NEW SPECIES OF HIPPARION FROM LA ROMA 2 (LATE VALLESIAN, TERUEL, SPAIN): A STUDY OF THE MORPHOLOGICAL AND BIOMETRIC VARIABILITY OF HIPPARION PRIMIGENIUM

Key words: Equidae - Hipparion - Multivariate analysis - Vallesian - Late Miocene - Teruel - Spain

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ABSTRACT- Morphological and biometrical variability is analyzed in Hipparion primigenium (V. Meyer) from four Vallesian and Turolian locations in Spain (Masía de Barbo, Puente Minero, Nombrevilla and Los Valles de Fuentidueña).

Previously unstudied remains of Hipparion from La Roma 2 (Teruel province, Spain) are described and tested by multivariate analysis. This form is compared with: 1) Hipparion

primigenium (or Hippotherium primigenium) from the above-mentioned Spanish localities, 2) large-sized specimens from Çalta (Turkey), and Pavlodar (Kazakhstan), 3) forms from the locality type of Eppelsheim, Höwenegg and Dürkheim (Germany), and Nikiti 1 (Greek) and 4) specimens from two other Spanish localities, Concud and Venta del Moro. Hipparion remains from La Roma 2 are identified as Hipparion laromae n. sp. by body mass and morphological characteristics, and confirmed by bivariate and multivariate analyses. The faunal assemblages indicate a late Vallesian age (MN10) for La Roma 2 locality and an early Turolian age (MN11) for the Puente Minero locality.

INTRODUCTION

THE GENUS Hipparion is recorded in Eurasia from the early Vallesian to the early Villafranchian (Upper Miocene-Upper Pliocene, *sensu* Bonadonna and Alberdi, 1987). During the Turolian, this genus was widely dispersed throughout Eurasia. We observe a size reduction from medium-sized species such as Hipparion mediterraneum Roth and Wagner and Hipparion concudense Pirlot to very small species, which are found not only in the Spanish Turolian (Hipparion gromovae Villalta and Crusafont, Hipparion periafricanum Villalta and Crusafont), but also in Russia and some Greek sites (Hipparion matthewi Abel, Hipparion macedonicum Koufos; the latter is considered by Forstén to be a synonym of Hipparion matthewi (Forstén, 1968; Alberdi, 1974; Koufos 1980, 1987; among others). The collection of Miocene and Pliocene Hipparion remains has increased substantially during the last fifteen years as a result of fieldwork carried out by the Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain) (Alberdi and Alcalá 1989-90, 1999; Alberdi and Morales, 1981). The abundant record of Eurasian Vallesian and Turolian Hipparion gave rise to a great

proliferation of taxonomic names. In 1968, Forstén first began to synthesize these names using statistical methods. Later, Alberdi (1974) used statistical methods that combined morphological and biometrical features to set limits to the reduced systematization made by Forstén. Alberdi (1989) established a total of six groups (“morphotypes” sensu lato) in an attempt to unify and group the Eurasian and African Hipparion species from the early Vallesian to the early Villafranchian.

Many early Vallesian species and subspecies were named, and most of them were later referred to the species Hipparion primigenium (Sondaar, 1961; Forsten, 1968; Alberdi 1974, 1989). Recently, several authors have proposed subdividing the species into different genera and subgenera. Based on Chinese Hipparion remains, Qiu et al. (1987) proposed grouping several chinese species into different subgenera. Bernor et al. (1996, p. 308) placed all species of Hipparion genus into the Hipparionini tribe and grouped them into several genera or group complexes. These genera or groups are: Cormohipparion, Neohipparion, Nanippus, Pseudohipparion, Hippotherium, Hipparion s.s., Cremohipparion, “Sivalhippus” Eurygnathohippus (= Stylohipparion), Plesiohipparion and Proboscidihipparion.

The aims of this study are to: (1) analyze the variability of Hipparion primigenium in 4 Spanish localities, (2) study the new data from specimens found at La Roma 2 locality (Teruel, Spain; Alcalá, 1994), and (3) to compare the specimens from these localities with populations from other Spanish localities and localities in Çalta, Pavlodar, Eppelsheim, Höwenegg, Dürkheim, Vienna Basin, and Nikiti1.

MATERIAL AND METHODS

Material

This study concentrates on the Hipparion morphotype 1 of Alberdi (1989). Also included

within this group the material from the first Hipparion appeared in Eurasia, H. primigenium. The material studied comes from La Roma 2, Teruel, Spain (Alberdi and Alcalá, 1989-1990). These Hipparion remains belong to a robust, large-sized animal, and due to their dental morphology and skeletal structure, were assigned to H. primigenium by Alberdi and Alcalá (1989-90).

La Roma 2 is located between the villages of Peralejos and Alfambra, close to Masía de La Roma (1° 1' 10" W; 40° 30' 8" N). The stratigraphical section and the mammal assemblage are described in detail in Alcalá (1994) and van Dam (1997). The faunal association indicates a late Vallesian age (MN10, Mein, 1990; Mein et al., 1989-1990; de Bruijn et al., 1992; local zone J3, van Dam, 1997). The faunal list includes: Progonomys hispanicus, Huerzelerimys minor, cf. Democricetodon, Hispanomys peralensis, Hispanomys sp., Myomimus sp., Galerix sp., Desmanella sp., Prolagus crusafonti, Ictitheriinae indet., Lycyaena chaeretis, Microstonyx major, Tragoportax gaudryi, Aragoral mudejar, Micromeryx sp., Hipparion primigenium, Alicornops alfambrense, Aceratherium incisivum, Lartetotherium schleiermacheri, Proboscidea indet. (Adrover et al., 1982; Cerdeño, 1989; Alcalá et al., 1989-90; Cerdeño and Alcalá, 1989-90; van de Made et al., 1992; Alcalá, 1994; van Dam, 1997; Alcalá and Morales, 1997). La Roma 2 is the type locality of the monospecific genus Aragoral (type species Aragoral mudejar) and the species Alicornops alfambrense.

Material for comparison includes: Vallesian-Turolian forms like Hipparion primigenium koenigswaldi (Sondaar, 1961) from Nombrevilla; Hipparion primigenium primigenium (Alberdi, 1974) from Can Llobateres; Hipparion primigenium melendezi (Alberdi, 1974; similar to Hipparion concudense after Forstén, 1982, and referred to as Hipparion melendezi by Eisenmann, 1995) from Los Valles de Fuentidueña; Hipparion mediterraneum (Alberdi and Montoya, 1988) from Crevillente; Hipparion concudense (Pirlot, 1956) from Concu; and

a small to medium-sized form and a large form, both as of yet unnamed, from Santiga, a locality recently studied by Forstén (1997). Specimens analyzed from the Pliocene levels are from Villalba Alta Río 1 and Layna. These latter specimens were recently studied by Alberdi and Alcalá (1999) and identified as Hipparion fissurae Crusafont and Sondaar. Large-sized Hipparion rocinantis Hernández Pacheco are studied from the early Villafranchian of Villarroja. From the early Turolian (MN11) we include three possible species of Spanish Hipparion recovered from Puente Minero (Alberdi and Alcalá, 1989-90; Alcalá and Montoya, 1989-90; Alcalá, 1994) as well as Hipparion primigenium from Masia del Barbo (latest MN10).

