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Gigantic horses

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Abstract - *The "largest in the world" monodactyl equids (modern draft horses,* E. calobatus, E. capensis, E. enormis, E. giganteus, E.major, E. singularis, E. suessenbornensis, E. verae*, and other fossils) are compared using different parameters: skull basilar lengths, occlusal dimensions of the upper cheek teeth, metapodial lengths and distal widths, estimated weights and withers heights. Although the estimations proved extremely difficult, some fossil equids could probably stand at least 180 cm at the withers and weighed more than 1000 kilos. Wild caballines and "gigantic" zebras never reached the size of Pliocene and Early Pleistocene equids. The North American stilt-legged equids have no equivalent among the Old World fossil or modern species.*

Keywords: Gigantic equids (*Equus calobatus, E. capensis, E. enormis, E. giganteus, E. major, E. singularis, E. suessenbornensis, E. verae*), Pliocene, Pleistocene, North America, Beringida, Asia, Europe, Africa.

Résumé - *Les plus grands Equidés monodactyles d'Amérique du Nord, Eurasie et Afrique du Pliocène au Pléistocène supérieur sont comparés suivant leurs dimensions crâniennes (longueur basilaire), dentaires (dimensions occlusales des dents jugales supérieures) et squelettiques (longueurs et largeurs distales des métapodes) et suivant les estimations qui peuvent être faites de leurs poids et hauteurs au garrot. Bien que ces estimations soient sujettes à caution, on peut admettre pour certains fossiles des hauteurs au garrot de 180 cm et des poids dépassant 1000 kilos. Les plus grands caballins sauvages* (E. mosbachensis) *et les plus grands zèbres apparentés aux zèbres de plaine (*E. capensis*) n'ont jamais atteint les dimensions observées au cours du Pliocène* (E. enormis) *et du Pléistocène inférieur* (E. singularis, E. suessenbornensis, E. verae). *Certaines espèces d'Amérique du Nord* (E. calobatus) *présentent des proportions squelettiques sans aucun équivalent dans l'Ancien Monde.*

Mots-clés: Equidés géants (*Equus calobatus, E. capensis, E. enormis, E. giganteus, E. major, E. singularis, E. suessenbornensis, E.verae*), Pliocene, Pléistocene, Amérique du Nord, Beringida, Asie, Europe, Afrique.

Introduction

Equus major, E. enormis, E. giganteus, E. singularis, all these specific names imply fossil horses of *"*out of common*"* large sizes. But what is *"*common*"* and what is *"*size*"*? The size of an extant horse is usually expressed in terms of weight and withers height of the living animal. Paleontologists have no direct access to these parameters and have to find ways of estimating them. On the other hand, paleontologists may have direct access to skulls, and be interested by skull lengths, which are not usually considered by zoologists or veterinarians. In the present paper, fossil *"*size*"* will be addressed under two aspects: observed dimensions (skull basilar lengths, upper cheek teeth occlusal diameters, limb bone lengths, metapodial widths); and estimations (weight, withers height).

What is "common" in matter of size is another point to address. Obviously, the usual size is not the same for all extant species, and probably was not for all geological periods. It is impossible, however, to avoid references to extant animals because the idea of what is "common" is based on them. Because of that, in the histograms illustrating the "world-wide records" of equid sizes, the ranges of variation are extended in the direction of "common" or even small size. Visual comparison between usual and large sizes may thus be helped.

Some of the questions I'll try to answer are: What are the maximal sizes observed in the fossil horses, and how do they compare with extant "records"? Are the maximal sizes the same for any species of monodactyl equid ? What are the practical possibilities and the limitations of estimating the weight and the withers height? Are there geological periods for maximal sizes? How many very large species may be distinguished ?

Most of these points could be better developed, with proper statistical studies and formal taxonomical conclusions. In the mean time, this work presents some methodological approaches and tentative conclusions that may be of interest.

Four groups of monodactyl equids were distinguished: Caballine horses, Plains zebras *sensu lato*, *Plesippus* and *Allohippus*, and (the paper-basket) "large fossil equids". The first group was chosen to represent as well as possible a single species over time. Naturally, there is no saying whether the horse of Mosbach and the horse of Alaska would have produced fertile hybrids. But, although separated by 0.5 Ma, their bones do globally look like those of extant *E. caballus*. In this group belong *E. scotti* (Texas), *E. mosbachensis*, and the large caballine of San Sidero (Italy).

Plains zebras *"sensu lato"* are not so well defined. The extant *E. burchelli* is very probably closely related to the recently extinct *E. quagga* and to the Middle Pleistocene *E. mauritanicus* (Algeria). But the age and the specific attribution of South African fossils, including those referred to *E. capensis*, are less clear. *E. capensis* is mostly defined by its large size. The skull found at Elandsfontein resembles that of *E. mauritanicus*, but is quite larger. Fossils of large size were found at both localities assigned to the Middle Pleistocene and to the Late Pleistocene. Elandsfontein yielded fossils of both ages. According to the fossilization, James Brink (*National Museum of Bloemfontein*) was able to assign, at least tentatively, some Elandsfontein fossils to Late Glacial or Cornelian (Middle Pleistocene) ages. The Elandsfontein skull is possibly Cornelian. The size and protocone lengths of the upper cheek are identical, no matter the assumed age but there are some differences in limb bones. At Equus Cave, the bulk of the material is probably Late Pleistocene, but may include older fossils. Smaller equids of uncertain position are present at most localities and predominate at Equus Cave, Black Earth Cave 3, Ochre Cave, and Gladysvale Cave. Fossils of the very small *E. lylei* were not included in the study.

Plesippus and *Allohippus* are represented by fossils referred to the Pliocene and the Earliest Pleistocene, i.e. before and just after the Olduvai event. *E. enormis* (California) is part of them.

During the Early Pleistocene Plesippine and Allohippine equids were probably replaced by modern Equus (EISENMANN & BAYLAC 2000a). When skulls are known, there are clear differences pointing to a subgeneric or generic distinction. But many teeth and limb bones cannot be referred to any of these groups with certainty. In addition, some large fossils are of very uncertain ages. Because of that, the "large fossil equids" group may include fossils of true *Equus* and/or of *Plesippus* or *Allohippus*. On the whole, it is mostly composed of late Early and Middle Pleistocene not caballine equids, such as *E. singularis* (Kuznetsk Basin), *E. major* (Chagny), *E. suessenbornensis* (Süssenborn, Akhalkalaki), *E. verae* (NE Siberia, Yukon).

Because of the vast geographical and chronological ranges of the considered equids, an exhaustive bibliography could not be given. But in addition to the papers explicitely quoted in the text, other publications, in particular those dealing with geological ages, were included in the list of references.

MATERIAL

Caballine horses

Modern horses are represented only by the wild (or Zoo bred) *E. przewalskii*. For many fossil samples the age is not precise. This imprecision is actually of no great importance because we distinguish here only two time categories: Middle Pleistocene and Late Pleistocene. To the first belong Clacton, Swanscombe, Brundon, Crayford, Erith, Ilford and Slades Green (Great Britain), Biache-Saint-Vaast, Châtillon-Saint-Jean, Chelles, La Caune de l'Arago and Orgnac 3 (France), Ehringsdorf and Mosbach (Germany), Vertesszöllos (Hungary), Missy, Tunguz and part of the collections of NE Siberia (Russia), Hay Springs and Rock Creek (United States). Late Pleistocene samples come from Arcy-sur-Cure, Chasse-sur-Rhône, Siréjol, and Jaurens (France), San Sidero and Val di Chiana (Italy), Bug, Mezin and Taburishche (Ukraine), Ural and NE Siberia (Russia), Lost Chicken and Tofty (Alaska), Dawson, Gold Run, and Sixty Mile (Yukon), Medicine Hat (Alberta).

Plains zebras "*sensu lato*"

Beside extant Plains zebras (*E. burchelli*) and recently extinct *E. quagga*, the group includes Middle Pleistocene and Late Pleistocene fossils. Were considered as Middle Pleistocene *E. mauritanicus* of Ternifine (Algeria), fossils from Cornelia, Florisbad, Mahemspan, Vlakkraal, and the fossils of Elandsfontein assumed as Cornelian, according to their fossilization. Were considered as Late Pleistocene samples from Equus Cave, Black Earth Cave 3, Ochre Cave, Gladysvale Cave, Besaansklip, Swartklip, and fossils of Elandsfontein assumed Late Glacial according to their fossilization. For the upper cheek teeth, all South African large specimens, irrespective of their age, were plotted as *E. capensis*.

Plesippus and *Allohippus*

In this group are included fossils of Koobi Fora (Kenya), Tegelen (Netherlands), Saint-Vallier and Senèze (France), Montopoli, Matassino, Olivola, and Valdarno (Italy), Huelago, La Puebla de Valverde, El Rincon, and Toledo (Spain), Schernfeld (Germany), Oasele and Tetoiu (Romania), Gerakarou and Vatera (Greece), Sarikol Tepe (Turkey), Khapry, Livenzovka and Morskaia (Russia), Kuruksai (Tadjikistan), Locality 32 of Zdansky, Madahai, and Nihowan (China), some localities of Anza Borrego, Blanco, Broadwater, Dry Mountain, Eleven Mile, Grand View, Hagerman, Lisco, Long Pine, Loup Fork, Metagorda, Rexroad, Sand Draw, San Pedro, Santo Domingo, South Wind (United States).

