

Functional Structure of Metapodial Bones of Cattle

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Abstract

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The supporting part of the metapodium skeleton of the thoracic limb consists of os metacarpale III et IV, developing through the fusion of two initially independent bones (III and IV). In the pelvic limb it is os metatarsale III et IV, developing analogically. In macerated bones of recent cattle at the age of 1-8 years and those from archaeological excavations (medieval, 9th–15th centuries) the length asymmetry of the above bones was studied by means of osteometry and the data obtained were evaluated statistically. In the thoracic limb metapodium, being the major supporting element in unguligrade paraxonic cattle, three possible relations between the lengths of metacarpals III and IV were observed, viz., (1) III longer than IV, (2) IV longer than III, and (3) both bones of the same length. In the metatarsus, i.e. the part of the pelvic limb with a largely locomotive function, bone IV was the longer one in all cases. Osteometric and statistical methods were also applied to the material mentioned above in order to examine the correlation of the width of cavum medullare with the overall width of a bone. While the relative width of the medullar cavity of the metapodium bones was found to be correlated with age, this correlation was negative in both the metacarpus and metatarsus ($r = -0.6778$ and -0.6294 , respectively). The relation between the resorptive and formative processes (R:F) in the bone of unguligrades tends to depend upon the requirements for mechanical strength and bone resistance.

Cattle, os metacarpale III et IV, os metatarsale III et IV, osteometry

In unguligrade quadrupeds, the bones of their metapodia are among the important limb long bones. In the thoracic limb, the position of metacarpal bones (os metacarpale III et IV), the same as those of the forearm, is perpendicular and the compact bone of the diaphysis equally supports the weight of the head, neck, and the anterior part of the trunk, whereas the scapula and the humerus are posited obliquely and the peripheral compact bone of their diaphysis is not equally poised. In the pelvic limb the metatarsal bones (os metatarsale III et IV) are the only ones that are perpendicular, the stylopodium (thigh bone) and the zeugopodium (shin bones) being oblique as well. As to locomotion, the pelvic limbs are of greater importance as they give the impulse for forward movement. The thoracic limbs support the cranial part of the animal and help it to move forward. Generally speaking, the long bones of the pelvic limb are longer and stronger than those of the thoracic limb.

Osteometric data on the lengths, widths, and circumferences of bones can provide fairly correct ideas of the sizes of the animals, their height at the withers, sex, and other characteristics. Bone dimensions are sex-dependent, as documented by Bartosiewicz (1984) who compared the lengths of three long bones in the thoracic limb of cattle (the humerus, the radius, and the metacarpus) and found them longer in bulls than in cows. The mean length of metacarpus of the bulls ($n = 26$) was 219.833 ± 4.762 mm; that of the cows ($n = 47$) 207.651 ± 4.259 mm.

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The skeleton of the metapodium (metacarpus and metatarsus) of cattle is known to develop through a fusion of two initially independent bones: os metacarpale III and os metacarpale IV in the metacarpus, and os metatarsale III and os metatarsale IV in the metatarsus. In the course of prenatal development, there also develop and ossify the cartilaginous rudiments of metacarpal (and metatarsal) bones II and V (Martin 1912; Petersen 1922; Küpfer and Schinz 1923; Gjesdal 1969). These rudiments, however, vanish already during intrauterine development, only the rudimentary os metacarpale V., lying lateral at the base of os metacarpale III et IV, persisting lifelong in cattle. The bone is quite unimportant functionally.

According to Kolda (1936), the two main bones (III and IV) are readily separated still in newborns. Küpfer and Schinz (1923) observed on their x-ray photographs that from 9 weeks of age, ca 65 days of ontogeny (DO), crown-rump length (CRL) 82 mm, until 6 months of intrauterine development (CRL 520 mm) the ossified diaphyses of bones III and IV of the metapodium are independent. In fetuses CRL 570 and 580 mm, from the same month, the ossified diaphyses lie in close contact, the same as in the fetus CRL 727 mm (end of the 7th month) where the onset of ossification is also observed in distal epiphyses.