From Central Europe and Asia, we analyzed remains from Eppelsheim (MTA data), Höwenegg and Dürkheim (Germany; Bernor et al., 1997; Bernor and Franzen, 1997); the Vienna Basin (Bernor et al., 1988); and Nikiti1 (Greece, Koufos, 2000); Pavlodar (Kazakhstan; Orlov, 1936), and Çalta (Turkey; Hipparion longipes Gromova) from both localities; and Hipparion crassum Gervais from Çalta only (MTA data; Heintz et al., 1975; Sen and Heintz, 1977), this last species was later assigned to Hipparion heintzi by Eisenmann and Sondaar (1998) (Fig. 1, Table 1).

The material from La Roma 2 was described in part by Alcalá (1992, 1994). Previously, Alberdi (1974) reported Hipparion material from Masía de La Roma 2 (Teruel, Spain) that showed many affinities with H. primigenium and H. concudense from Masía del Barbo and may be considered as an intermediate species between them. The material from La Roma 2 comes from the permanent collections of both the Museo Nacional de Ciencias Naturales and the Diputación General de Aragón.

Material remains from La Roma 2 - Upper teeth: a complete, flattened skull with right and left P²-M³ and anterior dentition (RO-2390). A right maxilla (P²-M³) (RO-2065), two right and

left series P^3-M^3 of the same individual (RO-171; RO-172; RO-173; RO-174; RO-175; RO-176; RO-177; RO-178; RO-179; RO-180. Isolated teeth: only a left M^{1-2} (RO-1413). Milk teeth: one left series D^2-D^3 (RO-126), one right series D^3-D^4 (RO-856), one right D^2 (RO-124), four rights and three left D^{3-4} (RO-113; RO-114; RO-118; RO-119; RO-121; RO-865-1; RO-865-2). Lower teeth: two mandibles with P_2-M_3 one left and one right (RO-1195; RO-1390), one left series M_1-M_2 (RO-187), and one right series $P_2-P_3-M_3$ broken (RO-115; RO-116; RO-117); isolated teeth: three left P_2 (RO-123; RO-376; RO-1081), four M_{1-2} (RO-120; RO-125; RO-1287; RO-2015), and one right M_3 (RO-115). Milk teeth: right mandible with D_2-D_4 and M_1 erupting (RO-9), one left series D_2-D_4 (RO-1406), two left and one right D_2-D_3 (RO-189; RO-862; RO-863), one left D_4 (RO-865) and one right D_4 (RO-864); and two petrosal bones (RO-1234; RO-1343).

Appendicular skeleton: a complete scapula and two fragment (RO-2290; RO-489; RO-25), 20 humeral distal fragments (10 left and 10 right: RO-14; RO-183; RO-285; RO-333; RO-337; RO-359; RO-487; RO-492; RO-556; RO-851; RO-1022; RO-1255; RO-1281; RO-1282; RO-1381; RO-1400; RO-1506; RO-1514; RO-2390; RO-2505), three complete left radii (RO-285; RO-487; RO-492) and 15 fragments (RO-24; RO-149; RO-201; RO-298; RO-334; RO-348; RO-490; RO-491; RO-555; RO-1035; RO-1144; RO-1221; RO-1235; RO-1336; RO-1416), 11 complete McIII (RO-288; RO-294; RO-551; RO-1087; RO-1131; RO-1164; RO-1186; RO-1193; RO-1511; RO-1576; RO-2425) and 13 fragments (RO-26; RO-28; RO-43; RO-79; RO-283; RO-335; RO-1054; RO-1058; RO-1130; RO-1136; RO-1168; RO-1194; RO-1321), 17 McII/IV (10 right and seven left: RO-504; RO-525; RO-632; RO-1039; RO-1083; RO-1109; RO-1182; RO-1183; RO-1192; RO-1230; RO-1279; RO-1436; RO-1528; RO-1531; RO-1541; RO-1544; RO-2429), two complete femora (RO-2291; RO-2294) and two fragments (RO-205; RO-1208), 21 tibiae (RO-44; RO-63; RO-71; RO-152; RO-168; RO-

264; RO-323; RO-330; RO-427; RO-468; RO-578; RO-849; RO-850; RO-1074; RO-1133; RO-1145; RO-1207; RO-1260; RO-1296; RO-1357; RO-2118), 17 complete calcanea (eight left and nine right: RO-20; RO-339; RO-498; RO-501; RO-582; RO-1021; RO-1044; RO-1117; RO-1316; RO-1350; RO-1398; RO-1446; RO-1516; RO-1557; RO-2113; RO-2146; RO-2246) and 16 fragments (RO-52; RO-58; RO-73; RO-128; RO-194; RO-304; RO-306; RO-495; RO-558; RO-1020; RO-1139; RO-1147; RO-1352; RO-1359; RO-1539; RO-1573), 34 complete astragali (15 right and 19 left: RO-31; RO-62; RO-67; RO-197; RO-200; RO-208; RO-305; RO-338; RO-413; RO-496; RO-500; RO-507; RO-512; RO-522; RO-619; RO-1001; RO-1048; RO-1051; RO-1096; RO-1106; RO-1146; RO-1165; RO-1184; RO-1233; RO-1248; RO-1309; RO-1310; RO-1351; RO-1353; RO-1371; RO-1428; RO-1560; RO-2147; RO-2153) and five fragmentes (RO-336; RO-1248; RO-2016; RO-2220; RO-2260), 17 complete MtIII (RO-277; RO-287; RO-289; RO-552; RO-580; RO-581; RO-848; RO-1023; RO-1080; RO-1280; RO-1291; RO-1324; RO-1572; RO-2028; RO-2185; RO-2430; RO-2770) and 27 fragments (RO-27; RO-61; RO-156; RO-192; RO-198; RO-206; RO-232; RO-237; RO-241; RO-260; RO-280; RO-282; RO-292; RO-326; RO-450; RO-530; RO-1140; RO-1180; RO-1295; RO-1328; RO-1339; RO-1372; RO-1379; RO-1383; RO-1447; RO-1558; RO-1574), 36 MtII/IV (17 right and 19 left: RO-547; RO-570; RO-571; RO-572; RO-608; RO-852; RO-853; RO-854; RO-855; RO-1014; RO-1038; RO-1071; RO-1085; RO-1086; RO-1121; RO-1155; RO-1181; RO-1125; RO-1209; RO-1257; RO-1263; RO-1267; RO-1273; RO-1385; RO-1417; RO-1431; RO-1535; RO-1552; RO-1554; RO-2111; RO-2145; RO-2187; RO-2188; RO-2261; RO-2460; RO-2493), four 1PhIII complete (RO-502; RO-1269; RO-1337; RO-2248) and one fragment (RO-515), three 2PhIII (RO-505; RO-510; RO-536), two 3PhIII complete (RO-1346; RO-2502); four right scaphoids (RO-1071; RO-1091; RO-1151; RO-1294), two magna (right and left: RO-511; RO-1368), five lunata (three