Large fossil equids

These equids come from East Runton (Great Britain), Oesterschelde (Netherlands), Chagny, Gannat, and Solilhac (France), Cueva Victoria (Spain), Süssenborn and Würzburg-Schalksberg (Germany), Kislang (Hungary), Feldioara and Rotbav (Romania), Akhalkalaki (Georgia), Lakhuti 2 (Tadjikistan), Itantsa, Kuznetsk Basin, Ol'khon, Tataourova, and part of the collections of NE Siberia (Russia), Old Crow (Yukon), some localities of Anza Borrego, Arkalon, Channing, Hay Springs, Holloman, Lissie Formation, Rock Creek, San Diego Creek and Trinity River (United States).

Most of the data are personal. Others were communicated by C. De Giuli or found in AZZAROLI (1995, 1998), AZZAROLI & VOORHIES 1993, DOWNS & MILLER 1994, FORONOVA 1998, GROMOVA 1949A, HIBBARD & DALQUEST 1966, HOWE 1979, KOUFOS 1992, LAZAREV 1980, LIU & YU 1974, MUSIL 1992, QUINN 1957, RUSSANOV 1968, SAMSON 1975, WINANS 1985 and ZDANSKY 1935.

OBSERVED DIMENSIONS

Histograms were drawn for basilar lengths of skulls, occlusal dimensions of upper P3-P4-M-M2, lengths of third metacarpals and metatarsals, and supra-articular widths of third metacarpals and/or metatarsals. When data were very numerous, only a part of them was plotted, but the largest observed data were always considered. Values were plotted inside the same range of variation, whatever the taxa, in order to help a direct comparison of sizes between the "Caballines", the "Plains zebras s.l.", the "Large fossil equids" and the "Plesippus and Allohippus" groups.

SKULL BASILAR LENGTHS (Fig. 1)

The largest basilar length I have observed is 662 mm in a domestic *E. caballus* (AMNH 16274). Basilar length was estimated at 621 mm in LACM 4338, a skull found in a locality of Anza Borrego, California, about 1Ma old. The next largest estimations are 616 mm for the type skull (IVCM 32) of *E.enormis* found in another locality of Anza Borrego, about 2.5Ma, and 615 mm for the Pliocene type skull (ZIN 31078) of *E.livenzovensis* (DOWNS & MILLER 1994). These fossil skulls are very fragmentary and the estimations were not plotted on the histogram.

Among well preserved fossil skulls, the largest basilar lengths belong to caballines: *E. scotti* (NMC 2381) of Rock Creek, Texas: 595 mm, *E.* cf. *scotti* (SI 160-455) of Ulakhan Sular, NE Siberia: 585 mm, *E. mosbachensis* (Germany): 612mm and the Late Pleistocene caballine (IGF 16328) of San Sidero, Italy: 590 mm. Among Plains zebras-like equids, the largest basilar length is only 560 mm in the possibly Middle Pleistocene *E. capensis* of Elandsfontein (ZM. E. 21025).

Taking into account the whole data set - without distinction of time or species - it seems that no wild equid has ever reached the basilar length observed in one domestic *E. caballus*.

UPPER CHEEK TEETH OCCLUSAL DIMENSIONS (Fig. 2)

Comparison of cheek teeth is more difficult, not only because of changes due to wear, but also because of the size differences between premolars (P3-P4) and molars (M1-M2) and uncertainties concerning the nature (P or M?) of some isolate teeth. The first difficulty may be palliated by using an average occlusal dimension: (occlusal length + occlusal width)/2. The reason is that occlusal surfaces of little worn teeth tend to be long, but narrow, while tending to be shorter but wider at later stages. To address the second point, I have chosen to take into consideration all the cheek teeth of the series excluding P2 and M3.

The largest fossil upper cheek tooth in the world is probably the type specimen (AMNH 1816) of *E. giganteus*. According to SELLARDS (1940), it may have been collected around 1888, in San Diego Creek, Texas, probably in Pleistocene deposits. WILLOUGHBY (1974) considers it to be a M2, but it could have been a P4. The section surface is 40 mm long and 39 mm wide. The rather short and plump protocone is not caballine. The other *"*very large*"* teeth are smaller. Occlusal dimensions larger than 35 mm are found in the Pliocene (*E. enormis* of Anza Borrego and the equid of Tegelen) but also in the Early and Middle Pleistocene (*E. singularis* of Kuznetsk Basin, *E. bressanus* of Chagny, *E. suessenbornensis, E. capensis*, and equids of Anza Borrego, Lakhuti 2, and Old Crow). The largest teeth of fossil caballine horses do not reach 35 mm. In modern *E. caballus*, the maximum value I have observed is 32.8 mm. It is interesting to remark that a very large skull had a surnumerary tooth.

Figure 2 shows a considerable overlap between the occlusal dimensions of *E. mauritanicus* and *E. capensis*. Teeth of *E. przewalskii* overlap with Late Pleistocene, and to some degree with Middle Pleistocene caballines. For both Plains zebras and horses, overlap is larger than for basilar lengths.

METACARPAL LENGTHS (Fig. 3)

The longest metacarpal (AMNH 116154: 307 mm), associated to a metatarsal, comes from Santo Domingo, New Mexico, and is Late Pliocene. It belongs to a very slender "stilt-legged" equid. During the Early-Middle Pleistocene of North America, metacarpals of stilt-legged equids are shorter. In the Old World, there were no large stilt-legged equids, but the longest metacarpal is almost as long: 301 mm. This specimen and the associated metatarsal belonged to the old collections of Clermont-Ferrand and are presently preserved at the Faculty of Sciences in Lyon. The locality is said to be Gannat, Allier. According to C. Guérin, the possible association with a peculiar *Megaceros* and a Merck Rhinoceros could indicate a late Early Pleistocene age. The next longest metacarpal, probably also late Early Pleistocene is 285 mm long and comes from Würzburg-Schalksberg, Germany (MAUSER 1992).

Caballine metacarpals are shorter: maximum 271.5 mm in 1973/157 of Mainz collections of Mosbach, Germany. Metacarpals of *E. capensis* are even shorter: 240 mm for Besaansklip n°190 and for Mahemspan n°2393.

METATARSAL LENGTHS (Fig. 4)

The Late Pliocene metatarsal of Santo Domingo is 344mm. Another stilt-legged horse is represented by an even longer metatarsal: 348 mm (AMNH 11642, Loup Fork). Similar dimensions may be observed in Middle Pleistocene stilt-legged equids (Arkalon Gravel Pit), which is remarkable since Middle Pleistocene metacarpals are shorter. We will come back later to the respective lengths of metacarpals and metatarsals. As already observed, there were no stilt-legged equids in the Old World but similar lengths may be found from the Pliocene to the Middle Pleistocene: 345 mm (Gannat, East Runton, NE Siberia), 342.7 mm (Würzburg-Schalksberg), 335 mm (Seneze), 334 mm (Cueva Victoria, Tataourova), 330 mm (Akhalkalaki, Kislang, Livenzovka, five specimens are more than 330 mm long in NE Siberia). In Yukon, at Old Crow, one metatarsal is about 340 mm long. In Oklahoma, one is 330 mm long at Holloman Gravel Pit. Caballine metatarsals do not reach 330 mm: the maximum observed is 322 mm (Mosbach 1961/425 and Verteszöllos II V69/789). For *E. capensis*, the maximum is 292 mm (Elandsfontein 2696).

SUPRA-ARTICULAR METAPODIAL WIDTHS (Fig. 5)

Data come from metacarpals and/or metatarsals measurements. The maximal observed value is 68 mm, both for a modern draft horse and for the metatarsal PIN 3659-721 (Adycha, NE Siberia). Many other Early-Middle Pleistocene NE Siberian metapodials have dimensions superior to 64 mm. Similar values may be found in the Kuznetsk Basin and at Akhalkalaki, Cueva Victoria, Gannat, and Würzburg-Schalksberg. In the New World, such dimensions are rare: 65mm for UNSM 49210 of Backus Biba, Nebrasaka, and for NMC 14484 of Old Crow, Yukon. During the Pliocene and Earliest Pleistocene, very wide metapodials are exceptional: Senèze (64.5 mm), Schernfeld (65 mm). The largest caballines (Mosbach) do not reach 62 mm. The largest *E. capensis* (Equus Cave) does not reach 64 mm.

ESTIMATIONS

Weight

According to Willoughby (1974), the largest draft horses weighed up to 1.450 kilos. In fossil equids, weight may be estimated on the basis of the surface of an upper M1 using the equation proposed by EISENMANN & SONDAAR (1998):

Ln weight = -6.388 + 1.873 (Ln surface of M1).

Estimated in this way, the weight of *E. singularis* was about 970 kilos. A weight of 714 kilos may be supposed for the type of *E. enormis* and slightly less (708 kilos) for the Early-Middle Pleistocene equid of Lakhuti 2. Unfortunately, M1 are not always available. In the case of *E. giganteus*, for example, the tooth is said to be a M2. In modern draft horses, the surface of the M1 is, on average, 28.6 square mm larger than the surface of the M2. But in *Allohippus stenonis* of Saint-Vallier, it is the surface of the M2 that is larger (by 16.6 square mm). Assuming that the tooth of *E. giganteus* was indeed a molar, the weight of the animal could have been around 1600 kilos. But it may have been a premolar.