According to Regli (1963), the metapodia start ossifying from 68 DO at the latest. His observations indicate that the osseous connection of bones III and IV in the metapodium begins developing from 200 DO in the proximal-distal direction and ends around 210 DO. In his paper, however, Regli (l.c.) demonstrates macerated bones of older fetuses, in which these bones are separated.

Having studied rather large series of metapodium bones, we have found that the individual metapodium bones (III and IV) are not equal in length and that not even os metacarpale III et IV, nor os metatarsale III et IV are symmetrical in length. While the literary sources contain data on autopodium asymmetry, such data are very rare and mostly pertain to the skeleton of digits, i.e., the acropodium. The morphological differences in the proximal sesamoid bones of the autopodium were described by Červený (1985a, 1985b) on the basis of osteological material and x-ray photographs. Červený (1983) also presented the time differences in the onset of ossification in these bones. Černý (2002) mentions asymmetry in the size of hooves III and IV on the thoracic limb, and he correlates it with their different mechanical load. However, the available literature does not contain sufficient data on the mutual length ratio of the fused bones (III and IV) of the cattle metapodium. For this reason, we have attempted to somewhat enlarge the existing observations.

With advancing age, even the bone structure will change. Numerous papers are available concerning this problem, especially in human bones, and most of them are concerned with the microscopic structure of bone tissue (e.g., Kerley 1965; Bouvier and Uberlaker 1977; Fiala 1978; Feik et al. 1997). The papers just mentioned also discuss the origin of the changes in macroscopic bone structure. Feik et al. (1997) described, in human femur, the correlation of endosteal resorption with periosteal apposition. Endosteal resorption predominates with advancing age, which results in increasing size of the medullar cavity in the bones affected. Likewise, Fiala (1978) mentions this correlation and states that, at the same time, the inner (medullar) layers of compact bone shows osteonal canals increasing in diameter (intracortical porosity). However, the available literary sources do not describe the relative increase in the cavum medullare in animal bones in relation to their age.

Materials and Methods

The development of macroscopic structure of the cattle metapodium skeleton was studied on both fresh and macerated material. The material of non-pregnant females (3-5 individuals i. e. 76 bones from left extremities) was obtained from the slaughter house of the University of Veterinary and Pharmaceutical Sciences. The animals came from healthy stocks kept in standard housing and feeding conditions. From each of the individuals, we removed the os metacarpale III et IV and the os metatarsale III et IV. The bones were classified by age in groups 1, 2, 3, 4,

5, 6, 7, and 8 years. They were treated using the method of biological maceration, cleaned and bleached with 8% solution of hydrogen peroxide. To obtain additional data and check the earlier observations, we also used macerated bones and fixed foetuses at the age of 8 months of prenatal development (40 bones from left extremities) from the collections of the Institute of anatomy, histology and embryology, of the Faculty of Veterinary Medicine, University of Veterinary and Pharmaceutical Sciences in Brno.

For the study of the macroscopic structure of metapodium bones of cattle from archaeological excavations, we used the complete bones (40 bones from left extremities) of metacarpale III et IV and os metatarsale III and IV of this kind from the collections of the Institute of Archaeology, ČSAV, in Brno, the Institute of Archaeology of the Moravian Museum in Brno, and the Archaeological Department of the Brno City Museum. The finds date from the period between 500 to 1000 years ago and come from medieval localities in Moravia.

The following dimensions were taken from the bones (Plate III, IV, Figs. 1, 2):

a) Os metacarpale III et IV

1. Physiological length of metacarpal III, i.e. distance between the most distal points of the edge of facies articularis basis ossis metacarpalis III and of the abaxial part of the trochlea of caput ossis metacarpalis III.

2. Physiological length of metacarpal IV, i.e. distance between the most distal points of the edge of facies articularis basis ossis metacarpalis IV and of the abaxial part of the trochlea of caput ossis metacarpalis IV.

3A. Width of os metacarpale III et IV at the level of 1/4 of its length (level A)

3B. Width of os metacarpale III et IV at the level of 1/2 of its length (level B)

3C. Width of os metacarpale III et IV at the level of 3/4 of its length (level C)

4A. Width of compact bone in margo medialis ossis metacarpalis III et IV at the level of 1/4 of its length (A) half the distance between facies dorsalis and facies palmaris ossis metacarpalis III et IV.

