In : Paleoclimate and Evolution, with Emphasis on Human Origins : 547pp.
E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burckle, editors. Yale University Press. New Haven and London.

Please use the original figures, page 152 and last page.
V. Eisenmann

Chapter 11

What Metapodial Morphometry Has to Say about Some Miocene Hipparions

Véra Eisenmann

Several myths have crystallized concerning the origins, migrations, diversifications, and adaptations of the Old World tridactyl horses named hipparions. Although new data have produced evidence to counter some of these myths, a few are still broadly accepted.

Since the late 1970s (Skinner and MacFadden, 1977), an enormous amount of work has been devoted to the morphology, systematics, and phylogeny of hipparions, most of which has been based on skull characters, particularly the pit situated in front of the orbit known as the preorbital fossa. Hipparions without any fossa, as well as hipparions not represented by skulls, have been more or less bypassed by the main flow of studies.

This chapter discusses some myths and looks at some rarely mentioned hipparions, taking the other end of the animal—not the skull but the foot—as the leading element of comparison. Appendixes 11.1–11.5 give metrical data for the forms discussed, either specimen by specimen or after statistical elaboration when the number of specimens is large. The system of measurements is illustrated in figures 11.1–11.5. Comparisons are made using ratio diagrams (Simpson, 1941) in which the reference line represents *H. mediterraneum* from Koufos (1987a). A more detailed study of the Pikermi material, however, convinced me that the fossils of two species were grouped under that name: *H. mediterraneum sensu stricto* and *H. dietrichi*. For this reason, the ratio diagram for what I believe are *H. mediterraneum* metacarpals (fig. 11.7) is not identical to the Koufos's *H. mediterraneum* reference line.

Naming morphotypes of metapodials that are not associated with skulls is rather like attempting a taxonomy of footprints. In the present chapter, in some cases I am fairly certain that the metapodials belong to a particular species, whereas in other cases my evaluation is more of a guess. Some of the resemblances may be due to parallelism. A study restricted to metapodials also precludes the application of formal taxonomy. Indeed, it would be premature to put species in synonymy just because the metapodials belong to the same morphotype. The specific or subspecific names used should therefore be considered as identifying terms for morphotypes, not as taxonomically valid names. Each subspecific name in the appendixes is included to remind the reader of the name previously used for the hipparion of the relevant locality. The biochronology is based on Mein (1990).

Monotypy of Vallesian Hipparions

Following the studies of Forsten (1968), there has been a general tendency to contrast the Vallesian large monotypic *H. primigenium*, with rather robust limb bones, with the diverse Turolian hipparions, among which figure small (*H. matthewi*), slender (*H. mediterraneum*), or very slender (*H. dietrichi*) forms.

It appears, however, that even in the Lower Vallesian (MN 9 zone of Mein) there are at least three morphotypes: 1) the very small *H. minus* (Pavlow, 1890) from Sebastopol; 2) the usually robust *H. primigenium* (Eppelsheim, Höwenegg, Germany; Can Llobateres, Spain; Yassiören, Turkey) possibly including very large variants (Nombrevilla, Spain), more slender variants (Rudabanya, Hungary; Gritzev, Russia), and variants with a large anteroposterior proximal diameter (Bou Hanifia, Algeria; Yassiören, Turkey); and 3) the slender

Copyright © 1995 by Yale University. All rights reserved.
ISBN 0-300-06348-2.

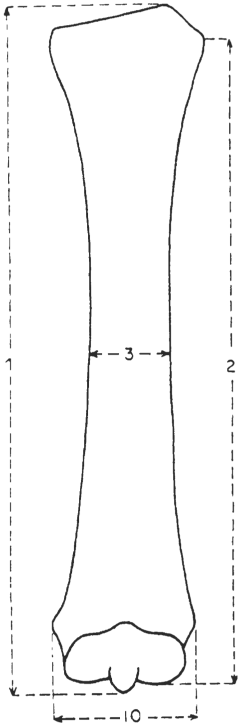


Fig. 11.1

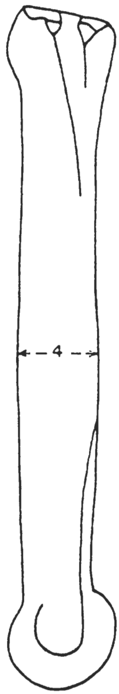


Fig. 11.2

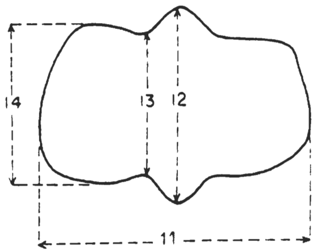


Fig. 11.3

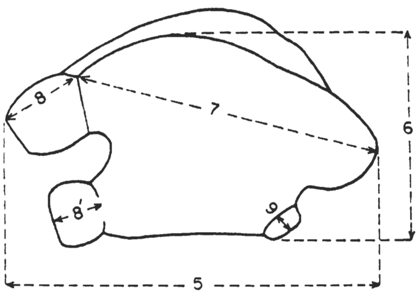


Fig. 11.4

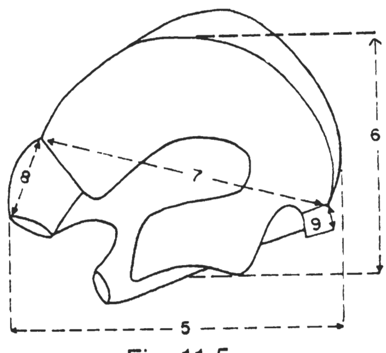


Fig. 11.5

Figs. 11.1 to 11.5. System of measurements of equid metapodials. The names of the measurements are given in appendixes 11.1 through 11.5.

H. sebastopolitanum, from Russia (Borisiak, 1914), also present at Yassiören (Turkey), Can Llobateres, Los Valles de Fuentidueña, and El Lugarejo (Spain). *H. melendezi* (Alberdi, 1974) described at Los Valles de Fuentidueña and El Lugarejo is probably a younger synonym of *H. sebastopolitanum*. *H. melendezi* was not mentioned at Can Llobateres, but at least one metatarsal probably belongs to this form.

During the MN 10 zone, *H. primigenium* is probably still present at Ravin de la Pluie, Greece, and Montredon, France (*H. depereti* of Sondaar, 1974, and Eisenmann, 1988), one variant or morphologically close species (*H. garedzicum*, Gabunia, 1959) is present at Udabno, Georgia, and two morphologically close species are present at Samburu, Kenya (Nakaya and Watabe, 1990). *H. sebastopolitanum* is still present at Masia del Barbo, Spain (Sondaar, 1974), and a new small species, *H. macedonicum* (Koufos, 1984), appears at Ravin de la Pluie and possibly at Montredon (Eisenmann, 1988).

Consequently, the presence during the Vallesian of at least four, and possibly seven, metapodial morphs of hipparion (fig. 11.6, table 11.1), some of which may be associated in the same site, does not support the classical concept of Vallesian monotypy. Neither does it support a contrast between "large-robust Vallesian" forms and "small-slender Turolian" forms. It is true that the most slender forms do not appear before the Turolian and that there are more morphotypes in the Turolian than in the Vallesian, but the diversity pattern based on metapodial morphology tends to minimize the usually accepted differences between Vallesian and Turolian hipparions and the classical notion of explosive diversification during the Turolian.

Turolian Diversity

I distinguish at least nine metacarpal morphotypes (figs. 11.7, 11.8, 11.9, table 11.2); if two, probably endemic Spanish hipparions, *H. periafricanum* and *H. gromovae* from El Arquillo (MN 13), are included, the number of morphotypes becomes eleven.

The *H. brachypus* morphotype is similar to, and sometimes difficult to distinguish from, *H. primigenium* (figs. 11.6 and 11.7). It is the only Vallesian morphotype that can be traced clearly into the Turolian. The metacarpal of *H. minus* is larger than that of *H. periafricanum* and flatter than that of *H. matthewi* (figs. 11.6, 11.8, 11.9). The metacarpal of *H. macedonicum* is about the same size

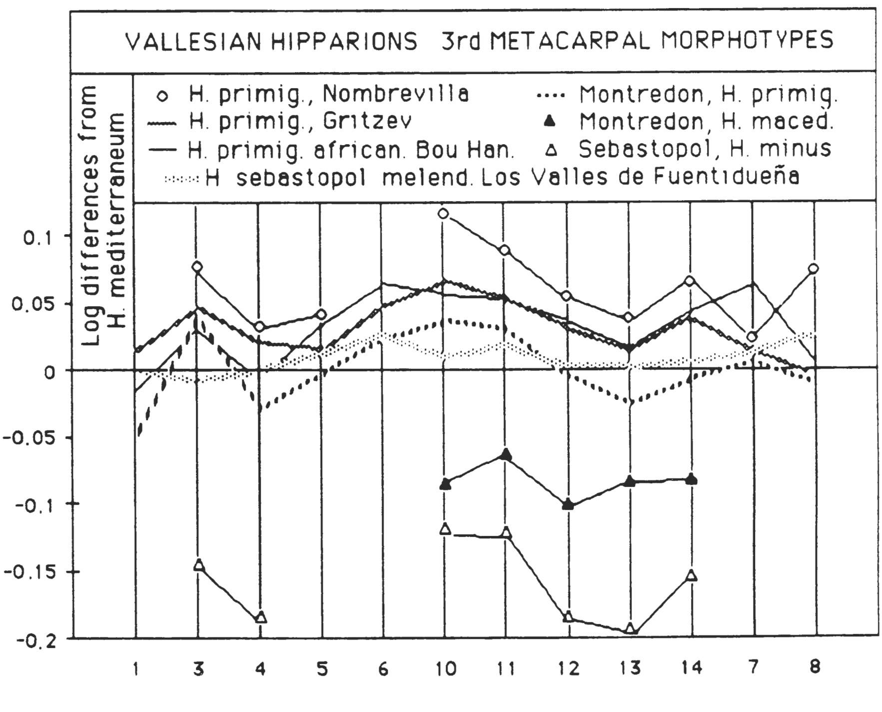


Fig. 11.6. Ratio diagrams of Vallesian hipparions metacarpals: H. = *Hipparion;* primig. = *primigenium;* african. = *africanum;* maced. = *macedonicum;* sebastopol. = *sebastopolitanum;* melend. = *melendezi;* Bou Han. = Bou Hanifia = Oued el Hammam. The names of measurements 1 through 14 are given in appendixes 11.1 through 11.5.