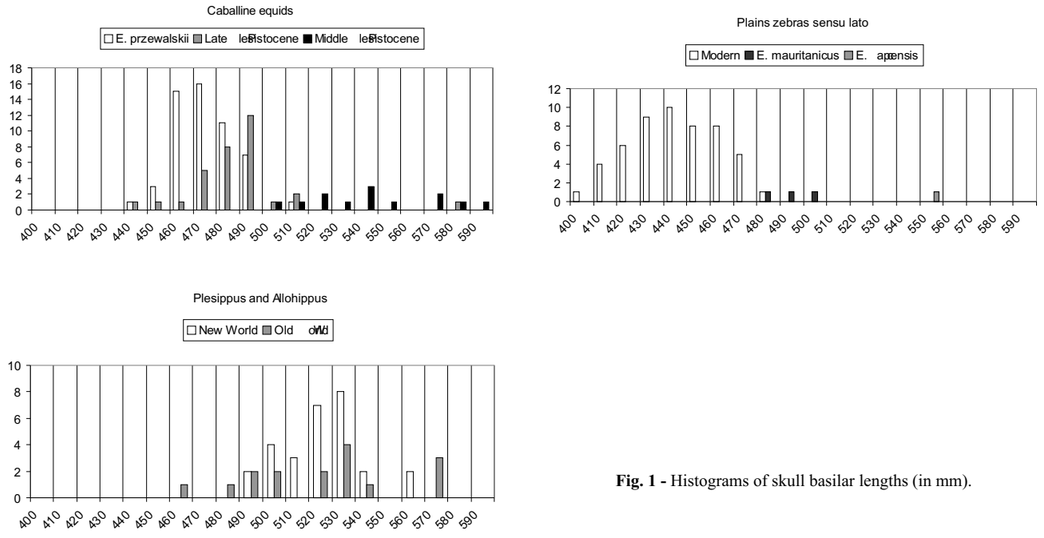

Fig. 1 - Histograms of skull basilar lengths (in mm).

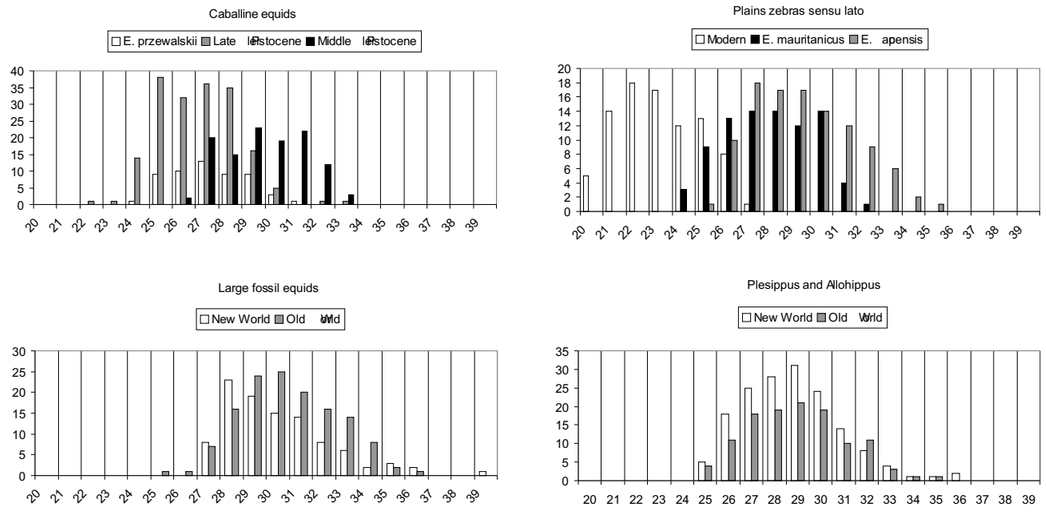

Fig. 2 - Histograms of upper cheek teeth occlusal dimensions (in mm).

In modern draft horses, the surfaces of the P3 and P4 are, respectively, about 131.5 and 108 square mm larger than the average surface of the M1. In *A. stenonis* of Saint-Vallier, the respective differences are 193 and 154 square mm. Accordingly, if the tooth of *E. giganteus* was a P4, the weight may have been only (!) 1250 kilos, and 1.320 kilos if it was a P3. This is still quite more than the average weight of a draft horse - 736 kilos according to WILLOUGHBY (1974). A weight of 730 kilos may have been reached by a caballine horse of Ehringsdorf. Maximal weight calculated on molars of *E. capensis* is about 600 kilos, but if the specimen 4864 of Florisbad is a molar, the weight it could reach is 800 kilos.

Weight may also be estimated, probably with better accuracy (EISENMANN & SONDAAR 1998), on the basis of the product of two distal diameters of the metacarpals (MC) or metatarsals (MT): the transverse maximum width (MC or MT10) and the antero-posterior minimal medial depth (MC or MT 13). The computed formulas are:

Ln Weight = -4,525 + 1,434 (Ln (MC10*MC13))

and

Ln Weight = -4,585 + 1,443 (Ln (MT10*MT13))

It is important to use a combination of width and depth because wide metapodials tend to be flat while narrow metapodials tend to be deep. Calculated thus, the maximal weights are those based on the metatapodials of Overstrand (BM 19242: 861 kilos) and NE Siberia (SI 160-268 : 833 kilos). As much as we know, the largest third metacarpal of a draft horse is the specimen AMNH 16274. The relevant measures are 68 and 39mm and the corresponding weight would be about 1.010 kilos. For fossil caballines, the biggest estimated weight is 740 kilos (Mosbach) and for *E. capensis,* 690 kilos.

Table 1 compares the maximal weight estimated on different bases. When metacarpals and metatarsals belong to the same animal (Chukochya (NE Siberia), San Sidero 6, Santo Domingo, Würzburg-Schalksberg), the concordance may be good (10 kilos for Würzburg- Schalksberg and Santo Domingo) or not so good (30 kilos for San Sidero, 45 kilos for Chukochya). Very large discrepancies (Old Crow: 104 kilos, *E. scotti*: 135 kilos) are probably due to aleas: the largest animal may be represented only by the anterior or posterior of its metapodials. If we compare the maximal weight obtained on a metapodial (anterior or posterior) to the maximal weight obtained on a M1, the discrepancies may be even larger (almost 190 kilos for Chagny). Clearly, the same aleas may be responsible, but there may be an additional cause: equid species may be relatively microdont or macrodont. Whatever the case, it is obvious that these estimations are very coarse.

Withers height

The height at the withers of a horse used to be expressed in "hands" (one hand = 4 inches) or in "feet" (one foot = 12 inches), and in "inches". Since one inch = 25.4 millimetres, a horse "21 hands high" or "7 feet high" stands 213.4 cm at the withers. According to Willoughby (1974) the largest draft horses may reach this height.

When live animals cannot be measured, the height at the withers is estimated by multiplying the length of one of the limb bones by an adequate number. Such numbers were proposed for horses by Kiesewalter in 1889 ("Kiesewalter's indices" of GROMOVA 1949a). But as already pointed by many authors, the results are not satisfactory. In cursorial animals, the proximal limb bones (humerus, femur, radius, tibia) tend to be relatively short while more distal limb bones, in particular metapodials, tend to be long (GREGORY 1912, OSBORN 1929). Applied to a cursorial equid the metapodial "indices" calculated for a draft horse will naturally overestimate the withers height as will be shown farther on. A sensible estimation of withers heights must depend on the knowledge of the proportions between all limb bone lengths.

WILLOUGHBY (1974) published the average limb bones lengths and withers height of many modern equids. On the basis of his data and my own, it appears that the Middle Pleistocene

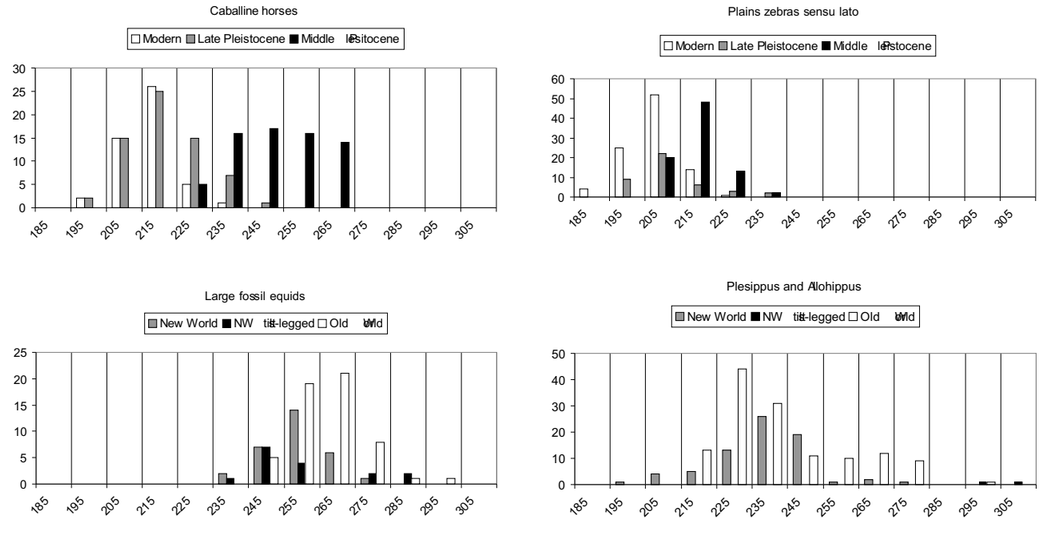

Fig. 3 - Histograms of third metacarpal lengths (in mm).

