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REMAINS OF *HIPPARION* (EQUIDAE, PERISSODACTYLA) FROM PUENTE MINERO (TERUEL PROVINCE, SPAIN) AND THEIR IMPLICATIONS FOR THE SYSTEMATICS OF THE TUROLIAN HIPPARIONINI

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Abstract: Morphological and biometrical variability of the equid *Hipparion* from Puente Minero and other localities from the Teruel Basin, Spain (MN10-MN13) is analysed. Three species of *Hipparion* are recognised in Puente Minero – *H. laromae*, *H. matthewi*, and *Hipparion* sp. cf. *H. longipes* – through comparison with other Spanish and Eurasian species (Samos, Greece; Höwenegg, Germany; Pavlodar, Kazakhstan, small and large forms; Akkaşdaği, Turkey; and the following Spanish sites, La Roma 2, Los Aljezares, Concud, Milagros, Las Casiones, and Venta de Moro). The majority of the *Hipparion* remains from Puente Minero and determined to be *Hipparion laromae* based on their size and morphology. This interpretation was confirmed by bivariate and multivariate analysis. These results suggest a Eurasian immigration of different *Hipparion* species into the Teruel basin.

Key words: Equidae, *Hipparion*, Multivariate analysis, Turolian, Late Miocene, Puente Minero, Teruel Basin, Spain.

THE genus *Hipparion* Christol, 1832 is recorded in Eurasia from the early Vallesian European Land Mammal Stage to the early Villafranchian European Land Mammal Stage (Upper Miocene-Upper Pliocene, *sensu* Bonadonna and Alberdi 1987). Many early Vallesian species and subspecies have been named, although most of them were later grouped into the species *H. primigenium* (Alberdi 1974; Forsten 1968). During the Turolian European Land Mammal Stage, the genus diversified widely throughout Eurasia. Size reduction of the medium-sized species (*H. mediterraneum*, *H. concudense*, etc) led to the appearance of some species of very small size. These are found in the Spanish Turolian, in Russia and in some Greek sites (*H. matthewi*, *H. macedonicum*, *H. periafricanum*) (Alberdi 1974; Forstén 1968; Koufos 1980, 1987; Pesquero *et al.* 2007).

As the abundant Eurasian record of Vallesian and Turolian *Hipparion* had given rise to a great proliferation of taxonomic names, in 1968 Forsten proposed a synthesis using statistical methods. Later, Alberdi (1974), by means of statistical methods that combined morphological and biometrical features, set limits to Forsten´s reduced systematization. Afterwards, Alberdi (1989) established a total of six morphotypes *sensu lato* in an attempt to unify the Eurasian and African species of *Hipparion* from the early Vallesian to the early Villafranchian. Recently, several authors have proposed subdividing the species into different genera and subgenera. Based on Chinese remains of *Hipparion*, Qiu *et al.* (1987) proposed grouping several Chinese species into different subgenera. Bernor *et al.* (1996, p. 333) placed all species of the genus *Hipparion* within the tribe Hipparionini and classified them into several genera or group complexes. These include a minimum of four super-specific evolutionary complexes: the *Hippotherium* complex (including 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.

This more and more complicated Systematics of the Hipparionini horses is in part due to differences related to the taxonomical meaning of the different characters used to compare both genera and species. In our opinion, a re-evaluation of these features is necessary in order to provide a global framework for defining the morphotype of *Hipparion sensu lato* (see Pesquero *et al.* 2006, 2007).

The early Turolian locality of Puente Minero, placed near the city of Teruel inside the Neogene continental Teruel Basin, is located in the right bank of the Rambla de Valdecebro (Alberdi and Alcalá 1989-1990; Alcalá 1994; Alcalá *et al.* 1991), quite close to other classical Turolian mammal localities such as Los Mansuetos (middle Turolian) and El Arquillo de la Fontana (= Valdecebro, late Turolian). The dark clayey marls bearing the fossil level are interpreted as deposits of small marginal swamps in a very shallow lacustrine environment. Excavations at the fossil site have provided an abundant assemblage of both micro- and macrovertebrates belonging to the upper Miocene (early Turolian, MN11 zone of Mein 1990, and local zone K of van Dam 1997). Some taphonomic features observed in the Puente Minero faunal assemblage indicate pre-burial biases: predominance of teeth, dominance of cubically and spherically shaped bone specimens (i.e., specimens with the three main lineal dimensions being of similar magnitude), and a homogeneous range of bone sizes and evidence of abrasion on some specimens. In addition, the presence of articulated and associated skeletal elements in the site indicates selection of elements from the carcasses before their complete disarticulation.

