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On the fossae nudatae in the basipodia of *Equus* and of some fossil tridactyl horses (Equidae, Mammalia)

Heinz Tobien

Tobien, H., Institut für Geowissenschaften, Paläontologie, Johannes Gutenberg-Universität, Postfach 3980, D-6500 Mainz, Germany

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By partial destruction or loss of the cartilage cover on the articulation surfaces of some joints in the carpalia and tarsalia of horses pits or elongated grooves appear. They often reach into the underlying bare bone. These fossae nudatae (or fossae synoviales) can thus be studied on macerated basipodia of living *Equus* species, and on fossil basipodia of mono- and tridactyl horses. The form, structure and different types of recent fossae nudatae and their palaeontological occurrences in Miocene, Pliocene and Pleistocene equids are reviewed. According to the majority of mammalian palaeontologists, the fossae are insertions of strong intrabasipodial ligaments, ensuring the immobility of the basipodial amphiarthrotic joints concerned. According to most veterinarians, the fossae are filled with synovia, the liquid acting as a joint lubricant. A dissection of a fresh horse foot strongly supports the latter interpretation.

1. Introduction

Fossae nudatae (or fossae synoviales) appear in some joints, mainly those of ungulates, "if the articular cartilage is destroyed or lost for some reason and fissures appear in the areas of bared bones. In the ungulates the articular surfaces of several joints, especially those of the extremities, have pit-like depressions devoid of cartilage" (Nickel et al. 1986:169). In Ellenberger-Baum (1977:12) these fissures, grooves and pits are called "fossae nudatae synoviales", because they have no cartilage cover, and are filled with synovia, the liquid secreted by the synovial capsule, and acting as a joint lubricant.

In fact the fossae are often deepened through the articular cartilage into the compacta and not uncommonly also into the upper levels of the spongiosa. They can therefore be observed on the articular facets of macerated bones of living horses and fossil *Equus* and tridactyl horses as well. In this context the denomination "fossae nudatae" seems to be more suitable as they are free of cartilage and of removed compacta. Furthermore the bottoms of the fossae have an irregular, rugose, sometimes porous surface (Fig. 2a, 25, 26).

The veterinary literature is not very concerned with this cartilage-bone-alteration (= cba-alteration) phenomenon, as far as it exists in the bared bony, and therefore also fossiliferous parts. In the text below some details of fossae nudatae in the bony basipodia of some recent and fossil equids will be described. The functions and causes attributed to the fossae nudatae by mammalian palaeontologists and veterinarians are discussed in the light of a recently undertaken dissection of a horse foot.

Abbreviations:

Coll. Utrecht: Instituut vor Aardwetenschappen, Universiteit Utrecht (The Netherlands) LSNK: Landessammlungen für Naturkunde, Karlsruhe (Germany) MB: Naturhistorisches Museum, Basel (Switzerland) PIM: Institut für Geowissenschaften, Paläontologie, Universität Mainz (Germany)

Measurements in the text in mm, scale bars of the figures in cm.

2. Fossae nudatae in the forelimb basipodium of *Equus*

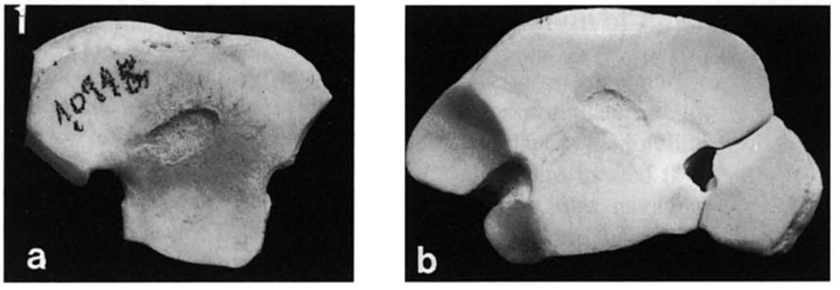
The basipodium of the equine forelimb consists of two rows of smaller bones from medially to laterally: the proximal row with scaphoid (= naviculare manus, radiale, Cr), lunatum (= semilunare, intermediale, Ci), triquetrum (= cuneiforme, pyramidale, ulnare, Cu), pisiforme (= accessorium carpi, Ca). Their proximal facets articulate more or less with the distal facets of the radius. The distal row includes: trapezium (= multangulum majus, carpale 1, Cl), trapezoideum (= multangulum minus, carpale 2, C2), magnum (= capitatum, carpale 3, C3), unciforme (= hamatum, carpale 4, C4). Their distal facets articulate with the proximal facets of mcII–mcIV. The largest bone in the distal row is the plate-like, trapezoidal magnum, which contacts proximally scaphoid and lunate, and distally a medial part of the mcIII (see veterinary text books).

In the present state of our knowledge the only fossae nudatae, at least in a bare bony state, exist in the articulation magnum/mcIII, i.e. on the distal facet of the magnum and the proximal one of the mcIII (Fig. 1, 2). Their fossae are congruent, i.e. size, shape, structure and position on the articular facets are similar or identical, mirrorlike. Thus both fossae represent a 3-dimensional, hollow structure with in addition to the dominant mediolateral extension a certain small proximo-distal component. In statu vivendi this distance would be enlarged by the cartilage thickness (several mm) to outside of the fossae, but is absent in the fossae themselves. It is a matter of conjecture what kind of matrix filled this cavity in life (p. 396 below).

There are two different modifications, at least, in the bony status: type 1 (Fig. 1) is represented by an isolated, mostly sharp ridged, rounded fossa with a rugose, sometimes poriferous bottom, located in the centre or near the borders of the facets mentioned, in congruent position and shape (fossa nudata type 1). Another habitus represents type 2 (Fig. 2): a more or less centrally situated fossa continues into a furrow or sulcus, which has an exit at an incisura mostly on the medial border of the mcIII, opposite the mcII capitulum. The corresponding furrow is situated at the medial border of the magnum (Fig. 2). In contact position both fossae form a channel several mm in diameter, in this case with a medial opening.

Both examples are represented by an *Equus zebra* and an *Equus grevyi* respectively (Fig. 1, 2), labelled as such in the collection of the Basel Nat.Hist.Mus., Dept. of Osteology. Other specimens in this rich collection offer type 1: *Equus somaliensis* (MB 10858), *Equus grevyi grevyi* (MB 10873) and *Equus przewalskii* (MB 10877). *E. zebra* (MB 10884) shows a beginning medial exit, connected with a diffuse central fossa. *E. hemionus hemionus* (MB 10883) has a small fossa in addition to the medial incisura. In another specimen of *E. przewalskii* (MB 10863) and *E. grevyi grevyi* (MB 10876) the fossae are missing (at least on the bony surfaces of the macerated skeletons). Thus the variation is obviously considerable. In the fossa nudata 2 case a magnum fossa of a large *Equus caballus* (ost. coll. Inst. Geowiss. Mainz, S-298) opens at the labial side (Fig. 3). On the mcIII (in a mcII – mcIV ensemble) of a recent zebra the type 2 fossa has an accessory aperture at the cranial border (Fig. 4).

In fossil horses, such as the early Pleistocene *Equus stenonis*, no true fossae have been de-



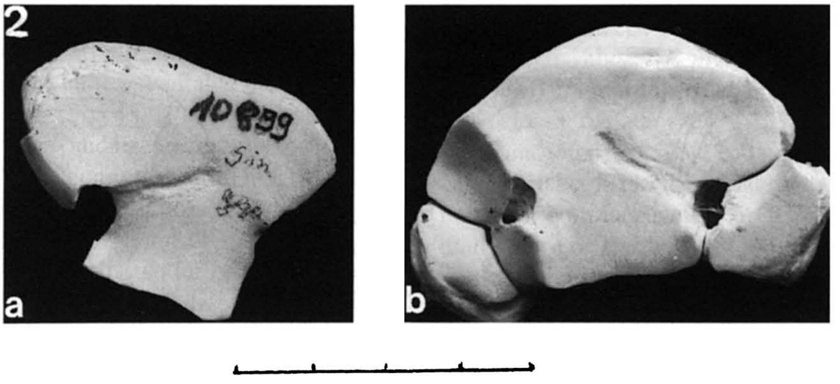


Fig. 1. *Equus zebra* L. (MB 10918). — a: left magnum, distal facet, fossa nudata isolated from the border, surrounded by bony compacta of articular facet. — b: left mcIII, proximal facet, fossa nudata mirror image of a. Fig. 2. *Equus grevyi* Oustalet (MB 10899). — a: left magnum, distal facet, fossa nudata connected with the medial border of the bone. — b: left mcIII, proximal facet, fossa nudata mirror image of a.

scribed or figured (Gromova 1955a: fig. 17E, F; Fig. 5, 6; see also Major 1880: pl.5; except Fig. 5: a pit only on mcIII). One of the earliest American monodactyl horses, however, the Pliocene *Pliohippus* (*Dinohippus*) *mexicanus*, has on its mcIII facet a large fossa nudata type 2, with a broad medial exit (Sondaar 1968:pl.4, fig. A3; fig. 9-3A shows only a fossa of type 1: this text Fig. 7b), yet a magnum facet from the same species and site has no fossa nudata (Fig. 7a).

3. Fossae nudatae in the forelimb basipodium of tridactyl horses

Among tridactyl horses the early Late Miocene (Vallesian) "*Hipparion*" *primigenium* from Eppelsheim (SW of Mainz, Tobien 1983) and Höwenegg (N of the Lake of Constance, SW Germany, Tobien 1986) fossae nudatae are mostly absent on the few mcIII (Eppelsheim) or on the dozen magna and mcIII of the more or less complete articulated skeletons (Höwenegg) (Fig. 8). Only the M-55 skeleton has a rather large (8 mm long) oval fossa nudata type 1 on the left magnum, 5 mm behind its cranial border, and in congruent size and position on the mcIII. The two facets of the right side bones, however, have only small pits (as can sometimes be seen on other Höwenegg specimens) in the corresponding locations: an unusual example of right/left asymmetry.

