New evidence of conspecificity between *Hipparion primigenium melendezi* Alberdi, 1974 from Los Valles de Fuentidueña (Segovia) and *Hipparion concudense concudense* Pirlot, 1956 from Concud (Teruel, Spain)

Nuevas evidencias de la coespecificidad entre Hipparion primigenium melendezi Alberdi, *1974 de Los Valles de Fuentidueña (Segovia) e* Hipparion concudense concudense *Pirlot, 1956 de Concud (Teruel, España)*

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ABSTRACT

This paper reports a morphological and biometric comparison of *Hipparion primigenium melendezi* from Los Valles de Fuentidueña (Segovia) and *Hipparion concudense concudense* from Concud (Teruel) to investigate their possible conspecificity. Comparisons with other Spanish (La Roma 2, Puente Minero, Milagros, Las Casiones and Venta del Moro) and Eurasian (Höwenegg, Germany; Pavlodar, Kazakhstan [small form]) material were also made. Based on their morphology, and on bivariate and multivariate analysis to establish size similarities, the *Hipparion* remains from Los Valles de Fuentidueña and Concud were both determined to belong to *Hipparion concudense*. However, differences in both dental morphology and limb slenderness could suggest differences at the subspecific level.

Keywords: Equidae, *Hipparion*, Multivariate analysis, Late Miocene, Los Valles de Fuentidueña, Concud, Spain.

RESUMEN

En este trabajo se realiza una comparación morfológica y biométrica de *Hipparion primigenium melendezi* de Los Valles de Fuentidueña (Segovia) e *Hipparion concudense concudense* de Concud (Teruel) con el fin de revisar la posible coespecifidad entre ellas. Se han realizado comparaciones con material de otras localidades españolas (La Roma 2, Puente Minero, Milagros, Las Casiones y Venta del Moro) y Euroasiáticas (Höwenegg, Germany; Pavlodar, Kazakhstan [forma pequeña]). A partir de los caracteres morfológicos y los análisis bivariantes y multivariantes de los restos de *Hipparion* de ambas localidades y su comparación con los restos de otras localidades españolas y euroasiáticas se confirma la relación coespecifica entre ambas especies de *Hipparion*. Sin embargo, tanto las diferencias encontradas en la morfología dental como en la gracilidad de sus metápodos podrían sugerir diferencias a nivel subespecífico.

Palabras clave: Equidae, *Hipparion*, Análisis multivariante, Mioceno superior, Los Valles de Fuentidueña, Concud, España.

Introduction

The genus *Hipparion* is recorded in Eurasia from the early Vallesian to the early Villafranchian (late Miocene-late Pliocene, *sensu* Bonadonna & Alber-

di, 1987). Many early Vallesian species and subspecies were proposed, but most were later grouped into the species *H. primigenium* (Alberdi, 1974; Forsten, 1968). During the Turolian, the genus diversified widely throughout Eurasia. Size reduc-

tion of the medium-sized species *H. mediterraneum* and *H. concudense*, among others, led to the appearance of very small taxa such as *H. matthewi* and *H. periafricanum*.

The abundant Eurasian record of Vallesian and Turolian *Hipparion* gave rise to a great proliferation of taxonomic names that Forsten (1968) tried to synthesize using statistical methods. Later, using other statistical methods that combined morphological and biometric features, Alberdi (1974) set limits to Forsten's reduced systematics. Alberdi (1989) then went on to establish six morphotypes *sensu lato* in an attempt to unify the Eurasian and African *Hipparion* species appearing from the early Vallesian to the early Villafranchian. A number of authors have recently proposed these species be assigned to different genera and subgenera. Based on *Hipparion* remains found in China, Qiu *et al.* (1987) proposed grouping a number of Chinese species into different subgenera. Bernor *et al.* (1996, p. 333) placed all species of the genus *Hipparion* into the Hipparionini tribe, and grouped them into several genera or group complexes. Following Bernor *et al.* (1996) these include four supra-specific evolutionary complexes: the *Hippotherium primigenium*-Complex (with 13 taxa), the *Hipparion* s.s.- Group (six taxa), the *Cremohipparion*-Group (seven taxa), and the "*Plesiohipparion*"- Group (six taxa) belonging to the "*Sivalhippus*" Complex.

The nomenclature of *Hipparion* species is, however, becoming more and more complicated, a likely consequence of the philosophical differences in taxonomic meaning employed when comparing genera and species. The examination of the morphological features of many remains of *Hipparion* could, however, provide a global framework for defining the morphotype of *Hipparion sensu lato* (see Pesquero *et al.*, 2006, 2007).

The Turolian mammal site of Concud, in the northeast of the Teruel Province, Spain, is home to accumulations of vertebrate bones, the richness, diversity, and special features of which render the faunal assemblages recorded a reference for studies on Eurasian Neogene mammals. The site is the type-locality of *Canis cipio* (the oldest canid - Caninae *sensu stricto* - of the fossil record), of the bovid *Hispanodorcas torrubiae*, of *Turiacemas concudensis* (one of the oldest three-tined deer), and of the tridactyl equid *Hipparion concudense*. The fossiliferous level was deposited during the progressive transition between alluvial and shallow lake envi-

ronments. The mammal assemblages, similar to that found at Los Mansuetos locality, typify the middle Turolian (MN12) (Alcalá, 1998; Alcalá *et al.*, 1999; Pesquero *et al.*, 2010).

The Vallesian mammal site of Los Valles de Fuentidueña (Segovia Province), located in the upper part of the Duero Basin, reflects a pond system, the bone material of which was provided via a small alluvial fan coming from a Cretaceous calcareous palaeorelief (Hoyos *et al.*, 1981). This site contains the remains of a diversified fauna of micro- and macromammals, and is highly important for the characterization of the early Vallesian of the Duero Basin as it allows correlations with faunal assemblages of the same age in other basins. The analysis of this fauna indicates that, during the late Aragonian and early Vallesian, the Duero Basin fauna was similar to that of the Calatayud-Teruel Basin. In fact, both can be included within a single biogeographic unit. This unit, however, shows clear differences to the faunal composition of the Vallés-Penedés Basin, which is more similar to German and French basins of the same age (Alberdi *et al.*, 1981).

The main aim of this paper is to review the Los Valles de Fuentidueña and Concud remains of *Hipparion*, checking against the work of Forsten (1982), who indicated a conspecific relationship between *Hipparion concudense* (Pirlot, 1956) from Concud and *Hipparion primigenium melendezi* (Alberdi, 1974) from Los Valles de Fuentidueña, referred to by Eisenmann (1995) as *Hipparion melendezi*.