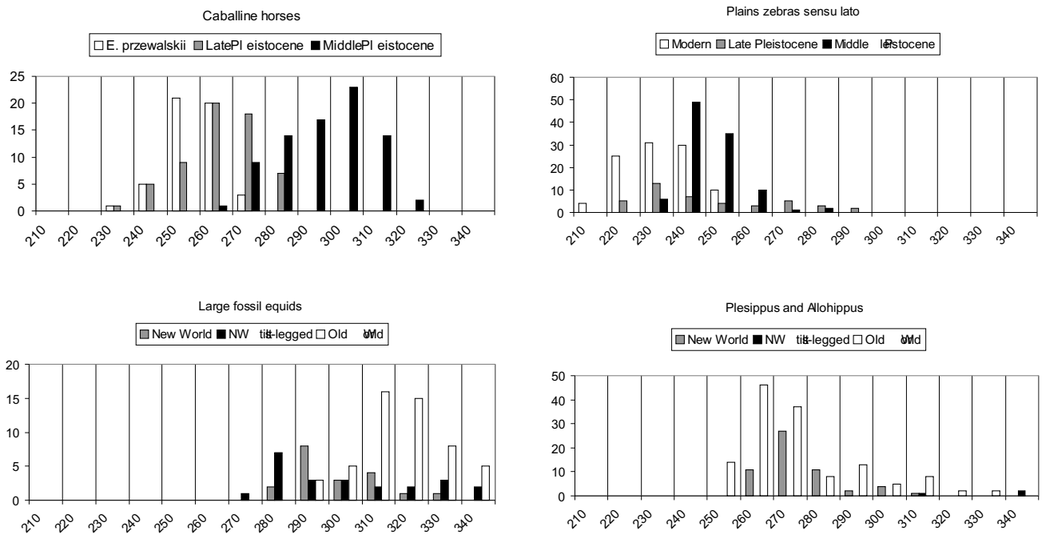

Fig. 4 - Histograms of third metatarsal lengths (in mm).

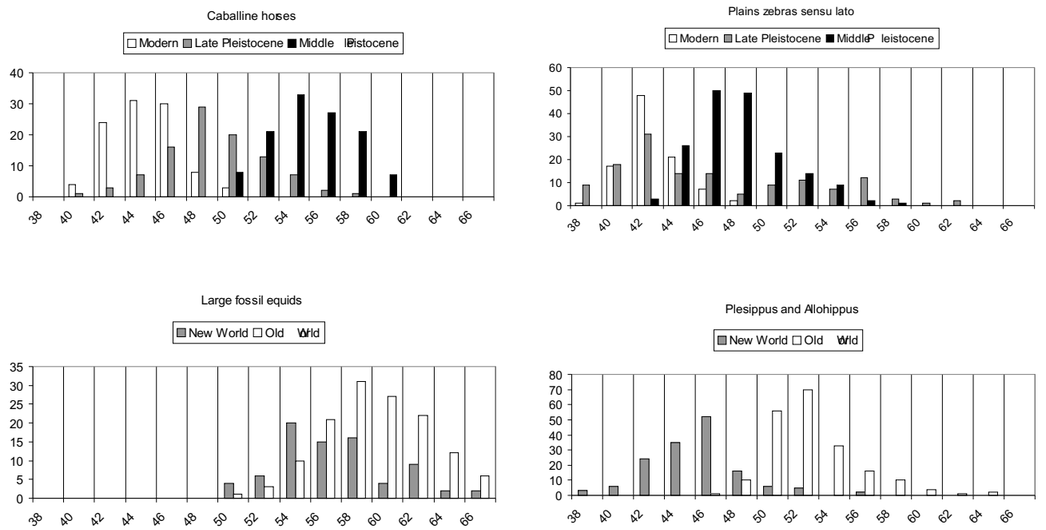

Fig. 5 - Histograms of third metacarpal and/or metatarsal supra-articular widths (in mm).

	Maximal estimated weights		
	On M1	On MC	On MT
E. major, Chagny	756,8		567,2
Old Crow	729,8	671,0	775,4
NE Siberia	689,0	789,9	833,1
Chukochya, PIN 3100-333		635,7	590,3
Tegelen	649,2	570,0	
Akhalkalaki	647,9	618,7	579,6
E. mosbachensis	629,7	660,4	740,9
San Sidero 6, IGF 16328	471,3	521,7	492,1
E. capensis	608,1	686,8	696,2
E. livenzovensis	556,4	629,3	661,3
E. scotti	538,8	614,3	479,2
E. suessenbornensis S	504,6	580,5	587,1
Santo Domingo, AMNH 11654		432,3	421,5
Gannat		818,9	761,2
Würzburg-Schalksberg		735,0	725,8

Table 1 - Comparison of weight estimations in kilos based on the occlusal surface of the upper M1, and on distal metapodial diameters (MC = third metacarpal, MT = third metatarsal).

caballine horse of Mosbach was intermediate by its proportions between one of my modern Arab and the average Draft horse of Willoughby. Using the corresponding indices, *E. mosbachensis* (the largest caballine) stood on average between 155 and 165 cm at the withers. A similar height is probable for the Pliocene *E.enormis* of Anza Borrego. The anterior limb of the Villafranchian *E. athanasiui* (SAMSON 1975) resembles that of one modern Hanover horse. The corresponding withers height would be again about 165 cm. For the very large metapodials not associated to any proximal bone, the estimation is more risky. In extant cursorial equids, the withers height may be obtained by multiplying the metapodial lengths by "indices" as small as 5.32 for the metacarpals and 4.52 for the metatarsals. In graviportal equids, however, the corresponding indices may reach respectively 6.72 and 5.87. Thus, the largest metapodials (Gannat) may point to withers heights of 156 cm if the equid of Gannat was extremely cursorial or 202 cm if it was extremely graviportal! Bad as it is, for Old World equids we feel at least entitled to apply modern models.

Things are even worse with North American stilt-legged equids because some of their proportions have absolutely no modern equivalent. In modern equids, the radius is always shorter than the tibia - its length is between 91.7 and 95.9% of the tibia length. This ratio reaches 96.5% in *E. semiplicatus* of Dalhart, Texas (AZZAROLI 1998), while in the associated skeleton of *E. calobatus* (Arkalon Gravel Pit, Kansas), the radius is even longer than the tibia (102.5%)! In modern equids, the metacarpal length represents 81.5 to 89.1% of the metatarsal length. In *E. semiplicatus*, it is only 74.9%. Still in modern equids, the metacarpal length represents 61.8 to 68.7% of the tibia length. The ratios are much bigger in *E. semiplicatus* (77%), the Pliocene equid of Santo Domingo, New Mexico (77.7%) and *E. calobatus* (80.7%). In these equids, the shortness of the tibia seems compensated by the elongation of the metatarsal. We may guess that these were cursorial equids and tentatively apply to them the indices of modern cursorial forms. In such case, the stilt legged equid of Santo Domingo stood *"only"* about 158.5 at the withers. If we apply the graviportal horse indices, the estimated height would reach 206 cm.

DISCUSSION AND CONCLUSIONS

Table 2 presents the maximal observed dimensions and estimated weights and withers heights of some very large equids and may help answer some of our initial questions.

1. Estimations of weights and withers heights

As demonstrated above, these estimations are very inaccurate and at times discordant. Equids differ greatly by the intrinsic proportions of their metapodials (length, width, depth), as well as by the relative lengths of their limb bones. The teeth may be big or small relative to the rest of the skeleton. Accordingly, no general equation may bring satisfactory estimations. Estimations should be done by comparisons with adequate models. Unfortunately, such models are hard to build because of the lack of data on weights and withers heights for most modern skeletons. In consequence, our estimations must be considered only as indicative in a very approximate way. It may still be reasonable to admit that *E. verae*-like equids reached a withers height close to that of a tall man (180 cm) and that *E. giganteus* may have weighed more than 1.000 kilos.

2. Were fossil equids bigger than the biggest extant ones?

Among the largest domestic caballines are found the maximal basilar length and metapodial width and possibly the largest weights. Metapodial lengths are far from maximal and teeth dimensions are relatively small.

3. Are maximal sizes observed in all specific groups ?

Leaving aside the poor documented basilar lengths, wild caballines (*E. mosbachensis*) and Plains zebras-like equids (*E. capensis*) never reached maximal sizes. In addition, the extant Plains zebras, overall smaller than extant wild horses, have also smaller *"*gigantic*"* fossil relatives. It seems that there is a limit to the factor by which *"*usual*"* size may be increased.

4. Are there geological periods for maximal sizes ?

Because the ages of most gigantic equids are unknown, there cannot be a precise answer. It is remarkable that a very large caballine is present in the Late Pleistocene (San Sidero) and that *E. capensis* seems to have been as large during the Late and the Middle Pleistocene. In general, however, gigantic horses are mostly represented during the Pliocene and the Early or Middle Pleistocene.

5. How many large equids ?

Obviously, the skeletal proportions of the North American stilt-legged *E. calobatus* are altogether different from almost all other equids (we do not know if the equid of Santo Domingo belonged to the same species). For more conventional taxa, observations of skeletal proportions may also help to distinguish taxa.