In stratigraphically later hipparionine horses fossae nudatae on the mcIII heads and/or on the magna also show considerable variation. Gromova (1955b:pl. 5, fig. 26 B) figured the distal facet of a magnum of "*Hipparion*" *elegans* from Pavlodar (Turolian, Central Asia) with a rather small fossa

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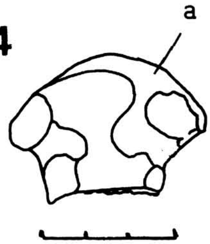

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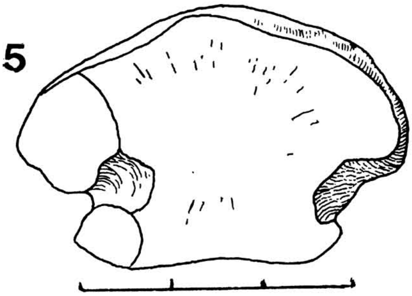

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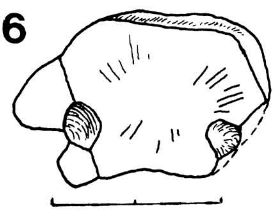

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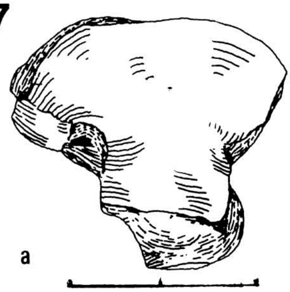

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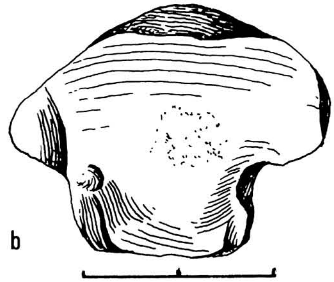

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Fig. 3. *Equus caballus* L.(PIM-S298). Left magnum, distal facet, fossa nudata with opening on the lateral side of the bone.
Fig. 4. *Equus zebra L.*, recent. Left mcIII, proximal facets, with fossa nudata type 2 and accessory aperture at the cranial border (after Kovalevsky 1873: pl. 2, fig. 26D).
Fig. 5. *Equus stenonis* cf. *major* Boule. Left mcIII, Pleistocene, coast of the Asov Sea (after Gromova 1955: fig. 17E).
Fig. 6. *Equus* cf. *stenonis* Cocchi. Right mcIII (reverted), Pleistocene, Psekups river, near Krasnodar (N of the Caucasus range) (after Gromova 1955: fig. 17F).
Fig. 7. *Pliohippus mexicanus* Lance, Pliocene, Chihuahua, Mexico. — a: right magnum (reverted), distal facet (after Sondaar 1968: fig. 7D). — b: left mcIII, proximal facet (after Sondaar 1968: fig. 9-3a).

nudata type 1 (Fig. 9), whereas the mcIII facet (same species, same site) shows no fossa nudata (Gromova l955b:pl. 8, fig. 41 B). These examples are similar to those from Vallesian sites, as e.g. Höwenegg. Gabuniya (1961) published several views of proximal mcIII facets from Odessa region species (Southern Russia): *Hipparion* sp., Meotian, liman of Kujalnik, with fossae nudatae type 1 (Fig. 10), and type 2, with narrow exit on the medial side (Fig. 11); with fossae nudatae type 1 (Fig. 13); "*Hipparion*" *moldavicum*, Meotian, Novo-Elisavetovka without any fossae nudatae, Fig. 14). "*H.*" cf. *verae* from Tchobrutchi has a large fossa nudata type 2 on the distal facet of a magnum (Gabuniya 1961:fig. 16A-c) and the proximal facet of an mcIII (Gabuniya 1961:fig. 16D-c) (Fig.12).

A right magnum of "*Hipparion*" *theobaldi mogoicum* Zhegallo (1978) from Chirgis-Nur II in the Mongolian PR has a fossa nudata type 2 with an unusual exit at the caudal border of the distal facet, protruding cranially (Fig. 16). The counterpart exists on the posterior border of a mcIII dext. (? of the same individual) (Fig. 15). The site is of "Pontian" age (Zhegallo 1978:fig. 1, no. 84, fig. 2, fig. 80). From the same locality comes an mcIII with fossa nudata type 1 ("*H.*" *theobaldi platyodus*), an mcIII with fossa nudata type 2 ("*H.*" *elegans*), and an mcIII without fossae nudatae (*H. sefvei*) (Zhegallo 1978: fig. 50b, fig. 58g, fig. 53b), all similar to Figs. 13, 12, 14, respectively. From Chamar comes an mcIII without fossae nudatae ("*H.*" *tchikoicum*) (Zhegallo 1978: fig 55v).

Among the earlier Indian hipparionine horses "*Hipparion*" *nagriense* offers a further fossa nudata example (Fig. 17): The mcIII sin. facet has a type 2 fossa nudata, with an opening at the medial side.

As far as the body dimensions in the mentioned *Hipparion* examples are concerned it should be pointed out that "*H.*" cf. *verae* belongs to the medium-sized European species, but nevertheless has a well developed fossa nudata type 2. Possibly fossae nudatae types are independent of individual size (see also the small living *E. somaliensis, E. hemionus*: p. 396, Table 1).

A European tridactyl horse earlier than *Hipparion* is the Middle and early Late Miocene *Anchitherium.* The few available mcIII facets of *A. aurelianense* (Fig. 18, 19) do not show indications of fossae nudatae. Presently nothing is known about the congruent distal magnum facet.

Resuming the occurrences of fossae nudatae in the magnum/mcIII joint of fossil horses, no true fossae nudatae has so far been described or figured for the European late Pliocene-early Pleistocene *Equus* (*Allohippus*) *stenonis.* The American *Pliohippus* (*Dinohippus*), considered directly ancestral to *Equus,* already exhibits a fossa nudata type 2, however.

The early European (Vallesian) tridactyl horses, like the immigrant *Hipparion,* appear to have fossae nudatae only rarely (as type 1). Yet one specimen of the Indian "*H.*" *nagriense* of Nagri (more or less Vallesian) age shows a progressive fossa nudata type 2. Type 1 and/or type 2 fossa nudata may be more common in later hipparionine horses of the late Late Miocene (Turolian) in the Palaearctic. The Middle Miocene immigrant *Anchitherium* lacks fossae nudatae as far as the two specimens available demonstrate.

Some American *Neohipparion* and *Merychippus* clearly testify to the presence of fossae nudatae. An mcIII of "*Merychippus paniensis*", Miocene, Nebraska, shows a fossa nudata type 1 with large grooves or pori at the bottom (Fig. 20). An mcIII of *Neohipparion floresi* lacks fossae nudatae (Fig. 21). The distal facet of a magnum of the same species has traces of a fossa nudata type 1 (Fig. 22). No fossae nudatae are developed on a magnum of *Parahippus leonensis* from the earlier Miocene of Florida (Fig. 23) and on an mcIII of *Archaeohippus blackbergi* (Sondaar 1968: fig 7D, 11-2B).

4. Fossae nudatae in the hindlimb basipodium of *Equus*

In the tarsal segment of living and fossil *Equus* the fossae nudatae are more abundant and diversified than in the forelimb. The congruent fossae nudatae are located (Fig. 24) in the astragalus/navicular joint, navicular/cuneiform 3 joint and the cuneiform 3 / mtIII joint, and all parts of the tarsal joint. As none of the text books and treatises mentioned on p. 381 and 397 contain figures and descriptions of the fossae nudatae on the articular facets, these details of living non-domesticated horses (*E. przewalskii, E. hemionus, E. grevyi*) are reproduced in Fig. 25.

A fossa nudata type 2 of the astragalus/navicular joint (Fig. 25a, b) is present and very characteristic. From the broad exit at the medial border of both facets the deep fossae extend laterally more or less halfway into the facet. Their borders are sharp, the bottom is uneven and rugose, in direct contrast to the smooth facet, and in vivo covered with cartilage. There are some fine pori, which probably reach down into the spongiosa. On the navicular there is a larger hole at the end of the fossa.

The fossa nudata type 2 in the navicular/cuneiform 3 joint (Fig. 25c, d) runs transversely in a sinusoidal course, thus separating a larger cranial from a smaller caudal facet part. The caudal part is subdivided by a caudally directed second outlet of the main fossa. This is not the case on the large cuneiform facet. Here the cuboid forms part of the support of the navicular. The morphological details of the fossa (borders, bottom, pori) are the same as in the preceding joint. The variations, particularly in the navicular, are considerable. Sometimes the medial or lateral opening is closed. The caudal outlet, however, seems to be present in all specimens. In the cuneiform 3 the lateral part of the fossa is missing, or the fossa is interrupted medially by a bony bridge.