Material and Methods

Material

The studied material comes from the Spanish fossil sites of Los Valles de Fuentidueña (Segovia) (Alberdi, 1974) and Concud (Teruel) (Alberdi, 1974; Alcalá, 1994) (fig. 1). This material is stored at the *Museo Nacional de Ciencias Naturales,* CSIC, Madrid.

Specimens from Los Valles de Fuentidueña. Upper teeth: 64 P3-4, 128 M1-2. Lower teeth: 66 p3-4, 107 m1-2. Appendicular skeleton: one distal humeral fragment, two proximal radial fragments, 35 McIII (ten complete), seven calcanei, 28 astragali, 49 MtIII (15 complete), seven 1PhIII, 13 first lateral phalanges, 39 2PhIII, 13 second lateral phalanges, one 3PhIII, 16 scaphoids, one magnum, six lunata, six pisiforms, six ectocuneiforms, 12 naviculars, and seven cuboids.

Specimens from Concud. Upper teeth: 128 P3-4, 121 M1-2. Lower teeth: 97 p3-4, 102 m1-2. Appendicular skeleton: 23 humeral fragments, 52 radial fragments, eight femur fragments,

Figure 1.—Geographic location of the sites - 1, Teruel area: Concud (CD), La Roma 2 (RO2), Puente Minero (PM), Milagros (ML), and Las Casiones (KS); 2, Venta del Moro (VM); 3, Los Valles de Fuentidueña (LVF); 4, Höwenegg (HO); 5, Pavlodar (PAV).

22 McIII (seven complete), one tibia and 24 fragments, 12 calcanei, 45 astragali, 22 MtIII (ten complete), 50 1PhIII, 86 first lateral phalanges, 94 2PhIII, 20 second lateral phalanges, 12 3PhIII, three third lateral phalanges, 40 scaphoid, 50 magna, 49 lunata, 14 pisiforms, 18 trapezoids, 66 ectocuneiforms, 83 naviculars, and 66 cuboids.

Material for comparison. This study compars the specimens from these localities with material from other Spanish sites in order to increase the reference framework and render multivariate analysis for establishing size limits more reliable. The Vallesian-Turolian forms from these sites include *Hipparion laromae* from la Roma 2 (Pesquero *et al*., 2006), *Hipparion laromae* from Puente Minero (Pesquero *et al*., 2011), *Hipparion matthewi* from Milagros; *Hipparion matthewi* from Las Casiones; and *Hipparion matthewi* from Venta del Moro (Pesquero, 2003; Pesquero *et al*., 2007). From Central Europe and Asia, specimens of *Hipparion primigenium* (or *Hippotherium*

primigenium sensu Bernor *et al*., 1996) from Höwenegg (Germany; Bernor *et al*., 1997; plus raw data kindly sent by Bernor) and *Hipparion matthewi* from Pavlodar, Kazakhstan (Orlov, 1936; plus our own data) were examined.

Methodology

The morphological and morphometric traits (fig. 2) proposed by Alberdi (1974) were examined. The hypsodonty index was calculated for unworn or only slightly worn teeth. This index is defined as the ratio between the mesio-distal length (2) and the height of the unworn teeth (1) (Eisenmann *et al*., 1988: Figs. 6-8). The dimensions of the teeth are presented in a bivariate plot using the customary P3-4, M1-2, p3-4, and m1-2 teeth. Two bivariate plots were generated to analyse the robustness or gra-
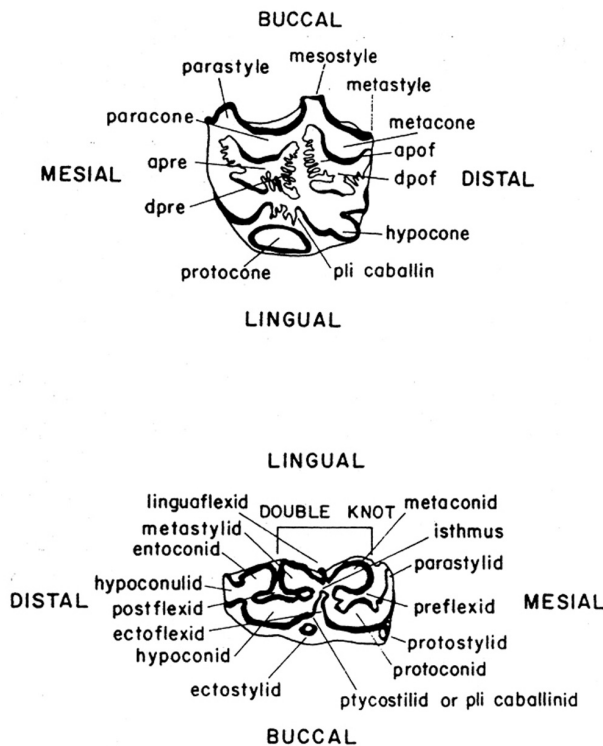
Figure 2.—Morphological characteristics of the upper (top) and lower (bottom) cheek teeth of *Hipparion*.

cility of the metapodials. One plot, produced according to Bernor *et al.* (1990), juxtaposed the maximum length (McIII1 or MtIII1) against the distal articular breadth (McIII11 or MtIII11). The second compared the maximum length against the minimal breadth of the diaphysis (McIII3 or MtIII3). Bivariate and multivariate analyses were performed with the numerical data to establish size similarities. Metapodials, astragali, calcanei and first phalanges were analysed using principal component analysis (PCA) to evaluate size similarities and/or differences among the different *Hipparion* remains. Groups were identified based on the outcome of PCA, and discriminant analysis (DA) then preformed using the Mahalanobis method with the aim of maximizing the separation between them. This determines whether the centroids differ significantly or not, and often identifies specimens not included in the original PCA. Body masses were estimated using the first phalanx, the Ph5 measurement (r = 0.991), and McIII and MCIII13 measurements (r = 0.982), according to Alberdi *et al.* (1995). Calculations were made using SPSS 15.0.

The nomenclature and measurements follow the recommendations of the "*Hipparion* Conference", New York, November 1981 (Eisenmann *et al.*, 1988). All dimensions are expressed in millimetres.