Table 11.1. Occurrences of Different Hipparion Metapodial Morphotypes during the Vallesian

	H. primigenium						
	1 Big	2 Normal	3 Slender	4 Deep	*H. sebast.*	*H. maced.*	*H. minus*
	Samburu		Samburu				
		Montredon				Montredon	
MN 10					Masia Barbo		
	Udabno	RPl				RPl	
		Can Llobat.					
				Bou Hanifia	Sebastopol		Sebastopol
MN 9		Yassiören	Rudabanya	Yassiören	Yassiören		
	Nombrevilla	Höwenegg	Gritzev		El Lugarejo		
		Eppelsheim			Los Valles F.		

Note: The biochronology is taken form Mein (1990). H. = *Hipparion*; sebast. = *sebastopolitanum*; maced. = *macedonicum*; RPl = Ravin de la Pluie; Can Llobat. = Can Llobateres; Los Valles F. = Los Valles de Fuentidueña.

as that of *H. matthewi* but flatter (figs. 11.6 and 11.8). Contrary to Forsten (1982), I do not think that the hipparions from Los Valles de Fuentidueña (MN 9) and Masia del Barbo (MN 10) are conspecific with the species from Concud (MN 12). In my opinion, the first two do belong to the same morphotype (*H. sebastopolitanum*), but *H. concudense* is more robust and lacks the proximal depth of the Spanish *H. sebastopolitanum*.

According to data published by Forsten (1968), *H. plocodus* is characterized by relatively small epiphyses (measurements 5, 6, 10 to 14; the numbered measurements referred to here and subsequently in the text are given in the appendixes) when compared to the diaphysis length (measurement 1). The diaphysis breadth is unknown. I tentatively refer to this morphotype (fig. 11.8) two specimens (FAM 23054 and FAM 23054e) from Samos 5 (Bernor and Tobien, 1989, table 5), although they would be much younger (MN 13 instead of MN 11, according to Qiu et al., 1987). The same figure shows how the *H. plocodus* morphotype differs from the other small hipparion metacarpals from Samos (Bernor and Tobien, 1989, table 5), which may be referred to *H. matthewi*.

Figures 11.8 and 11.9 show the differences between the small hipparions of Greece and Spain. Although *H. gromovae* (fig. 11.9) has about the same breadths as *H. matthewi*, it is much shorter and therefore more robust. *H. periafricanum* (fig. 11.9) is notably smaller.

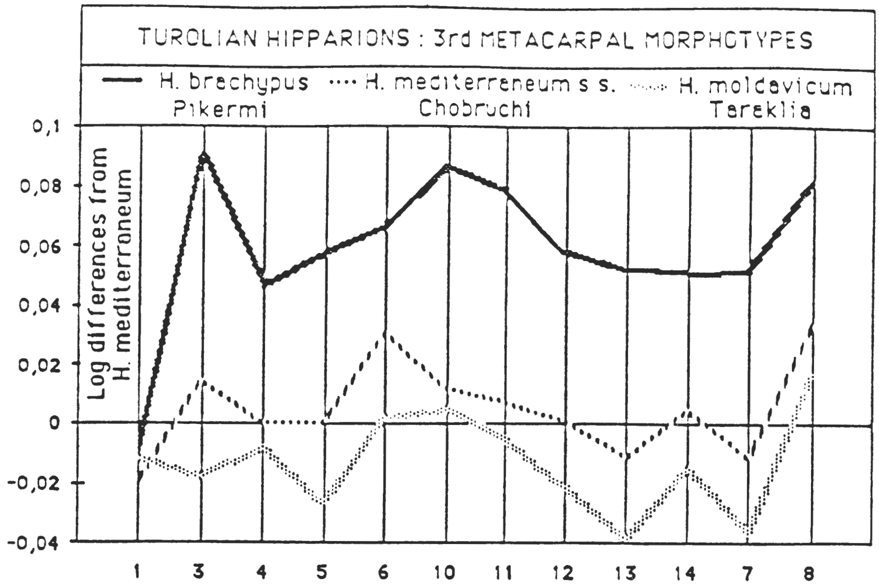
On the whole, the Turolian hipparions are more slender than the Vallesian forms, sometimes very much so, as in the case of *H. dietrichi* and *H. matthewi* (fig. 11.8). They are often deeper, either at the diaphysis level (measurement 4), at the proximal end (measurement 6), or at the distal end (measurements 12, 13, and 14). Usually, the anterior articular facet for the second metacarpal is more developed (measurement 8).

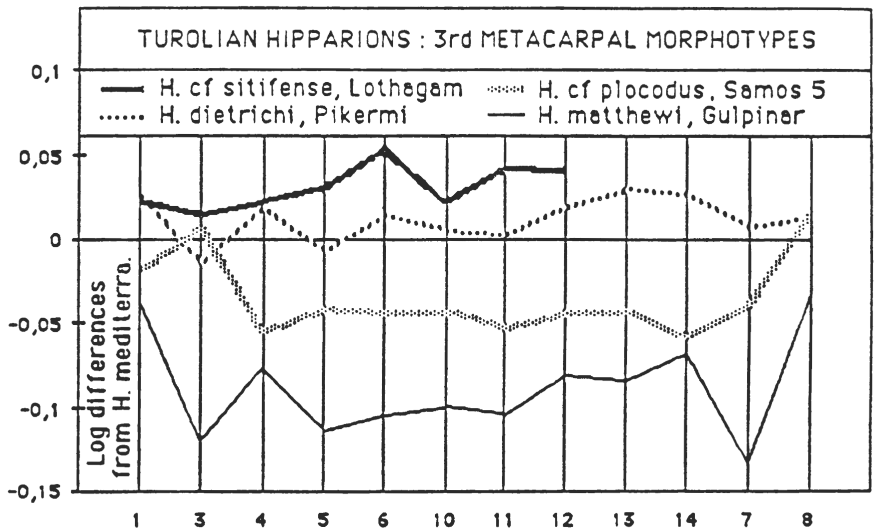
Functional, Evolutionary, and Ecological Interpretations of Metapodial Morphology

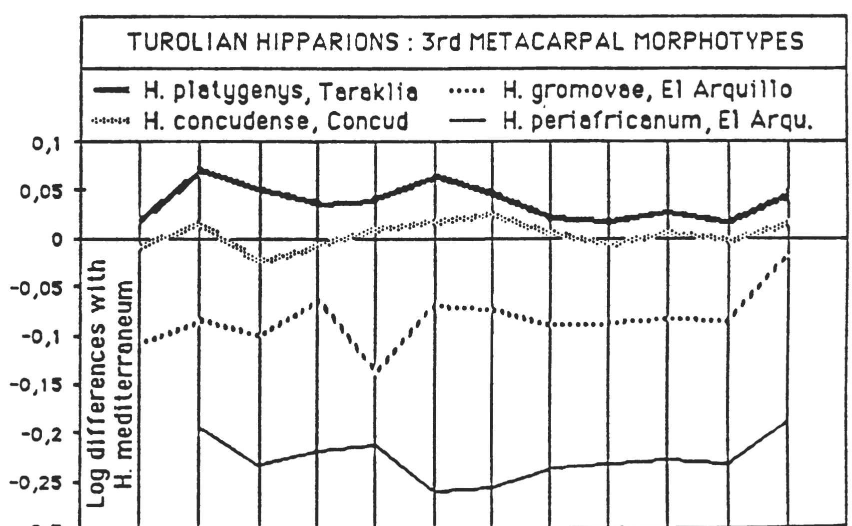
The gracility of the diaphysis may be just a matter of diminished breadth (measurement 3) relative to the length (measurement 1), or it may be partly related to the deepening of the diaphysis (measurement 4) or to the lengthening of the bone (measurement 1) relative to the other segments of the limb. In the first case, the character would indicate a drier climate (Gromova, 1952); in the second, a posterior shifting of the lateral metapodials (see below); and in the third, an adaptation for running (Gregory, 1912; Osborn, 1929).

The shifting of the lateral metapodials from a lateral to a posterolateral position relative to the third metapodial can be considered as an evolutionary change toward functional monodactyly and, thus, as a better adaptation for running (Gromova, 1952). This shifting is usually accompanied by a deepening of the whole bone (measurements 4, 6, 12, 13, and 14) and an effacement of the distal supra-articular tuberosities. As a result, the preeminence of the supra-articular breadth (measurement 10) appears decreased relative to the articular breadth (measurement 11).

The development of the sagittal keel (measurement 12) is a character that enhances pendular movements of the limbs and, again, is a sign of better adaptation for







Figs. 11.7 to 11.9. Ratio diagrams of third metacarpals of Turolian hipparions.

Table 11.2. Occurrences of Different Hipparion Metapodial Morphotypes during the Turolian

	H. primig. *H. brachyp.*	*H. platyg.*	*H. medit.* ss	*H. concud.*	*H.* cf. *plocod.*	*H. mold*	*H.* cf. *sitif.*	*H. dietrichi*	*H. matthewi*	*H. gromovae*	*H. periaf.*
	Sahabi						Sahabi				
							Lothagam	Pavlodar			
MN 13	Baltavar					Dytiko	Lukeino	Venta Moro	Dytiko	Arquillo	Arquillo
							Baccinello				
	Polgardi				Samos 5		Kujal'nik		Samos 5		
	Pikermi		Pikermi			Tudorovo		Pikermi	Gulpinar		
		Saloniki	Lubéron					Saloniki			
MN 12			Chobruchi	Concud					Kinik		
		Taraklia				Taraklia					
								Samos Andr			
MN 11	Sumeg										
	Piera							Vathylakkos	Vathylakkos		
	Grebeniki			Grebeniki				Ravin Zo.	Ravin Zo.		

Note: H. = *Hipparion*; primig. = *primigenium*; brachyp. = *brachypus*; platyg. = *platygenys*; medit. = *mediterraneum*; concud. = *concudense*; plocod. = *plocodus*; mold. = *moldavicum*; sitif. = sitifense; periaf. = *periafricanum*; Andr = Andrianos Quarry; Ravin Zo. = Ravin des Zouaves.

running (Gromova, 1952; Staesche and Sondaar, 1979; Eisenmann and Sondaar, 1989). This development may be accompanied by reduction of the minimal distal depth (measurement 13), together with enlargement of the maximal condyle depth (measurement 14). Altogether, these changes diminish lateral mobility still more and create better conditions for anteroposterior movements.

