A note on the systematic position of the Muntjac (Artiodactyla, Cervidae)

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The Muntjac and its relatives the Tufted deer (genera Muntiacus and Elaphodus) have always been assigned an isolated position among the Cervidae. It is true that they bear a fairly close resemblance to certain Miocene genera such as Euprox, but at the same time their relatively primitive features should not be allowed to obscure any similarities they may have with more specialised, recent groups.

Because of their supposed isolation, generally resulting in the muntjac being assigned a separate subfamily (Muntiacinae or Cervulinae), a consideration of their relationship may help to clarify the systematics of the living Cervidae as a whole. A brief summary of the history of the classification of this group will therefore be given.

The earliest attempt to split up the Cervidae into groups was by BROOKE (1878), who proposed a basic division into Plesiometacarpi (deer in which the rudiments of metacarpals II and V are retained at the proximal end of the cannons) and Telemetacarpi (in which it is the distal ends which are retained). To the first group belonged the muntjac and the Red Deer group; to the second, all the other deer. BROOKE also pointed out certain other features which help to divide up the Cervidae: division of the choanae, position of the metatarsal tuft, and premaxillary-nasal articulation. These subsidiary features did not, however, entirely agree in their distribution with the metacarpal characters, as BROOKE himself noted.

LYDEKKER (1915) did not divide up the Cervidae beyond putting the Musk deer (Moschus) into a subfamily of its own: but these latter are today not considered true deer in any case and are placed in a family, Moschidae, of their own (Flerov 1952).

POCOCK (1923) proposed a division into eight subfamilies of the Cervidae; his prime division being between the Plesiometacarpal and Telemetacarpal groups. Within the Telemetacarpal group, he used the character of the vomer mentioned by BROOKE to separate the Pudinae, Odocoileinae and Rangiferinae from the Hydropotinae, Capreolinae and Alcinae; with the Plesiometacarpal group he distinguished two subfamilies, Cervinae and Muntiacinae, on the grounds that 1. in the latter the naviculo-cuboid and external and median cuneiforms are all fused together, 2. the male muntjac has a long, daggerlike canine whereas cervine stags have the upper canine absent or minute, 3. the antler pedicels are very long in Muntiacinae, short in Cervinae.

SIMPSON (1945) also makes the Plesio- vs. Telemetacarpal division the primary one in his classification, recognising two large subfamilies, Cervinae for the Plesio- and Odocoileinae for the telemetacarpal groups, and two small ones, Moschinae (now removed from the Cervidae altogether: see above) and Muntiacinae. The theoretical standpoint therefore seems to be that BROOKE's divisions are of prime importance,

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except that the muntjac group is too primitive to be allowed to take its place in its respective group (which would be the plesiometacarpal group, the Cervinae of

The system adopted by Flerov (1952) is totally different from any of these. Roundly criticising SIMPSON for in effect making a division of the Cervidae on the basis of a single character, he uses skull-characters to reshuffle the various genera while retaining two subfamilies with the same nuclei as SIMPSON. Basically, Alces and Capreolus are now transferred to the Cervinae and Hydropotes is made the type of a special subfamily, Hydropotinae; the residue of the New World deer plus Rangifer are retained in a subfamily Neocervinae (basically, SIMPSON's Odocoileinae).

We thus have now two large subfamilies, distinguished by the presence or absence of a vomerine septum in the nasal cavity (and other skull characters) instead of by the metacarpal rudiments, and two "primitive" subfamilies instead of one. The main contribution in this scheme was to show that Alces and — more especially — Capreolus are really quite closely related to the Cervus group in spite of their metacarpal types. But still the muntjac is excluded because of its claimed primitive status, and indeed a second subfamily has now been erected on a similar basis.

The arrangement of HALTENORTH (1963) returns to a scheme like that of POCOCK, with a number of subfamilies rather than a basic division. Although Capreolus is retained in the Odocoileinae, both Alces and Hydropotes have been raised to subfamily rank, in addition to Rangifer; a curious move, as both SIMPSON and FLEROV agreed that this genus is close to Odocoileus and the true New World deer.

Two other studies that need to be mentioned, as they provide further bases for systematic conclusions without however, themselves making new subfamilial arrangements, are those of Pocock (1935) and Meunier (1963). The former is a survey of incisor forms in Cervidae, and has been subsequently extended by HALTENORTH (1963); the latter is a study of skull angles, especially the basicranial angulation.

If we take the results of all these studies together, character by character, we find

very definite indications as to the relationships of the muntjac group:

1. Like the Cervinae (Cervus, Elaphurus etc.), muntjac are plesiometacarpal; they are, moreover, the only other deer which are. As this implies a virtually nonfunctional role for the lateral digits - since these do not articulate with the lateral metacarpal rudiments — it seems likely that this is a strong specialisation. Indeed in Muntiacus, though not in the closely allied Elaphodus, the lateral digits are more or less absent and have no skeletal elements.

2. Again like the Cervinae, the choanal opening is undivided. In this case we have probably a resemblance due to retention of a primitive (symplesiomorph) condition; it is shared with Alces, Capreolus and Hydropotes, while the Odocoileinae have a specialised condition in which the vomer extends dorsally to fuse with

the palatines, making a septum for the nasal cavity.