Abbreviations

P/M: upper cheek teeth; p/m lower cheek teeth; L: length; B: breadth; HI: hypsodonty index; Apre: anterior-prefossette;

Dpre: distal-prefossette; Apof: anteriorpostfossette; Dpof: distal-postfossette; McIII and MtIII: metacarpal and metatarsal of the third digit respectively; GI: gracility index; 1PhIII, 2PhIII and 3PhIII: first, second and third phalanges of the third digit respectively; PCA: principal components analysis; DA: discriminant analysis.

Localities: CD: Concud; HO: Höwenegg; KS: Las Casiones; LVF: Los Valles de Fuentidueña; ML: Milagros; PAV: Pavlodar; PM: Puente Minero; RO2: La Roma 2; VM: Venta del Moro.

Systematic Palaeontology

Order PERISSODACTYLA Owen, 1848
Infraorder HIPPOMORPHA Wood, 1937
Superfamily EQUOIDEA Gray, 1821
Family EQUIDAE Gray, 1821
Genus HIPPARION Christol, 1832
Hipparion concudense Pirlot, 1956
Hipparion concudense melendezi Alberdi, 1974

Synonymy list:
1926 *Hipparion gracile* Kaup; Royo Gómez.
1944 *Hipparion gracile* Kaup; Meléndez, Crusafont and Villalta.
1944 *Hipparion gracile* Kaup; Almela, Bataller and Sampelayo.
1948 *Hipparion gracile* Kaup; Villalta and Crusafont.
1952 *Hipparion gracile* Kaup; Crusafont.
1968 *Hipparion* sp. Crusafont, Aguirre and García.
1974 *Hipparion primigenium melendezi* Alberdi; Alberdi.

Holotype: Right MtIII (MNCN-30654; ancient number collection: LVF-15019 and H- 988), stored at MNCN Collection. Referred to in Alberdi (1974: Lam 2-3 and Fig. 7).

Type locality: Los Valles de Fuentidueña, Segovia, Spain.

Stratigraphic distribution: Vallesian (late Miocene).

Geographic distribution: Spain.

Material: Specified in the "Materials and Methods" sections.

Description: The protocone shape is oval in premolars and molars, sometimes connected to the protoloph in stage of wear II in P2 and in stage of wear III in P3-4 and M1-2. In M1-2, the fossette folds show medium folding varying from 0 to 7 at Apre, 2-11 at Dpre, 2-7 at Apof, and 0-3 at Dpof. The modes are 2 plus 3, 7, 5, and 1 respectively. In P3-4, the fossette folds show medium folding varying from 0 to 3 at Apre, 3-10 at Dpre, 1-8 at Apof, and 0-3 at Dpof. The modes are 1, 6, 3, and 1 respectively. The pli caballin varies between 1 and 4, while the mode for premolars is 2 and for molars is 1. Hypsodonty index 2.1 in P3-4 and 2.5 in M1-2. In the lower cheek teeth the enamel is complex. Protostylid isolated on occlusal surface of unworn teeth, only joined to protoconid in stages of wear III. Hypsodonty index 2.2 in p3-4 and 2.4 in m1-2.

Postcranial remains are medium-sized and slender. Metapodials are elongated and slender. In McIII proximal articulation, the angle between the magnum and unciform facets varies from 124º to 134º. The gracility index of McIII1/McIII3 varies from 10.6 to12.3 (X = 11.3); that of McIII1/McIII11 is 15.2 (only one specimen was available).

Table 1.—**Hypsodonty index of Spanish *Hipparion*. N = number of specimens; Sd = standard deviation; X = mean**

	H. laromae (RO2)			*H. laromae* (PM)			*H. primigenium* (NO)			*Hipparion* (LVF)		
	N	Sd	X	N	Sd	X	N	Sd	X	N	Sd	X
P3-4	-	-	-	(2)	0.13	2.4	(6)	0.14	1.8	(5)	0.08	2.1
M1-2	-	-	-	(2)	0.08	2.6	(6)	0.14	2.5	(25)	0.14	2.5
p3-4	(1)	-	2	(2)	0.09	2.5	(2)	0.11	2.1	(4)	0.06	2.2
m1-2	(1)	-	2.2	(2)	0.04	2.6	(3)	0.1	2.4	(21)	0.16	2.4

	Hipparion (CD)			*H. matthewi* (VM)			*H. matthewi* (KS)			*H. matthewi* (ARQ)		
	N	Sd	X	N	Sd	X	N	Sd	X	N	Sd	X
P3-4	(13)	0.13	2.5	(1)	-	2.5	(3)	0.11	2.5	(3)	0.1	2.7
M1-2	(19)	0.12	2.6	(9)	0.04	2.4	(17)	0.16	2.7	(10)	0.11	2.8
p3-4	(16)	0.09	2.4	(1)	-	2.5	(2)	0.16	2.3	(1)	-	2.7
m1-2	(19)	0.12	2.6	(5)	0.16	2.7	(14)	0.18	2.7	(3)	0.05	2.8

Proximal articulation surface of MtIII shows a well developed cuboid facet. A small cuneiform facet is present in two specimens (four in total). Gracility index of MtIII1/MtIII3 varies from 9.4 to10.8 (X = 10.3); that of MtIII1/MtIII11 varies from 13.9 to 14.8 (X = 14.4).

Hipparion concudense concudense Pirlot, 1956

Synonymy list:
1850. *Hippotherium gracile* Kaup; Ezquerra del Bayo.
1852. *Hipparion prostylum* Gervais; Gervais.
1885. *Hipparion gracile* Kaup; Cortazar.
1903. *Hipparion gracile* Kaup; Woodward.
1914. *Hipparion gracile* Kaup; Hernández-Pacheco.
1947. *Hipparion gracile* Kaup; Villalta and Crusafont.
1952. *Hipparion mediterraneum* Roth & Wagner, not Hensel; Crusafont.
1954. *Hipparion mediterraneum* Roth & Wagner, not Hensel; Crusafont and Truyols.

Holotype: Not defined

Lectotype: Cheek tooth row (P40-1960) stored at IPPS. Referred to in Sondaar (1961: p. 229, Fig. 7a, Lam. IC).

Type locality: Concud, Teruel, Spain.

Stratigraphic distribution: Turolian (late Miocene).

Geographic distribution: Spain.

Material: Specified in the "Materials and Methods" sections.

Description: The protocone shape is oval, becoming quadrangular with wear. Sometimes connected to the protoloph in advanced stages of wear. M1-2 show deep-medium fossette folds varying from 1 to 6 at Apre, 2-12 at Dpre, 1-10 at Apof, and 0-4 at Dpof. The modes are 4, 6 plus 7, 5, and 1 respectively. In P3-4 the fossette folds vary from 0 to 9 at Apre, 3-14 at Dpre, 1-9 at Apof, and 0-4 at Dpof. The modes are 1, 7, 5, and 1 respectively. The pli caballin varies between 1 and 5, while the mode for both premolars and molars is 1. Hypsodonty index 2.5 in P3-4 and 2.6 in M1-2.