	Skulls	Teeth	Mc Length	Mt Length	Mp Width	Weight	Height	
Draft horses	662	32.8	288	324	68	1450 a	213 a	Modern
San Diego, *E. giganteus*		39.5				1250	225 a	Pleistocene ?
Anza Borrego, *E. enormis*	621 b	36.8 b	269 b	308 b	50.7 b	714	165	Pliocene
Kuznetsk Basin, *E. singularis*		36.3 c				969		Early Pleistocene
Chagny, *E. major*		35.5		320	58.5	757		Early Pleistocene ?
Livenzovka, Khapry	615 b	34.5	300	330	61	661		Pliocene ?
E. suessenbornensis , Süssenborn		35.8	282	327	60	587		Early Pleistocene
Akhalkalaki		34.8	282	330	64	648	168	Early Pleistocene
Old Crow		35	277	340	67	775	180	Early Pleistocene
NE Siberia, *E. verae*		34.3	277	345	68	833	180	Early Pleistocene
Chukochya, PIN 3100-333			261	312	62,5	636	159	Brunhes-Matuyama
Rock Creek, *E. scotti*	595	32	246	291	59	614		Early Pleistocene
Mosbach, *E. mosbachensis*	612	34	271,5	322	61.5	740	165	Middle Pleistocene
San Sidero	590	33.5	250	288	58.5	609	155	Late Pleistocene
South Africa, *E. capensis*	560	35.3	240	292	63.5	587	146	M and L Pleistocene
Santo Domingo			307	344	51	432		Pliocene
Gannat			301	345	64,7	790		Early Pleistocene ?
Würzburg-Schalksberg			285	343	65	735		Early Pleistocene
Tegelen		35.3	281		56	649		Early Pleistocene
Senèze				335	64,5	794		Early Pleistocene ?

Table 2 - Maximal dimensions of selected equids. Skull basilar lengths, occlusal dimensions of the upper cheek teeth, metapodial lengths and widths in millimetres. Weights in kilos. Wither heights in centimetres. Mc = third metacarpal, Mt = third metatarsal, Mp=third metapodial. a = according to WILLOUGHBY 1974, b = according to DOWNS & MILLER 1994, c = according to FORONOVA 1990.

Relative lengths of metacarpals and metatarsals (100*Mc length/Mt length)

Most stenonid equids have relatively long metacarpals - their average lengths equal more than 86% of the metatarsal average lengths at El Rincon, La Puebla de Valverde, Saint-Vallier, Matassino, Vatera, Sesklo, Dmanisi, Selvella, Pirro and Gerakarou. To this group belong the type skeleton of *E. enormis* (87.3%), the equid of Gannat (87.2%) and the largest equids of Livenzovka. The other large equids have relatively short metacarpals in average (less than 85%). In this second group fall the equids of Cueva Victoria, Süssenborn, Würzburg-Schalksberg, Akhalkalaki, NE Siberia and Old Crow. Unfortunately, only the metacarpal lengths are known for *E.major* euxinicus of Oasele, *E. athanasiui*, and the equid of Tegelen, and only the metatarsal length is known for *E. major* of Chagny and the large equids of Senèze and Kislang. Also unfortunate is the lack of an explanation that can be proposed for the observed differences.

Relative lengths of first anterior phalanges and metacarpals (100*PhI A length/Mc length)

In very cursorial equids such as extant Hemiones and Przewalski horses, the first anterior phalanges are short relative to the metacarpals (35.9-36.6%). In graviportal Draft horses, first anterior phalanges are relatively longer - 39.7%. Other extant equids are intermediate. We do not know what mechanical explanation can be given for that, or if similar differences in fossil horses are necessarily related to cursorial abilities, but differences certainly exist. The majority of large fossil equids have relatively long first phalanges: the percentages are between 36.3% and 39.6% at Sesklo, El Rincon, Würzburg-Schalksberg, Dmanisi, Akhalkalaki, Matassino, Süssenborn, Saint-Vallier, NE Siberia (Chukochya associated skeleton), Tetoiu, and Old Crow. The length of the first anterior phalanx of the large equid of Tegelen, associated to the metacarpal, equals only 35.6% of its length. Moreover, the metacarpal of Tegelen differs from most stenonid metacarpals: the widths (transverse diameters) are smaller and the depths (antero-posterior diameters) are larger. Large fossils of Morskaia, Khapry, and part of Livenzovka seem close to the Tegelen pattern.

To sum up, at least three specific groups of large "conventional equids" may be distinguished:

1. The slender and possibly cursorial Tegelen equid, probably also represented at Khapry, Morskaia, and Livenzovka (RGU 372).

2. Large and robust stenonids with long metacarpals relative to metatarsals: *E. enormis*, equids of Gannat and Livenzovka (RGU 451).

3. Large and robust equids with short metacarpals relative to metatarsals: Old Crow, NE Siberia (*E. verae*), Akhalkalaki, Würzburg-Schalksberg, Süssenborn (*E. suessenbornensis*), Cueva Victoria.

E. major, *E. major euxinicus* and the large equids of Senèze and Kislang may as well belong in the second or the third group because the relative length of metacarpals and metapodials are unknown. A character not studied here, the protocone length, brings no certainty either. Although the protocones are, on average, longer in the third than in the second group, they overlap. The single very large tooth of Senèze and the teeth of Chagny have small protocones but enter inside the range of variation of the third group. The distinction between stenonids and younger large and robust equids is very difficult.