right and two left: RO-520; RO-1115; RO-1148; RO-1555; RO-2222), two hamata (one right and one left: RO-533; RO-1556), five pyramidals (three right and two left: RO-16; RO-540; RO-1153; RO-1229; RO-1498), two pisiforms (right and left: RO-523; RO-1369), three right trapezoids (RO-1312; RO-1509; RO-1556); 16 ectocuneiforms (seven right and nine left: RO-77; RO-235; RO-270; RO-531; RO-538; RO-560; RO-601; RO-864; RO-1060; RO-1149; RO-1259; RO-1340; RO-1407; RO-1512; RO-1549; RO-2151), 16 naviculars (nine right and seven left: RO-69; RO-207; RO-503; RO-509; RO-518; RO-585; RO-593; RO-866; RO-1095; RO-1112; RO-1137; RO-1233; RO-1306; RO-1430; RO-1526; RO-2148), 16 cuboids (eight right and eight left: RO-77; RO-81; RO-270; RO-514; RO-516; RO-528; RO-541; RO-602; RO-607; RO-1150; RO-1169; RO-1253; RO-1275; RO-1438; RO-1561; RO-1571), four small cuneiforms (RO-54; RO-1520; RO-1537; RO-1565); seven complete first lateral phalanges (RO-2156; RO-2503; RO-1006; RO-524; RO-542; RO-605; RO-1548), three complete second lateral phalanges (RO-544; RO-546; RO-1011), and one third lateral phalanx (RO-1366); two proximal sesamoids (RO-1298; RO-1341) and six vertebra (RO-860; RO-1064; RO-1196; RO-1197; RO-1211; RO-1494).

Methodology

The nomenclature and measurements follow the recommendations of the ‘Hipparion Conference’, New York, November 1981 (Eisenmann et al., 1988). We used morphological and morphometric characters, and the wear degree on upper and lower cheek teeth (i.e. germ to very worn teeth, I, II, III, IV, and V) proposed by Alberdi (1974: figs. 1 and 2) (see Fig. 2). Whenever possible, we include references to cranial and mandibular characters on the few specimens that were available. We calculated the hypsodonty index on teeth that were unworn or only slightly worn. This index is defined as the ratio between the height of the unworn

teeth divided by the mesio-distal length at 10 mm from crown base (Alberdi, 1974).

Dimensions of the teeth are analyzed in bivariate plot diagrams using the customary P^{3-4} , M^{1-2} , P_{3-4} , and M_{1-2} . We generated two bivariate plot diagrams to analyze the robustness and/or slenderness of the metapodials. One plot, following Bernor et al. (1990), juxtaposed the maximum length (McIII1 or MtIII1) versus the distal articular width (McIII11 or MtIII11). The second compared maximum length versus minimal breadth of the diaphysis (McIII3 or MtIII3). We performed univariate and multivariate analyses with the numerical data to establish size similarities. Metapodials, astragali, and first phalanges were analyzed using principal component analysis (PCA) and discriminant analysis (DA). We utilized principal component analysis to evaluate similarities and/or differences among La Roma 2 remains and to assess their relationship with remains from other localities. It is also important to bear in mind that results can vary according to the age of the individual, which can differ greatly from one population to another. After similar groups were identified based on the PCA, we performed a discriminant analysis (DA) following the Mahalanobis method to evaluate the PCA results. We also studied body mass variability among Hipparion populations following Alberdi et al. (1995). We estimated the body masses using first phalanx, Ph5 measurement ($r = 0.991$). Calculations were made using SPSS 11.0.

For several of the Hipparion populations, we compared the mean ($\bar{X}$), standard deviation (δ), and sample number (N) using a t-test of significance between sample means that acted as a t of STUDENT with $N1+N2-2$ degrees of freedom; $N1$ and $N2$ being the respective value of each contrasted mean.

Abbreviations

Apre: Anterior-prefossette; Dpre: Distal-prefossette ; Apof: Anterior-postfossette; Dpof:

Distal-postfossette; DPOF: dorsal preorbital fossa; HI: Hypsodonty index; L: length; SI: Slenderness index; W: width; 1PhIII, 2PhIII and 3PhIII: first, second and third phalanges of the third digit respectively; McIII and MtIII: metacarpal and metatarsal of the third digit respectively; DA: Discriminant Analysis; PCA: Principal Component Analysis; RO 2: La Roma 2; PM: Puente Minero; NOM: Nombrevilla; MB: Masía del Barbo; CA: Can Llobateres; LVF: Los Valles de Fuentidueña; CD: Concud (Cerro de la Garita); CR: Crevillente 2; SAN: Santiga; VAR1: Villalba Ata Río 1; LAY: Layna; VILL: Villarroya; HO: Höwenegg; EP: Eppelsheim; DÜRK: Dürkheim; VIENN: Vienna Basin; NIK 1: Nikiti 1; PAV: Pavlodar; ÇA: Çalta.

All dimensions are expressed in millimeters.

RESULTS

Morphological and univariate analysis

Morphological analysis of the La Roma 2 remains reveals similarities in skeletal structure among the Spanish samples grouped as “H. primigenium” -morphotype 1 of Alberdi 1989- (‘morphotypes’ sensu lato). However, some morphological and size differences exist among teeth samples. La Roma 2 and Puente Minero equids have similar occlusal tooth morphology, which differs from the morphology found H. primigenium from the other localities (Nombrevilla, Los Valles de Fuentidueña and Masía del Barbo in Spain, and Höwenegg and Vienna Basin in Central Europe). Equids from these latter localities tend to have a more complicated enamel pattern on the occlusal surface (Alberdi, 1974). The dental morphology of La Roma 2 is medium-complicated, and simpler in the lower teeth than in the upper ones. Prefossette folds are more numerous in the La Roma 2 sample than in the sample of Puente

Minero. The protocone shape is essentially oval-elongated (depending on wear degree and size of the tooth) in all the Spanish specimens. The lower dentition from La Roma 2 shows a simple morphology and is heavily covered with cement. The ectoflexid practically touches the linguaflexid in the molars from La Roma 2. In Puente Minero equids, the ectoflexid only touches the linguaflexid in the premolars.

