

## Adaptive evolution of the equid foot

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The mode of evolution of equid foot anatomy and locomotion has repeatedly been subject for inquiry. CAMP and SMITH (1942) studied the phylogeny and function of the digital ligaments, ROBB (1936) and FORSTEN (1968, 1973) proportions of the distal limb bones, and SONDAAR (1968) anatomy and function of the front foot. The mode of inception of different locomotive adaptations in the Equidae is not fully known; the present paper is a discussion of some changes observed in fossil equids at the shift to monodactyly, and of parallel adaptations in a persistently tridactyl genus.

CAMP and SMITH (1942) and SONDAAR (1968) showed that in pad-footed tridactyl horses, i. e. the sub-family Anchitheriinae except the genera *Parahippus* and *Archaeohippus*, the foot was probably supported by pads, which were lost in the tip-toed tridactyl forms, i. e. polydactyl horses of the sub-family Equinae leaving the central toe supported by the distal phalanx alone. The monodactyl Equinae differ from the polydactyl ones in the side toes having become reduced to short splints. The inclination of the foot to the ground probably differed between these groups: SONDAAR showed that the angle of the central toe phalanges to the ground was probably sharper in pad-footed tridactyl than in tip-toed tridactyl forms. The sharp angle of the toe in pad-footed horses was due to the lack of strong supporting digital ligaments, and was made possible by the supporting pads and by relatively short central toe phalanges. In the tip-toed tridactyl horses and the monodactyl forms the position of the foot was stabilized by supporting digital ligaments.

ROBB (1936) showed that in the polydactyl horses growth of the side toes, i. e. metapodials and phalanges, in relation to cannon bone length can be expressed by the allometric formula  $1.5 (CB)^{0.97 \text{ to } 0.98}$ , and concluded that since the side toes are initially shorter than the central toe, i. e. cannon bone and phalanges, they would be lifted from the ground with the phyletic size-increase observed in most equid lineages. ROBB thought that the elevation of the side toes, which thus were rendered non-functional, finally caused the reduction in initial length of the splints of monodactyl horses. SONDAAR (1968), on the other hand, believed that the side toes underwent progressive reduction, whereas the central toe phalangeal part progressively increased in length with consequential alterations in functional foot type.

My data (FORSTEN 1973) supported ROBB's conclusions by confirming that throughout the evolution of the Equidae there was no progressive reduction in length of the side metapodials nor of the side toes in relation to cannon bone length, but showed an initial difference in central toe length between pad-footed tridactyl and tip-toed tridactyl horses: the former have a relatively shorter central toe phalangeal part, which makes the side toes appear relatively longer in relation to central toe length. The shift from the pad-footed tridactyl grade to the tip-toed tridactyl one may have proceeded over a stage with relatively short central toe phalanges lacking pads, as observed in some *Parahippus* (FORSTEN 1973). The shift in central toe length from one grade to the other was abrupt, indicating a quantum evolutionary step, for instance

a major mutation or a rapid shift from one adaptive peak to another brought about by strong directional selection of small cumulative mutations. In both groups central toe length increased relatively faster than side toe length with increase in over-all size, and thus in a large horse of either group the side toes would appear relatively "more reduced" than in a small horse, but increased size probably did not relieve the side toes of locomotive function. In all polydactyl horses high correlation of homologous measurements on the central toe and side toes indicate that the foot as a unit was subject to stringent selection pressure with side toes probably locomotively functional, possibly as braces. Increased body size and, consequently, weight must have caused greater dorsal flexion of the phalangeal joints, especially at the fetlock and demanded correspondingly stronger support. Allometric growth alone probably is not enough to explain the inception of monodactyly in tridactyl forms, nor relative lengthening of the central toe phalangeal part. In *Equus* the proximal phalanx is as a mean slightly longer relative to cannon bone length than in tip-toed tridactyl horses, but the two distal phalanges are short, and the total phalangeal part is hardly relatively longer in monodactyl than in tip-toed tridactyl forms. Increased support of the fetlock joint and development of a mechanism which functionally replaced the side toes in locomotion were necessary. CAMP and SMITH (1942) and SONDAAR (1968) have suggested that the digital ligaments fulfilled these demands.

CAMP and SMITH (1942) discussed the morphology and phylogeny of the digital ligaments of the horse and showed that the development of these ligaments in fossil forms can be interpreted on the basis of their volar attachment areas or scars on the proximal and medial phalanx. These scars changed in size and position evidently in correlation with the locomotive adaptations of the foot. The proximal phalanx of the pad-footed tridactyl horses had many small volar ligamental scars, but in the tip-toed tridactyl forms CAMP and SMITH observed an increase in the importance of the ligamenta sesamoidea obliqua, which culminated in the large oblique ligaments of *Equus* attaching along the long, flat V-scar on the proximal phalanx of the latter. The elastic digital ligaments furnish the automatic spring-mechanism of the equid foot (CAMP and SMITH 1942; SONDAAR 1968); in addition they brace the fetlock and prevent it from sinking through in gaits, such as gallop and fast trot, in which the body weight is supported on only one foot, respectively two feet at one time. The increase in size of the oblique ligaments, pulling against the interosseous tendon, may have been prerequisite to the development of monodactyly in the Equidae, as by bracing the fetlock they may have allowed the central toe to stand more vertically, thus causing the side toes to be lifted from the ground and become locomotory non-functional.

