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On functional fusions in footbones of Ungulates

By J. J. M. LEINDERS and P. Y. SONDAAR

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Introduction

During evolution, especially in the Orders Artiodactyla and Perissodactyla we find a reduction of number of footbones, elongation of the metapodials and phalanges and sometime fusions of bones.

Those changes can be explained functionally: to provide the animal with a locomotion which is more efficient in running. Usually the tibia and fibula, radius and ulna fuse tightly together, which restricts the lateral movement and the motion is confined to the sagittal plane. In the ruminantia we find also the metapodials of the third and the fourth digit joined into one cannon bone. Some of the carpals and tarsals fuse also like navicular and cuboid, trapezoid and magnum, giving the carpal and tarsal joints more strength to lateral movements.

The fusions cannot be followed step by step due to fact that the fossil record is not complete. Probably the changes, or in other words the selection of the genetically fixed favourable fusions, take place in a rather short period.

The purpose of this paper is to describe some less common fusions in Perissodactyla and Artiodactyla and further to attempt to give a functional analysis, and the evolutionary meaning of those fusions.

Material studied

Parahippus blackbergi stored in University of Florida, and the Museum of Comparative Zoology, Harvard.

Phanourios minor and *Cervus cretensis* stored in the Geological Institute, Utrecht.

Myotragus balearicus stored in the British Museum of Natural History and Deya Archeological Museum.

Cervids from Gargano, stored in the Rijksmuseum voor Geologie, Leiden. Recent comparative material from several museums.

Magnum with trapezoid in equids

In three of the fifteen available magnums of *Parahippus blackbergi* from the miocene of Thomas farm (Florida), the trapezoid is completely fused with the magnum (plate I, fig. A), while in the others the bone structure where the two bones are in contact, suggests that there was no movement between the bones. This was learned from the posterior part of the trapezoid and magnum. On the magnum we find at the medial posterior side a tuberosity which must have been in contact with a similar tuberosity on the trapezoid. This contact was not a facet as found in *Equus* (SONDAAR 1968) but a rough area.

If we try to analyse the functional meaning of this fusion in *Parahippus*, it is necessary to consider the bones separately. The scaphoid transfers the weight from the body to the magnum and trapezoid and those bones shift the weight to the third and second metacarpal respectively.

During the evolution of the horse we see a relative reduction of the second digit after a major change between the Anchitheriinae and Hipporioninae (SONDAAR 1969).

The genus *Parahippus* was the first representative in the family of the Equidae in which this change occurred, namely the lateral flexibility of the foot became restricted; further a clear lengthening of the central phalanges lifted the foot from the ground and led to loss of its pad.

The function of the lateral metapodials became reduced. When we follow the changes from *Parahippus* towards *Equus* we see, by changes in shape, size and position of the articulation facets of carpal bones, that more and more weight will be shifted towards the central metacarpal.

This is evident when we follow the changes in the trapezoid. In *Equus* for example this bone has a clear facet, on the posterior side, articulating with the third metacarpal so more of the weight is borne by this metacarpal.

The contact between the trapezoid and magnum is always by clear articulation facets. The described fusion in *Parahippus blackbergi* is clearly an exception in the phylogeny of the horse. This fusion can be explained in two different ways; pathological or functional. Though the fusion is complete, in only three of the fifteen magnums. We can exclude the pathological explanation as all other specimens show that there was no movement between magnum and trapezoid and the whole population cannot have been pathological. A good functional explanation exists: by fusion of the trapezoid and magnum more of the weight is borne by the third metacarpal at an evolutionary stage in which the function of the second metacarpal was reduced. We may mention a relevant parallelism with the Ruminantia in which the trapezoid and magnum are also fused (YALDEN 1971) but here this fusion is total. Concluding we may say that the fusion of trapezoid and magnum had a functional meaning to transfer more weight to the central metacarpal and in this *Parahippus blackbergi* was more advanced than the recent *Equus*. The question why this configuration which proved to be so successful in Ruminantia failed in the Equidae must stay open. Of course

we can speculate that the *Parahippus* of Florida was local evolved and isolated branch of the equids which failed to invade central North America by a less adapted chewing mechanism.