4B. Width of compact bone in margo medialis ossis metacarpalis III et IV at the level of 1/2 of its length (B) half the distance between facies dorsalis and facies palmaris ossis metacarpalis III et IV.

4C. Width of compact bone in margo medialis ossis metacarpalis III et IV at the level of 3/4 of its length (C) half the distance between facies dorsalis and facies palmaris ossis metacarpalis III et IV.

5A. Width of compact bone in margo lateralis ossis metacarpalis III et IV at the level of 1/4 of its length (A) half the distance between facies dorsalis and facies palmaris ossis metacarpalis III et IV.

5B. Width of compact bone in margo lateralis ossis metacarpalis III et IV at the level of 1/2 of its length (B) half the distance between facies dorsalis and facies palmaris ossis metacarpalis III et IV.

5C. Width of compact bone in margo lateralis ossis metacarpalis III et IV at the level of 3/4 of its length (C) half the distance between facies dorsalis and facies palmaris ossis metacarpalis III et IV.

b) Os metatarsale III et IV

6. Physiological length of metatarsal III, i.e. distance between the most distal points of the edge of facies articularis basis ossis metatarsalis III. and of the abaxial part of the trochlea of caput ossis metatarsalis III.

7. Physiological length of metatarsal IV, i.e. distance between the most distal points of the edge of facies articularis basis ossis metatarsalis IV and of the abaxial part of the trochlea of caput ossis metatarsalis IV.

8A. Width of os metatarsale III et IV at the level of 1/4 of its length (level A)

8B. Width of os metatarsale III et IV at the level of 1/2 of its length (level B)

8C. Width of os metatarsale III et IV at the level of 3/4 of its length (level C)

9A. Width of compact bone in facies medialis ossis metatarsalis III et IV at the level of 1/4 of its length (A) half the distance between facies dorsalis and facies plantaris ossis metatarsalis III et IV.

9B. Width of compact bone in facies medialis ossis metatarsalis III et IV at the level of 1/2 of its length (B) half the distance between facies dorsalis and facies plantaris ossis metatarsalis III et IV.

9C. Width of compact bone in facies medialis ossis metatarsalis III et IV at the level of 3/4 of its length (C) half the distance between facies dorsalis and facies plantaris ossis metatarsalis III et IV.

10A. Width of compact bone in facies lateralis ossis metatarsalis III et IV at the level of 1/4 of its length (A) half the distance between facies dorsalis and facies plantaris ossis metatarsalis III et IV.

10B. Width of compact bone in facies lateralis ossis metatarsalis III et IV at the level of 1/2 of its length (B) half the distance between facies dorsalis and facies plantaris ossis metatarsalis III et IV.

10C. Width of compact bone in facies lateralis ossis metatarsalis III et IV at the level of 3/4 of its length (C) half the distance between facies dorsalis and facies plantaris ossis metatarsalis III et IV.

In the same way we measured bones 500 and 1000 years old from archaeological excavations.

All measurements were taken using a calliper rule (in standard use in osteometry) and the data were entered in tables. The measurements were treated statistically using the Statistica 6 programme and the results were expressed graphically.

The correlation of the lengths of the IIIrd metacarpal (or metatarsal) with the IVth metacarpal (or metatarsal) bones was evaluated from dimensions 1, 2, 6, 7. For the selection of the optimum method of statistical evaluation, we first examined the distribution of the values by means of histograms. Wilcoxon's nonparametric paired test was used to compare the two series of data, determining the null hypothesis H_0 on the $P = 0.05$ significance level. For a comparison of the recent bones and those from archaeological excavations, we used diagrams with box-and-whisker plots indicating means, standard deviations, and minimum and maximum values of the bone dimensions taken.

To determine the development of the correlation of the size of cavum medullare with the total bone width, we employed dimensions 3 (A,B,C), 4 (A,B,C), 5 (A,B,C), 8 (A,B,C), 9 (A,B,C) and 10 (A,B,C). The mean values

calculated from dimensions taken at levels A, B, and C were used to compute the correlation of two variables by means of Pearson's correlation coefficient on 95% confidence level.