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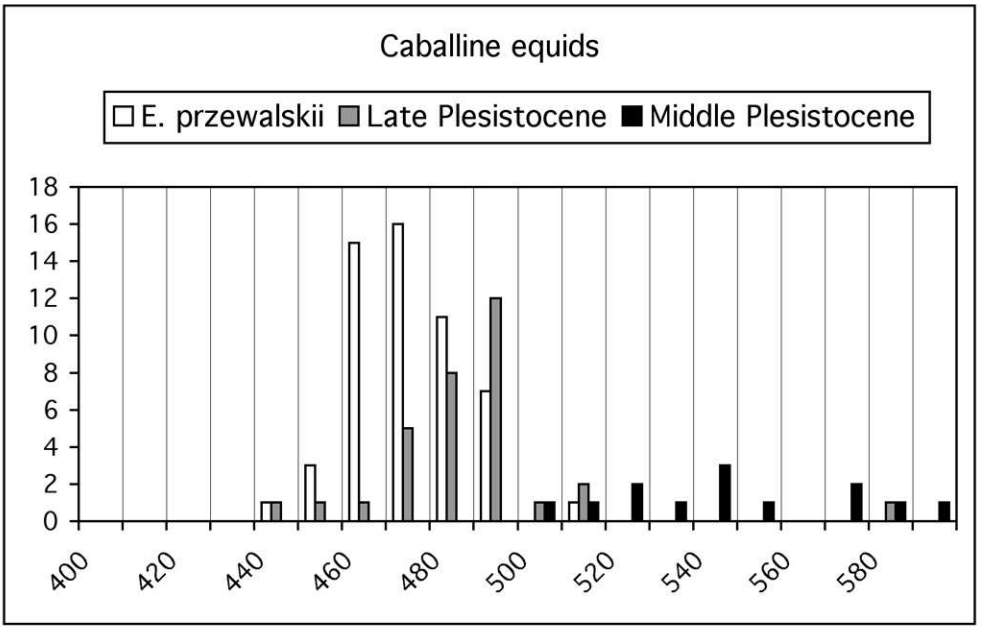
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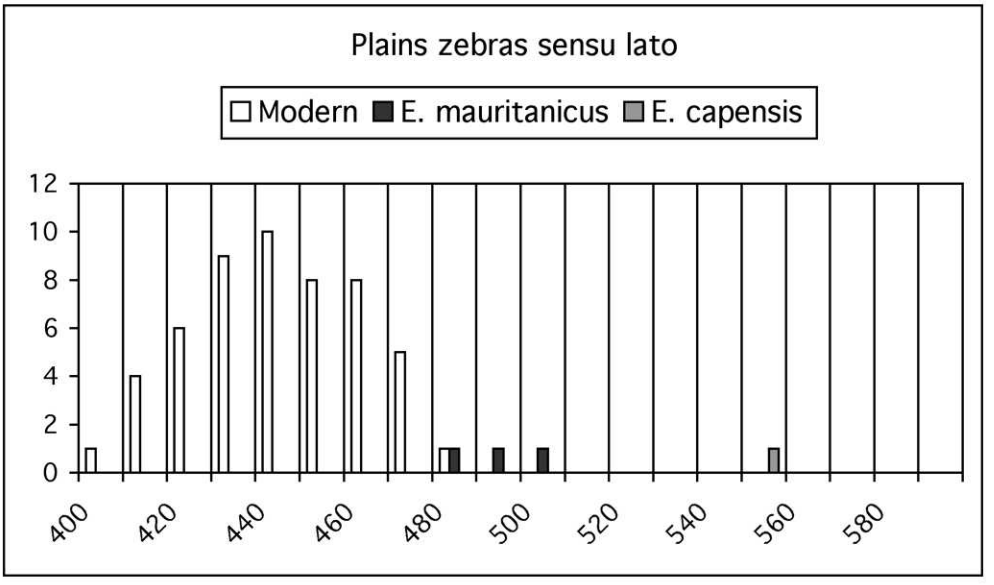
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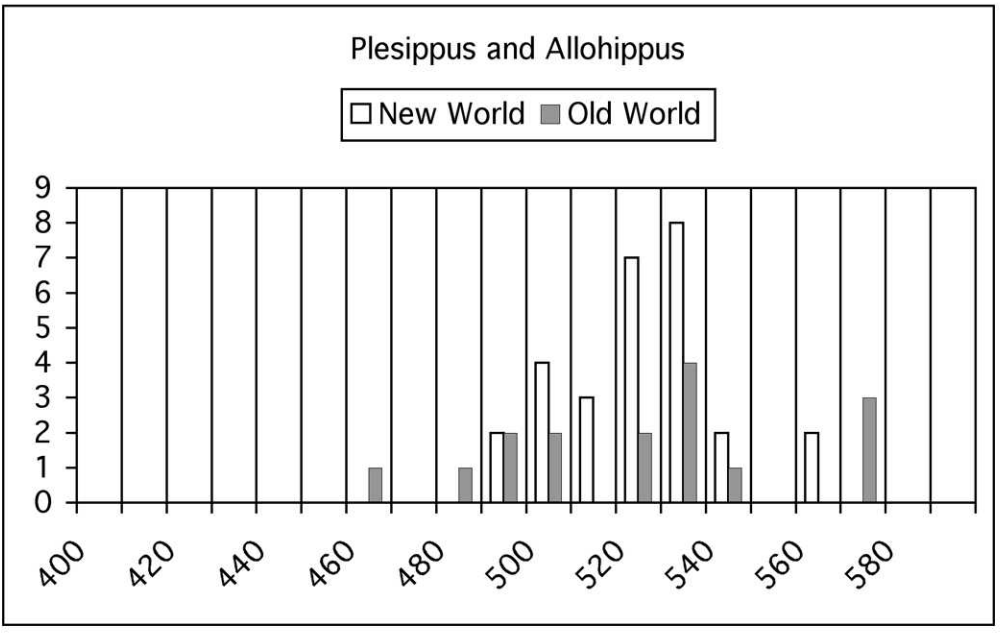
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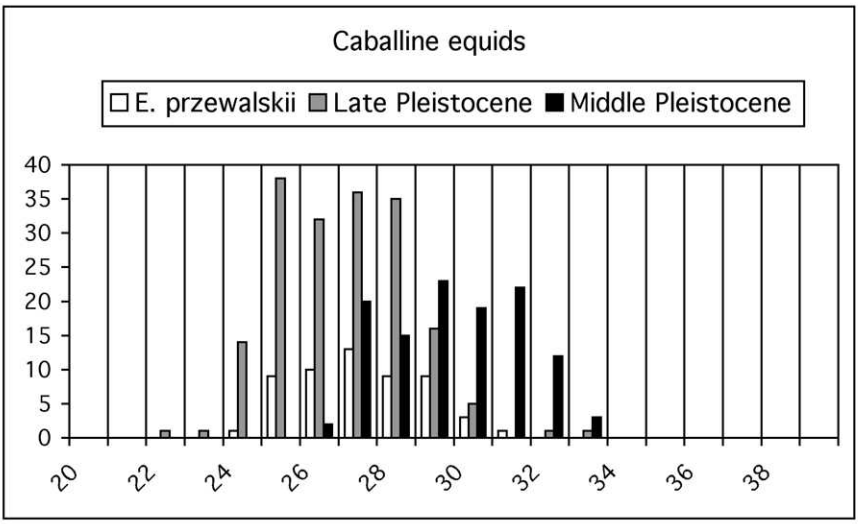
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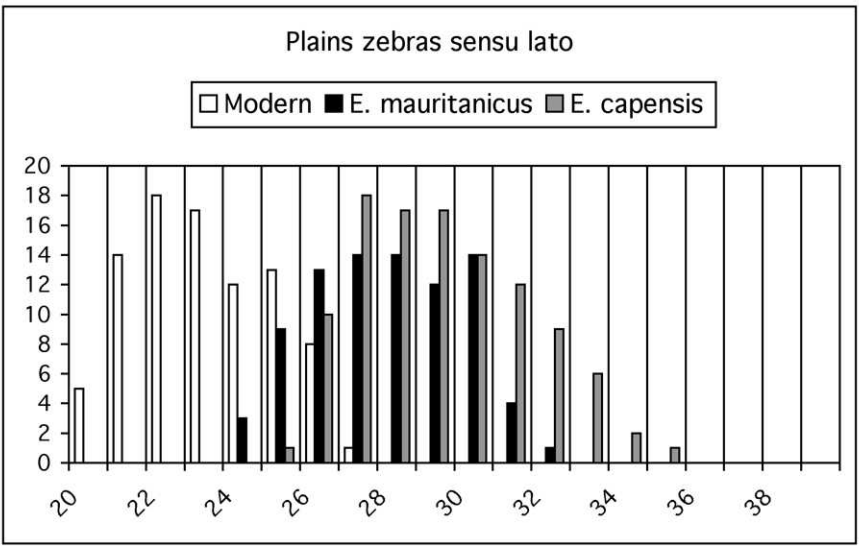
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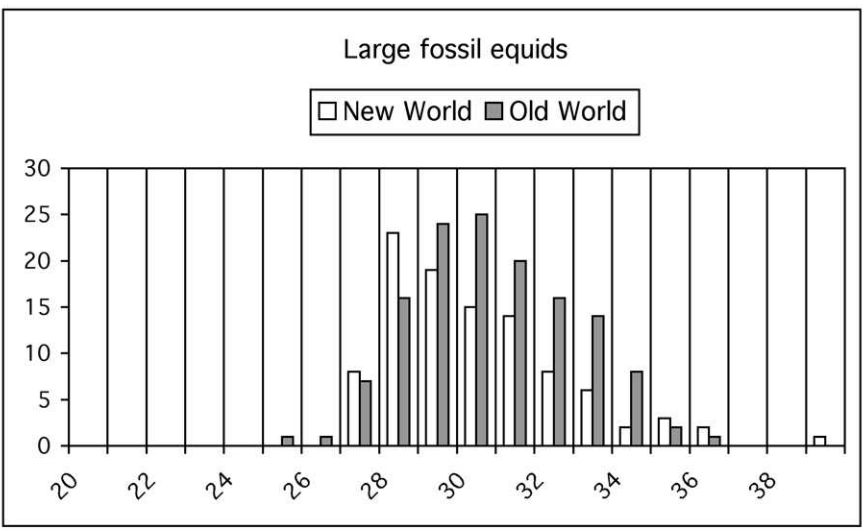
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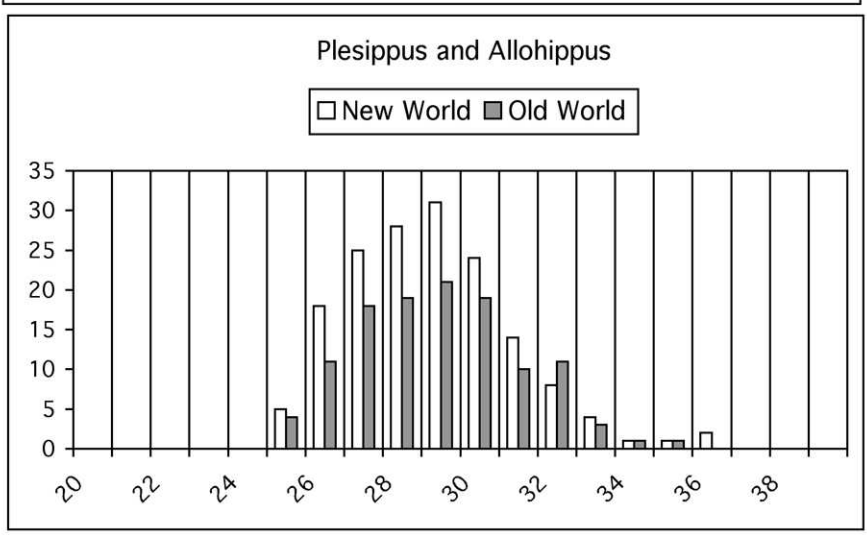