Navico — cuboid with the cuneiformes and the metatarsals in ruminants

Common characters of the fossil ruminants from the mediterranean islands are a secondary shortening of the lower part of the leg, a short skull, hypsodont teeth and further fusion of the tarsal bones. We observed these characters in:

- a. *Myotragus balearicus*, a bowid from the pleistocene of Mallorca.
- b. *Cervus cretensis*, a deer from the pleistocene of Crete.
- c. *Cervus elaphus* var. *barbarus*, a deer from the pleistocene of Malta.
- d. A still undescribed deer from the miocene of the Gargano region in Italy (FREUDENTHAL 1971).

It is remarkable that these skeletal characteristics occur in different families of the artiodactyla, on different islands and in deposits with a different geological age.

Normally in ruminants the following tarsal bones are fused:

- a. Metatarsus III and IV (cannon bone)
- b. Navicular and cuboid (navico-cuboid)
- c. Cuneiforms II and III (great cuneiform)

The further fusions of the tarsal bones from the ruminants of the endemic islands faunas are:

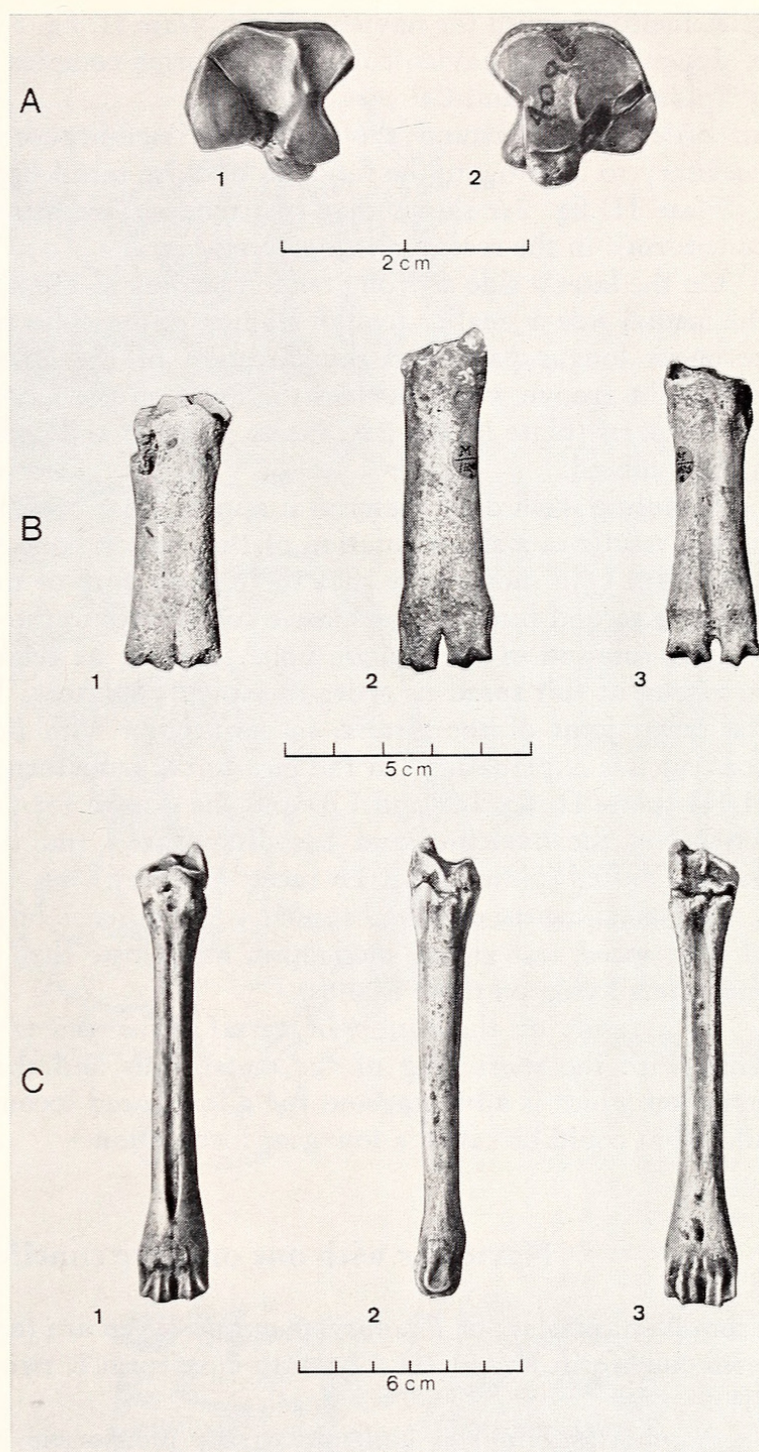


Plate I. A = *Parahippus blackbergi*, University of Florida, coll. no. 4096, magnum fused with trapezoid sin. 1 = proximal view; 2 = distal view. — B = *Myotragus balearicus*, British Museum coll. no. 1106, navico-cuboid-cuneiforme complex fused with the cannon bone dorsal views. 1 = juvenile individual; 2 = young individual; 3 = adult individual. — C = *Cervus cretensis*, coll. Geol. Inst. Utrecht, navico-cuboid-cuneiforme complex fused with the cannon bone dext. 1 = dorsal view; 2 = lateral view; 3 = volar view.

d. Cuneiforms with the navico-cuboid (plate II, fig. 3)

e. Frequently this navico-cuboid-cuneiforme complex is fused with the cannon bone (plate I, fig. B and C)¹

In order to understand the functional significance of these further fusions it is necessary to investigate the function of these tarsal bones in recent ruminants.

Plate II, fig. 2A shows that two tendons are attached to the cuneiform I (small cuneiform): in the recent *Antilope cervicapra*.

On the lateral side a strong tendon leading to the musculus peroneus longus and on the medial side a smaller tendon leading to musculus tibialis. The tendon of musculus peroneus longus passes, in the direction of the lateral side of the navico-cuboid, through a groove which divides the facet on the navico-cuboid for the cannon bone in two parts (plate II, fig. 2A, facets d and e) and continues on the lateral side of the navico-cuboid.