3. The basicranial axis is straight as in the Cervinae, Alces, Capreolus and Hydropotes, and contrasts with the typical Odocoileine condition which shows lordosis.

4. The anterior ends of the premaxillae are rounded as in the Cervinae and in the three genera listed above, not notched as in the Odocoileinae. This, like (2), may

well be a primitive character.

5. The angle between the palatal plane and the pharyngeal skull-base plane (MEUNIER 1963) is below 165° in Muntiacus as in the Cervinae. In this case, some of the Odocoileinae show values also under 165°, but the three other Old World genera mentioned above have values above this.

6. The choanal height angle lies between 10 and 15° as in the Cervinae and most of the Odocoileinae; Alces has an angle in this range, but in Hydropotes and certain Odocoileines it is lower, while in Capreolus alone in the family it is above 15°.

- 7. The rhinarium is large, enclosing the nostrils, in *Muntiacus*; this is likely to be a primitive character as only cold-adapted deer (*Alces, Rangifer, Pudu*) have smaller rhinaria.
- 8. The incisors show a characteristic size relationship in various deer. In muntjac, as in Axis and Dama (two of the cervine group), the breadth of I₁ is greater than the combined breadth of the other two incisors and the canine. In the other cervines, as well as in Hydropotes, I₁ breadth is about equal to the combined breadth of I₂ and I₃, or equal to these plus the canine. Capreolus falls into this group as well. But in the Odocoileinae and in Alces, the size discrepancy is far less, I₁ being only half the combined breadth of the other incisors plus the canine, and in some cases not much broader than I₂ alone.
- 9. The pedal glands of the hindfoot are long and deep in muntjac, as in *Dama* and *Axis*, *Hydropotes*, and some odocoileines (*Pudu* and *Mazama*). In other deer they are simple and pocket-like, but in other cervines (*Cervus*, *Rusa* etc.) lacking altogether.
- 10. The special features of muntjac are in most cases only exaggerations of tendencies already present in other deer, especially the Cervinae:
 - a. The nasal bones are very short, and fail to reach back to the level of the orbits. This character is less marked in *Elaphodus*, and foreshadowed in some individuals of other genera, e.g. *Axis*.
 - b. The orbits are not tubular like those of most deer. This seems to be partly dependant on size; in *Hydropotes*, *Pudu* and *Mazama* there are also non-tubular orbits, and those of *Axis porcinus* and some of the small Philippine *Rusa* are less so than most.
 - c. The long, dagger-like upper canines of males are shared only with *Hydropotes* among the Cervidae, and in the latter they are much more strikingly developed. Some deer have lost the upper canines entirely, which is why those of muntjac are so conspicuous, but small ones are regularly present in the Cervinae (except *Dama*) and in some Odocoileinae.
 - d. The facial "ribs" of *Muntiacus* downward prolongations of the antler pedicels and the great length of the pedicels themselves are only the extreme development of tendencies common among the smaller Cervinae (e.g. *Axis porcinus*, *Cervus nippon*,) and are seen much more exaggerated in *Muntiacus* than in *Elaphodus*.
 - e. The extensive fusion of tarsal bones is not seen in any other deer except *Pudu*, in which the medial cuneiform is still free, and in which, in any case, it is likely to be convergent. This is therefore a real special feature of muntjac.

An examination of a number of features has, therefore, shown that there is no reason to exclude *Muntiacus* from the Cervinae; it is indeed probably closer to the central group of cervina genera — Cervus, Axis, Dama, Elaphurus — than Alces, probably even than Capreolus. It is probable that Hydropotes is another member of this subfamily, though an aberrant one owing to its total lack of antlers: the question of this remarkable genus is more difficult it being uncertain whether its resemblance to the Cervinae are due to common retention of primitive features or not. But in the case of Muntiacus there is no doubt.

Summary

A survey of the features used to divide the subfamilies of Cervidae shows that the muntjac, *Muntiacus* and *Elaphodus*, are true cervines, and rather closely related to *Cervus* and its allies. There is no reason to refer them to a separate subfamily as has been done by almost all authors up to now.

Zusammenfassung

Eine Notiz über die systematische Stellung der Muntjacs (Artiodactyla, Cervidae)

Ein Merkmalsüberblick beschäftigt sich mit den Unterschieden der Unterfamilien innerhalb der Cervidae. Dabei zeigt sich, daß die Muntjacs Muntiacus und Elaphodus mit Cervus und dessen Verwandten eng verbunden sind und somit echte Cervinae darstellen. Es gibt keinen Grund, eine eigene Unterfamilie Muntiacinae aufzustellen, was bislang fast jeder Verfasser tat.

Résumé

Une note sur la position systématique du Muntjac (Artiodactyla, Cervidae)

Un aperçu sur les charactères employés à diviser les sous-familles des Cervidae a montré que les muntjac, *Muntiacus* et *Elaphodus*, sont des vrais cervinés, étroitement affinés à *Cervus* et ses parentés. Il n'y a pas de raison pour les separer en une sous-famille spéciale, comme a été fait par presque tous les auteurs jusqu'à maintenant.

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