Results

The following facts have been found in comparing the lengths of the IIIrd and IVth bones of both metapodia:

In the case of os metacarpale III et IV, the correlation of the lengths of the IIIrd and IVth bone was not constant. In some cases the IIIrd metacarpal was longer, and vice versa in others. In several cases the two bones were equal in length. This situation has been found in recent metacarpals as well as in those 500 and 1000 years old. The statistical evaluation of the distribution of mean lengths of the bones (III:IV) is shown in Diagram 1, indicating symmetrical (normal) distribution of mean values.

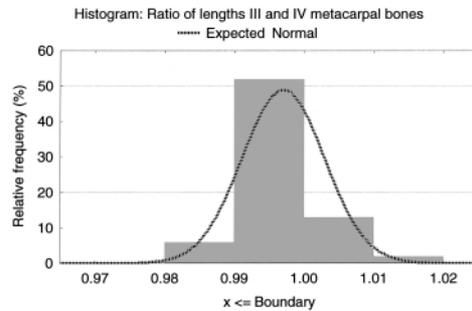


Diagram 1. Histogram showing distribution of computed ratios of metacarpal bones III:IV.

In all cases of the metatarsal bones from all three periods, the os metatarsale IV was longer than os metatarsale III. Diagram 2 shows asymmetrical (non-normal) distribution of the length ratios of bones III:IV.

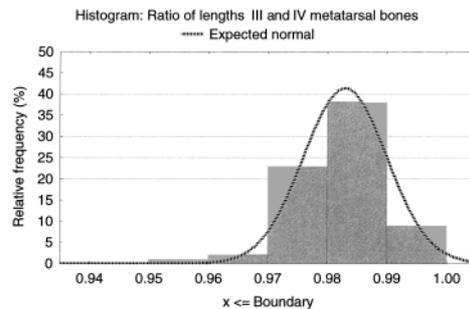


Diagram 2. Histogram showing distribution of computed ratios of metatarsal bones III:IV.

In testing the identity of the two series by means of Wilcoxon's test, the computed value $P = 1.72 e^{-13}$. This value indicates on the $P = 0.05$ probability level that the two series (i.e. metacarpals vs. metatarsals) differ significantly in the indices compared.

In comparing the dimensions of recent bones with those from archaeological excavations (Diagram 3), the metapodium bones of recent cows are absolutely longer than the respective

bones of cows 500 and 1000 years ago. Besides, we have confirmed that the IIIrd metapodium bone is invariably shorter only in the metatarsus.

The study of the width of cavum medullare in relation to the overall bone width has revealed the following:

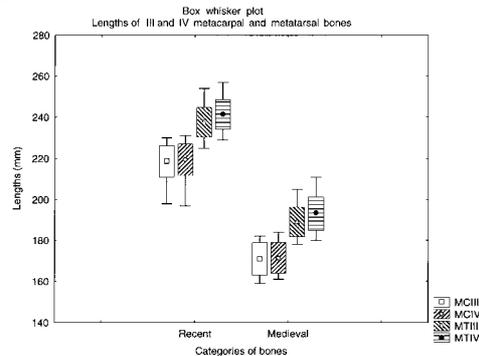


Diagram 3. Comparison of lengths of metapodial bones III and IV in recent and archaeological material. MCIII, os metacarpale III; MCIV, os metacarpale IV; MTIII, os metatarsale III; MTIV, os metatarsale IV. Box and whisker plots indicate means and standard deviations.

In the metacarpal bones of a foetus at eight months of intrauterine development the mean width of the medullar cavity amounts to 71.3% of the overall bone width; at one year of age, 65.9%; at two years of age, 61.1%; at three years of age, 61.6%; at four years of age, 62.9%; at five years of age, 60.4%; at six years of age, 60.8%; at seven years of age, 61.4%; and at eight years of age, 62.1%. Diagram 4 shows the statistical evaluation of the correlation of two variables on a 95% confidence level by means of Pearson's correlation coefficient. The relative size of the medullar cavity is negatively correlated with the animal's age from 8 months of intrauterine development until 8 years of postnatal ontogeny. The value of the correlation coefficient in this case was $r = -0.6778$.