Apart from *Hipparion* other identified macromammals include the carnivorans *Indarctos, Martes, Plioviverrops, Thalassictis,* and *Paramachaerodus*, the suid

Microstonyx, the ruminants *Birgerbohlinia, Tragoportax, Hispanomeryx,* and *Lucentia,* the rhinocerotid *Lartetotherium*, and the gomphoterid *Tetralophodon.* Most of the fossils are stored at the Palaeontological Museum of the Dinópolis Institution (Teruel, Aragón Government).

The most abundant large mammal remains from this locality correspond to a large-sized *Hipparion*, but there are also some other quite scarce smaller elements belonging to the same genus. Preliminarily, Alberdi and Alcalá (1989-1990) cited the possible presence of three different forms of *Hipparion* (*H. primigenium* and two smaller forms) while Alcalá (1994) indicated later the presence of only two different species, one of larger body size than the other one.

The main goals of this paper are: to describe the main characters of the specimens of *Hipparion* found in the early Turolian locality of Puente Minero (Teruel, Spain); to describe the systematic state of the Puente Minero remains; to identify if there are two or three different forms and what their taxonomical status is; to examine their relationships with other species from Spanish and Eurasian; and to frame their evolutionary history.

MATERIAL AND METHODS

Material

The studied material comes from the fossil locality of Puente Minero, Teruel, Spain (Alberdi and Alcalá 1989-90; Alcalá 1994; Alcalá and Montoya 1989-90) (Text-fig. 1). This material is stored at the Palaeontological Museum of the Dinópolis Institution, Teruel.

Material remains from Puente Minero. Upper teeth: two right and one left series P2-M3 of the same individual (PM-596 and PM-880, PM-881); one right series P2-M3 (PM-

1350-2/PM-1350-7); and one right series P3, M1-M3 and one left series P3, M1-M2 of the same individual (PM-487 - PM-492). Isolated teeth: four P2, 22 P3-4, 18 M1-2 and six M3.

Lower teeth: one left mandible with p2, d3, d4, m1-m3 (PM-512); isolated teeth: 11 p2, 10 p3-4, 31 m1-2 and nine m3.

Appendicular skeleton: two distal humeral fragments; one distal radial fragment; 14 McII fragments, seven McIII (four complete), 10 McIV fragments; one distal tibial fragment; eight calcanea (five complete); 12 astragali (10 complete); 10 MtII fragments, 17 MtIII (five complete), nine MtIV fragments; seven complete 1PhIII, eight complete first lateral phalanges, 12 complete 2PhIII, four complete second lateral phalanges, two 3PhIII, one third lateral phalanx; one scaphoid, two magna, three lunata, one pyramidal, three pisiforms, two trapezoids, eight ectocuneiforms, eight naviculars and six cuboids.

Material for comparison. This study compared the specimens from Puente Minero with populations from other Spanish localities (La Roma 2, Los Aljezares, Concud, Milagros, Las Casiones, and Venta de Moro), in order to improve the description and make the multivariate analysis more complete.

Vallesian-Turolian forms from Spanish localities, such as *Hipparion laromae* Pesquero et al., 2006 from la Roma 2; *Hipparion* sp. from Los Aljezares; *Hipparion concudense* (Pirlot 1956) and *Hipparion* sp. from Cerro de la Garita (Concud); *Hipparion matthewi* (Pesquero *et al.* 2007) from Milagros; *Hipparion matthewi* and *Hipparion periafricanum* from Las Casiones (Pesquero 2003) and *Hipparion matthewi* (Pesquero *et al.* 2007) from Venta del Moro. In order to make a comparison with other remains from Central Europe and Asia, we analysed specimens from Höwenegg (Germany; Bernor *et al.* 1997; and raw data that Bernor sent us from Höwenegg), large-sized specimens from Çalta (Turkey; Heintz *et al.* 1975; Eisenmann and Sondaar 1998, and own data herein), specimens from Akkaşdaği (Turkey; Koufos and Vlachou 2005; Scott and Maga 2005), and both small and large-sized specimens from Pavlodar (Kazakhstan; Orlov 1936; and own data herein).