The fossa nudata type 2 in the cuneiform 3 / mtIII joint (Fig. 25e, f) is rather large. On the cuneiform 3 the fossa covers a round quadrangular area with a broad exit on the lateral side and a narrow exit on the medial border. Thus the remaining articular facet, in vivo covered with cartilage, is subdivided into a larger cranial and a

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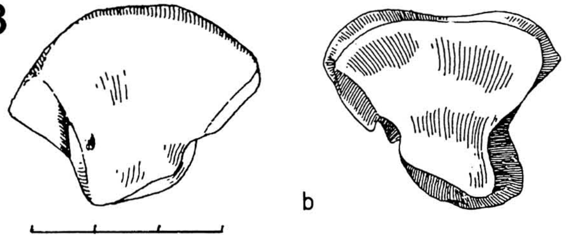

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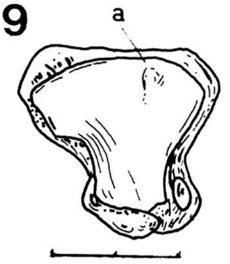

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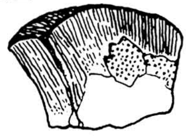

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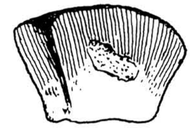

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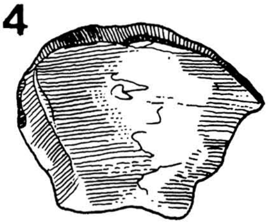

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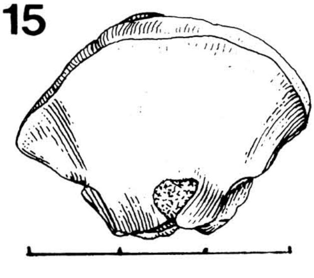

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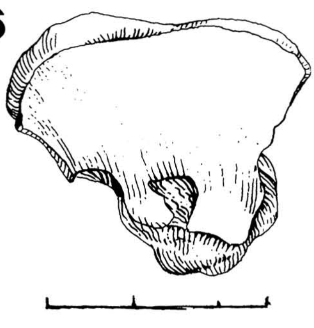

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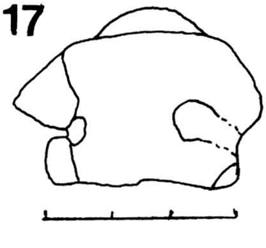

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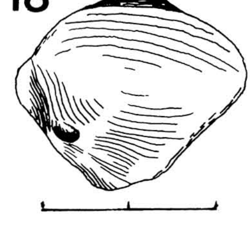

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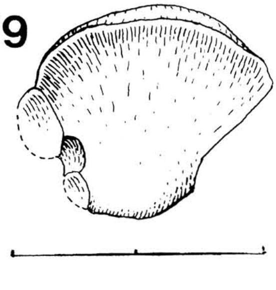

Fig. 8. "*Hipparion*" *primigenium* (von Meyer), Vallesian, Höwenegg, SMNK. — a: left mcIII, proximal facet, Hö-A skeleton, with small fossa nudata at the medial incisura. — b: left magnum, distal side, from the same skeleton A, with congruent fossa nudata at the medial border.

Fig. 9. "*Hipparion*" *elegans* Gromova, Turolian, Pavlodar (after Gromova 1955b: pl. 5, fig. 26B). Left magnum, distal facet, with a small fossa nudata type I(a) on the cranio-lateral corner.

Fig. 10–11. *Hipparion* sp. Meotian, Liman of Kujalnik (after Gabuniya 1961: fig. 16D-a,b). — Fig. 10. Right mcIII (reverted), with fossa nudata type 1, unciforme facet uniform, with small incisura. — Fig. II. Left mcIII, with fossa nudata type 2, exit on the medial side, unciforme facet uniform, with small incisura.

Fig. 12–13. "*Hipparion*" *verae* Gabuniya, Meotian, Tchobrutchy (SW of Odessa) (after Gabuniya 1961: fig. 16D-d,c). — Fig. 12. Right mcIII (reverted), fossa nudata type 2 with medial exit, unciforme facet uniform. — Fig. 13. Right mcIII (reverted), fossa nudata type 1.

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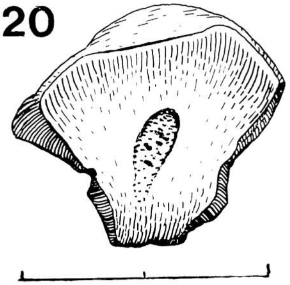
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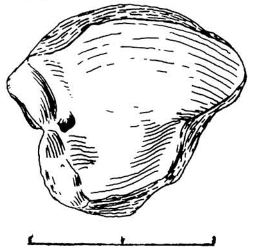
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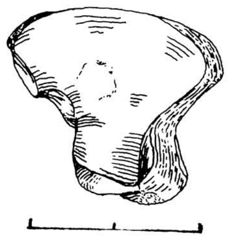
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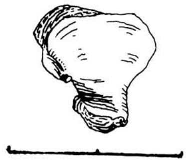

Fig. 20. "*Merychippus paniensis*" (Cope), Miocene, Nebraska (1959 XXIII 435, Staatl. Sammlung Paläontol. Histor. Geol. München, complete mcIII). Left mcIII, proximal facet, fossa nudata type 1, unciforme facet bipartite.
Fig. 21–22. *Neohipparion floresi* (Stirton), Hemphillian, Chihuahua, Mexico (after Sondaar 1968: fig. 9-1A, 7D). — Fig. 21. Right Mc III (reverted), proximal facet, without fossa nudata, unciforme facet bipartite. — Fig. 22. Right magnum (reverted), distal facet, with traces of a fossa nudata type 1.
Fig. 23. *Parahippus leonensis* Sellards, Lower Miocene, Thomas farm, Ghilchrist co., Florida (after Sondaar 1968: fig. 7D). Right magnum (reverted), distal facet, without fossa nudata.

smaller caudal section. The mtIII facet shows the same arrangement: a broad lateral opening behind the cuboid facet and a narrower opening on the medial side. Thus the facet is divided into a cranial, crescentoid, larger and a smaller square-like caudal part. The details of the fossa are similar to those of the two preceding ones, with more proximal articulations. The main variation is that the medial exit may be closed. By this means a more or less broad medial bony connection results between the caudal and cranial segments of the joint.

It is beyond the scope of this account to discuss the reasons for the variation in the carpal and tarsal joints. Due to the lack of systematically gathered data nothing can be said about the amount of interspecific, intraspecific, ontogenetic or sexual variation. As far as the individual age of the appearance of the fossae nudatae is concerned, a ten-month old foal of a zebra shows incipient fossae in the three joints (Fig. 26). In the astragalus/navicular joint (Fig. 26a, b), the fossae are short, narrow, flat, with already removed compacta, as the bottom of the fossae shows. The navicular part of the navicular/cuneiform 3 joint (Fig. 26c, d) exhibits three oval alterations of the compacta, which by their shape and arrangement predict the adult's complete transverse fossa and its caudal outlet (compare Fig. 25c). The cuneiform 3 facet (Fig. 26d) exhibits a fossa still interrupted by a bridge connecting the two articular facets. The cuneiform 3 / mtIII congruence (Fig. 26e, f) has no medial exit, present in

Fig. 14. "*Hipparion*" *moldavicum* Gromova, Novo-Elisavetovka (N of Odessa) (after Gabuniya I961: fig. 16 V-a). Right mcIII (reverted), without fossa nudata, only slight indentation on medial side, unciforme facet uniform.
Fig. 15–16. "*Hipparion*" *theobaldi mogoicum* Zhegallo, Pontian, Chirgis-Nur II, Mongolian PR (after Zhegallo 1979: fig. 33v, 26g). — Fig. 15. Right mcIII (reverted), with fossa nudata type 2 at caudal border of facet, directed cranially. — Fig. 16. Right magnum (reverted), with short fossa nudata type 2 at caudal border.
Fig. 17. "*Hipparion*" *nagriense* Hussain, Nagri Gorge, Nagri fm. (NG 53, coll. Utrecht). Left mcIII, proximal facet with fossa nudata type 2, unciforme facet subdivided in cranial and caudal part.
Fig. 18. *Anchitherium aurelianense* Cuvier, Middle Miocene, Steinheim (after Sondaar 1968: fig. 9-2A). Left mcIII, proximal facet, without fossa nudata, unciforme facet bipartite.
Fig. 19. *Anchitherium aurelianense*, Middle Miocene, Sansan (after Kovalevsky 1873: pl. 2, fig. 24A, from a set of McII–McIV). Left mcIII, proximal facet, without fossa nudata, unciforme bipartite.

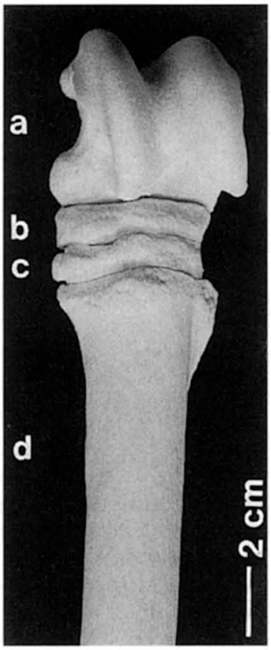

Fig. 24. *Equus przewalskii* Poljakow, recent (MB 10881). Left basipodium, cranial view, location of the three joints with fossae nudatae: astragalus / naviculare (a/b), naviculare / cuneiforme 3 (b/c), and cuneiforme 3 / mtIII (c/d).

adult individuals (Fig. 25 e, f). Some of these details coincide with those encountered in fossil horses (p. 397, Table 2).

In the normal standing position of the tarsus (Fig. 24, 27) the fossae nudatae form four channels, similar to the magnum/mcIII channel. They have clearly visible outlets, at least in macerated skeletons, here that of *E. przewalskii.* The proximal channel 1 and its exit 1(1, Fig. 27a) corresponds to the fossa nudata in the navicular facet of the astragalus and the fossa nudata of the navicular. Further distally channel 3 and its exit 3 (3, Fig. 27a) are enclosed by the fossa nudata of the distal cuneiform 3 facet and the proximal mtIII facet.