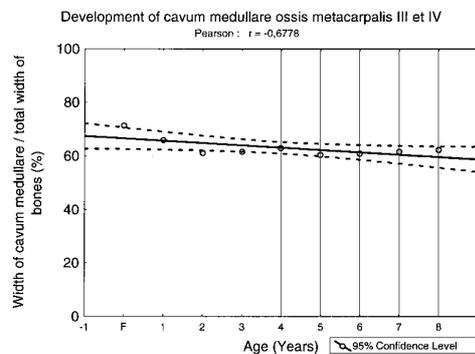


Diagram 4. Correlation of width of cavum medullare with overall width of os metacarpale III et IV. F - foetus 8 months of age.

In the metatarsal bones of a foetus at 8 months of intrauterine development the share of the width of the medullar cavity in the overall bone width amounts to 67.5%; at one year of age, 61.7%; at two years of age, 50.3%; at three years of age, 52.7%; at four years of age, 57.2%; at five years of age, 55.1%; at six years of age, 51.2%; at seven years of age, 51.9%; and at eight years

of age, 54.9%. Even in this case the measured and computed values were evaluated by means of the same method. The result is shown in Diagram 5. In the case of the metatarsal bones, the width of the medullar cavity was negatively correlated with the animal's age during the period indicated. The correlation coefficient $r = -0.6294$.

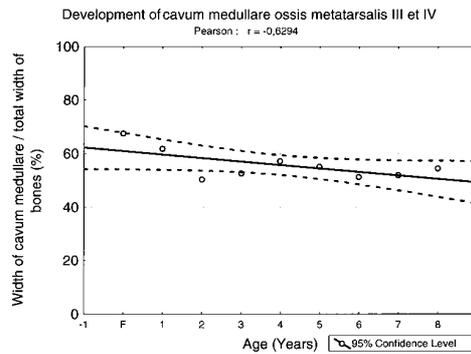


Diagram 5. Correlation of width of cavum medullare with overall width of os metatarsale III et IV. F - foetus 8 months of age.

Discussion

The observation that bone IV is invariably longer of the two in the metatarsus and occasionally in the metacarpus is of interest in connection with the fact that, on the other hand, it is the bone III that is slightly more robust in both the metacarpus and metatarsus. It is worthwhile to give a thought to the relation between the greater massiveness of bone III and the lesser one of bone IV and the order in which toes are reduced during phylogeny. Apparently, the difference between the metacarpus and metatarsus as regards the length of their individual bones is just one of many morphological expressions of the different function of the two kinds of limb. Due to the structure of all its joints, the thoracic limb of a paraxonic artiodactyl, such as cattle, is only capable of flexion and extension. Besides, *m. pectoralis transversus*, inserting as far as fascia antebrachii, limits abduction in the spherical shoulder joint. Thus, the dorsal surface of the autopodium points "forward" all the time, and the thoracic limbs are almost incapable of "straddling". For such posture, which is primarily of advantage for the supporting function of the thoracic limbs, the approximately equal length of the trochleae of the IIIrd and IVth metacarpal bones is probably most suitable. The minor differences in the length of either of the bones are probably due to individual variability. The joints of the pelvic limb of cattle are also only capable of flexion and extension, except for the hip joint, which can also perform other movements including abduction. The greater freedom of the posture of the stylopodium against the pelvis, and thus of the whole pelvic limb, agrees with the predominantly locomotive function. Thus, one may assume that the invariably greater length of the IVth autopodium ray is of advantage for a limb with a wider range of movements. It is interesting to compare our measurements taken on the metacarpus and metatarsus with the literary data on the remaining parts of the autopodium. Černý (2002) states that on the thoracic limb of cattle the IVth hoof is bigger than the IIIrd one, as it carries greater weight. On the contrary, on the pelvic limb, in which we invariably found IVth metatarsal bones being longer than the IIIrd ones, Černý (2002) described symmetrical development of hooves. In his study of proximal sesamoid bones, Červený (1985a, 1985b) found, in both thoracic and pelvic limbs, that the topography of these bones (belonging to the IVth toe) is more distal.