Lower cheek teeth are medium-sized. Occlusal morphology not complicated. Molars with a protostylid isolated on occlusal surface in unworn teeth, only joined to protoconid in stage of wear I in molars and II in premolars. Hypsodonty index 2.4 in p3-4 and 2.6 in m1-2.

Appendicular skeleton remains well preserved, characterizing an animal of medium size. In McIII proximal articulation, the angle between the magnum and unciform facets is 130º. The gracility index of McIII1/McIII3 varies from 11.2 to14.5 (X = 12.7); that of McIII1/McIII11 varies from 13.9 to 16.7 (X = 15.9). In MtIII, cuboid facet not well developed. Gracility index of MtIII1/MtIII3 varies from 10.7 to12.7 (X = 11.8); that of MtIII1/MtIII11 varies from 14.1 to 15.3 (X = 14.8).

Results

Morphological and univariate analysis

Morphological analysis revealed similarities in skeletal structure between the *Hipparion* remains from LVF and CD. Both show similar occlusal tooth morphology, although the enamel is more complicated in the LVF lower cheek teeth. *Hipparion* from LVF differs from *H. primigenium* from Nombrevilla in Spain and HO in Central Europe (Pesquero *et al.*, 2006), which tend to have a more complicated enamel pattern on the occlusal surface (Alberdi, 1974).

The hypsodonty index indicates that, in general, the teeth of the CD form are somewhat more hypsodont than those from LVF (table 1), and that both CD and LVF teeth are more hypsodont than those of either *H. primigenium* from Nombrevilla (Pesquero *et al.*, 2006) or *H. laromae* from RO2, and similar to those of *H. laromae* from PM.

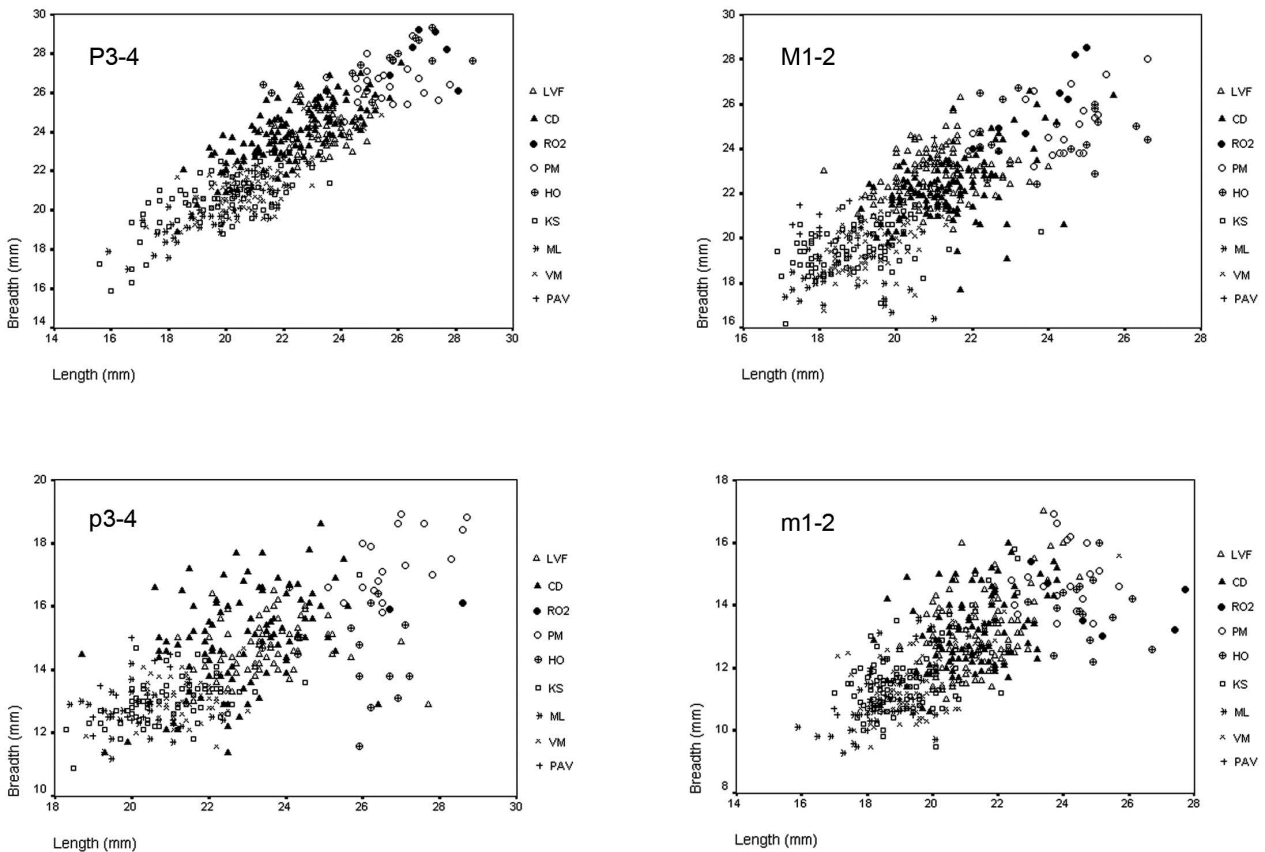The bivariate plot of the dental measurements indicates that the remains of *Hipparion* from LVF

Figure 3.—Occlusal length vs. occlusal breadth plotted for upper and lower cheek teeth (P3-4, M1-2, p3-4, m1-2) of Spanish and Eurasian *Hipparion* material.

clearly fall within the distribution of the CD remains. In both forms the length and breadth of the lower and upper cheek teeth are similar. The teeth of *Hipparion* from CD and LVF are larger than those of *H. matthewi* from KS, ML, VM, and PAV and clearly rest outside of the distribution of *H. primigenium* from HO and *H. laromae* from RO2 and PM (fig. 3).