Unfortunately, relative lengths of the limb bones, which can be compared easily in modern equids and even in some fossil species (Eisenmann, 1984), are difficult to compare in hipparions, because the long bones are usually broken or distorted. Other proportions can be compared, however, using ratio diagrams.

Figure 11.10 illustrates the morphological and functional differences between a Vallesian *H. primigenium* (Yassiören, Turkey) and the Turolian *H. brachypus* (Pikermi, Greece). Although the Turolian form is more robust (measurement 3 is large relative to measurement 1), in the Vallesian hipparion the diaphysis is flatter (measurement 4), the preeminence of the distal supra-

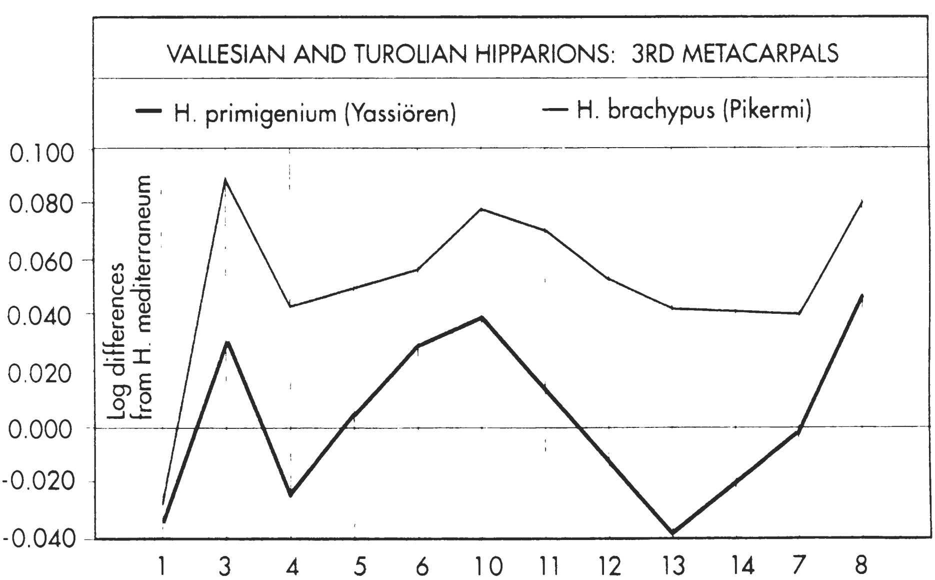


Fig. 11.10. Ratio diagrams of the third metacarpals of Vallesian (*H. primigenium*) and Turolian (*H. brachypus*) hipparions.

articular breadth (measurement 10) on the distal articular breadth (measure 11) is more pronounced, and the distal depths (12, 13, 14) are less developed. In the Vallesian form, these differences are probably linked to a lateral position of the lateral metapodials, whereas in the Turolian hipparion they have shifted to a more posterior position.

Figure 11.11 illustrates the differences between two Turolian forms, *H. brachypus* from Pikermi and *H. dietrichi* from Saloniki. The Saloniki hipparion is a good example of a slender (3), deep (4) diaphysis, with a deep proximal end (6) and two deep anteroposterior distal diameters (12 and 14) on each side of the condylar constriction (13). The distal breadths (10 and 11) are subequal and not very developed.

The anatomical characters allow only tenuous inferences of climate. Gracility may well be the only character that directly indicates climatic conditions (Gromova, 1952). The inference that deep metapodials are associated with savanna conditions is based on several probable, but not quite certain, suppositions: that the depth is the result of the shifting of the lateral metapodials; that this shift is beneficial to rapid locomotion; that rapid locomotion is beneficial only in open landscapes; and that open landscapes are dry. The assumption linking robust, flat metapodials to forest environments is valid only if 1) flatness is linked with lateral metapodials in a lateral position such that lateral movements are not altogether suppressed, 2) lateral mobility is more beneficial on uneven ground on which there are obstacles such as trees; and 3) trees grow mostly in humid conditions.

If all these suppositions are true, the study of the metapodials of some Miocene hipparions suggests the following conclusions (fig. 11.12):

1. The *H. primigenium* populations from the Vallesian (Yassiören, Nombrevilla, Höwenegg, Eppelsheim, Ravin de la Pluie, Montredon) and from the Turolian (Piera, Sumeg, Baltavar), noted as *H. primigenium* 1 and 2 in figure 11.12, were in general forest dwellers. Because of the flatness of the diaphysis, this is also probably true of the very small Vallesian *H. minus* and the small Vallesian *H. macedonicum*. But because we do not know the metapodial length, these species are not included in figure 11.12, where morphotypes are listed according to their robustness or gracility.
2. The slenderness of some Vallesian variants of the *H. primigenium* morphotype indicate drier conditions: Samburu, Gritzev, Rudabanya (*H. primigenium* 3 in fig. 11.12).
3. Some Vallesian variants of the same morphotype (Can Llobateres, Bou Hanifia, Yassiören) were better adapted to open landscapes (*H. primigenium* 4 in fig. 11.12).
4. This adaptation is even more pronounced in the Vallesian *H. sebastopolitanum* morphotype (Los Valles de Fuentidueña, El Lugarejo, Masia del Barbo,

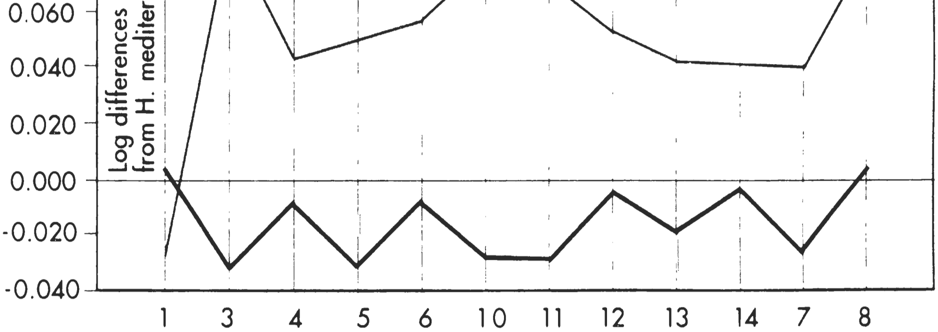


Fig. 11.11. Ratio diagrams of third metacarpals of two Turolian hipparions.

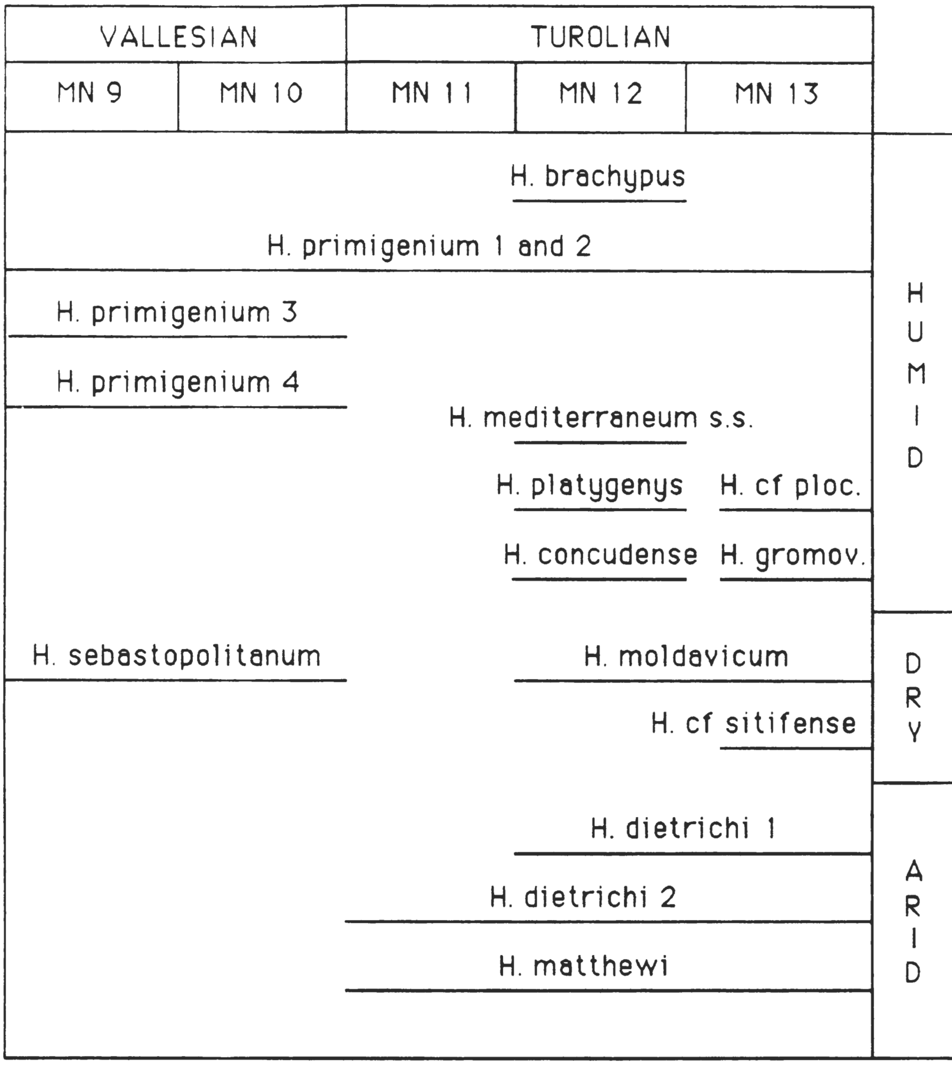


Fig. 11.12. Ratio diagrams for the four species of tridactyl equids present in the sample of Christmas Quarry.

Sebastopol, Yassiören), which also indicates dry conditions.