Handling fresh dead material it appears that contraction of the musculus peroneus longus results in a slight rotation of the cannon bone caused by the movement of the cuneiform I, in such a way that the plantar face of the foot turns to the lateral side and as a second function the muscle contributes to the extension of the tarsal joint.

This rotation of the cannon bone seems to be related to the ability of ruminants to zigzag at full speed in order to escape predators. The contrasting construction of the tarsal joint of the giraffe, in connection with its inability to zigzag, seems to confirm this explanation. In the giraffe the cuneiform I is fused with the cuneiform II/III (plate II, fig. I A and I B) and the groove for the tendon of musculus peroneus longus on the navico-cuboid has disappeared and the facets for the cannon bone become united (plate II, fig. I B facets d and e).

A typical aspect of island faunas is the absence of predators and as a consequence of this, speed and zigzag mechanism have lost their functional significance for the ruminants living on those islands.

As a result of the fusion of tarsal bones the tarsal joint becomes more solid. This, with the shortening of the metatarsals and the phalanges, gives a foot construction which is advantageous for a low speed locomotion in a varied environment and what could be called a low gear locomotion.

Navicular with one or more cuneiforms in hippos

From 25 naviculars of *Phanourias minor*, seven are fused with the cuneiform III, one with cuneiform II and III, one with cuneiform I, two with all cuneiforms (I, II and III).

Phanourias minor is endemic to the pleistocene of Cyprus and most probably descended from *Hippopotamus amphibius*. In the fossil and recent Hippopotamidae such fusions are otherwise unknown. BOEKSCHOTEN and SONDAAR (1972) note in *Phanourias minor* that the movement in lateral sense of the legs are restricted, but more extended in anterior-posterior sense than in *Hippopotamus amphibius*. This is learned from the tarsal joint where the movement between cuboid and navicular is more restricted while more movement between these two bones and the astragalus is possible in anterior-posterior direction. In this the hippo from Cyprus resembles *Hippopotamus creutzburgi* from Crete. This change in movement of the joints can be explained by an adaption to an island life where natural meadows along big rivers were absent and so a locomotionary system adapted to walking, to reach the more rugged grazing sides was a necessity, BOEKSCHOTEN and SONDAAR (1966).

¹ The first author has the intention to give quantitative data in a further publication.