Comparing the lengths of the bones under study in recent cattle and those kept in the middle ages (bones 500 and 1000 years old), we have found greater absolute bone lengths in recent cattle. This is in agreement with literary data on medieval cattle (e.g. Kratochvíl 1969, 1988; Walcher 1976, and others). The metacarpal: metatarsal length ratio of bones III:IV, practically identical in medieval and recent cattle, suggests that the structure of metapodium skeleton did not change in this respect in the course of the past millennium.

In studying the correlation of bone width and size of cavum medullare, we had to consider the difference between a metacarpus and a metatarsus. In sections of the metapodium of the thoracic limb the thickest compact bone is found in the place of maximum bone width, the margo lateralis/medialis forming a pillar that strengthens the diaphysis wall (Plate III, Fig. 1). To avoid bias in the data on the width of the compact bone due to this local strengthening, the wall thickness was measured halfway between facies dorsalis and facies palmaris ossis metacarpalis III et IV. In the corresponding bone of the pelvic limb, however, the place of the greatest width of the bone does not correspond with that of the thickest compact bone. Here the strengthening pillars are distinct on the facies dorsalis and less so on the facies plantaris ossis metatarsalis III et IV and they are parallel with the respective sulci longitudinales (Fig. 3). Therefore, in the case of the metatarsus, we measured the thickness of compact bone in the place identical with that of the overall width of the bone. Apparently, the strengthening pillars in the lateral parts of the metacarpus fit with the increased requirement for static firmness of this bone in its supporting and carrying function. On the contrary, the strengthening of the metatarsus on its dorsal and less so on its plantar surface is probably connected with somewhat different requirements for mechanical strength of the pelvic limb metapodium in its locomotive function.

It is evident from Diagrams 4 and 5 that the share of the medullar cavity in the overall width of the bones under study is correlated with the animal's age. In contrast to the changes observed in human femur (Feik et al. 1997; Fiala 1978), however, the medullar cavity decreases in size with increasing age. Thus, the compact bone in the wall of the diaphysis becomes thicker. The curve showing the trend of this development in the diagrams is the steepest during the first two years of life. The relative size of the medullar cavity is the greatest in the 9th month of intrauterine development of the foetus and decreases thereupon. The drop is so abrupt that the cavum medullare is the smallest at the age of 2 years. In the diagram the percentage value lies in the line limiting the 95% confidence level. In subsequent years of life the variation in these values is not as marked. Pearson's correlation coefficient r expresses the strength of the correlation of two variables, in this case the size of the medullar cavity and the animal's age, and varies between -1 and +1. The lower is the r value, the weaker the correlation. Comparing the two diagrams, it is evident that the correlation of relative size of the medullar cavity with age is stronger in the case of the metacarpus than in that of the metatarsus. The two bones also differ in the share of the medullar cavity in the overall bone width, the values being somewhat lower in the case of the metatarsus. The question remains why these two variables are negatively correlated. Feik (1997) describes the intracortical porosity of compact bones in senescent humans. In the present study, cows up to the age of 8 years were examined. Cattle are known to attain higher age than that, but then cattle are slaughtered before they attain old age. Hence, it was impossible to obtain sufficient material of older individuals, and the question remains whether cattle are already old at the age of eight. Moreover, it is very difficult or even impossible to find any way of mutually converting human and animal ages, as different mammal species differ considerably in the duration of development, growth, and natural ageing. In unguligrades, therefore, the correlation of resorption (R) with formation (F) may not tend towards R being greater than F but, rather, it may reflect the requirement for mechanical firmness and resistance of bones.