5. During the Turolian, the morphotype of *H. matthewi* indicates very dry conditions and open landscapes (Vathylakkos, Ravin des Zouaves, Kinik, Gulpinar, Samos 5, and Dytiko). The Turolian *H. dietrichi* (Vathylakkos, Ravin des Zouaves, Samos Andrianos, Saloniki, Pikermi, and Venta del Moro) suggests dry conditions and variable adaptations to open landscapes, more so in the Thessaloniki area (Vathylakkos, Ravin des Zouaves, Saloniki = *H. dietrichi* 2 in fig. 11.12) than elsewhere (Samos Andrianos, Pikermi, Venta del Moro = *H. dietrichi* 1).
6. Continuing dry conditions, though not so pronounced, and imperfect adaptation to open landscapes are suggested by the *H.* cf. *sitifense* morphotype (Lothagam, Sahabi, Baccinello, Kujal'nik). It is interesting to note that the same morphotype seems to be represented by the *Neohipparion* from Chihuahua, Mexico (Hemphillian-Blancan according to Lundelius et al., 1987).
7. The *H. moldavicum* morphotype (Taraklia, Tudorovo, Dytiko) is close to that of *H.* cf. *sitifense.*
8. The remaining morphotypes (table 11.2) indicate more humid conditions—very humid in the case of *H. brachypus* (Pikermi)—but with better adaptation to open landscapes than in the typical *H. primigenium.*
9. On the whole, there is certainly evidence for drier

conditions and more open landscapes in the Turolian than in the Vallesian and a progression of the number of dry morphotypes during the Turolian: two in the Early (*H. dietrichi* and *H. matthewi*); three in the Middle (*H. dietrichi*, *H. matthewi*, and *H. moldavicum*); and four in the Late Turolian (*H. dietrichi*, *H. matthewi*, *H. moldavicum*, and *H.* cf. *sitifense*).
10. There is no evidence for abrupt climatic changes, possibly because the dating of the fossils is not precise enough.

Origins

The North American *Cormohipparion occidentale* is richly represented at Christmas Quarry, Nebraska (Skinner and Johnson, 1984). Christmas Quarry is situated in the higher parts of the Ash Hollow Formation, above the Cap Rock Member, and is probably younger than 10 myr (Tedford et al., 1987). *H. primigenium*, the most ancient Old World Hipparion, belongs in the MN 9 zone (Mein, 1990) and is dated at around 10.5 myr (Sen, 1990; Bernor and Lipscomb, this vol.).

The questions of how many species are included under the name *Cormohipparion occidentale* at Christmas Quarry, and of which one might be the sister group of Old World hipparions, have been discussed previously (Eisenmann et al., 1987). More recently, Bernor et al. (1990, p. 294), using scatter diagrams of distal widths to maximal lengths of third metapodials from the same quarry, concluded that a detailed morphological study "is needed to determine . . which of these morphs is . . . more similar to *H. primigenium*."

Such a study has been done. The late C. De Giuli and I measured all the relevant metapodials from Christmas Quarry, and I have completed individual ratio diagrams with twelve measurements for each bone, as well as ratio diagrams for the average of each group. These diagrams (fig. 11.13) clearly show four different kinds of metacarpals. One has the *H. primigenium* morphology. A second one is close in size to the smallest European hipparion: *H. periafricanum* from El Arquillo, Spain (MN 13). A third resembles, in size and slenderness, *H. matthewi* from Samos Quarry 5 and Dytiko, both in Greece, and Gulpinar, in Turkey (all MN 13 zone). The fourth morphotype is very close in size and proportions to *H. mediterraneum* of Upper Chobruchi, Moldova, and to the slender hipparion from Lubéron, France (MN 12).

If the respective dates are confirmed, the existence of an *H. primigenium* morphotype earlier in Europe than in Christmas Quarry suggests that the immediate ancestor of *H. primigenium* will be found in older American sites.

If Christmas Quarry tridactyl horses belonged to

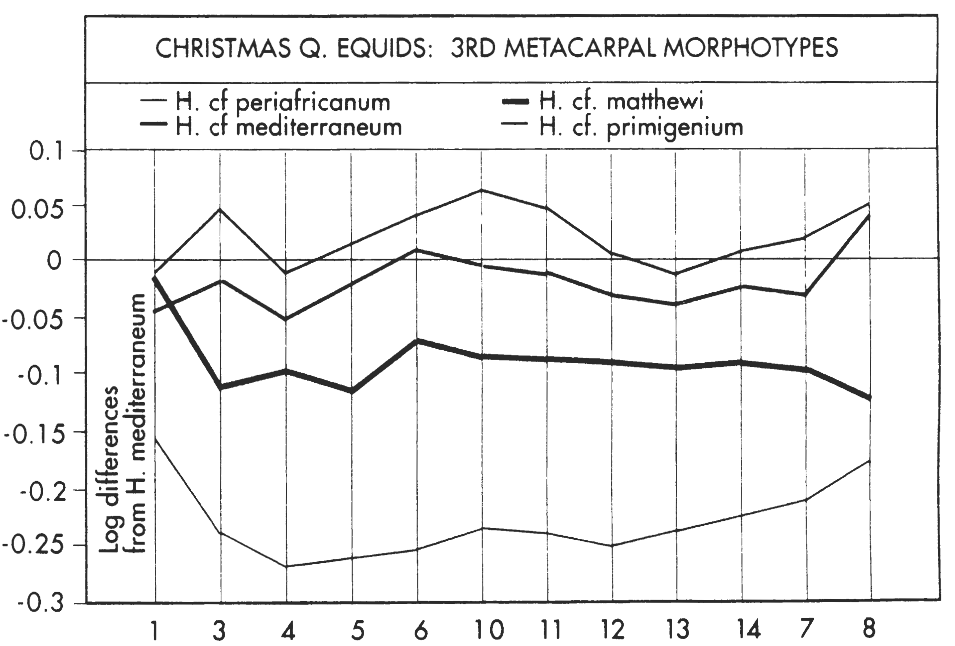


Fig. 11.13. Chronostratigraphical distribution of Vallesian and Turolian hipparions according to the robustness or slenderness of their metacarpals and the inferred humid or dry climatic conditions.

European instead of North American sites, they would indicate a Middle, or even Late, Turolian rather than a Vallesian age. Their age being fixed at somewhere around 9.5 myr, it seems that the conditions existing at this time in Nebraska had led to adaptations to dry conditions, although marked adaptation to open landscapes is not present in these forms. With the exception of the *H. primigenium* morphotype, already present in the European Vallesian, and the *H. periafricanum* morphotype probably representing a *Calippus* (Sondaar, pers. comm.), the other forms found at Christmas Quarry may have migrated later in Europe, when conditions there became dry enough.

Alternatively, parallel evolution may have resulted in European morphotypes similar to North American ones. Such a parallel evolution seems possible in the case of the Mexican (Chihuahua) and Old World hipparions belonging to the *H.* cf. *sitifense* morphotype. As is often the case, the answers to these questions depend on better data, particularly with regard to Asiatic hipparions.

References

Alberdi, M.-T. 1974. El género *Hipparion* en España. Nuevas formas de Castilla y Andalucia, revisión e historia evolutiva. *Trabajos sobre Neogeno-Cuaternario,* 1:1–146.

Bernor, R. L., and Tobien, H. 1989. Two small species of *Cremohipparion* (Equidae, Mamm.) from Samos, Greece. *Mitteilungen der bayerischen Staatssammlung für Paläontologie und historische Geologie,* 29:207–226.

Bernor, R. L., Tobien, H., and Woodburne, M. O. 1990. Patterns of Old World hipparionine evolutionary diversification and biogeographic extension. In *European Neogene mammal chronology,* ed. E. H. Lindsay et al., Plenum Press, New York. Pp. 263–319.

Borisiak, A. A. 1914 Sevastopol'skaja fauna mlekopitajuschchikh, vol. 1 *Trudy Geologicheskovo Komiteta,* n.s., 87:1–154.

Eisenmann, V. 1984. Sur quelques caractères adaptatifs du squelette d'*Equus* et leurs implications paléoécologiques. *Bulletin du Muséum National d'Histoire Naturelle,* 4th ser., 6, sec. C:185–195.

——— 1988. Les Périssodactyles Equidae. In *Contribution à l'étude du gisement miocène supérieur de Montredon (Hérault): Les grands mammifères. Palaeovertebrata,* special issue, 65–96.

Eisenmann, V., Sondaar, P., Alberdi, M.-T., and De Giuli, C. 1987. Is horse phylogeny becoming a playfield in the game of theoretical evolution? *Journal of Vertebrate Paleontology,* 7:224–229.

Forsten, A.-M. 1968. Revision of the Palearctic Hipparion. *Acta Zoologica Fennica,* 119:1–134.

———. 1982. *Hipparion primigenium melendezi* Alberdi reconsidered. *Annales Zoologici Fennici,* 19:109–113.

Gabunia, L. K. 1959. *K istorii gipparionov (po materialam Neogena SSSR).* Izdatel'stvo Akademii Nauk SSSR, Moscow.

Gregory, W. K. 1912. Notes on the principles of quadrupedal locomotion and on the mechanism of the limb bones in hoofed animals. *Annals of the New York Academy of Sciences,* 22:267–294.

Gromova, V. I. 1952. Gippariony (rod *Hipparion*) po materialam Taraklii, Pavlodara i drugim. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR,* 36:1–475.

Koufos, G. D. 1984. A new *Hipparion* (Mammalia, Perissodactyla) from the Vallesian (Late Miocene) of Greece. *Paläontologische Zeitschrift,* 58:307–317.

———. 1987a. Study of the Pikermi Hipparions. Pt. 1, Generalities and taxonomy. *Bulletin du Muséum National d'Histoire Naturelle,* 4th ser., 9, sec. C:197–252.

———. 1987b. Study of the Pikermi Hipparions. Pt. 2, Comparisons and odontograms. *Bulletin du Muséum National d'Histoire Naturelle,* 4th ser., 9, sec. C:327–363.

Lundelius, E. L., Churcher, C. S., Downs, T., Harington, C. R., Lindsay, E. H., Schultz, G. E., Semken, H. A., Webb, S. D., Zakrzewski, R. J. 1987. The North American Quaternary sequence. In *Cenozoic mammals of North America,* ed. M. O. Woodburne, University of California Press, Berkeley. Pp. 211–235.

Mein, P. 1990. Updating of MN zones. In *European Neogene mammal chronology,* ed. E. H. Lindsay et al., Plenum Press, New York. Pp. 73–90.