Fig. 27b shows the left tarsus in caudo-lateral view with cuboid removed. Channel 2 and its exit 2 (2, Fig. 27b), intermediate between channel 1 and 3 and their exits, is embraced by the caudal openings of the distal navicular facet and the fossa nudata of the proximal cuneiform 3 facet (Gromova 1955b: pl. 7, fig. 37A figured this exit of a recent horse). The most distal channel 4 (Fig. 27b) has a tiny exit 4, enclosed by the small fossa nudata on the medial side of the distal cuneiform 3 facet and the proximal mtIII facet (see Figs. 25e, f).

This rather detailed description of the fossae and their exits with their positions in the tarsus is motivated by the fact that these structures, like those in the carpus, are also known in the fossil state, and therefore of importance to mammalian palaeontologists.

Three mtIII heads of *Equus stenonis* from Pleistocene deposits N of the Caucasus range and one of *Equus caballus* show different development of their fossae nudatae: A type 1, with the not yet connected exit at the lateral wall (Fig. 28), with type 2 fossae, with completed exit and tendencies to form a medial one (Fig. 29 and 30). Fig. 31 represents the final stage with complete fossa nudata type 2, as in the recent *Equus* (Fig. 25f) (after Gromova 1955a: fig. 17, see also Major, 1880:pl. 5: fig. 10, cuneiform 3, dist., fig. 31: navicular, dist; pl. 6: fig. 35, 43 navicular facet of astragalus, fig. 40: mtIII, prox.).

Data on the pelvic limb in fossil and recent North American Equidae are available in the outstanding study of Hussain (1975), who figures a tarsal series with fossae nudatae in columns 1–4 (Fig. 32). The recent *Equus* shows no differences in the facets against the Plio-Pleistocene *Equus (Dolichohippus)* (see also Fig. 25), including the astragalar and metapodial congruencies. *Equus (Dolichohippus)* lacks its medial exit (Fig. 32-B4). The Late Miocene/Pliocene *Pliohippus* (Fig. 32 D1-4) has a type 2 fossa lacking a medial outlet. Furthermore the contours and the borders of the fossae are vague and indistinct. Here the dissolution of the cartilage that forms the fossae is evident, but the destruction of the deeper bony parts has only begun. This condition appears to be primitive.

5. Fossae nudatae of the hindlimb basipodium of tridactyl horses

In the A-skeleton of the Höwenegg *Hipparion* there is a complete set of fossa nudata type 2 (Fig. 33). As can be expected, the development of the fossae is clearly below the level of recent and Pleistocene European and North American monodactyl horses (Fig. 25, 32A, B). Nearest

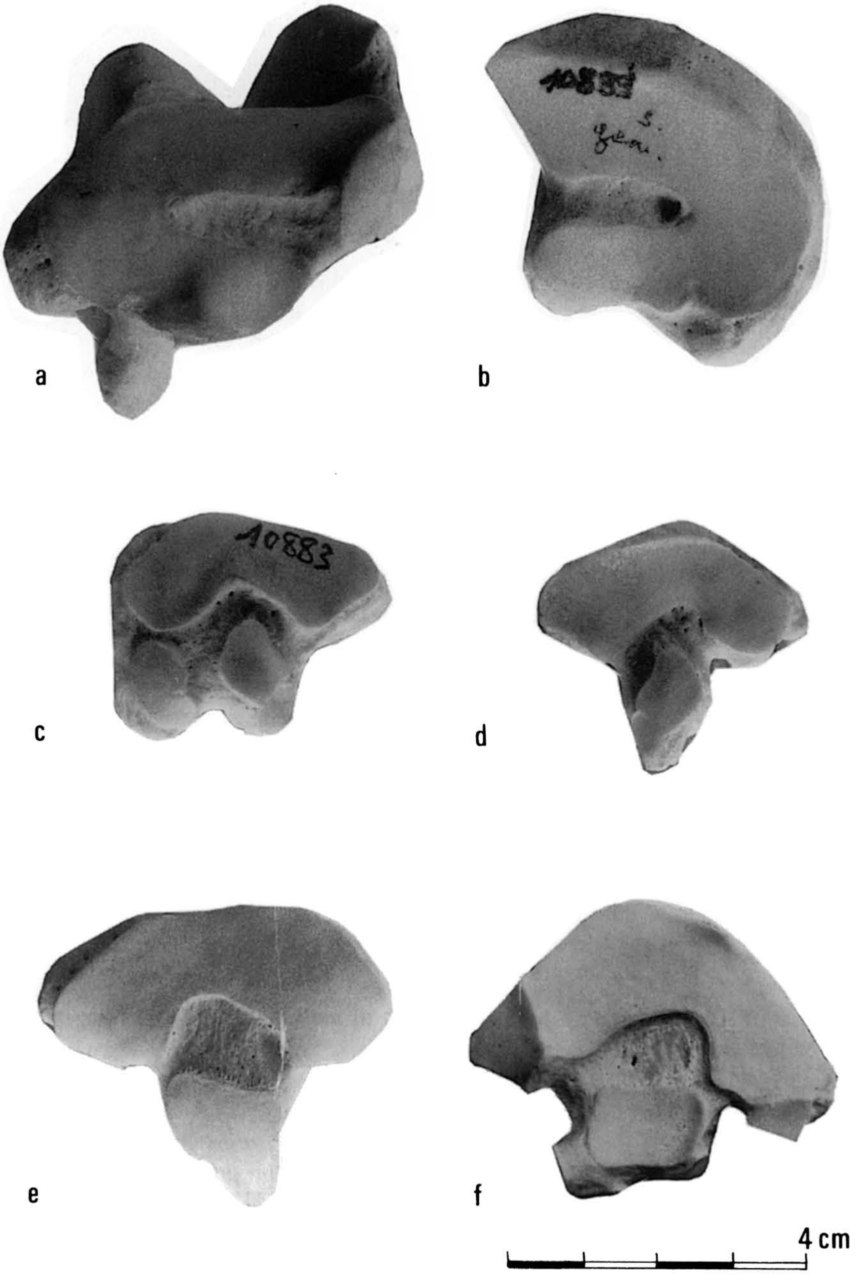

Fig. 25. Fossae nudatae type 2 of the three tarsal joints defined in Fig. 24. — Navicular facet of astragalus (a) and counterpart on proximal facet of naviculare (b); *Equus grevyi*, 5 years, sex?, MB 10899. — Distal facet of naviculare (c) and counterpart on proximal facet of cuneiforme 3 (d); *Equus hemionus hemionus* Pallas, 5 years, sex?, MB 10883. — Distal facet of cuneiforme 3 (e) and counterpart on proximal facet of mtIII (f); *Equus przewalskii*, 2 years, sex?, MB 10877.

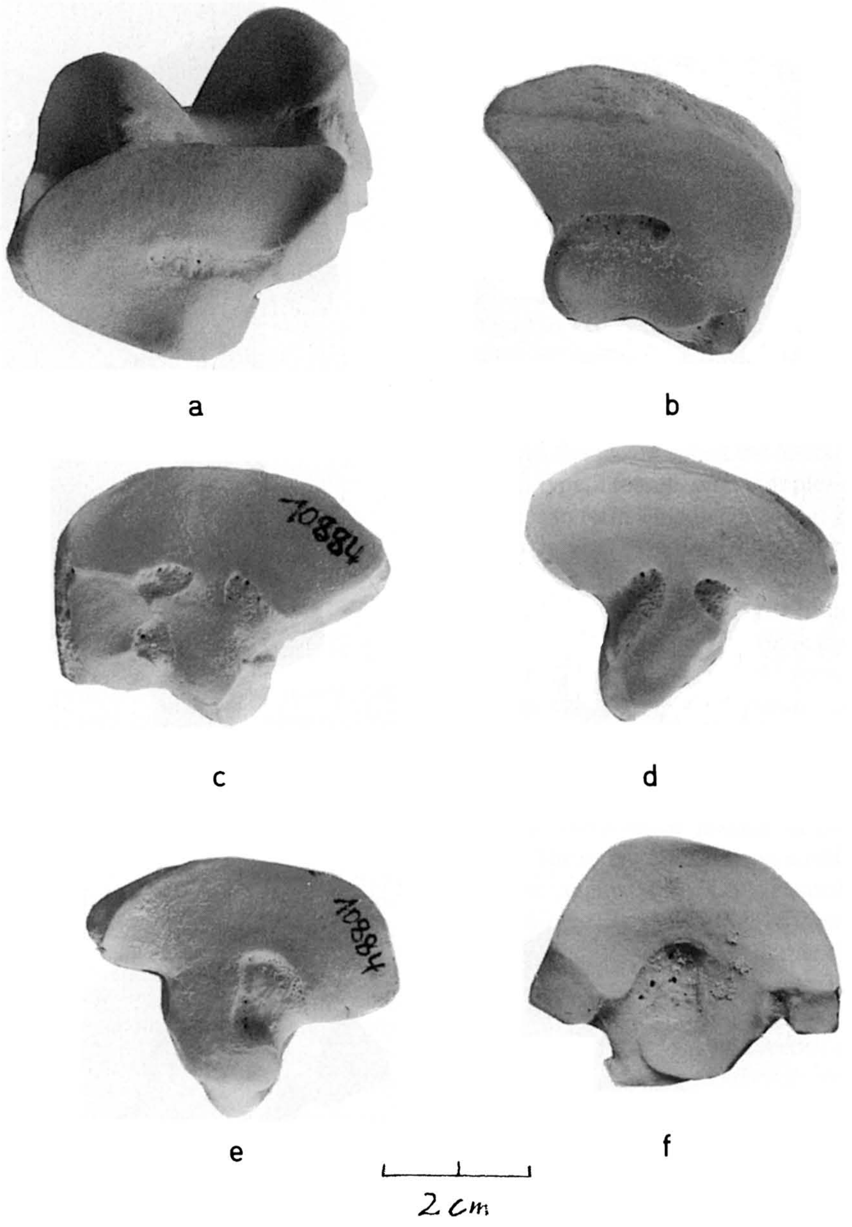

Fig. 26. Incipient fossae nudatae of the three tarsal joints defined in Fig. 24. *Equus zebra* L., recent, foal, age 10 months, sex?, MB 10884. — Navicular facet of astragalus (a) and counterpart on proximal facet of naviculare (b). — Distal facet of naviculare (c) and counterpart on proximal facet of cuneiforme 3 (d), incomplete fossae in “statu nascendi”. — Distal facet of cuneiforme 3 (e) and counterpart on proximal facet of mtIII (f), incomplete “Orimentary fossae” without a medial continuation and exit as in the adult in Figs. 25e and f.