We are able to establish two well-differentiated groups based on the comparison of the size of the upper and lower dental series. Remains from La Roma 2, Puente Minero, and Nombrevilla have longer dental series than specimens from Los Valles de Fuentidueña, Masía del Barbo, the Vienna Basin and Höwenegg. These differences are greater on the upper series than they are on the lower series. While Nombrevilla specimens have smaller premolars than La Roma 2 equids, both in the upper and lower dentition, molars of the Nombrevilla locality are larger than those of La Roma 2 and Puente Minero. H. primigenium of Los Valles de Fuentidueña has the smallest molars of all forms, which are similar in shape to those found in H. primigenium populations from Masía del Barbo and Höwenegg. The La Roma 2 hypsodonty index was calculated from only two available teeth (one P₃₋₄ and one M₁₋₂). The hypsodonty index is lower for La Roma 2 remains than it is for remains from Puente Minero (Table 2). Puente Minero is the most hypsodont of all forms studied. The hypsodonty index of Puente Minero was not only higher than that of Los Valles de Fuentidueña, but it was also higher than the index of the more robust equids from La Roma 2 and Nombrevilla (Table 2). The bivariate plot diagram of the dental measurements also indicates that La Roma 2 and Puente Minero specimens are larger in size than the specimens from other localities. Due to greater tooth length, the L/W ratios of both the lower and upper cheek teeth (at the same wear stage) are greatest for La Roma 2 and Puente Minero specimens. In comparison with equids from Nombrevilla, Los Valles de Fuentidueña, Masía del Barbo, Höwenegg and the Vienna

Basin, the postcranial skeletal remains of La Roma 2 and Puente Minero specimens are the largest.

Most of La Roma 2 metapodials are complete. Bivariate plots of McIII1 vs. McIII3 and McIII1 vs. McIII11 show that the bones from La Roma 2 are smaller than those from Puente Minero, but larger than those from Nombrevilla and Los Valles de Fuentidueña. Analysis of the MtIII yields similar results, but in this instance greater affinities between Los Valles de Fuentidueña and La Roma 2 are observed.

The gracility index indicates that the La Roma 2 form is more robust than forms from Puente Minero and Los Valles de Fuentidueña, and more slender than those from Nombrevilla, Höwenegg, Eppelsheim and the Vienna Basin (Table 3).

The length and the width of both the astragali and calcaneum are greatest in La Roma 2 and Puente Minero specimens.

1PhIII are scarce and very similar among localities. The most slender are the anterior 1PhIII from La Roma 2 and Puente Minero.

The paired comparison of the different bone parameters (McIII-MtIII-AST-CAL-1PhIII) means of t-test of significance between 2 sample means reveals a high degree of similarity between La Roma 2 and Puente Minero forms: McIII, $p \geq 0.01$ in parameter 1 and $p \geq 0.05$ in parameter 11; MtIII, $p \geq 0.05$ in parameter 7. Very similar results were obtained for the astragalus, calcaneum and 1PhIII (Table 4). The comparative analysis between remains from La Roma 2 and Los Valles de Fuentidueña shows significant difference of up to 99 percent ($p \geq 0.01$) in practically all bone parameters considered. Moreover, La Roma 2 remains were significantly different from those of Höwenegg, Eppelsheim, Dürkheim, the Vienna Basin and Nombrevilla for almost all analyzed parameters. There were only minor differences between La Roma 2 and Nikiti 1 (Table 4).

The morphological analysis of La Roma 2 remains suggests a strong, large-sized animal. In comparison to other remains from the Vallesian, certain characters of La Roma 2 forms are more primitive and less accentuated, such as the following features of the dental morphology (Fig. 2): shape of the protocone, presence of a protostylid, long tooth rows, presence of a small cuneiform facet, etc. In addition, the analysis of body mass following Alberdi et al. (1995) indicates that La Roma 2 forms were considerably larger than the other Vallesian forms of H. primigenium (Table 3).

Multivariate analysis

Principal component analysis (PCA)

Principal component analysis, based on skeletal measurements, permits us to identify two main groups on the basis of size (Fig. 3). The largest specimens are from La Roma 2, Puente Minero, Pavlodar, Çalta, and Villarroja. Within this group, the greatest affinities exist between La Roma 2 and Puente Minero. Generally, the second group consists of relatively smaller specimens from Los Valles de Fuentidueña, Concud, Santiga, Crevillente, Villalba Alta Río 1 and Layna. The McIII and MtIII of Höwenneg fall between the two previous groups, while there is a certain overlapping with respect to the 1PhIII. The metapodials most clearly identify the differences and similarities among samples. In the PCA of the McIII, the distal characters (McIII11, McIII12 and McIII13) and proximal articular breadth (McIII5 and McIII7) carry the most weight for the first component. The McIII PCA further differentiates two groups; one with a larger McIII and another with a shorter McIII. This analysis separates the samples into groups based on skeletal size. The minimal breadth of the McIII (McIII3) and the diameter of the anterior facet of the fourth carpal (McIII8) influence and carry the

most weight in the second component.

Although the results of the MtIII PCA are similar to those of the McIII, there is a wider range of intervals for La Roma 2 due to a greater quantity of remains (Fig. 3). In the first component, the most influential characters are the maximum diameter of the articular facet for the third tarsal (MtIII7), the minimum distal depth of the lateral condyle (MtIII13), and the maximum distal suparticular-breadth (MtIII10). In this component we observe, as we did with the McIII, two well-differentiated groups: (1) that with larger MtIII, and (2) that with shorter MtIII. The most robust MtIII is observed in Hipparion from La Roma 2, Höwenegg, Villarroya, Çalta and Pavlodar, while the most slender MtIII appears in the material from Los Valles de Fuentidueña, Layna, Villalba Alta Río 1, Concud, Crevillente, Santiga and Can Llobateres. The only notable difference between the PCA of the McIII and the MtIII is that in MtIII analysis, values for Puente Minero and Höwenegg remains are intermediate between the two differentiated groups (Fig. 3).

As we suspected, despite an abundance of astragali remains, the astragali PCA did not distinguish groups as clearly as the above-mentioned PCAs. Remains from La Roma 2, Puente Minero, Villarroya, Höwenegg, Çalta and Pavlodar form the larger groups, while smaller groups consist from the remains of Nombrevilla, Los Valles de Fuentidueña, Layna, Villalba Alta Río 1, Concud, Crevillente and Santiga. In this analysis, the characters that are most influential in the first component are: (AS2) the maximal diameter of the medial condyle, (AS5) the distal articular breadth and (AS6) distal articular depth. The maximal breadth (AS4) carries the most weight in the second component (Table 5). The first component clearly separates the first and second group of localities mentioned above (Fig. 3, Table 5). No differences among localities were detected in the principal component analysis of the calcaneum.

Discriminant analysis (DA)

DA was performed using the two main groups that had been established by principal component analysis. The first group, consisting of relatively small-sized remains, was divided into three subgroups: a) Los Valles de Fuentidueña + Can Llobateres + Santiga + Vienna Basin, b) Crevillente, and c) Concud. The second group, with larger remains, was divided into six subgroups: a) La Roma 2, b) Puente Minero, c) Höwenegg, d) Villarroya, e) Pavlodar + Çalta, f) Villalba Alta Río 1 + Layna. H. crassum remains were excluded from the analysis because they were clearly distinguishable from other Hipparion species.

In contrast with the abundance of postcranial remains, there is a scarcity of dental material; therefore, discriminant analysis of the dentition of La Roma 2 forms was not possible.