Nakaya, H., and Watabe, M. 1990. Hipparion from the Upper Miocene Namurungule Formation, Samburu Hills, Kenya. Phylogenetic significance of newly discovered skull. *Géobios,* 23:195–219.

Osborn, H. F. 1929. *The Titanotheres of ancient Wyoming, Dakota and Nebraska.* 2 vols. Monographs of the United States Geological Survey, no. 55, vol. 2. Washington, D.C.

Pavlow, M. 1890. Etudes sur l'histoire paléontologique des Ongulés. Pt. 4, Hipparions de la Russie. Pt. 5, Chevaux pléistocènes de la Russie. *Bulletin de la Société Impériale des Naturalistes de Moscou,* n.s., 3:653–716.

Qiu Zhansiang, Huang Weilong, and Guo Zhihui. 1987. The Chinese hipparionine fossils. *Palaeontologica Sinica,* 175, ser. C, 25:1–250.

Sen, S. 1990. *Hipparion* datum and its chronologic evidence in the Mediterranean area. In *European Neogene mammal chronology,* ed. E. H. Lindsay et al., Plenum Press, New York. Pp. 495–505.

Simpson, G. G. 1941. Large Pleistocene felines of North America. *American Museum Novitates,* 1136:1–27.

Skinner, M. F., and Johnson, F. W. 1984. Tertiary stratigraphy and the Frick collection of fossil vertebrates from north-central Nebraska. *Bulletin of the American Museum of Natural History,* 178:215–368.

Skinner, M. F., and MacFadden, B. J. 1977. *Cormohipparion* n. gen. (Mammalia, Equidae) from the North American Miocene (Barstovian-Clarendonian). *Journal of Paleontology,* 51:912–926.

Sondaar, P. Y. 1974. The Hipparion of the Rhone Valley. *Geobios,* 7:289–306.

Sondaar, P. Y., and Eisenmann, V. 1989. *L'évolution de la famille du Cheval.* Instituut voor Aardwetenschappen, Universiteit Utrecht. Pp. 1–43.

Staesche, U., and Sondaar, P. Y. 1979. *Hipparion* aus dem Vallesium und Turolium (Jungtertiar) der Turkei. *Geologisches Jahrbuch*, 33:35–79.

Tedford, R. H., Skinner, M. S., Fields, R. W., Rensberger, J. M., Whistler, D. P., Galusha, T., Taylor, B. E., Macdonald, J. R., and Webb, S. D. 1987. Faunal succession and biochronology through Hemphillian interval (Late Oligocene through earliest Pliocene epochs) in North America. In *Cenozoic mammals of North America*, ed. M. O. Woodburne. University of California Press, Berkeley. Pp. 153–210.

Appendix 11.1. In appendixes 11.1–11.4: Measurements (in mm) of third metacarpals (MC III) and third metatarsals (MT III) of tridactyl equids. Abbreviations: n = number of measures; x = mean; min = minimal observed value; max = maximal observed values; s = standard deviation; v = coefficient of variation (v = 100x/s); sebastopol. = *sebastopolitanum*.

	H. primigenium africanum, Bou Hanifia						*H. primigenium catalaunicum*, Can Llobateres					
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	4	207.5	204.0	211.0	3.11	1.50	8	207.5	199.0	215.0	5.53	2.67
3: Minimal breadth	5	27.0	25.5	28.0	1.06	3.93	11	28.0	26.0	29.0	1.07	2.82
4: Depth at level of 3	5	21.1	20.0	22.0	0.74	3.51	10	21.6	19.0	23.0	1.36	6.30
5: Proximal articular breadth	3	39.3	38.0	41.0	1.53	3.88	12	38.6	37.0	41.0	1.51	3.91
6: Prox. art. depth	3	28.7	26.0	30.0	2.31	8.06	11	27.0	25.0	29.0	1.24	4.59
10: Distal max. supra-art. breadth	4	37.3	37.0	38.0	0.50	1.34	10	38.0	36.0	42.0	1.87	4.92
11: Dist. max. art. breadth	4	35.9	35.5	36.0	0.25	0.70	11	36.7	35.0	40.1	1.44	3.92
12: Dist. max. depth of keel	4	28.8	28.0	30.0	0.87	3.01	11	28.1	26.2	29.5	1.03	3.67
13: Dist. min. depth of medial condyle	4	24.0	23.5	24.5	0.41	1.70	11	24.4	23.0	25.6	0.95	3.89
14: Dist. max. depth of med. condyle	4	26.8	26.0	27.5	0.65	2.41	11	26.2	23.6	28.5	1.23	4.69
7: Max. diameter facet 3rd carpal	3	36.2	34.0	38.0	2.02	5.59	12	33.1	31.0	35.0	1.58	4.77
8: Diam. anterior facet 2nd carpal	2	9.8	9.0	10.5	1.06	10.88	13	10.6	9.5	12.0	0.81	7.64
MT III												
1: Maximal length	5	240.7	234.0	247.0	4.66	1.94	4	234.5	228.0	245.0	7.33	3.13
3: Minimal breadth	7	26.1	25.0	27.0	0.61	2.33	11	29.4	27.0	32.0	1.43	4.86
4: Depth at level of 3	4	28.2	26.0	30.0	1.72	6.10	10	27.7	26.0	30.0	1.29	4.66
5: Proximal articular breadth	7	38.1	36.5	40.0	1.17	3.07	6	43.1	41.0	46.0	2.01	4.66
10: Distal max. supra-art. breadth	4	36.5	35.5	37.5	0.91	2.50	9	39.4	37.0	43.0	2.28	5.79
11: Dist. max. art. breadth	5	35.6	34.5	37.0	0.96	2.70	9	37.0	34.0	40.1	2.13	5.76
12: Dist. max. depth of keel	6	29.8	29.0	31.0	0.75	2.52	10	30.4	27.8	32.0	1.26	4.14
13: Dist. min. depth of medial condyle	6	23.9	23.0	26.0	1.11	4.66	8	24.8	23.5	27.2	1.09	4.40
14: Dist. max. depth of med. condyle	6	27.3	27.0	28.0	0.52	1.89	8	28.1	26.0	31.5	1.77	6.30
7: Max. diameter facet 3rd tarsal	7	36.0	34.0	38.0	1.41	3.93	6	39.6	38.0	41.0	1.02	2.58
8: Diam. facet 2nd tarsal	5	8.0	7.0	9.5	1.06	13.26	8	9.1	7.0	10.0	1.25	13.74

	H. sebastopol. melendezi, Los Valles de Fuentidueña						*H. primigenium*, Piera					
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	7	215.7	207.0	222.0	5.15	2.39	10	199.0	187.0	203.5	5.59	2.81
3: Minimal breadth	17	24.7	22.7	26.0	1.10	4.43	16	26.6	24.7	29.0	1.21	4.55
4: Depth at level of 3	20	21.4	19.0	23.7	1.27	5.93	15	19.9	17.5	22.5	1.60	8.04
5: Proximal articular breadth	13	37.4	36.0	41.0	1.41	3.77	15	37.1	35.5	38.5	0.90	2.43
6: Prox. art. depth	14	26.3	24.2	29.0	1.34	5.11	13	25.5	24.0	26.5	0.84	3.29
10: Distal max. supra-art. breadth	18	33.6	31.0	36.0	1.49	4.44	18	35.7	32.0	38.0	1.64	4.59
11: Dist. max. art. breadth	18	33.2	31.0	36.0	1.35	4.08	18	33.8	32.0	35.5	1.20	3.55
12: Dist. max. depth of keel	15	26.6	24.0	29.5	1.23	4.62	15	27.0	25.0	29.0	1.32	4.89
13: Dist. min. depth of medial condyle	18	23.2	22.0	25.0	0.81	3.49	19	22.9	20.0	25.5	1.52	6.64
14: Dist. max. depth of med. condyle	15	24.6	23.0	26.0	0.78	3.16	16	24.7	22.8	27.0	1.37	5.55
7: Max. diameter facet 3rd carpal	14	32.3	31.0	34.5	1.11	3.43	13	31.4	28.0	33.0	1.27	4.04
8: Diam. anterior facet 2nd carpal	13	10.3	8.5	12.0	1.09	10.63	12	10.9	10.0	12.5	0.76	6.97
MT III												
1: Maximal length	10	249.0	242.0	255.0	4.88	1.96	15	232.1	222.0	242.0	6.76	2.91
3: Minimal breadth	31	24.9	22.0	27.0	1.25	5.02	37	27.2	23.5	31.0	1.61	5.92

MT III		*H. sebastopol. melendezi*, Los Valles de Fuentidueña						*H. primigenium*, Piera				
	n	x	min	max	s	v	n	x	min	max	s	v
4: Depth at level of 3	28	26.3	24.0	28.0	1.19	4.52	36	26.9	24.0	31.0	1.42	5.28
5: Proximal articular breadth	25	38.8	36.0	42.0	1.54	3.97	27	38.8	35.0	44.0	2.04	5.26
10: Distal max. supra-art. breadth	29	34.8	32.0	38.0	1.73	4.97	28	37.7	32.7	41.0	1.94	5.15
11: Dist. max. art. breadth	28	34.0	30.0	37.0	1.81	5.32	26	35.3	33.0	38.0	1.18	3.34
12: Dist. max. depth of keel	15	29.0	27.0	31.0	1.41	4.86	26	29.0	27.0	33.0	1.51	5.21
13: Dist. min. depth of medial condyle	27	24.1	21.0	26.0	1.36	5.64	27	23.9	22.0	27.0	1.27	5.31
14: Dist. max. depth of med. condyle	26	26.7	23.0	29.0	1.54	5.77	27	26.8	25.0	29.0	1.30	4.85
7: Max. diameter facet 3rd tarsal	23	36.2	34.0	42.0	1.74	4.81	22	36.7	34.0	40.5	1.69	4.60
8: Diam. facet 2nd tarsal	24	9.3	7.0	11.0	1.12	12.04	21	8.6	6.7	11.2	1.41	16.40

Appendix 11.2. In appendixes 11.1–11.4: Measurements (in mm) of third metacarpals (MC III) and third metatarsals (MT III) of tridactyl equids. Abbreviations: n = number of measures; x = mean; min = minimal observed value; max = maximal observed values; s = standcrd deviation; v = coefficient of variation (v = 100x/s)