comes the habitus of the American *Pliohippus* (Fig. 32D). An example is the astragalus/navicular congruence, which is relatively stable (Zhegallo 1978:fig. 28G): Figures of the other congruencies or parts of them in Gromova (1955b:pl. 6, 7, 8) and Zhegallo (1978: figs. 28, 31, 34, 52, 55,

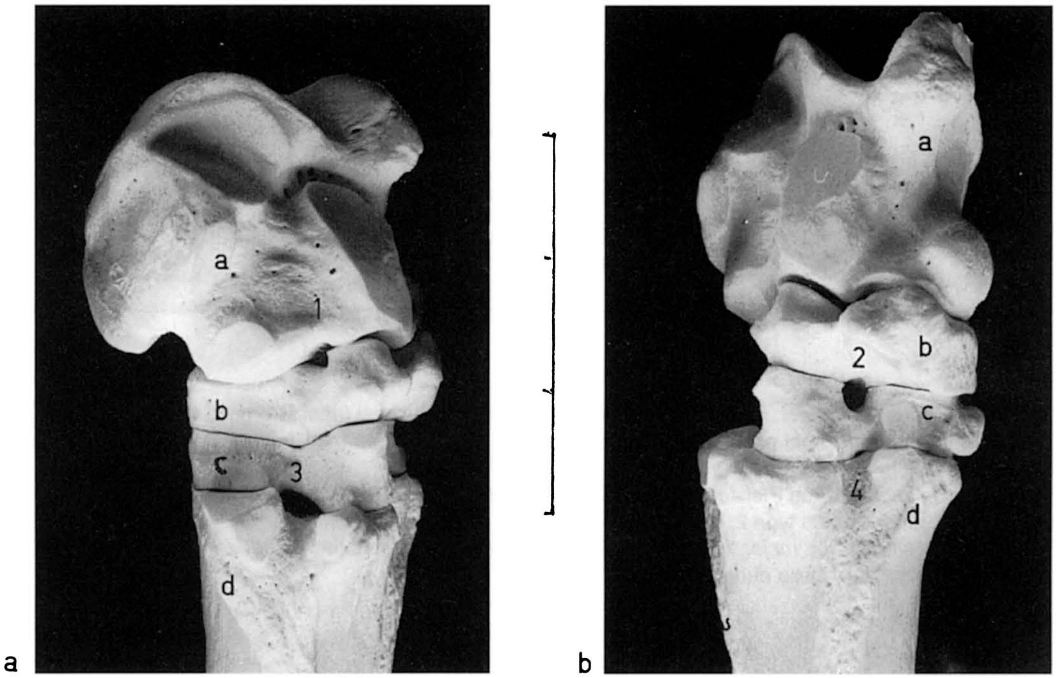

Fig. 27. Openings of fossae nudatae (1–4) on left tarsus and proximal part of mtIII (bones a–d as in Fig. 24). *Equus przewalskii*, 7 years, female, MB 10881. — Left figure in lateral view, right in caudal view, cuboid and calcaneum removed.

76, 77) show some individual variation. The proximal facet of a navicular of "*H.*" *sefvei* is remarkable for its fossa nudata type 1 (Zhegallo 1978:fig. 52e).

As in *Equus*, the development of fossae nudatae is stronger in the hindlimb than in the forelimb in *Hipparion*.

Not much was known about the hindlimb basipodium of *Anchitherium*. Kovalevsky (1873) in his classic monograph reproduced fossae nudatae of some tarsalia and an mtIII (Fig. 34a-d). The navicular facet of the astragalus has a small type 2 fossa with a narrow caudolateral exit (34a). On the proximal facet of a navicular there is a slight indication of a fossa nudata (34b). A distal facet of the same bone has a broadly incurved fossa nudata on its lateral border (34c). The distal facet of a cuneiform 3 has a narrow fossa with a lateral exit, which is congruent with a similar fossa in an mtIII head (34d, e). Vidalenc (1979) has recently added to these data. According to him, better developed type 2 fossae nudatae occur on the navicular facet of an astragalus (fig. 22-C2); on the proximal navicular facets (fig. 28A, 28B-6); on the distal facet of a cuneiform 3 (fig. 32B); and on the mtIII head. However, in this material the variation is considerable. For the proximal facet of an mtIII fossa nudata development ranges from non-existent (1 specimen), to very large fossae nudatae (12 specimens), and there are 24 specimens with fossae nudatae of intermediate size (Vidalenc 1979:173). *Anchitherium* appears advanced compared with the American *Parahippus* (Fig. 35-G).

Thanks to the monograph by Hussain (1975: figs. 7, 8, 11) there are data available on fossae nudatae of tridactyl horses from North America. They are reproduced here in Figs. 35C, F, E, G, H (using Hussain's capitals). The four columns show the proximal facet of the navicular, (which can be completed by the astragalus congruent facet); the distal facet of the navicular, the proximal and distal facets of cuneiform 3 (the latter completed by the congruent mtIII facet). This illustrates the se-

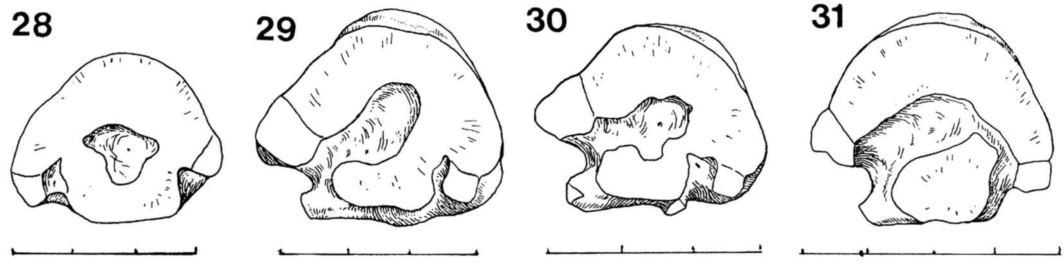

Fig. 28–29. *Equus stenonis* cf. *major*, Pleistocene, Khopry, Azov sea coast (after Gromova 1955a: fig. 17C,A). — Fig. 28. Right mtIII, proximal part, fossa nudata type 1. — Fig. 29. Right mtIII (reverted), proximal part, fossa nudata type 2.
Fig. 30. *Equus caballus*, late Pleistocene, Northern Asia (after Gromova 1955a: fig. 17D). Right mtIII (reverted), proximal part, fossa nudata type 2.
Fig. 31. *Equus stenonis* cf. *major*, Pleistocene, Psekups river, near Krasnodar (after Gromova 1955a: fig. 17B). Left mtIII, proximal part, fossa nudata type 2.

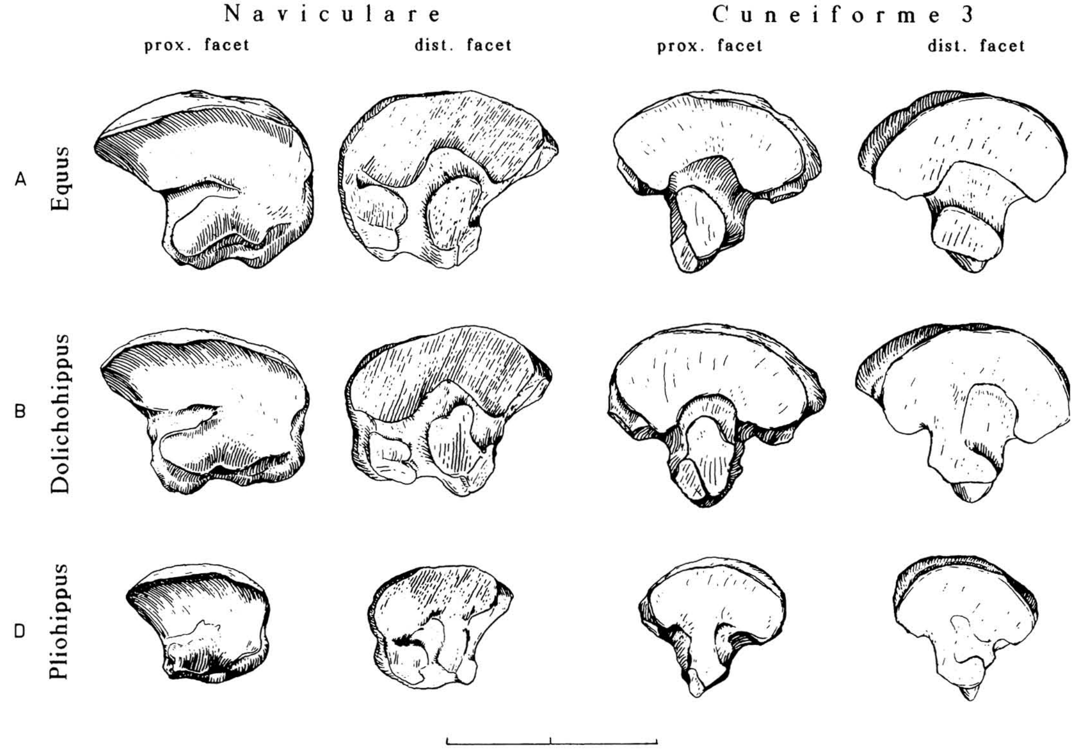

Fig. 32. Fossae nudatae on left tarsals of North American Equidae. — *Equus,* recent, *Dolichohippus*, Plio-Pleistocene, *Pliohippus*, Upper Miocene/Pliocene (after Hussain 1975: fig. 7, 8).