The bivariate plots for McIII and MtIII indicate differences between the LVF and CD *Hipparion* remains and those from the other sites (fig. 4). The McIII from LVF and CD are longer than those of *H. matthewi* from KS, ML, VM, and PAV, and similar to that of *H. primigenium* from HO. Nevertheless, the diaphysis breadth of the LVF and CD forms is larger than that of *H. matthewi* from VM and smaller than that of *H. primigenium* from HO, this is, the McIII from LVF and CD are slender than those from HO. Only one McIII from CD is similar in length and breadth to those from HO. The MtIII of LVF and CD forms clearly lie outside the distribution of the *H. matthewi* and *H. laromae* remains. In both Spanish forms the length of the MtIII is similar, but the breadth is wider in CD metatarsals than in the LVF samples and closer to that of *H. primigenium* from HO, although the latter has greater length.

The gracility index indicates the LVF specimens to be more slender than those of CD. Both forms are more slender than *H. primigenium* from HO and more robust than *H. matthewi* from KS, ML, VM, and PAV (table 2).

The analysis of body mass following the methodology of Alberdi *et al*. (1995) indicated the LVF and CD forms to be of similar weight, while both are considerably smaller than *H. laromae* from RO2 and PM or *H. primigenium* from HO, but larger than *H. matthewi* from KS, ML, and VM.

Multivariate analysis

Principal component analysis of the skeletal measurements identified four main groups based on size
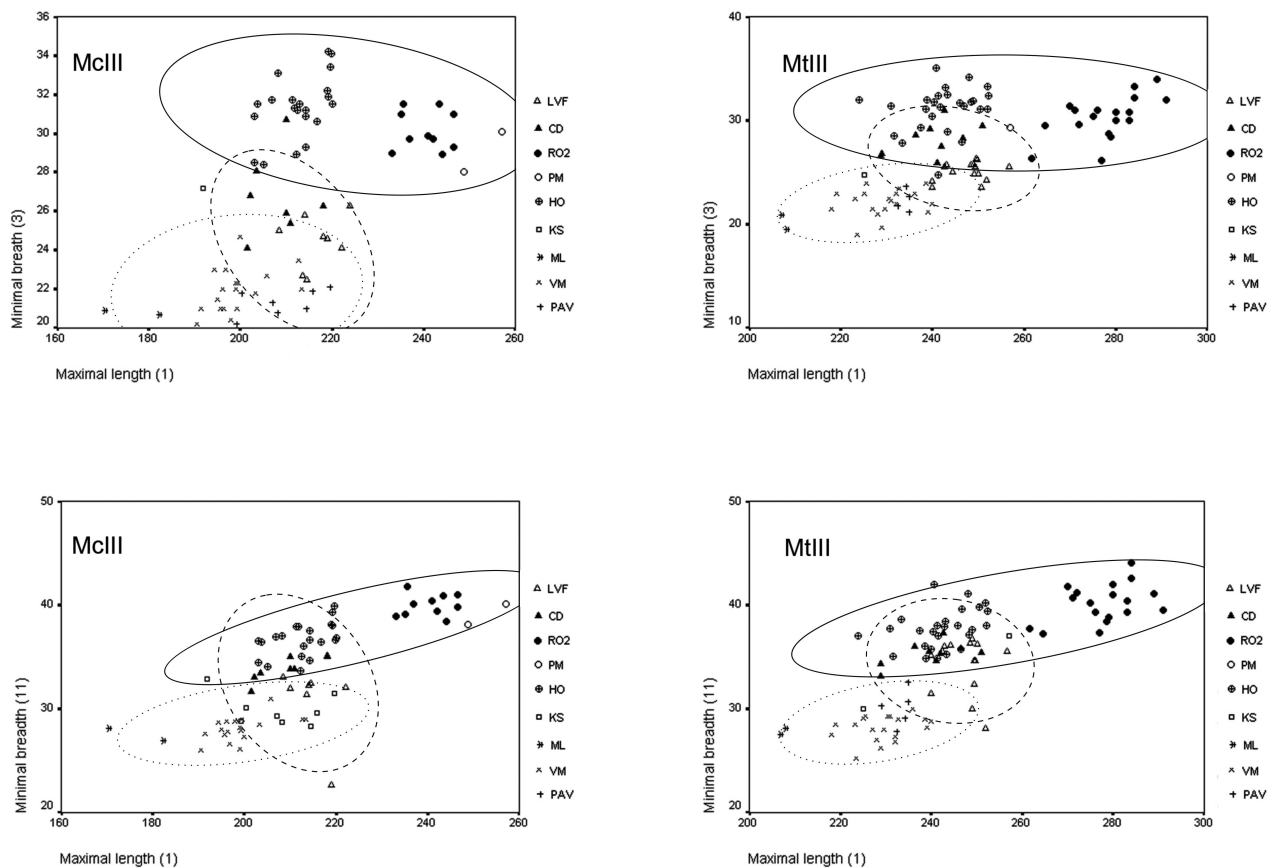
Figure 4.—Scatter diagram of McIII and MtIII (dimension 1 vs. dimension 3, and dimension 1 vs. dimension 11) of Spanish, and Eurasian *Hipparion* material.

Table 2.—**Gracility index and body mass estimation of Spanish, European, and Asian *Hipparion*. Abbreviations as in Table 1**

