgenannten Gattungen stehen einander näher als jede von ihnen zu *Bos*. Innerhalb der Gattung *Bos* ist nicht, wie meist angenommen, *Bos* die phylogenetisch am höchsten entwickelte Art, sondern der Gaur; danach kommt der Banteng. Bison, Yak, Kouprey und Auerochse stellen eine Gruppe dar, in welcher, wenn auch nicht-kraniologische Merkmale berücksichtigt werden, Bison/Yak und Kouprey/Auerochs engere Beziehungen zueinander haben. Daten aus anderen Bereichen, so der Karyologie und Palaeontologie, stehen mit diesem Schema im Einklang.

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