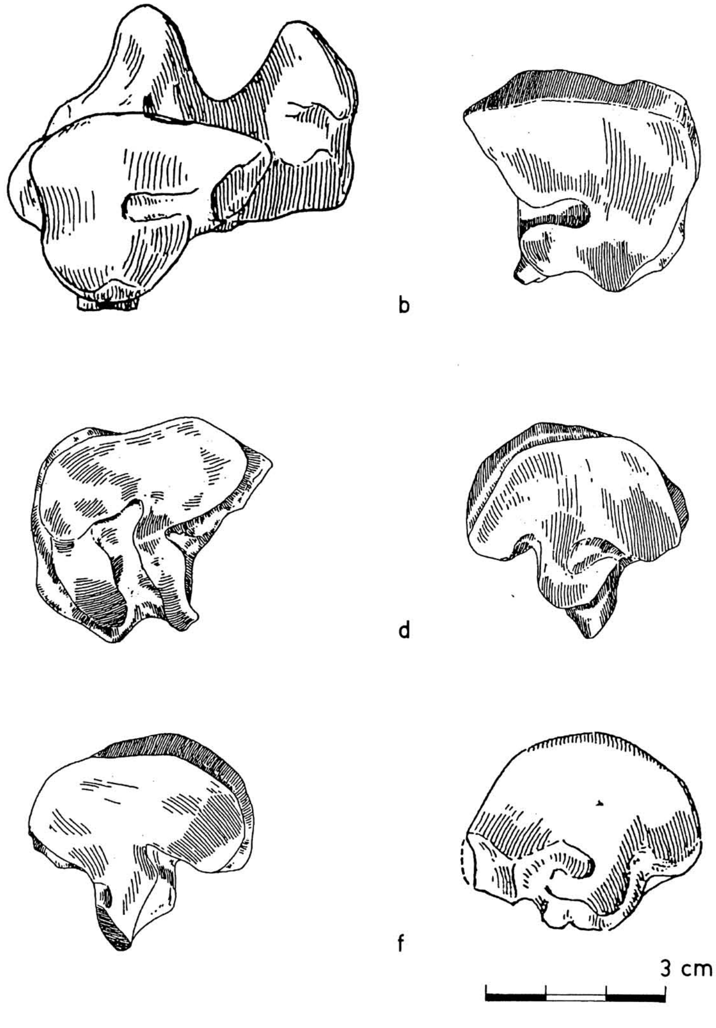

Fig. 33. Fossae nudatae type 2 of the three tarsal joints defined in Fig. 24. "*Hipparion*" *primigenium*, Vallesian, Höwenegg, A-skeleton. Original SLNK. — Navicular facet of astragalus (a) and counterpart on proximal facet of naviculare (b). — Distal facet of naviculare (c) and counterpart on proximal facet of cuneiforme 3 (d). — Distal facet of cuneiforme 3 (e) and counterpart on proximal facet of mtIII (f).

quence of development of fossae nudatae in *Mesohippus - Hipparion* in the North American Neogene. No further detailed description seems to be necessary in this context. It seems that in *Merychippus* the modern fossa nudata scheme — present in the recent horse — takes its origin.

6. Discussion

The data above (Table 1 and 2), unsystematically collected, permit only some grosso-modo remarks about the appearance, i.e., the "palaeontological history" of the fossae nudatae in the articulation joints of Neogene equids discussed above.

6.1. Europe and some Old World occurrences

The material does not reflect an evolutionary sequence, but represents successive immigrations of *Anchitherium-*, *Hipparion-*, and *Equus-*populations into the Old World in the Middle Miocene (Orleanian) – Late Miocene (Vallesian) and Pliocene, respectively.

According to the available information, *Anchitherium* is not provided with fossae nudatae in the fore limb magnum/mcIII joint. At present nothing is known about the terminal Vallesian *Anchitherium* (e.g. Eppelsheim) in this respect.

At the early "*Hipparion*" *primigenium* level (Vallesian) fossae nudatae appear to be rare in

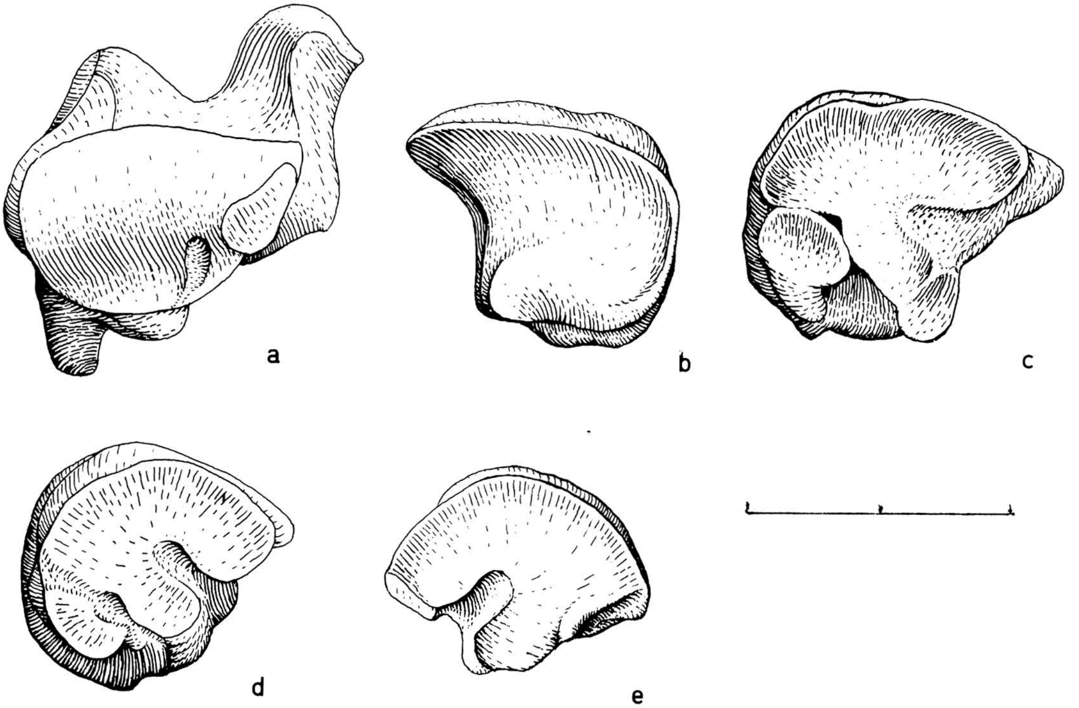

Fig. 34. Fossae nudatae type 2 of the left three tarsal joints defined in Fig. 24. *Anchitherium aurelianense*, Middle Miocene, Sansan (after Kovalevsky 1873: pl.2, fig. 14A, 17A, 33A, 23A, 28A). — Navicular facet of astragalus (a) and proximal facet of naviculare (b), incipient fossae; distal facet of naviculare (c) with broad fossa, entocuneiforme and cuboid facet; distal facet of cuneiforme 3 (d) with narrow fossa and entocuneiforme; proximal facet of mtIII (e) with narrow fossa.

the magnum/mcIII joint. In the later (Turolian) populations, however, fossae nudatae may be more widespread and diversified. On the basis of the very poor data at hand, the early Nagri "*Hipparion*" also seems to be somewhat more advanced than the European *"H." primigenium*. In the light of the very poor material reviewed here, it thus appears that fossae nudatae may have increased in size and frequency with time. It is an open question whether this trend, if real, was caused by local, provincial or continental level evolutionary processes.

In the *Equus* group a seemingly similar situation exists. *Equus stenonis* seems to have not yet evolved fossae nudatae in the magnum/mcIII joint, but later horses probably did, and living ones certainly did so. However, in the supposedly ancestral, North American *Pliohippus (Dinohippus)*, a variably expressed fossa nudata was already present (p. 396, Table 1).

In the three hind limb joints the situation is as follows:

Anchitherium: There are clear signs of a beginning fossa type 2 formation. The indentations begin at the lateral walls of the tarsal elements and the mtIII, penetrating in a medial direction halfway into the respective facets.

Hipparion: The Vallesian Höwenegg-*Hipparion* already shows a complete set of type 2 fossae nudatae in the three joints, and later taxa corroborate this picture, but with certain variations in the direction of type 1. Generally speaking, the state is intermediate between *Anchitherium* and *Equus*.