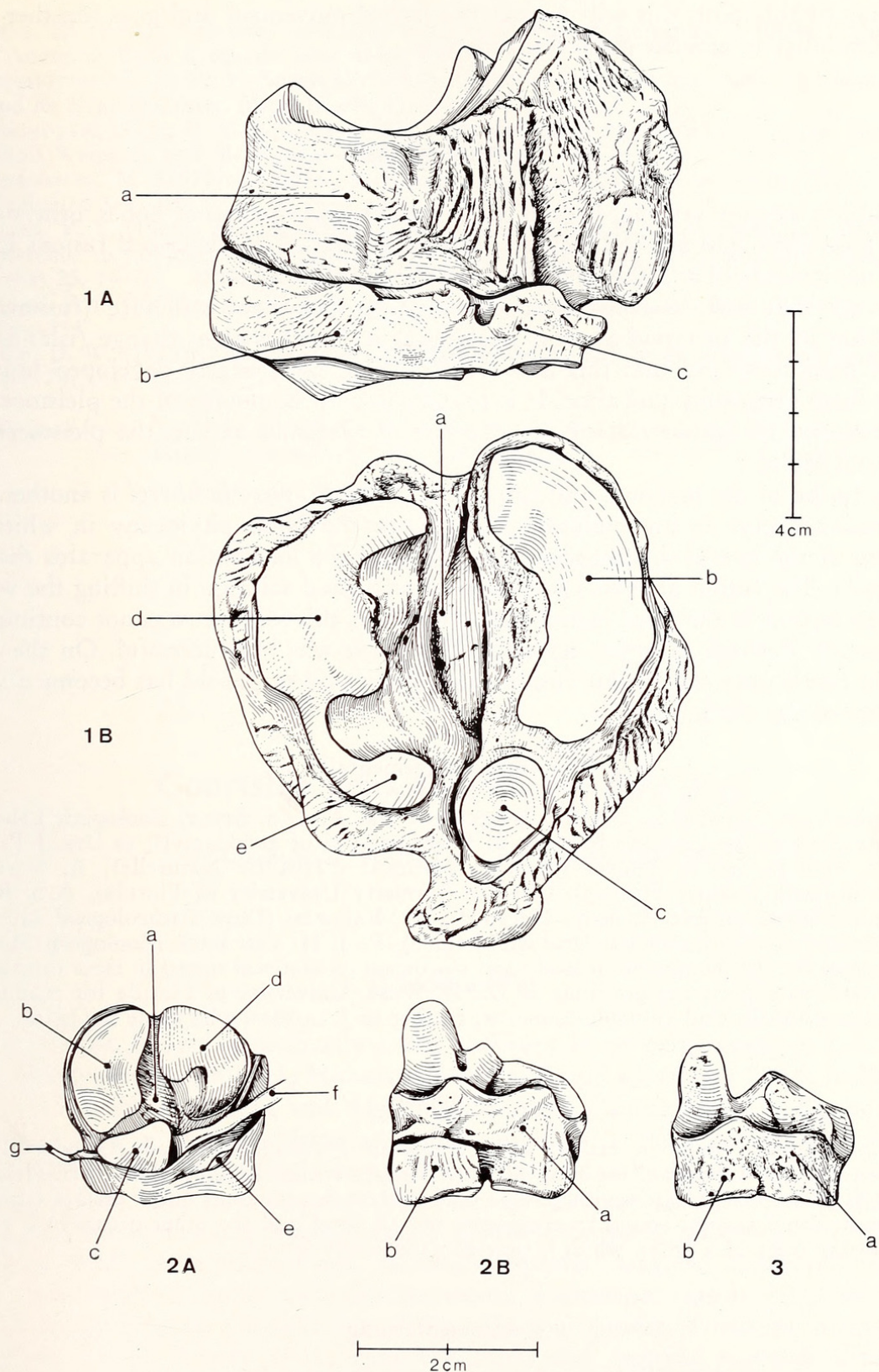


Plate II. — Fig. 1. *Giraffa camelopardalis* dext. Coll. Zool. Museum, Amsterdam (No. 964). A = medial view; B = distal view. — Fig. 2. *Antilope cervicapra* sin. Coll. Geol. Inst. Utrecht. A = distal view; B = dorsal view. — Fig. 3. *Cervus cretensis* sin. Coll. Geol. Inst. Utrecht, dorsal view. a = navico-cuboid; b = cuneiforme II/II; c = cuneiforme I; d = anterior facet for the cannon bone; e = posterior facet for the cannon bone; f = tendon leading to musculus peroneus longus; g = tendon leading to musculus tibialis.