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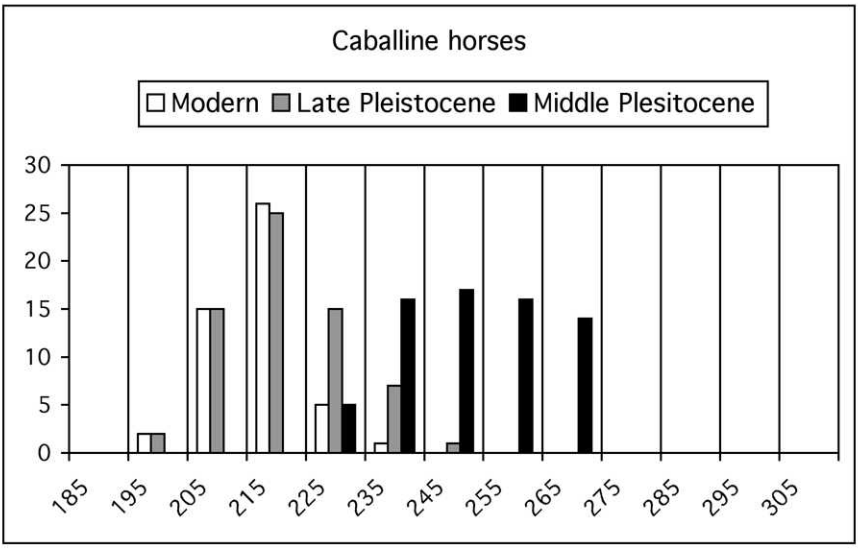
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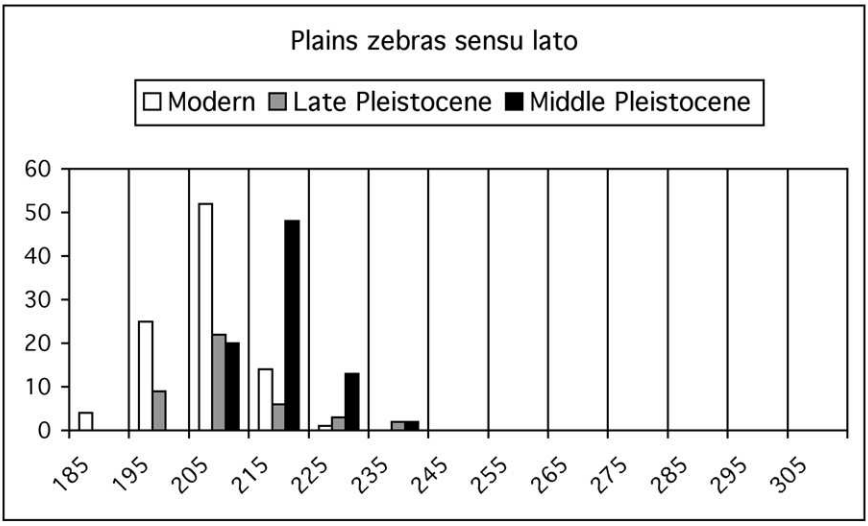
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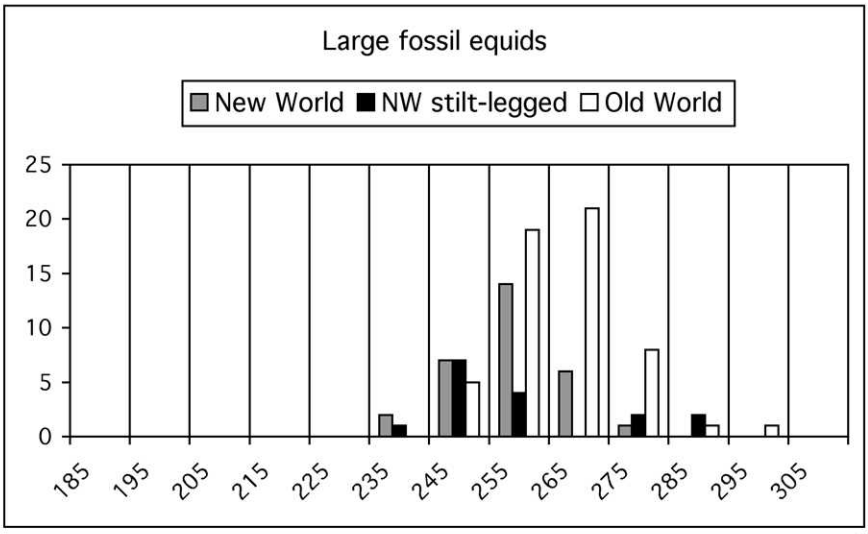
Large fossil equids
New World
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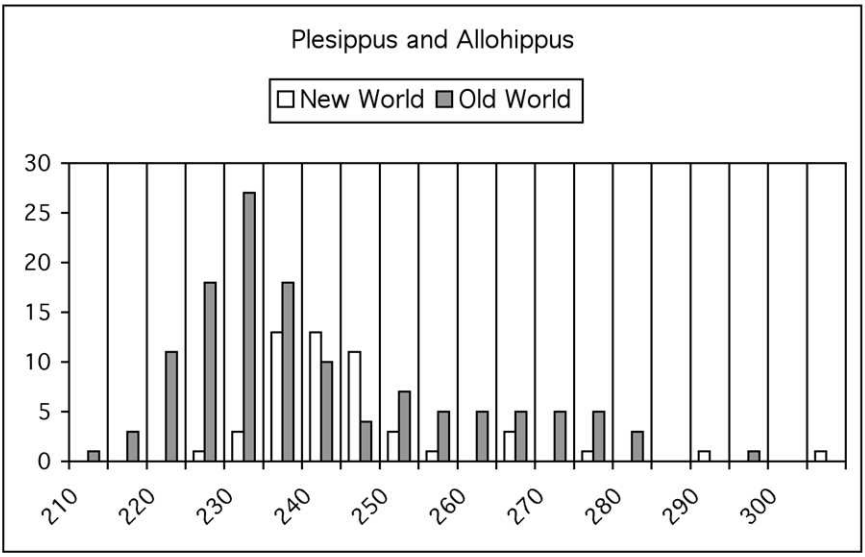
Plesippus and Allohippus
New World
Old World
30
25
20
15
10
5
0
210
220
230
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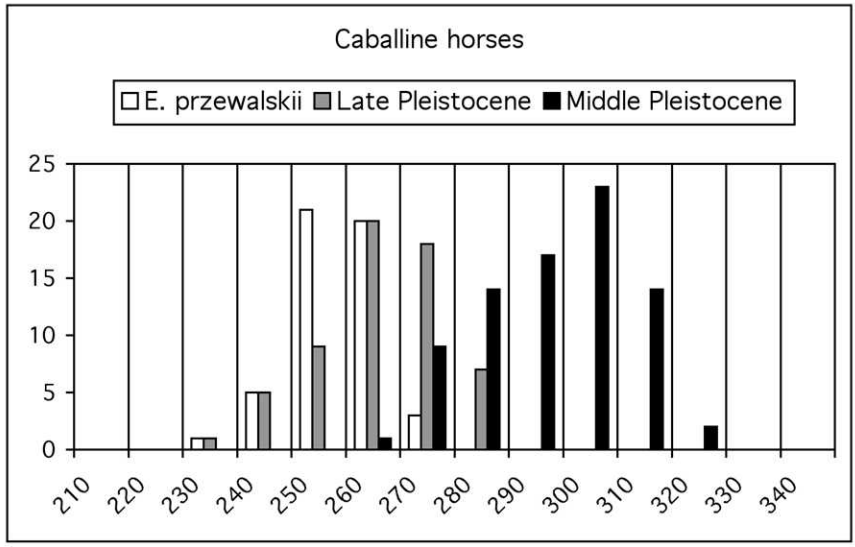
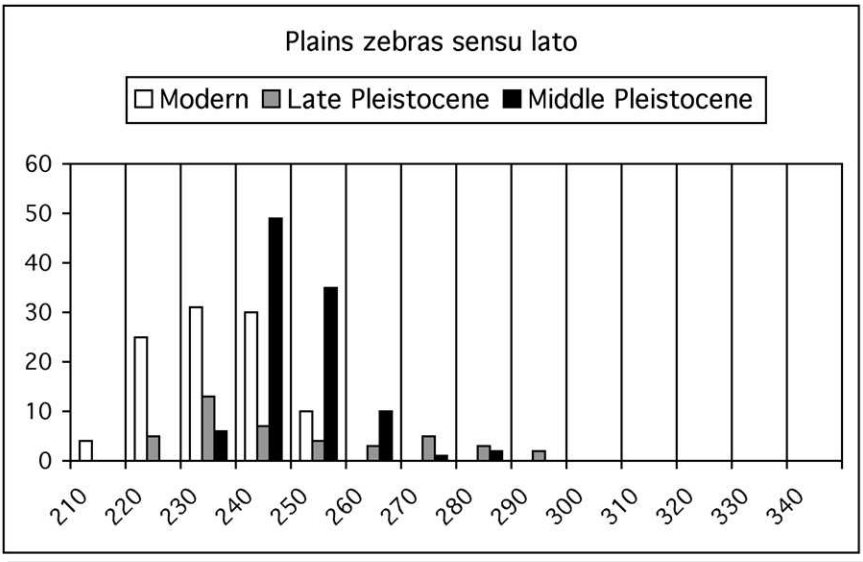
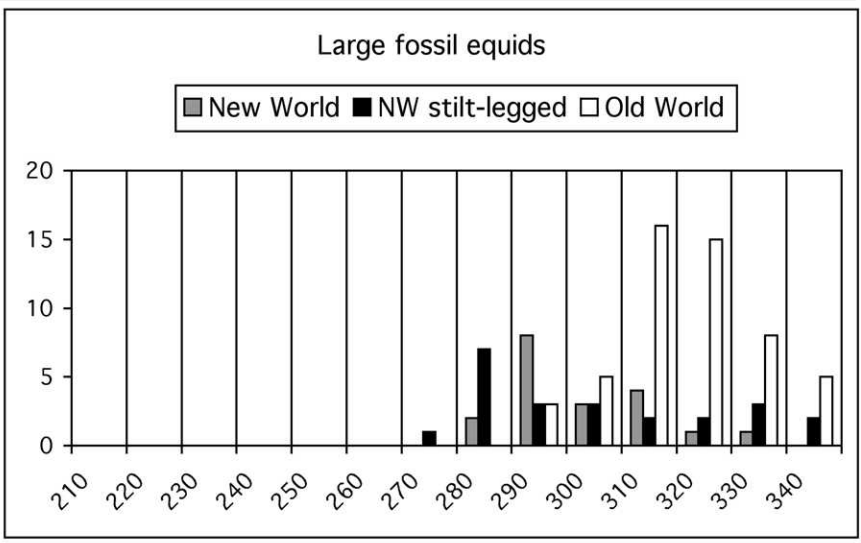
270
280
290
300