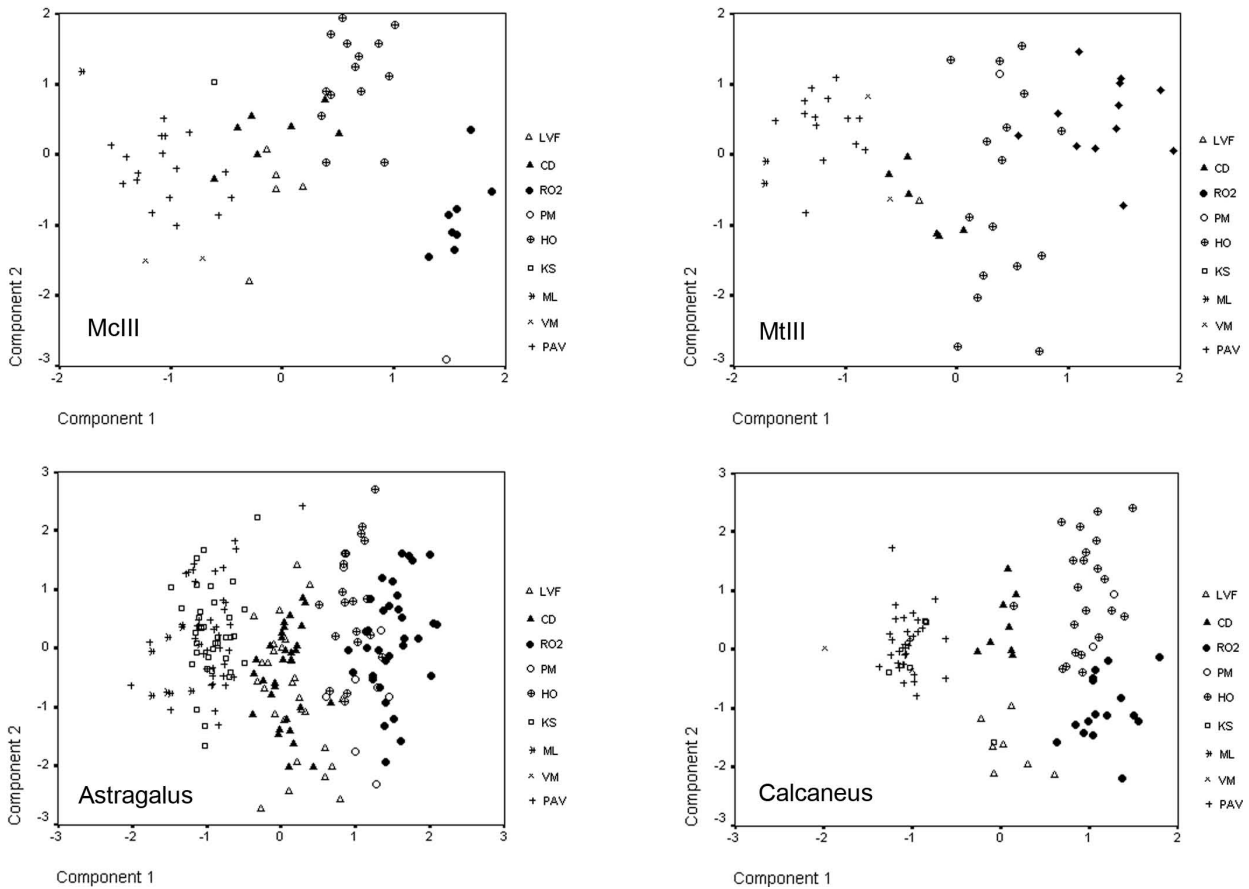| | MtIII1/MtIII3 | | | McIII1/McIII3 | | | MtIII1/MtIII11 | | | McIII1/McIII11 | | | Body mass (Kg.) | |
| | | | | | | | | | | | | | 1FII | McIII |
	(min.)	X	(max.)	(min.)	X	(max.)	(min.)	X	(max.)	(min.)	X	(max.)	(5)	(13)
Puente Minero														
(*H. laromae*)	-	11.4	-	11.3	11.5	11.7	-	14.4	-	15.3	15.5	15.6	331	338
La Roma 2 (*H. laromae*)	9.2	10.8	11.7	11.9	12.5	13.4	13.5	14.4	15.5	15.7	17.2	17.7	349	328
Howenegg														
(*H, primigenium*)	10.3	12.8	14.5	13.6	14.7	15.89	14.5	15.6	15.9	15.9	17.2	18.2	277	236
Nombrevilla														
(*H. primigenium*)	-	12.6	-	-	13.8	-	-	-	-	-	-	-	178	-
L.V.F.	9.4	10.3	10.8	10.6	11.3	12.3	13.9	14.4	14.8	-	15.2	-	170	186
Concud	10.7	11.8	12.7	11.2	12.7	14.5	14.1	14.8	15.3	13.9	15.9	16.7	160	178
Venta del Moro														
(*H. matthewi*)	9	9.5	10.1	9.8	10.2	10.8	12	12.8	13.9	13.2	14.1	15	111	123
Las Casiones														
(*H. matthewi*)	-	11	-	-	14.2	-	-	13.3	-	-	17.1	-	117	117
Milagros (*H. matthewi*)	9.4	9.7	10.1	11.3	11.8	12.2	13.3	13.4	13.5	14.7	15.6	16.5	75	114
Pavlodar (*H. matthewi*)	9.5	9.5	9.5	10.6	10.9	11.3	12.9	12.9	13	14.3	14.6	14.9	121	133

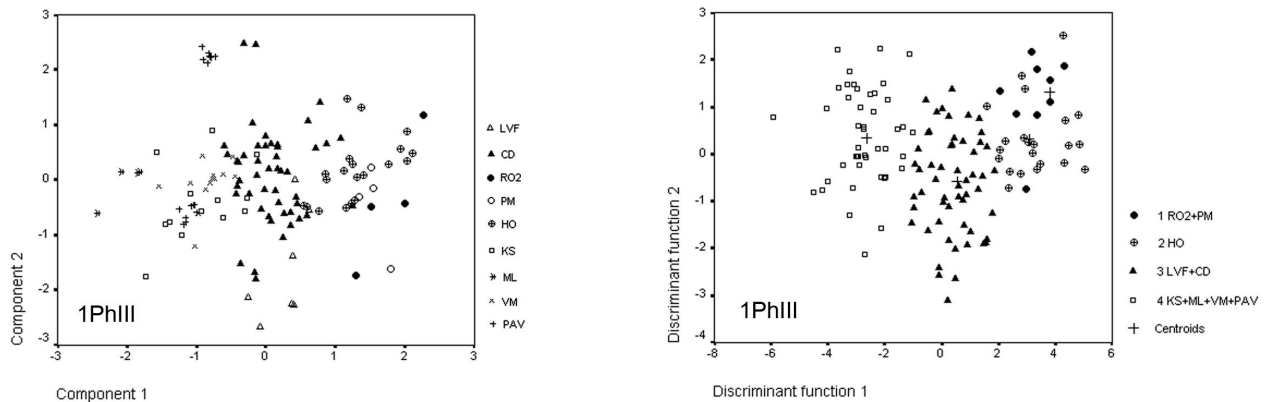Figure 5.—Principal component analysis of McIII, MtIII, astragalus, and calcaneus.

Figure 6.—Principal component analysis for the first phalanx III and discriminant analysis based on PCA results.

(figs. 5 and 6). The first clustered the specimens belonging to the large PM and RO2 forms, while the second contained the specimens from HO. The third group included the LVF and CD forms, and the fourth group contained the relatively small specimens of *H. matthewi* from VM, KS, PAV, and ML.

In the PCA for McIII, all variables influenced the first component with the skeletal size carrying the greatest weight (fig. 5, table 3). The most influential traits were the proximal articular breadth (McIII5), the proximal articular depth (McIII6), and the maximal distal depth of the medial condyle (McIII14).