MC III		*H. brachypus giganteum*, Grebeniki						*H. concudense verae*, Grebeniki				
	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	9	213.8	201.0	230.0	8.87	4.15	16	211.7	199.0	222.0	6.55	3.09
3: Minimal breadth	11	28.0	27.0	29.0	0.80	2.86	18	25.5	23.5	27.1	1.14	4.46
4: Depth at level of 3	9	22.0	20.0	24.0	1.23	5.60	17	20.8	19.0	22.0	0.88	4.24
5: Proximal articular breadth	10	38.8	36.0	40.5	1.23	3.18	14	37.2	35.0	40.0	1.74	4.68
6: Prox. art. depth	6	27.0	25.0	28.1	1.28	4.74	15	25.7	24.0	28.0	1.14	4.46
10: Distal max. supra-art. breadth	11	37.6	36.7	39.0	0.80	2.12	18	33.9	31.5	35.1	1.13	3.34
11: Dist. max. art. breadth	10	36.1	34.0	39.0	1.65	4.56	18	33.4	31.7	35.0	1.05	3.15
12: Dist. max. depth of keel	8	28.8	28.0	30.0	0.76	2.63	16	26.9	26.0	28.0	0.84	3.11
13: Dist. min. depth of medial condyle	8	24.7	23.7	26.0	0.75	3.05	18	22.7	21.0	24.0	0.80	3.54
14: Dist. max. depth of med. condyle	9	26.4	25.0	27.0	0.73	2.76	17	24.7	23.0	26.0	0.77	3.12
7: Max. diameter facet 3rd carpal	8	32.8	32.0	35.0	0.98	2.97	14	31.8	28.5	34.0	1.79	5.65
8: Diam. anterior facet 2nd carpal	9	11.4	10.0	12.5	0.77	6.82	15	10.9	10.0	12.1	0.77	7.02
MT III												
1: Maximal length	9	248.6	235.0	259.0	8.13	3.27	16	247.4	236.0	254.0	6.33	2.56
3: Minimal breadth	11	31.2	28.0	33.5	1.85	5.94	19	26.6	24.0	29.0	1.25	4.71
4: Depth at level of 3	8	30.2	26.7	32.0	1.82	6.00	18	26.4	24.5	30.0	1.44	5.43
5: Proximal articular breadth	10	44.4	43.0	47.0	1.15	2.59	16	40.0	37.0	43.0	1.59	3.96
10: Distal max. supra-art. breadth	11	42.6	38.1	45.0	1.87	4.39	19	36.0	33.0	38.0	1.64	4.56
11: Dist. max. art. breadth	11	39.9	37.3	42.0	1.62	4.07	19	35.0	33.0	37.0	1.16	3.32
12: Dist. max. depth of keel	9	33.3	31.5	36.0	1.36	4.08	19	29.2	27.0	31.0	1.01	3.47
13: Dist. min. depth of medial condyle	11	26.5	24.5	28.5	1.10	4.15	19	23.8	22.0	25.5	1.07	4.51
14: Dist. max. depth of med. condyle	10	30.1	28.0	32.0	1.29	4.27	19	26.7	24.5	28.5	0.97	3.64
7: Max. diameter facet 3rd tarsal	8	41.4	39.0	43.3	1.32	3.18	14	36.1	32.5	38.0	1.50	4.14
8: Diam. facet 2nd tarsal	7	11.3	7.5	13.0	1.78	15.78	14	10.0	9.0	12.0	1.07	10.69

MC III		*H. moldavicum moldavicum*, Taraklia						*H. moldavicum tudorovense*, Tudorovo				
	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	13	210.4	193.0	219.0	6.32	3.00	11	206.5	199.0	216.0	5.95	2.88
3: Minimal breadth	14	24.1	22.5	25.0	0.78	3.23	12	24.2	22.0	26.0	1.33	5.50
4: Depth at level of 3	14	21.0	20.0	22.0	0.66	3.12	12	20.2	18.0	21.5	0.99	4.90
5: Proximal articular breadth	13	34.2	31.5	36.0	1.30	3.80	11	34.6	32.0	39.0	2.17	6.27
6: Prox. art. depth	10	24.9	23.0	27.0	1.27	5.11	9	24.2	23.5	25.0	0.53	2.20
10: Distal max. supra-art. breadth	13	33.2	31.7	35.0	1.02	3.07	11	32.7	31.2	34.7	1.06	3.25

(Continued)

Appendix 11.2. (*Continued*)

		H. moldavicum moldavicum, Taraklia						*H. moldavicum tudorovense*, Tudorovo				
MC III	n	x	min	max	s	v	n	x	min	max	s	v
11: Dist. max. art. breadth	13	31.4	29.8	33.0	0.87	2.78	10	31.4	29.5	33.0	1.34	4.28
12; Dist. max. depth of keel	12	25.2	24.0	27.0	0.73	2.89	11	25.6	24.0	28.0	1.15	4.47
13: Dist. min. depth of medial condyle	14	21.1	20.0	22.0	0.49	2.30	11	21.8	21.0	24.0	0.96	4.40
14: Dist. max. depth of med. condyle	12	23.4	23.0	25.0	0.63	2.71	10	23.6	22.0	25.2	1.02	4.32
7: Max. diameter facet 3rd carpal	12	28.7	26.5	30.0	1.03	3.60	11	24.8	26.0	30.7	1.37	4.81
8: Diam. anterior facet 2nd carpal	13	10.1	7.5	12.0	1.24	12.30	10	9.9	9.0	13.0	1.19	12.06
MT III												
1: Maximal length	14	231.1	216.0	241.0	7.45	3.22	9	240.3	228.0	257.0	8.03	3.34
3: Minimal breadth	14	23.6	22.0	25.0	0.75	3.18	11	25.0	23.0	27.0	1.41	5.65
4: Depth at level of 3	14	24.7	23.0	26.5	0.98	3.98	10	25.6	23.0	27.1	1.44	5.61
5: Proximal articular breadth	13	36.1	33.5	39.0	1.81	5.02	8	36.0	32.0	38.0	1.98	5.51
10: Distal max. supra-art. breadth	14	33.4	31.0	35.0	1.37	4.11	13	34.2	33.0	37.0	1.11	3.24
11: Dist. max. art. breadth	14	31.4	30.0	33.0	0.88	2.82	13	32.3	31.0	34.2	1.00	3.09
12: Dist. max. depth of keel	14	26.9	24.0	29.0	1.31	4.88	13	27.2	24.5	29.0	1.03	3.79
13: Dist. min. depth of medial condyle	14	21.6	19.0	23.0	1.14	5.29	13	22.5	20.2	24.0	0.89	3.97
14: Dist. max. depth of med. condyle	13	24.3	22.5	26.0	1.16	4.77	12	24.9	22.7	26.0	0.94	3.78
7: Max. diameter facet 3rd tarsal	13	32.7	30.0	35.0	1.40	4.26	8	33.2	30.0	35.5	1.82	5.48
8: Diam. facet 2nd tarsal	13	7.7	6.0	9.5	1.07	13.88	7	9.4	8.0	10.5	1.02	10.79

Appendix 11.3. In appendixes 11.1–11.4: Measurements (in mm) of third metacarpals (MC III) and third metatarsals (MT III) of tridactyl equids. Abbreviations: n = number of measures; x = mean; min = minimal observed value; max = maximal observed values; s = standard deviation; v = coefficient of variation (v = 100x/s)

		H. mediterraneum s.s., Chobruchi						*H. concudense concudense*, Concud				
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal legnth	4	206.8	203.0	210.0	2.99	1.44	5	211.9	187.5	230.0	18.02	8.50
3: Minimal breadth	10	26.0	23.0	27.7	1.49	5.72	9	26.0	24.0	29.0	1.71	6.57
4: Depth at level of 3	10	21.4	20.0	22.2	0.72	3.37	10	20.3	19.0	21.6	0.76	3.76
5: Proximal articular breadth	7	36.4	36.0	37.5	0.73	2.01	11	35.8	32.8	38.0	1.75	4.90
6: Prox. art. depth	5	26.6	25.0	28.0	1.14	4.29	9	25.3	23.0	27.5	1.60	6.32
10: Distal max. supra-art. breadth	8	33.7	32.0	36.0	1.35	3.99	19	34.2	31.0	36.5	1.44	4.22
11: Dist. max. art. breadth	8	32.3	30.0	34.0	1.33	4.12	18	33.7	31.7	35.3	1.11	3.29
12: Dist. max. depth of keel	8	26.5	24.0	28.7	1.37	5.16	19	26.8	25.1	28.0	0.83	3.10
13: Dist. min. depth of medial condyle	8	22.5	21.0	24.5	1.02	4.54	19	22.7	21.8	24.0	0.67	2.95
14: Dist. max. depth of med. condyle	8	24.5	22.7	26.5	1.10	4.49	17	24.5	23.5	26.0	0.67	2.74
7: Max. diameter facet 3rd carpal	5	30.5	29.0	32.0	1.11	3.63	11	31.1	29.0	33.0	1.23	3.94
8: Diam. anterior facet 2nd carpal	6	10.5	9.0	11.5	0.99	9.45	13	10.1	9.0	11.7	0.97	9.67
MT III												
1: Maximal length	4	250.0	247.0	255.0	3.56	1.42	6	237.8	230.0	248.0	8.68	3.65
3: Minimal breadth	10	24.9	22.0	27.0	1.47	5.90	21	27.1	24.0	31.0	1.93	7.12
4: Depth at level of 3	10	25.5	24.0	27.0	1.22	4.78	17	26.4	22.0	29.0	1.82	6.91
5: Proximal articular breadth	11	38.0	33.0	42.0	2.72	7.16	11	38.8	36.3	42.0	1.67	4.31
10: Distal max. supra-art. breadth	7	34.9	34.0	37.0	1.02	2.91	29	35.4	30.0	39.0	2.14	6.04
11: Dist. max. art. breadth	7	33.3	32.0	36.7	1.57	4.72	29	34.2	30.0	37.0	1.89	5.53
12: Dist. max. depth of keel	6	28.8	28.0	30.0	0.71	2.46	25	29.3	25.0	32.5	1.86	6.35
13: Dist. min. depth of medial condyle	6	23.3	23.0	24.0	0.52	2.21	30	23.5	21.0	27.0	1.46	6.19
14: Dist. max. detp of med. condyle	6	25.8	25.2	26.0	0.32	1.24	28	25.8	22.5	29.0	1.31	5.08
7: Max. diameter facet 3rd tarsal	9	34.4	30.0	38.0	2.50	7.26	11	36.2	34.0	39.0	1.60	4.42
8: Diam. facet 2nd tarsal	9	9.6	9.0	10.0	0.49	5.06	11	9.2	7.5	11.8	1.27	13.78