The V-scar of the proximal phalanx in tip-toed horses varies in extent but is mostly short, sometimes the two lateral scars of the oblique ligaments do not even meet at the midline, and there is a more or less well defined, rugose or concave scar of the ligamentum sesamoideum centrale. This is the situation in the tridactyl forms of the genera *Parahippus*, *Archaeohippus*, *Merychippus*, *Pseudhipparion*, *Hipparion*, *Neohipparion*, *Nannippus*, *Calippus*, and *Pliohippus*. In monodactyl equids the central ligamental scar is rudimentary or absent, and the V-scar is very large and flattened.

The oblique ligaments seem to have increased in size shortly before the side toes were reduced to splints. An enlarged, somewhat flattened V-scar occurs occasionally in the proximal phalanx of *Pliohippus* (*Pliohippus*) cf. *supremus* and *P. (Astrohippus) martini* from the Clarendonian Lapara Creek fauna of the Texas Gulf Coastal Plain, but in these pliohippines the side toes were long, judging from their long attachment areas on the cannon bone and development and position of the distal protuberances of the latter. The V-scar is similarly enlarged in proximal pha-

langes referable to *P. (Pliohippus)* sp. and is especially long in the narrow phalanges of *P. (Astrohippus)* sp., both from Quarry FT-40, Clarendonian-Hemphillian of Nebraska, although the side toes were probably long. Not until the Hemphillian did most *Pliohippus* populations consist mainly or only of individuals with splint-like side toes, judging from their cannon bone morphology. The enlarged oblique ligaments in Clarendonian *Pliohippus* may have been a preadaptation, which made the loss of the locomotively functional side toes possible. It is interesting that the genus *Hipparion* in the Old World evolved similarly enlarged oblique ligaments, although as far as known all forms of that genus were tridactyl.

WEKUA (1972) identified *Hipparion crusafonti* Vill. in a fauna from the Middle Pliocene of Kvabebi, Georgian SSR. This species was originally described from the Villafranchian (Middle to Late Pliocene) of Villaroya, Spain (Villalta 1952). FORSTEN (1968) synonymized *H. crusafonti* with *H. rocinantis* Hern. Pacheco, and the synonymy was recently confirmed by ALBERDI (1972, unpubl. diss.). In the proximal phalanx from Kvabebi and Villaroya the V-scar is large and dominates the volar surface. A similar structure of the proximal phalanx characterizes *Hipparion* from Chamar, Mongolia; the age of this find is also Villafranchian (VANGENHEIM et al. 1972). The equally progressive, roughly contemporaneous Chinese *H. boufenense* Teilh. et Young seems also to have a long and well defined V-scar (TEILHARD and YOUNG 1931, Pl. VIII, fig. 1, 1a). I observed an incipiently enlarged V-scar in Pliocene *Hipparion* from Chia-Mo-Ssu, China, and referred this form to *H. hippidiodus* Sefve on limb bone size and proportions (FORSTEN 1968). Some proximal phalanges from Chia-Mo-Ssu have an enlarged, flattened V-scar and lack a central scar, although in other specimens the central scar is large and the V-scar short. An enlarged V-scar very occasionally occurs in the proximal phalanx of even earlier hipparions, as in the specimens PIN 2346–7347 (Museum of Paleontology, Moscow) and –7296, and PIN 2413–5212 of *H. elegans* Gromova from Pavlodar, and PIN 1256–4485 and –69HK of *H. "moldavicum"* Gromova from Taraklia, both Late Miocene.

In these hipparions the V-scar is long, broad, and flattened with a distal rugose part, sometimes with paired central volar ligamental scars in contact with the V-scar distally, but lacking a central ligamental scar. Small paired lateral volar ligamental scars occur high on the diaphysis. The characteristic, large V-scar resembles that in *Equus* more than in other hipparions or most other tridactyl equids, but these hipparions were fully tridactyl with complete lateral toes as in other members of the genus. CAMP and SMITH (1942, fig. 31 A, B) figured Hemphillian and Blancan *Nannippus* proximal phalanges with an enlarged V-scar, but phalanges referable to *Nannippus* in the Hemphillian Coffee Ranch material which I have seen have a short V-scar, as have *Nannippus* phalanges in the Uptegrove sample, Kimballian of Nebraska. Occasionally the V-scar in proximal phalanges of *Nannippus* is probably enlarged, as it is in some Old World early hipparions.