Table 3.—**Most influential traits with respect to components1 and 2 in PCA**

Principal component of limb bones	Number of character	Eigen value	Principal component of limb bones	Number of character	Eigen value
McIII			**Astragalus**		
First component	5	0.971	First component	2	0.978
	6	0.962		5	0.973
	14	0.952		4	0.971
Second component	8	0.511	Second component	3	0.318
	3	0.363		4	0.058
	11	0.168	**Calcaneus**		
MtIII			First component	1	0.976
First component	7	0.980		5	0.963
	10	0.969	Second component	3	0.427
	12	0.966		4	0.195
Second component	9	0.593	**First phalanx**		
	8	0.319	First component	7	0.968
	2	0.225		4	0.963
				6	0.953
			Second component	2	0.623
				1	0.540

These components clearly separate the McIII of the large PM and RO2 forms from the rest of the smaller remains. The McIII of HO fell in-between. The second component was mainly influenced by the diameter of the anterior facet of the fourth carpal (McIII8) and the minimal breadth (McIII3).

The results for the PCA of MtIII were similar to those of the McIII (fig. 5, table 3). In the first component the most influential character was size. The most influential variables were the maximal diameter of the articular facet for the third tarsal (MtIII7), the maximal distal supra-articular breadth (MtIII10), and the maximal distal articular breadth (MtIII11). In the second component the most important variables were the diameters of the articular facets for the second and fourth tarsals (MtIII 8 and MtIII9) and the maximal lengths (MtIII2 and MtIII1). In this analysis the large PM specimen fell among the values for the HO remains, those from LVF grouped with those from CD, and those from VM, ML, and PAV were clearly separated.

In the PCA for the astragalus, the distributions were similar to those recorded in the analysis of MtIII (fig. 5, table 3). All variables influenced the first component, emphasizing the size of the different specimens. The breadth of the trochlea (AS3) carried the most weight in the second component.

In the PCA for the calcaneus the distribution was again similar (fig. 5, table 3). All variables influenced the first component; the minimal breadth (CAL3) carried the most weight in the second component.

In the PCA for the first phalanx the most influential variable in the first component was skeletal size (fig. 6, table 3). The maximal length was the most important variable (1PhIII1) in the second component. In figure 6, the results for the 1PhIII PCA are similar to those for the calcaneus and astragalus in general terms, but the PCA for 1PhIII indicated large differences between the anterior and posterior phalanges.

Discriminant analysis was performed on the PCA results to maximize the separation among the groups produced. The first group included the largest remains, i.e., those from RO2 and PM; the second included the large sized remains from HO, the third consisted of the relatively middle remains from LVF and CD, and the fourth included the small-sized remains from VM, KS, ML, and PAV.

The DA for McIII clearly separated the LVF and CD group from the samples of *H. primigenium* from HO, and indeed from other sites (fig. 7, table 4). The results indicate this group to be well classified in 91.7% of cases, with only one of 12 specimens overlapping with some of *H. primigenium* from HO. The first and the second group were always correctly identified. The DA for MtIII reproduced these results. Only one specimen out of 13 (7.1%) from the third group overlapps with some specimens of *H. primigenium* from HO (fig. 7,
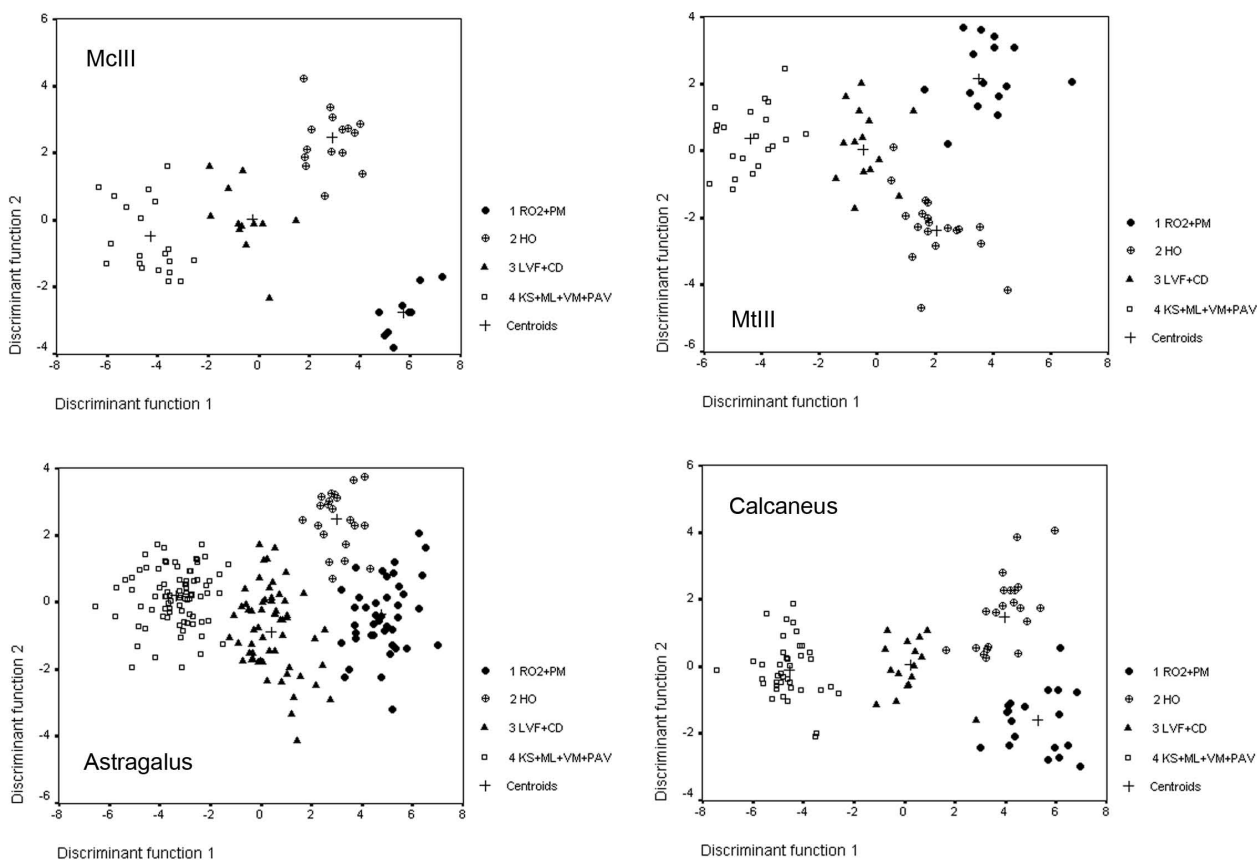
Figure 7.—Discriminant analysis based on PCA results for MtIII, McIII, astragalus and calcaneus.