Funkční stavba kostí metapodia skotu

Nosnou část skeletu metapodia hrudní končetiny tvoří os metacarpale III. et IV., která vzniká srůstem dvou samostatně založených kostí (III. a IV.), u pánevní končetiny je to os

metatarsale III. et IV., která vzniká obdobně. Na macerovaných kostech recentního skotu ve věku 1–8 let věku i na kostech z archeologických výzkumů (středověk, 9.–15. stol.) byla osteometricky studována a statisticky hodnocena délková asymetrie uvedených kostí. Na metapodiu hrudní končetiny, která má u unguigrádního paraxonického skotu převážně nosnou funkci, byly zjištěny tři možnosti vztahu délek III. a IV. metakarpální kosti: 1. delší III., 2. delší IV. a 3. obě stejně dlouhé. Na metatarzu, tedy části pánevní končetiny s funkcí převážně pohybovou, byla ve všech případech delší IV. kost. Osteometrickými a statistickými metodami byl na uvedeném materiálu rovněž sledován vztah šířky cavum medullare k celkové šířce kosti. Bylo zjištěno, že relativní šířka dřevné dutiny kostí metapodia je sice v korelaci s věkem, ale jak na metakarpu, tak na metatarzu se jedná o korelaci negativní ($r = -0,6778$ a $-0,6294$). Vztah mezi resorpčními a formativními procesy (R:F) v kosti unguigrád spíše vychází z požadavků na mechanickou pevnost a odolnost kosti.

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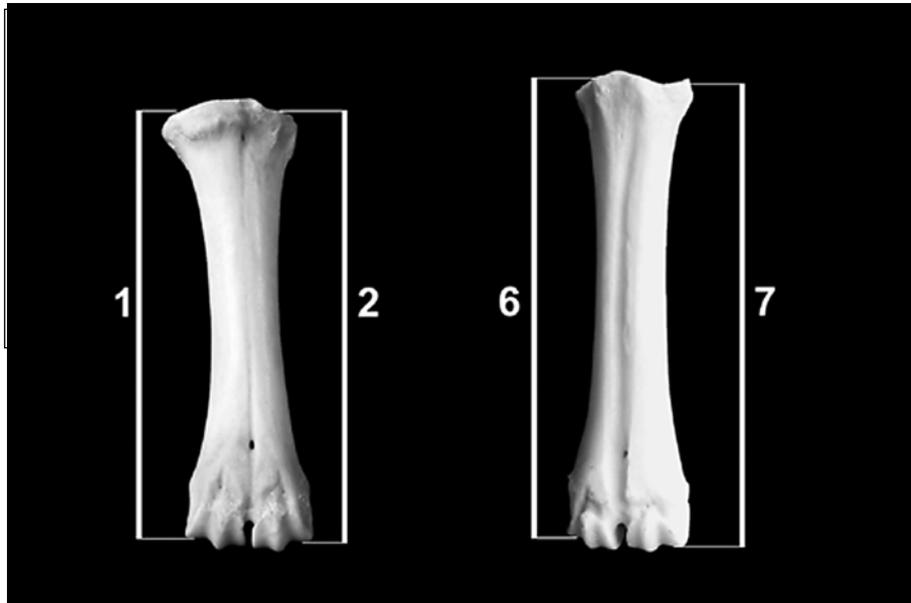


Fig. 1. Bones of cattle metapodium in dorsal view. Left, os metacarpale III et IV; right, os metatarsale III et IV. Osteometric dimensions taken: 1 – length of metacarpal bone III, i.e. distance between the most distal point in the margin of facies articularis ossis metacarpalis III and that on the abaxial part of trochlea of caput ossis metacarpalis III; 2 – length of metacarpal bone IV, i.e. distance between the most distal point in the margin of facies articularis ossis metacarpalis IV and that on the abaxial part of trochlea of caput ossis metacarpalis IV; 6 – length of metatarsal bone III, i.e. distance between the most distal point in the margin of facies articularis ossis metatarsalis III and that on the abaxial part of trochlea of caput ossis metatarsalis III; 7 – length of metatarsal bone IV, i.e. distance between the most distal point in the margin of facies articularis ossis metatarsalis IV and that on the abaxial part of trochlea of caput ossis metatarsalis IV.