		H. gromovae, El Arquillo						*H. dietrichi*, Venta del Moro				
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	1	169.0					3	206.7	200.0	215.0	7.64	3.70
3: Minimal breadth	8	20.7	19.0	22.5	1.06	5.11	6	21.8	20.1	23.5	1.15	5.27
4: Depth at level of 3	7	17.0	15.0	18.0	1.04	6.12	5	19.4	18.2	20.0	0.82	4.20
5: Proximal articular breadth	4	31.3	29.0	32.0	1.50	4.80	7	32.6	31.0	34.7	1.47	4.50
6: Prox. art. depth	1	18.0					7	22.8	22.0	23.0	0.39	1.73
10: Distal max. supra-art. breadth	7	27.9	27.0	30.0	1.03	3.70	6	30.2	29.0	31.0	0.71	2.36
11: Dist. max. art. breadth	7	26.8	25.0	28.0	1.22	4.53	6	29.5	28.7	30.0	0.61	2.08
12: Dist. max. depth of keel	7	21.5	20.0	23.0	0.96	4.45	6	24.5	23.5	26.0	1.04	4.25
13: Dist. min. depth of medial condyle	7	18.8	17.7	20.0	0.71	3.75	6	20.8	20.0	22.0	0.91	4.35
14: Dist. max. depth of med. condyle	6	19.9	18.3	21.5	1.11	5.57	6	21.8	21.0	22.7	0.60	2.76
7: Max. diameter facet 3rd carpal	3	25.5	23.0	27.5	2.29	8.99	4	28.4	27.0	29.5	1.11	3.91
8: Diam. anterior facet 2nd carpal	4	9.3	8.0	10.0	0.96	10.35	7	8.4	7.0	9.0	0.81	9.62
MT III												
1: Maximal length	1	203.0					2	235.0	233.0	237.0	2.83	1.20
3: Minimal breadth	7	21.7	21.0	22.5	0.70	3.22	14	22.1	20.5	23.0	0.68	3.06
4: Depth at level of 3	6	22.7	20.0	25.0	1.66	7.34	13	24.2	22.5	25.2	0.87	3.61
5: Proximal articular breadth	8	32.5	30.0	36.7	2.39	7.36	7	34.4	32.5	37.0	1.97	5.71
10: Distal max. supra-art. breadth	3	28.5	27.5	29.0	0.87	3.04	6	31.2	29.0	33.7	1.82	5.85
11: Dist. max. art. breadth	3	27.9	27.7	28.0	0.17	0.62	8	30.3	28.3	33.0	1.78	5.88
12: Dist. max. depth of keel	3	23.6	23.0	24.5	0.79	3.36	7	26.6	24.5	29.0	1.68	6.30
13: Dist. min. depth of medial condyle	3	20.0	19.0	21.0	1.00	5.00	8	21.1	19.0	23.0	1.25	5.90
14: Dist. max. depth of med. condyle	3	21.8	21.7	22.0	0.15	0.70	7	23.4	22.0	25.5	1.28	5.47
7: Max. diameter facet 3rd tarsal	5	29.9	27.0	33.5	2.46	8.23	6	32.5	30.0	35.0	1.89	5.83
8: Diam. facet 2nd tarsal	5	9.0	8.0	10.5	1.17	13.03	5	8.3	6.5	9.0	1.10	13.20

Appendix 11.4. In appendixes 11.1–11.4: Measurements (in mm) of third metacarpals (MC III) and third metatarsals (MT III) of tridactyl equids. Abbreviations: n = number of measures; x = mean; min = minimal observed value; max = maximal observed values; s = standard deviation; v = coefficient of variation (v = 100x/s)

		H. cf. ***primigenium***, Christmas Quarry						*H.* cf. ***mediterraneum***, Christmas Quarry				
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	23	209.2	200.8	216.9	4.87	2.33	7	194.6	188.5	201.5	4.76	2.44
3: Minimal breadth	22	29.2	26.7	32.9	1.82	6.25	7	24.5	23.8	25.4	0.55	2.24
4: Depth at level of 3	22	20.9	18.9	23.2	1.19	5.69	7	19.1	17.5	20.3	1.02	5.37
5: Proximal articular breadth	19	37.6	35.4	40.1	1.27	3.39	6	34.1	32.8	36.9	1.62	4.77
6: Prox. art. depth	20	27.5	25.0	30.2	1.56	5.68	7	25.4	24.2	28.2	1.45	5.68
10: Distal max. supra-art. breadth	23	37.4	34.7	40.8	1.76	4.72	7	32.3	31.2	34.4	1.02	3.16
11: Dist. max. art. breadth	22	34.9	31.8	37.4	1.62	4.64	7	30.9	29.9	32.2	0.93	3.02
12: Dist. max. depth of keel	21	26.8	24.4	29.0	1.13	4.23	7	24.6	22.9	27.2	1.50	6.10
13: Dist. min. depth of medial condyle	22	22.3	20.9	23.8	0.81	3.65	7	21.1	20.1	22.4	0.81	3.83
14: Dist. max. depth of med. condyle	20	24.7	22.2	26.6	1.22	4.95	7	22.9	21.8	23.5	0.55	2.40
7: Max. diameter facet 3rd carpal	17	32.4	29.0	34.5	1.60	4.93	6	29.2	27.1	31.8	1.73	5.94
8: Diam. anterior facet 2nd carpal	18	10.3	8.6	12.4	0.94	9.11	6	10.2	8.9	12.5	1.46	14.40

		H. cf. ***matthewi***, Christmas Quarry						*H.* cf. ***periafricanum***, Christmas Quarry				
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	6	208.2	200.4	218.2	5.82	2.80		147.5				
3: Minimal breadth	6	19.8	17.7	22.5	1.71	8.66		14.8				
4: Depth at level of 3	5	17.7	15.9	18.5	1.06	5.97		12.0				

(Continued)

Appendix 11.4. (*Continued*)

	H. cf. *matthewi*, Christmas Quarry						*H.* cf. *periafricanum*, Christmas Quarry					
MC III	n	x	min	max	s	v	n	x	min	max	s	v
5: Proximal articular breadth	6	29.2	27.0	32.5	1.92	6.59		20.6				
6: Prox. art. depth	6	22.2	20.1	25.5	1.81	8.13		14.8				
10: Distal max. supra-art. breadth	6	27.2	24.9	31.6	2.28	8.40		20.1				
11: Dist. max. art. breadth	6	26.3	24.3	31.0	2.46	9.35		19.2				
12: Dist. max. depth of keel	6	22.7	21.1	25.8	1.79	7.91		15.2				
13: Dist. min. depth of medial condyle	6	19.6	18.2	22.1	1.38	7.06		13.4				
14: Dist. max. depth of med. condyle	6	21.0	19.5	23.8	1.67	7.93		14.5				
7: Max. diameter facet 3rd carpal	6	26.1	25.0	28.4	1.29	4.95		19.2				
8: Diam. anterior facet 2nd carpal	6	7.4	6.4	8.1	0.73	9.99		6.5				

	H. dietrichi, Saloniki						*H. mediterraneum* s.s., Pikermi					
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	5	220.0	218.0	222.0	1.41	0.64	21	214.9	202.0	221.7	5.55	2.58
3: Minimal breadth	6	23.5	22.5	24.0	0.77	3.30	21	25.5	23.5	27.0	1.10	4.31
4: Depth at level of 3	6	21.2	20.0	23.0	1.17	5.52	20	21.3	20.1	23.5	0.84	3.93
5: Proximal articular breadth	5	34.1	32.0	36.5	1.75	5.12	22	36.7	33.5	40.0	1.94	5.28
6: Prox. art. depth	6	24.5	23.0	27.0	1.52	6.19	19	25.0	22.0	29.0	1.57	6.28
10: Distal max. supra-art. breadth	5	30.9	29.0	32.0	1.34	4.34	20	32.5	30.5	34.5	1.30	3.99
11: Dist. max. art. breadth	5	29.9	29.0	31.0	0.89	2.99	21	31.6	30.0	33.5	1.05	3.31
12: Dist. max. depth of keel	4	26.0	25.0	26.8	0.81	3.12	22	26.3	23.0	29.5	1.46	5.54
13: Dist. min. depth of medial condyle	4	21.9	21.7	22.0	0.15	0.68	22	22.9	20.1	26.5	1.26	5.51
14: Dist. max. depth of med. condyle	3	24.0	23.0	25.0	1.00	4.17	20	24.1	21.0	27.0	1.31	5.46
7: Max. diameter facet 3rd carpal	5	29.4	27.0	31.0	1.52	5.16	20	31.2	29.0	34.5	1.58	5.08
8: Diam. anterior facet 2nd carpal	5	9.8	8.3	11.0	0.98	10.05	20	9.9	8.0	11.5	0.99	10.00

	H. primigenium, Sumeg						*H. mediterraneum*, Lubéron					
MC III	n	x	min	max	s	v	n	x	min	max	s	v
1: Maximal length	1	191.0	191.0	191.0			4	200.8	191.5	207.0	6.58	3.28
3: Minimal breadth	14	29.3	26.5	33.0	1.92	6.54	13	24.1	22.0	25.0	0.96	3.97
4: Depth at level of 3	14	20.9	19.0	22.1	1.10	5.25	13	20.1	18.0	21.0	1.02	5.09
5: Proximal articular breadth	14	37.5	35.3	41.0	1.75	4.66	10	34.1	33.0	36.0	1.06	3.10
6: Prox. art. depth	12	26.5	24.0	28.0	1.27	4.79	11	24.5	23.0	26.0	0.94	3.82
10: Distal max. supra-art. breadth	11	36.6	33.0	39.0	1.88	5.14	11	31.1	29.7	34.1	1.55	4.99
11: Dist. max. art. breadth	11	35.0	33.0	37.6	1.66	4.76	10	29.9	28.0	32.5	1.45	4.86
12: Dist. max. depth of keel	9	27.1	25.0	29.0	1.20	4.43	11	25.2	24.0	27.0	0.74	2.94
13: Dist. min. depth of medial condyle	10	23.1	21.0	24.5	1.10	4.75	11	22.0	20.7	23.8	0.99	4.51
14: Dist. max. depth of med. condyle	10	24.9	23.0	26.0	0.95	3.80	8	23.1	22.0	24.0	0.75	3.26
7: Max. diameter facet 3rd carpal	12	31.8	30.0	34.0	1.21	3.80	11	29.2	28.0	30.5	0.91	3.13
8: Diam. anterior facet 2nd carpal	12	10.6	10.0	12.0	0.65	6.15	8	9.6	9.0	12.0	1.06	11.02