The explanation or consequence of the fusion in the tarsus can be sought in a stiffening of the joint, this will restrict the lateral movement and goes together with more flexibility in anterior-posterior direction.

Conclusions

Concluding we may say that besides the general known fusions of bones, others occur which must have had also a functional meaning. One of the described fusions is that of the navico-cuboid and the metatarsals in the island ruminants.

We see that such specialized runners evolve their foot structure (fusions and shortening of the metapodials and phalanges) if circumstances change (islands and lack of predators) and that this new structure will be similarly developed independently from geography and time. It is found so far in the bovids of the pleistocene of Mallorca and in the cervids of the miocene of Gargano and in the pleistocene of Crete and Malta.

The fusion of the magnum and trapezoid in *Parahippus blackbergi* is another case. This fusion occurs in an evolutionary stage in the horse phylogeny in which the function of the lateral digits become reduced and the locomotion apparatus changed essentially. The fusion of these two bones seems a good solution in shifting the weight from the second to the third metapodial. However, this solution was not continued in later horses. Perhaps in other characters this horse was less successful. On the other hand in ruminantia the similar fusion of magnum and trapezoid has become a stable character of the whole group.

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Summary

Some uncommon fusions in tarsals and carpals in Perissodactyla and Artiodactyla are described and the functional meaning of those fusions is discussed. In the described fusions two kinds of origins are distinguished. One kind evolves in ruminants under certain ecological conditions (those are not bound to geography nor to time) and the other occurs in a certain evolutionary stage of a group which is time-geographically-bound.

Zusammenfassung

Funktionelle Verwachsungen von Fußknochen bei Ungulaten

Einige ungewöhnliche Verwachsungen von Tarsal- und Carpalknochen bei Perissodactyla und Artiodactyla werden beschrieben, und die funktionelle Deutung dieser Verwachsungen wird diskutiert.

Die beschriebenen Verwachsungen kann man sich wie folgt entstanden denken: Eine Art entsteht bei den Ruminantia unter bestimmten ökologischen Bedingungen, die nicht geographisch oder zeitlich gebunden sind. Die andere Art kommt in einer Phase der Evolution einer Gruppe vor, die sowohl geographisch als auch zeitlich gebunden ist.

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Courtship behaviour of the wild goat

By GEORGE B. SCHALLER and ANDREW LAURIE

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Introduction

The wild goat, known scientifically either as *Capra hircus* or *C. aegagrus* (see ELLERMAN, MORRISON-SCOTT 1951; HARRISON 1968) is found on several Greek islands, in parts of Turkey, Iraq, Iran and Afghanistan, in the Caucasus and Turkmenia areas of Russia, and in the Baluchistan and Sind provinces of Pakistan. Because the wild goat of Pakistan supposedly lacks prominent knobs on the horns, and is said to be smaller in size, and have a paler coat than the animals farther west, it has been given the subspecific name *blythi* (LYDEKKER 1900). However, as STOCKLEY (1928) and ROBERTS (1967) have pointed out, the two subspecies (*aegagrus* and *blythi*) of wild goat are so similar in appearance that taxonomic distinctions may be unjustified. Published observations on the behavior of the wild goat consist of natural history notes (DANFORD 1875; WAHBY 1931; ROBERTS 1967) and hunting accounts (STOCKLEY 1928; MAYDON 1937). To add to the meager knowledge of this species, we studied one population in the Karchat Hills, western Sind, Pakistan, from September 6 to October 3, 1972.

The Kirthar Range borders the Indus plain along its southwestern margin. Near the southern tip of this range, at 25° 50' N, 67° 40' E, are the Karchat Hills, an isolated massif some 20 km in length and 6 km in width. The hills consist of a central convex plateau, 1030 m above sea level at the highest point, whose edges drop 300 m or



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