Large oblique ligaments must have been functionally adaptive in tridactyl cursorial horses. They allowed the animal to run faster by supporting the fetlock, thus causing greater verticality of the distal leg to the ground, and by adding bounce. Although this adaptation was tried already in Late Miocene *Hipparion*, it was evidently not selected for in this genus until Middle to Late Pliocene when the enlarged oblique ligaments became a constant feature in one or a few closely related species. Miocene *Hipparion* adapted to plains conditions mainly by evolving longer distal limbs; especially the metapodials became very long and narrow in some local forms. Villafranchian *Hipparion* was among the largest in the genus and among tip-toed tridactyl horses. They had long, robust metapodials and long phalanges; in these hipparions the oblique ligaments may have enlarged as a means to meet



demands for more effective support of the fetlock in an increasingly heavy animal. Clarendonian *Pliohippus*, on the other hand, was middle-sized as tip-toed tridactyls go, and the increase in oblique size does not appear to have been initiated by increased weight. In the sub-genus *Astrohippus* the proximal phalanx was relatively longer, although body-size was less, than in contemporaneous forms of the sub-genus *Pliohippus*; thus there was probably greater shear on the long phalangeal part in *Astrohippus* than in *Pliohippus*, which may have necessitated an increase in ligamental support in the former. The oblique ligaments increased in size and monodactylly evolved simultaneously in both sub-genera, probably mainly as an adaptation to a cursorial mode of life (SHOTWELL 1961). SHOTWELL suggested that the side toes in the tridactyl horses were advantageous in quick, dodging movements as they may have supplied traction; the elevated fetlock of the monodactyl forms, and possibly also of advanced *Hipparion*, and consequent lifting of the side toes, were probably advantageous in sustained locomotion over even and firm ground.

Thus given an initially longer central toe than side toes and a supporting but rather weak ligamental apparatus, by increase in strength of the ligaments, especially the oblique ligaments, the fetlock would be elevated to make the toe stand more vertically thus adding to limb length and leverage and also elevating the side toes. As locomotory non-functional, the side toes would be withdrawn from earlier selection which kept them closely correlated with the central toe, and become targets for "reducing" mutations, which were possibly selected for since dew-claw-like, fully developed side toes would affect the free movement of the limbs. ROBB (1936) showed that the shift in side toe length from the tip-toed tridactyl grade to the monodactyl one was sudden, "step-wise", but it may have proceeded over a brief stage with side toes running the full length of the cannon bone but ending in a thin tongue of bone without phalanges. Three metapodials of *Pliohippus*, two MT III (field nos. 4-17-6-15 and 5-17-6-15) and one MC III (field no. 6-17-6-15) in the University of Nebraska State Museum, from "Upper Reaches of Pine Creek, Brown county, Nebraska", have such side toes. The horse was functionally monodactyl, although the cannon bones are morphologically similar to those of a tridactyl tip-toed form. *Pliohippus* from Lapara Creek and FT-40 with precociously enlarged V-scar may have had such long side toes lacking phalanges.

Acquisition of the enlarged oblique ligaments in Villafranchian *Hipparion* is a parallel to that in *Pliohippus*, although *Hipparion* evolved the large V-scar much later. In *Pliohippus* elevation of the fetlock resulted in rapid loss of the locomotively functional side toes, but in *Hipparion*, although the prerequisites for monodactylly seem to have been present, the side toes with phalanges were fully developed. Possibly the time for "reducing" mutations to spread widely enough for mutants to show up among the fossils was too short, as the genus *Hipparion* became extinct soon after, or such mutants were selected against as before because the side toes were still functional, perhaps owing to the great weight of these forms.

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#### Summary

The article discusses some changes in the structure of the foot in fossil equids at the shift to monodactylly, as well as parallel adaptations in a persistently tridactyl genus.

## Zusammenfassung

*Adaptive Evolution des Fußes der Equiden*

Dieser Artikel diskutiert einige Veränderungen im Bau des Fußes fossiler Equiden während des Übergangs zur Einzebigkeit sowie parallele Anpassungen in einer fortdauernd dreizehigen Gattung.

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## Notes on the Gazelles

1. *Gazella rufifrons* and the zoogeography of Central African Bovidae

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## Introduction

Taxonomy retains its fundamental importance today as the "donkeywork" end of Systematics, if indeed the two are properly to be distinguished. Systematics may be looked on as the central unifying area in biology: the part without which none of the rest makes sense. While this claim is true in regard to all fields, from palaeontology to molecular biology, from ethology to conservation, its direct impact is perhaps nowhere more obvious than in the field of zoogeography.

An often neglected key paper on the mammalian zoogeography of Africa is ERNST SCHWARZ'S "Huftiere aus West- und Zentralafrika" (1926). Based primarily on the

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