Appendix 11.5. Measurements (in mm) of third metacarpals (MC III) of hipparions. Abbreviations: H. = *Hipparion*; primig. = *primigenium*; sebast. = *sebastopolitanum*; periaf. = *periafricanum*; platyg. = *platygenys*; sitif. = *sitifense*; concud. = *concudense*; Höwen. = Höwenegg; Nomb. = Nombrevilla; Yass. = Yassiören; Gritz. = Gritzev; El Lug. = El Lugarejo; Arqu. = Arquillo; Piker. = Pikermi; Tarak. = Taraklia; Salon. = Saloniki; Baccin. = Baccinello; Lubér. = Lubéron; n = number of measures.

MC III	*H. primig.* Eppelsheim	*H. primig.* Höwen. n = 3	*H. primig.* Nomb. n = 1–3	*H. primig.* Yass. 13	*H. primig* Rudabanya	*H. primig.* Gritz. n = 2–3	*H. primig.* Yass. n = 3–4	*H. sebast.* El Lug. n = 2–4	*H. sebast.* Yass. 12
1: Maximal length	215.0	214.0		198.0	226.0	224.0	205.9	210.5	222.0
3: Minimal breadth	28.6	31.5	30.0	27.0	27.1	28.0	27.5	25.3	24.2
4: Depth at level of 3	23.0	22.1	23.0	20.0	22.0	22.4	21.3	21.6	21.1
5: Proximal articular breadth	40.1	40.6	40.0	37.0	33.5	37.7	37.2	35.0	36.2
6: Prox. art. depth	28.9	28.6		26.5		27.7	26.6	25.1	23.3
10: Distal max. supra-art. breadth	40.3	39.3	43.0	36.0	38.0	38.3	34.9	33.4	34.2
11: Dist. max. art. breadth	37.1	37.3	39.0	33.0	36.0	35.9	33.5	32.6	33.0
12: Dist. max. depth of keel	28.0	28.0	30.0	25.5	28.0	28.4	27.2	25.3	27.8
13: Dist. min. depth of medial condyle	24.1	23.3	25.2	21.0	22.5	23.8	24.0	22.4	23.1
14: Dist. max. depth of med. condyle	26.0	26.8	28.1	23.0	24.2	26.4	26.1	24.0	25.0
7: Max. diameter facet 3rd carpal	36.0	33.5	33.0	31.0	29.3	32.3	31.8	30.6	31.0
8: Diam. anterior facet 2nd carpal	10.0	10.5	11.5	11.0	10.0	9.6	9.7	10.8	9.5

MC III	*H. minus* Sbastopol	*H. periaf.* Arqu. n = 1–2	*H. matthewi* Gulpinar n = 1	*H. dietrichi* Piker. n = 3–6	*H. platyg.* Tarak. n = 2–3	*H. platyg.* Salon. n = 1–2	*H. cf. sitif.* Baccin. n = 2	*H. cf. concud.* Lubér. n = 1–5	*H. brachypus* Polgardi
1: Maximal length			198.0	229.8	226.0	223.5		210.4	210.0
3: Minimal breadth	18.0	16.1	19.0	24.3	29.5	29.5		27.8	28.2
4: Depth at level of 3	14.0	12.5	17.9	22.3	24.0	24.0		20.5	22.3
5: Proximal articular breadth		22.0	28.0	35.8	39.5	38.0		36.1	40.0
6: Prox. art. depth		15.2	19.5	25.6	27.2	28.0			
10: Distal max. supra-art. breadth	25.0	18.0	26.1	33.2	38.0	38.0	33.7	33.1	38.7
11: Dist. max. art. breadth	24.0	17.6	25.0	31.9	35.3	33.5	34.5	31.6	37.0
12: Dist. max. depth of keel	17.3	15.3	22.0	27.6	27.8	26.5	27.4	26.3	28.2
13: Dist. min. depth of medial condyle	14.8	13.5	19.0	24.7	24.0	23.1	22.6	23.3	25.0
14: Dist. max. depth of med. condyle	17.0	14.3	20.7	25.7	25.8	25.1	24.4	24.6	26.0
7: Max. diameter facet 3rd carpal		18.3	23.0	31.8	32.5	33.0		29.4	33.0
8: Diam. anterior facet 2nd carpal		6.3	9.0	10.0	10.8	9.0		10.5	11.0

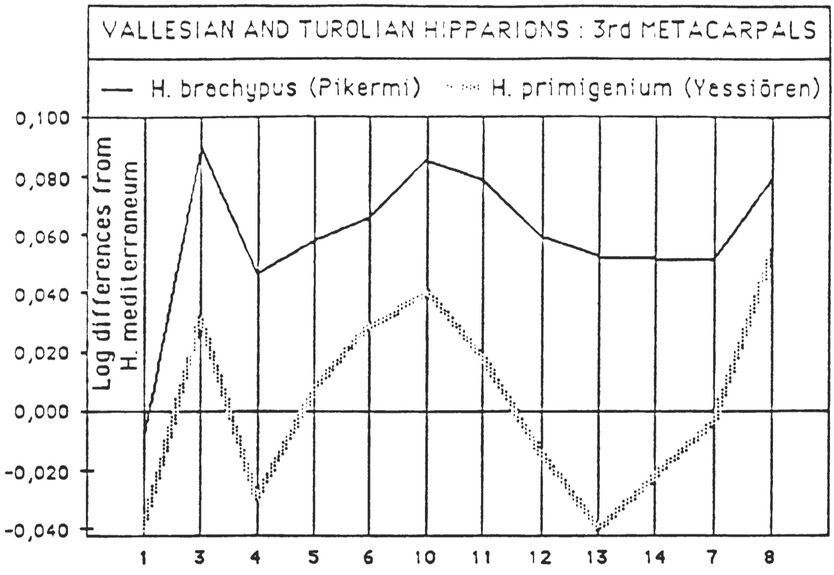


Fig 11.10

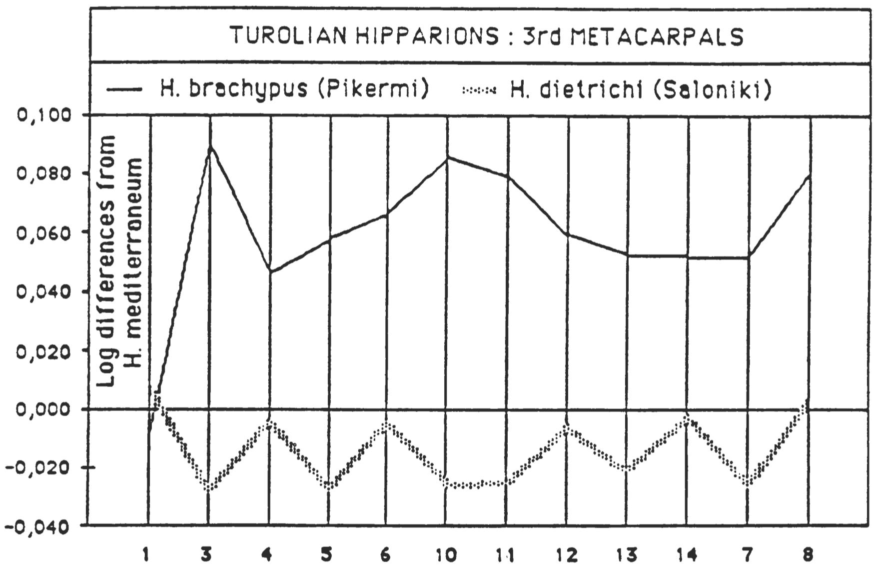


Fig 11.11

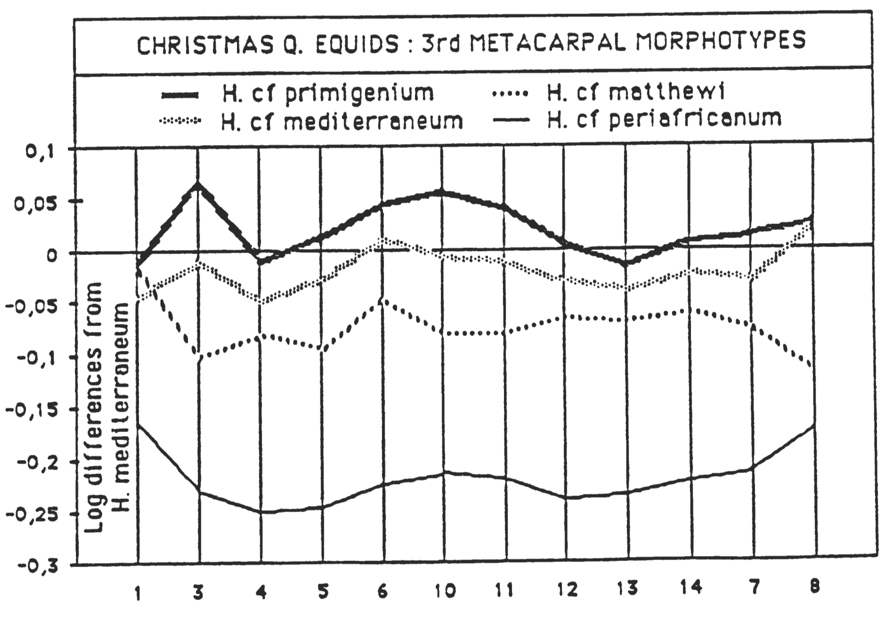


Fig 11.13