North American tridactyls: The development of the fossa is demonstrated by the sequence:

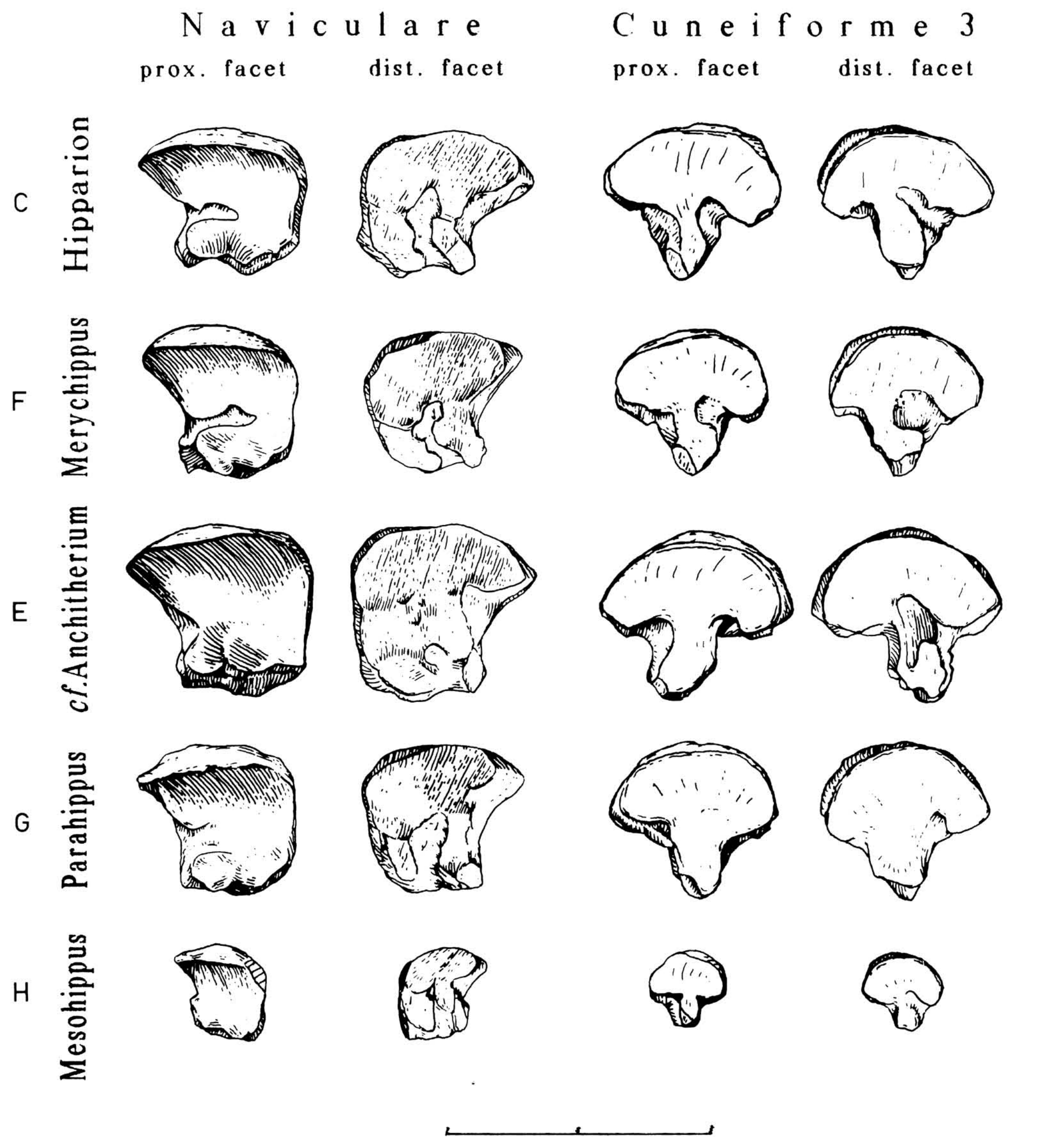

Fig. 35. Fossae nudatae on left tarsals of North American late Oligocene and Miocene tridactyl horses (after Hussain 1975: fig. 7, 8).

Mesohippus – Parahippus – Merychippus – "*Hipparion*". It seems that the merychippine level represents the origin of the modern fossa types.

Equus: As far as the very limited data indicate, the Plio/Pleistocene *Equus stenonis* may not yet have reached the level of later Pleistocene and recent horses in the differentiation of the fossae of the three tarsal joints.

6.2. Fossae nudatae in the podialia

Fossae nudatae of type 1 or 2 appear — at least in the basipodia of later Equidae in flat, platelike podialia, such as the magnum, navicular, cuneiform 3, and the adjacent metapodialia, astragalus included, with large articulation surfaces in congruent arrangement.

The articulations in the magnum/mcIII joint and in the hindlimb joints, described above, are amphiarthroses, i.e. they are joints in which little or no movement is possible, at least in the living horses.

Obviously the platelike podialia with their congruent facets, the fossae nudatae on their surfaces and their amphiarthroses represent a morpho-functional system with a real evolutionary background. It was brought into action in the tridactyl horses and reached its extreme in morphologically and functionally monodactyl horses.

Table 1. Occurrence of fossae nudatae in forelimbs of some recent and fossil Old World mono- and tridactyl horses. — Mg = distal facet of magnum, Mc = proximal facet of MtIII. One specimen studied, except for noted cases.

Taxon	Age	Mg	Mc	Source
Monodactyls				
Equus somaliensis	Recent	1	1	cf p. 3
E. przewalskii	Recent	1	1	cf p. 3
E. przewalskii	Recent	0	0	cf p. 3
E. g. grevyi	Recent	1	1	cf p. 3
E. g. grevyi	Recent	0	0	cf p. 3
E. grevyi	Recent	2	2	Fig. 2a,b
E. zebra	Recent	1	1	Fig. 1a,b
E. zebra	Recent	2	2	cf p. 3
E. zebra	Recent	—	0	Fig. 4
E. domesticus	Recent	2	—	Fig. 3
E. h. hemionus	Recent	2	2	cf p. 3
E. stenonis	Pleistoc.	—	0	Fig. 5, 6
Pliohippus mexicanus	Pliocene	0	—	Fig. 7a
P. mexicanus	Pliocene	—	2	Fig. 7b
P. mexicanus	Pliocene	—	0	cf p. 4
Tridactyls				
Hipparion primigenium	Vallesian	0	0	cf p. 4[a]
H. primigenium	Vallesian	2	2	Fig. 8a,b, cf p. 8[b]
"Hipparion" elegans	Turolian	2	—	Fig. 9
"H." elegans	Turolian	—	0	cf p. 4
"Hipparion" sp.	Meotian	—	1	Fig. 10
"H." sp.	Meotian	—	2	Fig. 11
"H." sp.	Meotian	—	1	Fig. 13
"H." moldavicum	Meotian	—	0	Fig. 14
"H." cf. *verae*	Meotian	2	2	Fig. 12
"Hipparion" theobaldi mogoicum	"Pontian"	2	—	Fig. 16
"Hipparion" theobaldi mogoicum	"Pontian"	—	2	Fig. 15
"Hipparion" nagriense	Vallesian	—	2	Fig. 17
Anchitherium aurelianense	Miocene	—	0	Fig. 18,19

[a] *N* = 12 [b] *N* = 2

6.3. The function of the fossae nudatae

Two disparate views regarding the function of the fossae nudatae exist in the literature. Palaeontologists have interpreted them, without much discussion, as attachment areas of strong ligaments: Major (1880:51, 58, 60, 62, 74 etc.): "Ansatzstellen der Ligamente", "rauhe Buchten für Ligamente" in the fossae nudatae of tarsalia and mtIII; Gromova (1955b) p. 104: "A la surface distale d'os naviculare tarsi d'*Hipparion*, les parties rugueuses (i.e. fossae nudatae) separant les facettes articulaires et servant d'attache aux ligaments unissant navicular à cuneiform III, sont plus petits que chez le cheval"; p. 105: "des fossettes ligamentaires indiquant des ligaments, reliant les deux series d'element du tarse ..."; see also pp. 107, 113; Gabuniya (1961) p. 46: os cuneiform III with "rugosité des ligaments interarticulaires", see also pp. 71, 83, 84, 108, 121 etc.; Hussain (1975) p. 198: "This rugose area serves for the attachment of the intertarsal ligaments" (fig. 7A-a, g: "non-articular area"); Zhegallo (1978) fig. 31: cuneiform III: li 3, li 4 = "ligamentum interosseum"; Renders & Sondaar (p. 473 in Leakey 1987: "Only [astragalus] LAET 2944 from Loc. 16 showed a ligamentary scar in the facet for the navicular. This scar is characteristic for most *Hipparion* species..."); Vidalenc (1979) fig. 28B-6: "insertio-ligamentae distolaterale of navicular dist.; fig. 29A-9: lig. talonaviculare inteross. of navicular prox.; fig. 32-7: lig. tarsometarsalis III interosseum III of cuneiform dist.; fig. 40-E: lig. tarsometarsalis interosseum III of mtIII. These authors accept the presence of strong intertarsal ligaments, rooting in and filling completely the congruent fossae nudatae, thereby reinforcing the stiffness of the respective articulations.

In standard veterinarian literature the fossae nudatae are interpreted as grooves or channels through which the liquid synovia is introduced between the amphiarthrotic joints of the basipodia as a lubricant for the cartilage cover (Ellenberger-Baum 1977:12; Nickel et al. 1986:169, 170). Getty (1975) describes and figures a horse magnum (distal facet), a navicular, a cuneiform 3 and an mtIII, all in proximal aspects with type 2 fossa nudata as "nonarticular depressions" (p. 289, figs. 15-101, 15-103, 15-108), without making allusions to a synovial function. However, nothing is said in the syndesmology chapter of intratarsal ligaments located in these nonarticular depressions (Getty 1975:370–374).