Caballine horses
E. przewalskii
Late Pleistocene
Middle Pleistocene
25
20
15
10
5
0
210
220
230
240
250
260
270
280
290
300
310
320
330
340


Plains zebras sensu lato
Modern
Late Pleistocene
Middle Pleistocene
60
50
40
30
20
10
0
210
220
230
240
250
260
270
280
290
300
310
320
330
340


Large fossil equids
New World
NW stilt-legged
Old World
20
15
10
5
0
210
220
230
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250
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270
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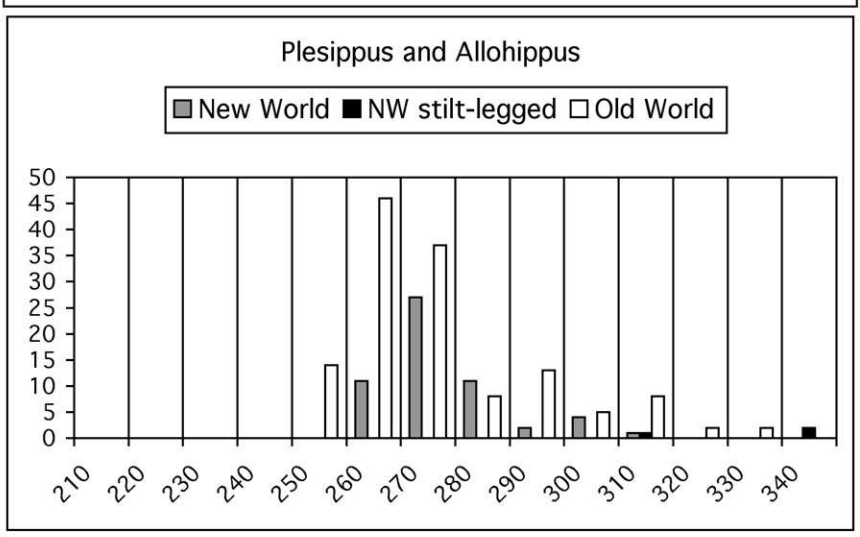
300
310
320
330
340


Plesippus and Allohippus
New World
NW stilt-legged
Old World
50
45
40
35
30
25
20
15
10
5
0
210
220
230
240
250
260
270
280
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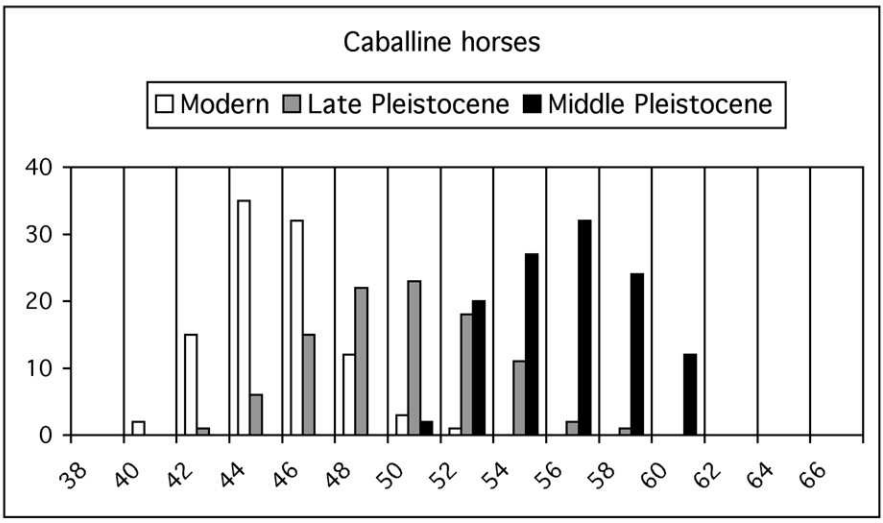
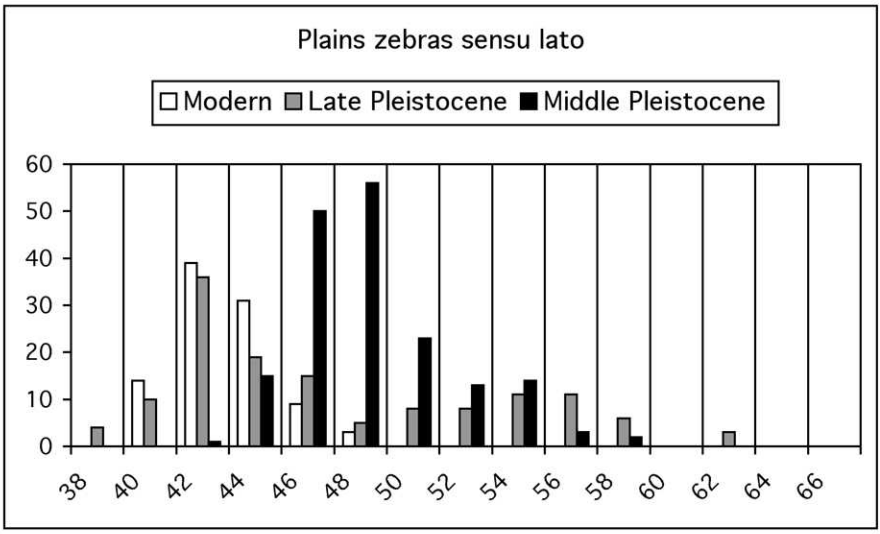
300
310
320
330
340


Caballine horses
Modern
Late Pleistocene
Middle Pleistocene
40
30
20
10
0
38
40
42
44
46
48
50
52
54
56
58
60
62
64
66


Plains zebras sensu lato
Modern
Late Pleistocene
Middle Pleistocene
60
50
40
30
20
10
0
38
40
42
44
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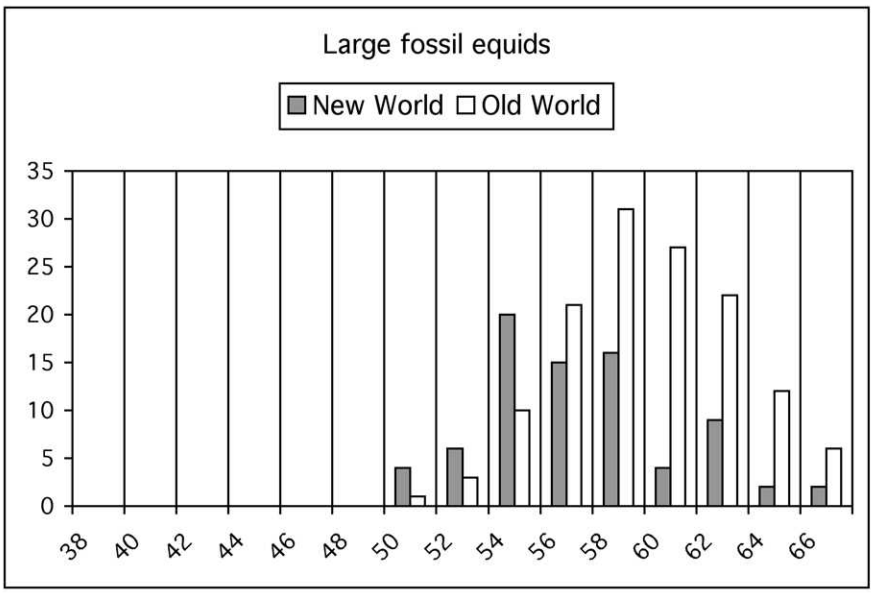
48
50
52
54
56
58
60
62
64
66


Large fossil equids
New World
Old World
35
30
25
20
15
10
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0
38
40
42
44
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52
54
56
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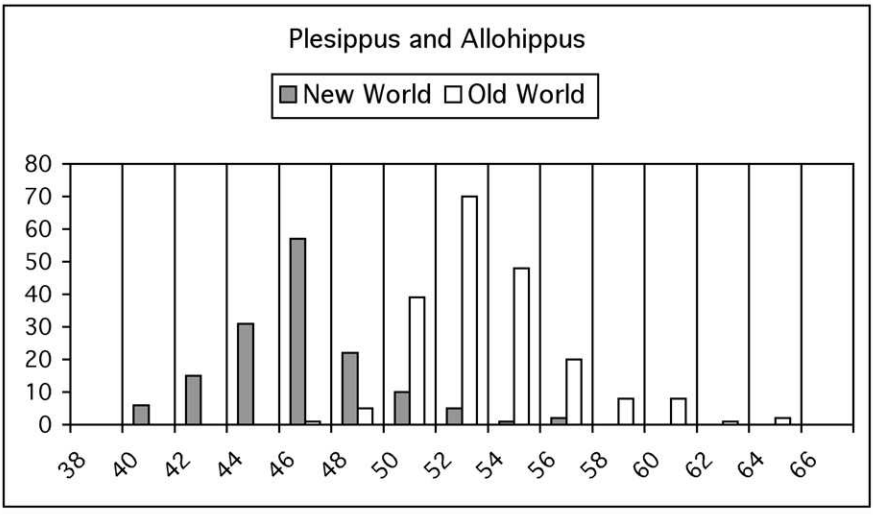
Plesippus and Allohippus
New World
Old World
80
70
60
50
40
30
20
10
0
38
40
42
44
46
48
50
52
54
56
58
60
62
64
66