Table 4.—**Percentage of correct classification as determined by cross-validation. 1: *Hipparion laromae* (RO2+PM); 2: *Hipparion concudense* (CD+LVF); 3: *Hipparion primigenium* (HO); 4: *Hipparion matthewi* (VM+KS+ML+PAV)**

	Original	N	1	2	3	4
McIII	1	9	100% (9)	0%	0%	0%
	2	14	0%	100% (14)	0%	0%
	3	12	0%	8.3% (1)	91.7% (11)	0%
	4	12	0%	0%	4.8% (1)	95.2% (20)
MtIII	1	17	94.1% (16)	0%	5.4% (1)	0%
	2	19	0%	100% (19)	0%	0%
	3	14	0%	7.1% (1)	92.9% (13)	0%
	4	21	0%	0%	0%	100% (21)
Astragalus	1	42	9.2% (39)	4.8% (2)	2.4% (1)	0%
	2	20	5% (1)	95% (19)	0%	0%
	3	59	1.7% (1)	0%	96.6% (57)	1.7% (1)
	4	85	0%	0%	1.2% (1)	98.8% (84)
Calcaneus	1	18	100% (18)	0%	0%	0%
	2	22	4.5% (1)	95.5% (21)	0%	0%
	3	15	0%	0%	100% (15)	0%
	4	41	0%	0%	2.4% (1)	97.6% (40)
First	1	8	75% (6)	85% (2)	0%	0%
phalanx	2	20	10% (2)	85% (17)	5% (1)	0%
	3	56	18% (1)	5.4% (3)	91.1% (51)	1.8% (1)
	4	47	0%	0%	6.4% (3)	93.6% (44)

table 4). The DA for the astragalus confirmed the separation observed in PCA (fig. 7, table 4). The remains from LVF and CD were clearly separated from those from the other sites. Only one of the 57 specimens (1.7%) overlapps *H. matthewi* from VM, KS, ML, and PAV. In the DA for the calcaneus, the remains from LVF and CD were also clearly separated from the rest. This group was well classified in 100% of cases (fig. 7, table 4). The DA for 1PhIII reproduced these results, but some specimens from LVF and CD overlapps the distribution of the HO specimens (fig. 6, table 4). The remains were well classified in 91.1% of cases, with one of 51 specimens (1.8%) overlapping with those of RO2 and PM, another (1.8%) with *H. matthewi* from VM, KS, ML, and PAV, and three more (5.4%) with *H. primigenium* from HO. These results indicate a strong similarity between the LVF and CD forms (table 4).

Discussion

The present results show that the remains of *Hipparion* from LVF and CD have similarities that clearly differentiate them from the materials from the other studied sites. Morphological affinities between them were confirmed in the bivariate and multivariate analyses, although some differences in dental and postcranial morphology were apparent. The hypsodonty index of the LVF specimens is lower than that of the CD specimens, and the occlusal morphology of the lower cheek teeth is more complicated in the LVF specimens (fig.8, table 1). These characters, hypsodonty and plication, would be related to different paleoenvironment conditions and consequently to the diet. The higher hipsodonty and the more complicated enamel plication are related with the drier conditions of the LVF environment. With respect to the postcranial skeleton, the metapods of both forms are slender, although the gracility index indicates the LVF specimens to be more slender than those from CD (the former are somewhat longer and the width of the diaphysis is smaller) (fig.8, table 2). These kinds the analyses confirmed the remains from LVF and CD to be very similar. Only a few morphological differences exist in the postcranial bones, PCA analysis showed them to overlap, and they merged in the DA analysis. The LVF and CD forms are clearly distinguished from the large forms from HO, PM, and RO2. The gracility indices also show that

the LVF postcranial skeletons more closely resemble those from CD than those of *H. primigenium* from HO (table 2), although the MtIII, astragalus, calcaneus, and 1PhIII from LVF are more slender than the homologous bones from CD. Nonetheless, the body masses of the LVF and CD *Hipparion* taxa are similar (table 2). It is important to note the differences between the LVF and CD taxa and other Spanish *Hipparion* (Ortiz Jaureguizar & Alberdi, 2003). The mean body mass of *Hipparion* from LVF was 170 kg with 1PhIII5, and 186 kg with McIII13. This is close to the mean weight of 160 kg with 1PhIII5 and 178 kg with McIII13 for the CD form (table 2). These similarities in weight, morphological features, and the results of the bivariate and multivariate analyses suggest, as Forsten pointed out (1982) that the *Hipparion* from LVF and CD should be included within *Hipparion concudense*, although as belonging to different subspecies. In accordance with the priority rules (ICZN, 2000) the name of *Hipparion concudense* is prioritary. Thus, the taxonomical separation between *H. c. melendezi*, from the Duero Basin, and *H. c. concudense*, from the Calatayud-Teruel Basin, would be consequence of different environmental conditions between both Basins, an idea supported by the presence in LVF of a faunal assemblage which suggests drier environment than that from CD.

Conclusions

The present results show the similarities between *H. concudense* from Concud and *H. p. melendezi* from LVF, to be sufficient to assign them to the same species, *H. concudense*, agreeing with previous Forsten's (1982) proposal. However, these taxa are different enough to represent two subspecies: *H. concudense melendezi* Alberdi, 1974, and *H. concudense concudense* Pirlot, 1956, by the morphological and biometrical differences.

The dental morphology of *H. concudense melendezi* is somewhat more complicated, and the distal parts of its limbs (McIII, MtIII, AST, CAL, and 1PHIII) are more slender than those of *H. concudense concudense*.

Figure 8.—*Hipparion concudense concudense* from Concud (Teruel, Spain) vs. *Hipparion concudense melendezi* from Los Valles de Fuentidueña (Segovia, Spain). a) MNCN-17685, right p3-4 from CD. b) MNCN-17679, right p3-4 from CD. c) MNCN-17765, right m1-2 from CD. d) MNCN-17753, m1-2 from CD. e) MNCN-30152, MNCN-30212, MNCN-30226, MNCN-30196, MNCN-30206, right lower series p2-m3 from LVF. f) MNCN-30593, left McIII from LVF. g) MNCN-17204, right McIII from CD. h) MNCN-30654, right MtIII from LVF. i) MNCN-17150, left MtIII from CD.

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