I discussed these problems with Dr. F. Schrenk, Landesmuseum Darmstadt, who proposed an autopsy of a freshly killed horse. From a butcher's shop we received in May 1990 the fore and hind feet of a 10-12 year old gelding. One left hind foot had already been cut off along the astragalus/navicular joint by the butcher. By this means the joint capsule had been destroyed and the synovial liquid - if such had been present - had escaped from the two fossae. The fossae were empty, however, not filled with ligaments, as postulated by the above mentioned authors. The dissection was continued in the Darmstadt Museum laboratory by Dr. F. Schrenk, with the assistance of Dr. E. Frey, now in Karlsruhe, Staatl. Museum f. Naturkunde, and the author. Cutting the extremely firm connection between the navicular and cuneiform 3, formed by the stiff, inelastic, thick ligaments at the cranial borders of both tarsals, revealed two facets with congruent type 2 fossae, similar to Fig. 25c, d respectively. Both were without synovia, probably because of the destruction of the joint capsule. The bottom of the fossa was rugose, free of cartilage and with small, irregularly distributed pori. The sharp borders, and in part the bottoms, were provided

Table 2. Occurrence of fossae nudatae in hindlimbs of some recent and fossil Old World mono- and tridactyl horses. — As = navicular facet of astragalus, Np = proximal facet of naviculare, Nd = distal facet of naviculare, Cp = proximal facet od cuneiforme 3, Cd = distal facet of cuneiforme 3, Mc = proximal facet of MtIII, co = coossified. One specimen studied, except for noted cases.

Taxon	Age	As	Np	Nd	Cp	Cd	Mc	Data source
Monodactyls								
Equus przwalskii	Recent	2	2	2	2	2	2	Fig. 24, 27
E. przwalskii	Recent	2	2	2	2	2	2	MB 10863 own observ.[b]
E. przwalskii	Recent	2	2	2	2	2	2	Fig. 25e,f & own observ.
E. zebra	Recent	2	2	2	2	2	2	Fig. 26
E. zebra	Recent	2	2	2	2	2	2	MB 10918 own observ.[e]
E. grevyi grevyi	Recent	2	2	2	2	2	2	MB 10873 own observ.[c]
E. grevyi grevyi	Recent	2	2	2	2	2	2	MB 10876 own observ.[d]
E. grevyi	Recent	2	2	2	2	2	2	Fig. 25a,b & own observ.
E. somaliensis	Recent	2	2	co	co	2	2	MB 10858 own observ.[a]
E. h.hemionus	Recent	2	2	2	2	2	2	Fig. 25c,d & own observ.
E. caballus	Late Pleistocene	—	—	—	—	—	2	Fig. 30
E. stenonis cf. *major*	Pleistocene	—	—	—	—	—	1	Fig. 28
E. stenonis cf. *major*	Pleistocene	—	—	—	—	—	—	Fig. 29
E. stenonis cf. *major*	Pleistocene	—	—	—	—	—	—	Fig. 31
Tridactyls								
Hipparion sefvei	Pliocene	—	1	2	—	—	—	cf p. 10
H. tchikoicum	Pliocene	—	—	—	—	—	2	cf p. 10
H. (Neohipparion) houfenense	Pliocene	—	2	2	—	—	2	cf p. 10
H. theobaldi mogoicum	"Pontian"	2	2	2	2	2	2	cf p. 10
"Hipparion" elegans	Turolian	2	2	2	2	—	2	cf p. 10
"H." primigenium	Vallesian	2	2	2	2	2	2	Fig. 33[f]
Anchitherium aurelianense	Miocene	2	1	2	—	2	2	Fig. 34
A. aurelianense	Miocene	1 or 2	2	2	2	2	2	Vidalenc 1979[g]
A. aurelianense	Miocene	0	0	0	0	0	0	Vidalenc 1979[h]

[a] Age 3 years, sex? [b] Juvenile, sex? [c] Age?, sex? [d] Age?, sex? [e] Age 7—8 years, sex?
[f] N = 20—30 [g] N = 56, 11, 16, 12, 11, 36, respectively [h] N = 19, 7, 2, 0, 0, 1, respectively

with short, tiny, soft and flexible organic filaments. Otherwise the fossae were empty.

The separation of the cuneiform 3 from the mtIII was easier. There were no ligaments filling the fossae (similar to Figs. 25e, f). As in the preceding articulation the bottom of the fossae nudatae were rugose, free of cartilage, with some pores, and filamentous, soft, tuffy tissue fibres along the borders, but lacked synovia.

Dr. Schrenk and Dr. Frey provided a brief report of their dissection:

> Hier ist das Protokoll zur Sektion des Pferdefußes, den Sie mitgebracht hatten. Leider lassen sich die Befunde fotografisch nicht so dokumentieren, wie wir es ursprünglich geplant hatten. Die Fasern und Faserbündel sind so stark zerfetzt, daß die entscheidenden Strukturen auf den Fotografien einfach nicht erkennbar sind. Wir können Ihnen daher nur eine kurze Beschreibung der Befunde liefern.
>
> In beiden Gelenken stellten wir fest, das auf den Fossae nudatae kurze weiche, elastische Fasern und Faserbündel angeheftet sind, welche von Knochen zu Knochen verlaufen. Ein Teil dieser Faserbündel hat ihren Ursprung in der Tiefe der Fossae. Die Anheftstellen dieser Faserbündel befinden sich ausschliesslich im marginalen Bereich der Fossae, der zentrale Bereich ist völlig frei davon. Offen bleibt, ob diese Zone mit Synovialflüssigkeit gefüllt war. Die genaue Lage und der Verlauf dieser intratarsalen Fasern und -bündel war mit unserer recht groben Präpariermethode nicht rekonstruierbar, weil sie unter Gewalteinwirkung unkontrolliert zerrissen.
>
> Wir planen, mehrere Carpal- und Tarsalgelenke von Pferden zu plastinieren, um u.A. genaue Aussagen über Lageverhältnisse und Ausdehnung der intratarsalen Faserserien etc. u. -bündel, sowie deren histologische Beschaffenheit machen zu können.

As the report shows, the dissection was unfortunately not a complete success, obviously because of "recht grobe Präparationsmethoden, unkontrolliertes Zerreissen der Fasern unter Gewalteinwirkung". Furthermore a detailed description of the fibres is missing. This fibrous, filamentous soft, intratarsal tissue looks very different from the intertarsal ligaments at the cranial walls of the navicular and cuneiform 3. These fibres were unable to hold the tarsals referred to firmly together, to produce an immovable amphiarthrosis. Probably they are structural elements, at least in the type 2 fossa nudata, with unknown function. What keeps these tight joints together in living horses is the stiff, inelastic and thick lig. dorsi centrale (Getty 1975: fig. 16–25), and this would also apply to fossil species. (The toughness of this ligament is demonstrated by the fact that Schrenk's scalpel was unable to cut through it; he had to use a hammer and chisel, due to lack of time). The planned plastinisation should provide additional and more accurate information.

Schulz (1915:253–254) long ago described a fossa nudata on the distal facet of the magnum (his os capitatum) of a domestic horse. The fossa begins in the middle of the lateral border of the facet and extends medially and parallel to the cranial border of the magnum (similar to Fig. 3). It is characterized by areas of deep reaching bony destruction. A congruent fossa is developed on the corresponding head of the mcIII (= basis metacarpi of the author). Nothing is mentioned of the presence of typical ligaments filling the fossae. Unfortunately Schulz's investigation is restricted — as far as the basipodia are concerned — to these data. So far this appears to be the sole published dissection of carpal and tarsal articulations of living horses in which the fossae nudatae are discussed.

To summarise the above remarks, in the cases discussed above, the fossae of type 2 are involved in making available synovia as a joint lubricant. In all probability the type 1 fossae are incipient stages.

Veterinarians are not unanimous about the appearance of the fossae synoviales (or nudatae) in domesticated mammals, mainly ungulates. Thus Schulz (1915) described 14 fossae nudatae from 12 horses of different individual ages, from the articular facets of the atlas down to the distal ends of the metapodials, and concluded (p. 269) that the cartilage disappears (i.e., the fossae nudatae appear) in locations where stress is minimal. Bürki (1905) studied the fossae nudatae of 26 individuals of slaughtered domestic cattle, describing examples from the basipodia (p. 247, 253) and suggested (p. 297) that the formation of the fossae synoviales might be related to high stress. In a study of 12 lambs, Mehlfeld et al. (1984) assume that synovial pits develop where tensile strength is high and compressive strength low. Dämmrich et al. (1977) deduced a positive relationship between individual body mass and size of the fossa nudata in a study of 12–18 month-old bulls.

The question of how fossae nudatae relate to stress can be addressed in relation to the phylogenetic development of fossae nudatae in the basipodia of horses. The evolution of tridactyl equids shows an increasing relative size of the medial metapodia (mcIII and mtIII) and their phalanges, suggesting that a greater proportion of body mass was carried by these central elements. This shift also concerned those basipodia that transfer stress to the medial metapodials. When first functional and later structural monodactyly evolved, these medial joints came to support the entire body mass. If the fossae nudatae are indeed more developed in monodactyl horses, as the available data seem to suggest, then the relationship between stress and fossa nudata size would appear to be a positive one. This question cannot, however, be resolved on the basis of fossil evidence alone.

Furthermore, palaeontologists are unable to say anything about the agents that produce the fossae nudatae by removal of the cartilage and part of the bony underlayer, i.e, about the causes of what may be called, in a very general sense, "cartilage-bone-alterations" (cba-alteration = "Knorpel-Knochen-Veränderungen") (Hembach-Gerleve 1986:66).

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