However, the teeth can be well distinguished among the different species by their morphological characters and size.

The DA carried out with the McIII clearly separates La Roma 2 specimens from the other localities with which it was grouped (Fig. 4). Discriminant analysis confirms the PCA results 96 percent of the time.

DA of the MtIII also separates the La Roma 2 form from the other samples of Hipparion primigenium (or Hippotherium primigenium sensu Bernor et al., 1996) studied. Nevertheless, La Roma 2 overlaps with some specimens from Villarroya and Puente Minero (Fig. 4).

The DA of the astragalus neither provide much information nor differentiate the groups. The DA of the calcanea defines the groups more clearly. In this analysis, La Roma 2 group overlaps with Puente Minero 18.8 percent of the time, while Santiga, Villarroya and Pavlodar remains are correctly identified 100 percent of the time.

In the DA of the 1PhIII, La Roma 2 overlaps with Puente Minero 50 percent of the time. This

broad overlapping of values is likely due to the difficulty in separating the anterior from the posterior phalanges.

INTERPRETATION AND DISCUSSIONS

With respect to the nomenclatorial situation of the species of Hipparion, Hiparionine tribu, we believe that Bernor's nomenclature disregards the global perspective and does not clarify the position of the genus Hipparion. The Hipparion genus is defined by 1) the presence of an isolated protocone and, 2) a tridactyl foot. In our opinion, the classification of Qiu et al. (1987), in which they grouped the species into several subgenera based on different assemblages of characters all considered belonging to Hipparion genus, is more elucidating and comparable to the groups established by Alberdi (1989) as morphotypes sensu lato. The classification of Bernor et al. (1996) is based on predominant character DPOF (10 characters from 16, see Bernor et al., 1988), consequently too much weight is given to the DPOF character on the whole. In our opinion, this is a variable character and its function is unknown. In addition, in localities where there are no skull remains, there are also no DPOF remains, thus making this systematic study impossible. Almost all Spanish localities lack skull remains.

From a philosophical point of view, we believe that including the Hipparion species into different genera obfuscates rather than clarifies the taxonomical situation of this group. The nomenclatorial history of hipparions species got more complicated the more and more and in our opinion it is necessary to find the similarities that representing global frame or estructure building of the mainly morfotype sensu lato of the Hipparion species.

Von Meyer 1829 names Equus primigenius and in 1933 describes three different varieties without changing the genus name from Equus: Equus caballus primigenius, Equus asinus

primigenius and Equus mulus primigenius. In 1832, Christol names a new genus of equids: Hipparion. Kaup (1833) describes a new genus: Hippotherium for a horse with the same characters as Hipparion. He includes the remains of Eppelsheim in a new species he calls gracile, to which he also assigns the material described by von Meyer (1833: 174) as Equus caballus primigenius and Equus mulus primigenius. Consequently, the priority correspond to Hipparion of Christol and, in fact, all hipparionine have the same characteristics of the genus that Christol used to define the genus Hipparion. Therefore, we maintain that Hippotherium does not have priority over Hipparion.

Morphological comparison and multivariate analysis reveal that La Roma 2 and Puente Minero equids share similarities that clearly differentiate them from the other H. primigenium populations studied. Affinities between La Roma 2 and Puente Minero remains are detected in overall dental morphology and in the structure of the McIII and MtIII. The equids from these two localities are clearly distinguished from the smaller-sized forms characteristic of Nombrevilla, Los Valles de Fuentidueña, Masía de Barbo and Höwenegg. It is important to note the differences in body mass of the Spanish Hipparion (Ortiz Jaureguizar and Alberdi, 2003). The La Roma 2 equid reach a mean weight of 349 kg, which following the methodology of Alberdi et al. (1995) could indicate a highly significant difference. Nevertheless, results of the analysis demonstrate that this second group of equids is not homogenous. We observe that the dental series of Nombrevilla are more similar in length to La Roma 2 and Puente Minero than they are to other populations within the second group of localities. Additionally, comparison of gracility indices reveals that the postcranial skeletons of Los Valles de Fuentidueña more closely resemble those of Puente Minero and La Roma 2 than those of other populations in the second group (Table 3). This suggests that the early Vallesian forms of H. primigenium were more robust, while those of late Vallesian were

taller and more slender. Despite all this, the La Roma Hipparion has some of the most extreme sizes of this group. The forms with the largest body mass were recorded in MN10 and MN16, while throughout their biochron, Hipparion remains fundamentally within the 100 to 200 Kg range. Similar weights are only found in the horse-like hipparions (Hipparion cabaloids: H. rocinantis, see Ortiz Jaureguizar and Alberdi, 2003). Therefore, the enormous weight difference between La Roma 2 and the other localities makes us inclined to separate the La Roma 2 form into a different species.

The other Spanish Hipparion samples are clearly differentiated. Except for the dimensions of the MtIII, Villalba Alta Río 1 and Layna forms are very similar (Alberdi and Alcalá, 1999) (Fig. 4). These equids correspond to Hipparion fissurae (see Alberdi, 1974; Alberdi and Alcalá, 1999). The distribution of dimensions varies greatly among Spanish Miocene Hipparion samples from Los Valles de Fuentidueña, Crevillente and Concud, but they are clearly separated by the size and morphology of the 1PhIII (Fig. 3). The DA of the McIII and MtIII from these three localities distinguishes them from each other 100 percent of the time. Therefore, we believe these three species should be correctly identified as: H. primigenium melendezi, H. mediterraneum, and H. concudense respectively. The form from Los Valles de Fuentidueña was identified as H. primigenium melendezi (Alberdi, 1974), while Forstén (1982) indicated that it could be considered conspecific with the typical H. concudense. Eisenmann (1984; 1995) regarded it as H. melendezi or possibly a synonym of H. sebastopolitanum (different from the ‘primigenium’ group). H. mediterraneum was identified at Crevillente 2 by Alberdi and Montoya (1988), and H. concudense was recognized at Concud (Pirlot, 1956; Sondaar, 1968; Forstén, 1979; Alberdi, 1974).

The Eastern European and Asian forms are also clearly differentiated. The large forms from both Pavlodar and Çalta are clearly identified as H. longipes (Gromova, 1952; Heintz et al.,

1975; Eisenmann and Sondaar, 1998).

The primary purpose of this analysis was to compare La Roma 2 remains with other H. primigenium forms. Although Hipparion remains from La Roma 2 vary greatly (possibly because of the large quantity of specimens), our multivariate analysis clearly distinguishes them from remains of Nombrevilla, Los Valles de Fuentidueña, Masia del Barbo, Höwenegg and from other Miocene groups.

Despite their similar size, the relationship between La Roma 2 and Puente Minero forms is not completely clear. While the astragali and first phalanges often overlap, analyses of McIII and MtIII maximal lengths clearly differentiate these localities (Figs. 3 and 4).