Plate IV

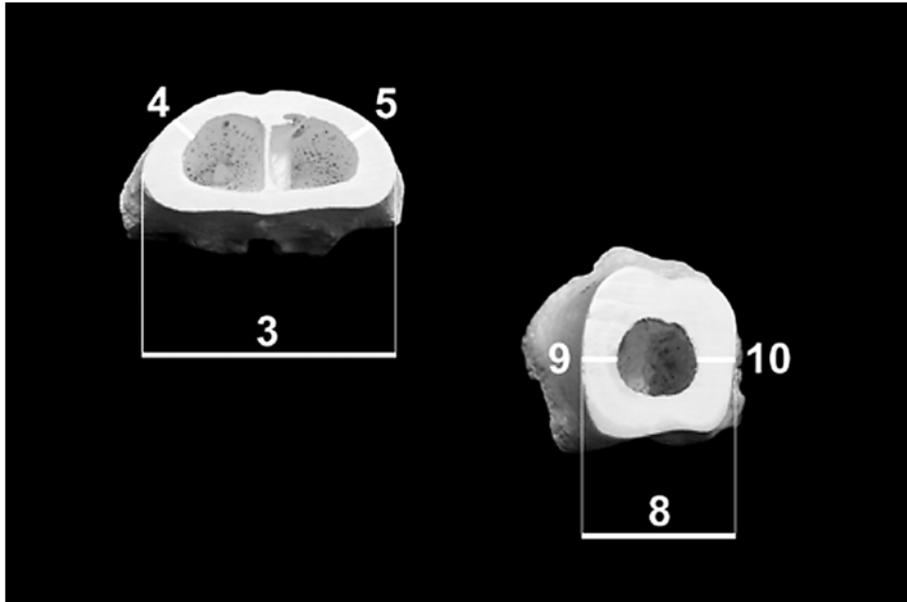


Fig. 2. Osteometric dimensions taken from transversal section. 3 – width of os metacarpale III et IV; 4 – thickness of compact bone in the medial part of os metacarpale III et IV; 5 – thickness of compact bone in the lateral part of os metacarpale III et IV; 8 – width of os metatarsale III et IV; 9 – thickness of compact bone in facies medialis ossis metatarsalis III et IV; 10 – thickness of compact bone in facies lateralis ossis metatarsalis III et IV.

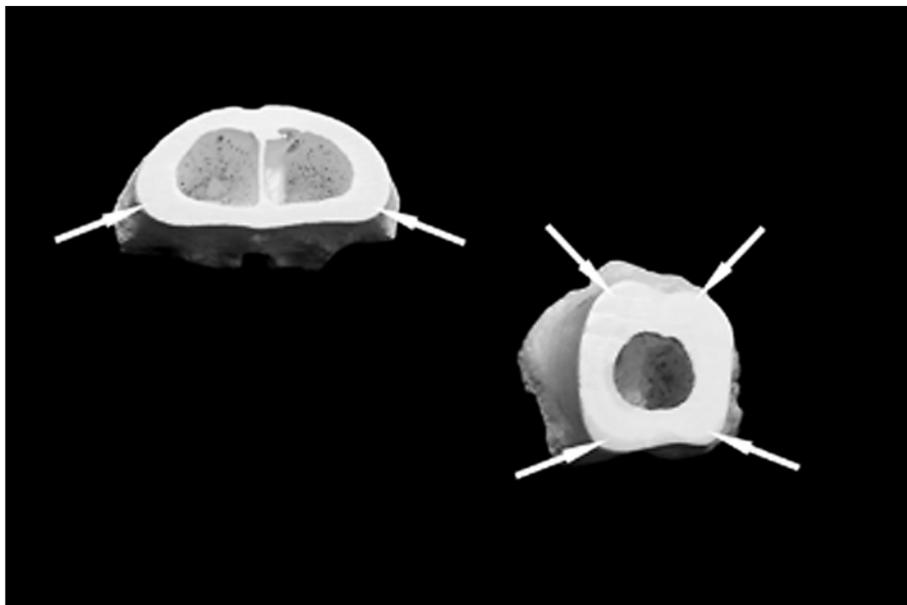


Fig. 3. Metapodial bones in transversal section. Left, os metacarpale III et IV; right, os metatarsale III et IV, arrow indicates pillar-like strengthening of compact bone in diaphysis.