Both morphological and biometrical analyses show that Hipparion forms from La Roma 2 were robust and possessed various primitive characters (i.e., the presence of a protostylid, a small cuneiform facet, etc.). Comparative analysis suggests that Hipparion from La Roma 2 were larger than the classical H. primigenium from Central Europe and Spain (Eppelsheim, Höwenegg, the Vienna Basin, Nombrevilla and Los Valles de Fuentidueña localities). This may be a result of an adaptive response to the different types of environments.

Alcalá (1994) suggests small environmental differences existed between La Roma 2 and Puente Minero. He considered that La Roma 2 was relatively drier, colder and less vegetated than Puente Minero. Referring globally to the Teruel Basin he indicated that during Vallesian-Turolian levels (in which the two above mentioned localities correspond) environmental conditions were colder and more open than they were in localities situated in later Pliocene levels.

The Hipparion specimens from La Roma 2 show a slightly smaller hypsodonty than those from other Vallesian sites studied here (Nombrevilla, Los Valles de Fuentidueña, Masia del Barbo, Santiga and Eppelsheim) (Table 2). These differences, again, can be correlated with

the type of environment each inhabited. MacFadden and Shockey (1997) attempted to establish a correlation between high-crowned teeth and expansion of C4 biomass, while Cerling (1993) and Cerling et al. (1997) found no evidence of significant C4 biomass in the Mediterranean ecosystems during the last 20 Ma. We are currently analyzing carbon isotopic samples on mammalian teeth collected from Teruel (Spain) to test the results obtained by Cerling et al. (1997). This area, which can be characterized as a small, closed basin contains the La Roma 2 locality. The focus of the ongoing study is to determine the degree to which changes can be detected in a closed basin that in a much larger area would go unnoticed.

CONCLUSIONS

Due to a significant difference in body mass, we conclude that the La Roma 2 equid remains correspond to a new species of Hipparion and not to Hipparion primigenium (or Hippotherium primigenium sensu Bernor et al., 1996). It is further differentiated by (1) large cheek teeth with a plicate occlusal surface that decreases with wear, and (2) a robust, well-developed DPOF. La Roma 2 has longer metapodials, therefore making it more slender than the Höwenegg form. Its body mass also surpasses Höwenegg's by nearly 70 kg. Even though some of these differences may be attributable to paleoenvironmental conditions, we are given to separating La Roma 2 at the species level due to the weight difference.

Our analyses indicate that early Vallesian Hipparion are smaller in size and more robust than those originating in late Vallesian. Late Vallesian Hipparion, in which La Roma 2 forms are included, tend to be taller and more slender.

The principal differences between La Roma 2 and Puente Minero Hipparion are size differences; the weight of the La Roma 2 form being greater. The distal parts of the extremities, mainly the metapodials, are longer in the Puente Minero form, making it more

slender and better adapted to running. This character may be attributable to minor habitat differences. Puente Minero Hipparion may have inhabited areas where the substratum was slightly drier and harder, while the morphology of the metapodials and robust 1PhIII suggest that La Roma 2 Hipparion may have lived in more open environments, such as tropical savannas, with slightly harder substratum, under climatic conditions that were relatively colder and drier. To a certain degree this contradicts paleoecological analyses that suggest the landscape of La Roma 2 was both more open and more sparsely vegetated than other Turolian localities (Alcalá, 1994).

SYSTEMATIC PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848

Infraorder HIPPO MORPHA Wood, 1937

Superfamily EQUOIDEA Hay, 1902

Family EQUIDAE Hay, 1902

Genus HIPPARION Christol, 1832

HIPPARION LAROMAE New species

Synonymy list: Hipparion primigenium v. Meyer, in Alberdi and Alcalá, 1989-90.

Type: First phalanx of the third digit (RO-1269 in anterior view; Fig. 5e), from La Roma 2 (Teruel, Spain).

Paratype series: Right upper series P3-M3 (RO-180, RO-178, RO-177, RO-179, RO-173 in occlusal view; Fig. 5a); right lower series P2-M3 (RO-1195 in occlusal view; Fig. 5b), right McIII (RO-1131 in anterior view; Fig. 5c), left MtIII (RO-2430 in anterior view; Fig. 5d), 2PhIII (RO-510 in anterior view; Fig. 5f) and 3PhIII (RO-2502 in anterior view; Fig. 5g). All remains

from La Roma 2 (Teruel, Sapin)

Etymology: derives from La Roma (Teruel, Spain), the locality where the fossil was discovered.

Type locality: La Roma 2, Teruel, Spain.

Occurrence: Late Vallesian (Late Miocene).

Geographic distribution: Spain.

Material: specified above.

Diagnosis: robust Hipparion species, having a significantly greater body mass than H. primigenium; well developed DPOF; large upper and lower cheek teeth, with characteristic enamel “wrinkled” plications that decrease with wear. Robust metapodials that become more slender in comparison with other Vallesian populations.

Description: Incomplete and crushed skull, with only lateral face and right and left upper cheek teeth ($P^2 - M^3$). Symphysis and distal part of skull absent, only some isolated fragments of occipital condyles. Right side of skull with facial crest starting at P^4 mesostyle level. DPOF incomplete, orbit deformed and subquadrangular. Distance between both: 50 mm.

Upper teeth, wear stage 2 following Eisenmann et al. (1988) (II sensu Alberdi, 1974), with quadrangular premolars and molars (Fig. 5a). Protocone elongated-oval and sometimes connected to the protoloph in advanced stage of wear; hypocone has open distal postfossette in M^3 (RO-172, RO-173). Premolar parastyle larger than mesostyle, some specimens with small mark in parastyle. Pli caballin double, only one germinal premolar multiple (1/21). Fossette folds marked, showing deep-medium folding (varying from 1 to 5 at Apre / 6 to 10 at Dpre / 4 to 8 at Apof / 1 to 3 at Dpof; mode as follows: 4 / 7 / 6 / 1, respectively). Hypocone characteristic, hypoconal groove deep in little worn teeth, decreasing with wear (Fig. 5a). Lower cheek teeth also large-sized. Premolar row longer than molar row, with abundant cement.

Occlusal morphology not complicated, with oval-elongated double knot (type 1, in Eisenmann et al., 1988), wide linguaflexid, ectoflexid deep in molars, reaching linguaflexid. Molars with protostylid, sometimes isolated on surface, depending on wear degree, not present in the unique premolar series available (Fig. 5b). Hypsodonty index 2 in P_{3-4} and 2,23 in M_{1-2} (only observed on a specimen) (Table 2).

Appendicular skeleton remains well preserved, characterising large-sized animal with robust extremities. Humerus, radius, femur, and tibia indicate a strong, robust animal.

Metapodials long, wide, and robust (Fig. 5c and 5d). In McIII proximal articulation, angle between magnum and hamatum facets varies from 131° to 147° (12 specimens). Hamatum facet (McIII8 and McIII16) consists of two isolated subfacets, continuous in some specimens; only five specimens with contact point (or small appendix). Two facets for McII, one placed anteriorly and the other posteriorly, more or less rounded; sometimes both facets with contact point. Magnum facet slightly elongated on medial border (RO-1511, RO-1054). Supra-articular distal breadth variable. Gracility index McIII1 vs. McIII3: from 11.9 to 13.4 ($X = 12.5$), and McIII1 vs. McIII11: from 15.7 to 17.7 ($X = 17.2$).

Proximal articulations of MtIII with well delimited facets. Cuboid facet quadrangular and variable in size, and forms a wide angle with the facet of the big cuneiform. Small cuneiform facet reduced and sometimes curved upwards, but absent in three of 25 specimens (RO-1280, RO-1372, RO-1572). Two facets for MtIV, variable in size, anterior facet triangular and posterior rounded. Two facets for MtII, posterior subdivided. Large, variable cuneiform facet. Distal articulation with supra-articular breadth (measure 10) sometimes very large (RO-580, RO-1280), intermediate in RO-2185, reduced in RO-1023. Supra-articular fosette well pronounced, more than in metacarpals. Diaphysis cross-section greater antero-posteriorly than transversally, gracility index varies between 9.2 and 11.7 ($X = 10.8$) for MtIII1 vs. MtIII3,

and from 13.5 to 15.5 ($X = 14.4$) for MtIII1 vs. MtIII11.

Calcanea and astragali large. Calcaneum facet C of astragali (nomenclature from Eisenmann et al., 1988) vertically elongated and large in almost all specimens. This facet usually in contact with posterior part of large condyle of pulley (30 specimens), but in some cases with a small groove between them (nine specimens). Calcaneum facet B situated in two planes, sometimes continuous (16 specimens), sometimes isolated (five specimens). Navicular facet subtriangular and variable in size; muscular insertion with differential development, varying from absent to well developed in relation with the animal age. Cuboid facet forms angle with navicular face; navicular facet protrudes and flanges with facet C of calcaneum.

In calcaneum, internal facet of sustentaculum tali more or less elongated, isolated, and variable in size and articulates with astragalus facet C. Cuboid facet elongated and variable.

Tuber calcis strongly developed.

1PhIII, 2PhIII and 3PhIII wide and robust (Fig. 5e, 5f and 5g). Although anterior and posterior 1PhIII can be well distinguished following Prat (1957), we do not separate them because they are scarce and differences are unclear in the analyzed localities. Proximal part of anterior 1PhIII rounded and deeply grooved; posterior 1PhIII shorter than anterior and more robust, with quadrangular and wide proximal facet. In general, trigonum phalangis are not well marked. Anterior and posterior 2PhIII are more difficult to distinguish than 1PhIII.

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TEXT-FIGURE CAPTIONS

FIGURE 1. Geographic distribution of the localities. 1, Teruel area: La Roma 2 (RO2), Masia del Barbo (MB), Puente Minero (PM), Concud (CD) and Villalba Alta Río 1 (VAR1); 2, Nombrevilla (NOM); 3, Los Valles de Fuentidueña (LVF); 4, Layna (LAY); 5, Villarroya (VILL); 6, Crevillente (CRE); 7, Can Llobateres (CA) and Santiga (SAN); 8, Höwenegg (HO), Eppelsheim (EP) and Dürksheim (DÜRK); 9, Viena Basin (VIENN); 10, Nikiti 1 (NIK 1); 11 Çalta (ÇA); 12 Pavlodar (PAV).

FIGURE 2. Morphological characters of the upper (top) and lower (bottom) cheek teeth of Hipparion.

FIGURE 3. Principal component analysis of the distribution of 11 Spanish, 2 Central Europe and 3 Asiatic Hipparion localities using the McIII, MtIII, astragalus and 1PhIII. The parameters used follow the “Hipparion Conference” recommendations (Eisenmann et al., 1988).

FIGURE 4. Discriminant analysis based on the PCA results (see Fig. 2) of the McIII and MtIII of Spanish, Central Europe and Asiatic Hipparion localities . Specific names as in figure 3.

FIGURE 5. Hipparion laromae new sp. from La Roma 2 (Spain). –a. Right upper series P3-M3 in occlusal view (RO-180, RO-178, RO-177, RO-179, RO-173). –b. Right lower series P2-M3 in occlusal view (RO-1195). –c. Right McIII in anterior view (RO-1131). –d. Left MtIII in anterior view (RO-2430). –e. 1PhIII in anterior view (RO-1269). –f. 2PhIII in anterior view (RO-510). –g. 3PhIII in anterior view (RO-2502).

TABLE LEGENDS

TABLE 1. Material for comparasion used in this study. We translated the exact names from the literature.

TABLE 2. Hipsodonty index of the Spanish Hipparion. Abbreviations: P: premolars; M: molars; N: number of specimens; min.: minimum; max.: maximum; X: mean value. Nomenclature following Eisenmann et al (1988).

TABLE 3. Gracility index of the Spanish and Asian Hipparion, and body mass in Kg. Abbreviations and nomenclature same as in Table 1.

TABLE 4. Correlations coefficients between different parameters of the analyzed bones of Roma 2 locality versus Puente Minero, Los Valles de Fuentidueña and Nombrevilla (Spain), Eppelsheim (Alberdi, 1975), Höwenegg (Bernor et al., 1987), Dürkheim (Bernor and Franzen, 1997) and Nikiti 1 (Koufos, 2000). Probability: * = $p < 0.005$ and ** = $p < 0.001$.

TABLE 5. Characters that are most influential for component 1 and component 2 in the Principal Component Analysis (PCA).

NOTE: additional raw data are available on the website of the Journal of Paleontology .

Measurements following nomenclatorial recommendations as Eisenmann et al. (1988).

(Website address: <http://journalofpaleontology.org>)

Figure 1

Figure 3

Figure 4

- + Centroids
- × Çalta (*H. longipes*) + Pavlodar
- ▣ Villarroja
- ◆ Layna + Villalba Alta Rio 1
- × Vienna Basin + Santiga +
Los Valles de Fuentidueña
+ Can Llobateres
- ◊ Concud
- △ Puente Minero
- ◁ Crevillente
- Howenegg
- La Roma 2

1

2 cm

2

2 cm

3

4

5

6

7

2 cm

2 cm

Table 1

Level	Species	Locality	Country
Vallesian (MN9)	<i>Hipparion primigenium koenigwaldi</i>	Nombrevilla	Spain
Vallesian (MN9)	<i>Hipparion primigenium primigenium</i>	Can Llobateres	Spain
Vallesian (MN10)	<i>Hipparion primigenium melendezi</i>	Los Valles de Fuentidueña	Spain
Vallesian (MN10)	<i>Hipparion primigenium</i>	Masia del Barbo	Spain
Vallesian (MN10)	small to medium sized form (unnamed)	Santiga	Spain
Vallesian (MN10)	large form (unnamed)	Santiga	Spain
Turolian (MN11)	<i>Hipparion mediterraneum</i>	Crevillente	Spain
Turolian (MN11)	<i>Hipparion primigenium</i>	Puente Minero	Spain
Turolian (MN11)	<i>Hipparion gromovae</i>	Puente Minero	Spain
Turolian (MN11)	<i>Hipparion periafricanum</i>	Puente Minero	Spain
Turolian (MN12)	<i>Hipparion concudense</i>	Concud	Spain
Alfambrian (MN14)	<i>Hipparion fissurae</i>	Villalba Alta Río 1	Spain
Alfambrian (MN15)	<i>Hipparion fissurae</i>	Layna	Spain
Villafranchian (MN16)	<i>Hipparion rocinantis</i>	Villarroya	Spain
Valesian (MN9)	<i>Hippotherium primigenium</i>	Vienna Basin	Austria
Vallesian (MN9)	<i>Hippotherium primigenium</i>	Eppelsheim	Germany
Vallesian (MN9)	<i>Hippotherium primigenium</i>	Höwenegg	Germany
Vallesian (MN10)	<i>Hipparion primigenium</i>	Nikiti 1	Greece
Turolian (MN11)	<i>Hippotherium primigenium</i>	Dürkheim	Germany
Turolian (MN12)	<i>Hipparion longipes</i>	Pavlodar	Kazakhstan
Ruscinian (MN15)	<i>Hipparion crassum</i>	Çalta	Turkey
Ruscinian (MN15)	<i>Hipparion heintzi</i>	Çalta	Turkey

Table 2

HIPSODONT INDEX

	P ₃₋₄			M ₁₋₂			P ³⁻⁴			M ¹⁻²		
	min.	X	max.	min.	X	max.	min.	X	max.	min.	X	max.
Can Llobateres				(5)			(2)			(3)		
	-			2,21	2,39	2,49	1,80		2,12	2,23	2,38	2,50
Nombrevilla	(2)			(3)			(6)			(6)		
	2,04		2,08	2,20	2,39	2,59	1,70	1,81	2,05	2,26	2,47	2,54
Los Valles de Fuentidueña	(4)			(21)			(5)			(25)		
	2,13	2,24	2,40	2,12	2,45	2,76	2,04	2,09	2,17	1,96	2,47	2,78
La Roma	(1)			(1)								
	2			2,23			-			-		
Puente Minero	(2)											
	2,45		2,58	-			-			-		
Concud	(1)			(3)						(8)		
	2,26			2,65	2,69	2,75	-			2,31	2,47	2,84

Table 3

	MtIII1/MtIII3			McIII1/McIII3			MtIII1/MtIII11			McIII1/McIII11			Body mass Kg.
	(min.)	X	(máx.)	(min.)	X	(máx.)	(min.)	X	(máx.)	(min.)	X	(máx.)	
Can Llobateres	-	12,4	-	-	-	-	-	16,34	-	-	-	-	174
Nombrevilla	-	12,6	-	-	13,8	-	-	-	-	-	-	-	178
L.V.F.	9,4	10,3	10,8	10,6	11,3	12,3	13,9	14,43	14,77	-	15,23	-	170
Santiga	11,3	12	12,8	12,3	14,5	15,4	14,82	15,28	16,08	17,3	17,56	17,87	167
La Roma 2	9,2	10,8	11,7	11,9	12,5	13,4	13,47	14,44	15,52	15,73	17,19	17,74	349
Nikiti 1	-	12,14	-	-	15,6	-	-	15,07	-	-	17,9	-	272
Dürkheim	-	-	-	-	12,62	-	-	-	-	-	15,88	-	218
Howenegg	10,3	12,8	14,5	13,6	14,72	15,89	14,46	15,57	15,86	15,87	17,23	18,16	277
Crevillente	-	12,2	-	12,9	14,7	16,5	-	16,22	-	-	18,13	-	180
Puente Minero	9,8	10,5	11,5	11,2	11,6	11,8	13,11	13,59	14,44	14,28	14,73	15,46	249
Concud	10,7	11,8	12,7	11,2	12,7	14,5	14,14	14,83	15,35	13,92	15,92	16,66	160
Vienna Basin	11,67	12,21	12,91	13,44	13,9	14,3	14,97	15,47	15,97	16,57	17,8	19,37	229
Villalba Alta Rio 1	8,5	8,8	9	-	9,6	-	12,2	12,24	12,28	-	14,17	-	126
Layna	-	11,3	-	10,8	10,85	10,9	-	12	-	13,29	13,48	13,67	185
Villarroya	10,8	11,3	11,7	-	-	-	13,82	14,78	15,9	15,22	15,87	16,57	391
Pavlodar	9,5	9,5	9,5	10,6	10,9	11,3	12,9	12,95	13	14,32	14,58	14,94	231
Çalta (<i>H. crassum</i>)	12,4	13,5	14,5	15,6	16,6	17,8	18,18	18,32	19,1	22,72	22,96	23,09	320
Çalta (<i>H. longipes</i>)	9,3	9,6	9,8	-	-	-	11,63	11,92	12,21	-	-	-	301

Table 4

		<i>t</i> of Student							
		PM	LVF	NOM	HO	EPP	NIK 1	DÜRK	VIENN
RO2 (McIII)	1	-5,734*	5,84		9,467	11,617	8,425	3,729*	8,481
	7	-0,547*	9,015		7,062		1,529**	7,017	5,56
	11	2,254**	12,432		6,258		3,584*	8,319	3,902
RO2 (MtIII)	1	-1,372*	10,858	5,799	12,534	9,384	6,491		10,596
	7	2,127**	12,392		5,757		4,019	5,53	5,284
	11	0,802*	11,975		4,724		3,638	8,862	5,31
RO2 (As)	1	1,893*	11,031	8,401	9,181	10,839	5,57	10,788	7,282
	2	2,565**	18,806	8,135	5,635	8,159	5,193	8,314	5,144
	4	2,508**	16,363	13,639	0,808*	18,102	2,827*	5,214	2,431*
RO2 (Ca)	1	0,76*	11,368		6,842	3,118			2,876*
	2	0,509*	0,396*		-0,11*	1,218	0,637**	-0,001**	0,045**
	6	1,648*	8,023		4,264		3,824	5,191	3,189*
RO2 (1PhIII)	1	0,331*	-0,067	4,757	-0,067*	2,049*	-0,112**		1,077**
	3	0,259*	4,132		4,132		0,748**		3,288*
	5	2,166*	4,686	5,867	4,686	11,365	1,101**		1,82**

Table 5

Principal component of limb bones	Number of character	Eigen value	Principal component of limb bones	Number of character	Eigen value
Third metatarsal			Third metacarpal		
First	7	0,937	First	5	0,955
	13	0,93		13	0,95
	10	0,906		7	0,935
	11	0,904		11	0,892
	12	0,895		12	0,867
Second	1	0,423	Second	3	0,647
	6	0,289		8	0,421
	3	-0,273		10	0,379
	4	0,17		11	0,225
	14	0,144		14	0,133
Astragalus			First phalanx		
First	2	0,953	First	6	0,964
	5	0,914		4	0,956
	6	0,894		3	0,949
Second	4	0,425	Second	8	0,656
	5	0,138		3	0,091
	6	-0,209		4	0,038