Methodology

We used morphological and morphometric characters (Text-fig. 2), and the degree of wear on upper and lower cheek teeth (i.e. germ to unworn teeth, I, II, III, IV, and V), proposed by Alberdi (1974: figs. 1 and 2). We calculated the hypsodonty index on unworn or only slightly worn teeth. This index is defined as the ratio between the mesio-distal length (2) and the height (1) of the unworn teeth (Eisenmann *et al.* 1988: figs. 6-8). Dimensions of the teeth are presented in bivariate plots using the categories P3-4, M1-2, p3-4, and m1-2. Two bivariate plots were generated in order to analyse the robustness and/or slenderness of the metapodials. One plot, following Bernor *et al.* (1990), juxtaposes the maximum length (McIII1 or MtIII1) against the distal articular breadth (McIII11 or MtIII11). The second plot compares maximum length versus minimal breadth of the diaphysis (McIII3 or MtIII3). Bivariate plots were also generated for 1PhIII. Bivariate and multivariate analyses were performed with the numerical data to establish size similarities. Metapodials, astragali, and first phalanges were analysed using principal component analysis (PCA) to evaluate similarities and/or differences among size and length of the different remains of *Hipparion* from Puente Minero and to assess their relationship with the remains from other localities. After these groups were identified, based on the PCA, we performed a discriminant analysis (DA) following the Mahalanobis method with the aim of maximizing the separation between the identified groups, to evaluate whether the centroids differ significantly or not, and often to identify specimens that were not included in the original analysis that established the groups. We estimated the body masses using the first phalanx, Ph5 measurement (r = 0.991) following Alberdi *et al.* (1995). Calculations were made using SPSS 15.0.

With regard to the smallest remains of the population of *Hipparion* from Puente Minero, we compared the single specimens with a large well-known sample following Simpson *et al.* (1963) to investigate if this specimen falls inside or outside of the normal distribution of the well-known sample. We used STUDENT's t-test with N -1 degrees of freedom

$$t = \frac{(0 - X) \sqrt{N/N+1}}{Sd}$$

where 0 is the mean of the well-know sample, X is the value of the single specimen, Sd is the standard deviation of the well-know sample, and N is the sample number.

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

DPOF: dorsal preorbital fosse; P/M: upper cheek teeth; p/m lower cheek teeth; L: length; W: breadth; HI: Hypsodonty index; Apre: Anterior-prefossette; Dpre: Distal-prefossette; Apof: Anterior-postfossette; Dpof: Distal-postfossette; McIII and MtIII: metacarpal and metatarsal of the third digit respectively; SI: Slenderness index; 1PhIII, 2PhIII and 3PhIII: first, second and third phalanges of the third digit respectively; PCA: Principal Components Analysis; DA: Discriminant Analysis. Localities: PM: Puente Minero; RO2; La Roma 2; ALJ: Aljezares; ML: Milagros; KS: Las Casiones; VM: Venta del Moro; CD: Concud, HO: Höwenegg; ÇA: Çalta; AK: Akkaşdaği, PAV: Pavlodar.

SYSTEMATIC PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848

Infraorder HIPPOMORPHA Wood, 1937

Superfamily EQUOIDEA Gray, 1821

Family EQUIDAE Gray, 1821

Genus HIPPARION Christol, 1832

Hipparion laromae Pesquero *et al.* 2006

(*Hippotherium laromae*, sensu Bernor *et al.* 1996)

Plates 1-2

Synonymy list.

1989-90 *Hipparion primigenium* on v. Meyer; Alberdi and Alcalá, p. 107.

1994 *Hipparion primigenium* on v. Meyer; Alcalá, p. 265.

Holotype. First phalanx of the third digit (RO-1269 in anterior view), from La Roma 2 (Teruel, Spain), stored at the Palaeontological Museum of the Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel. Referred in Pesquero *et al.* (2006: Fig. 5e).

Type locality. La Roma 2, Teruel, Spain (MN10).

Stratigraphic distribution: Late Vallesian - Early Turolian (Upper Miocene).

Geographic distribution. Spain.

Material. Specified in the "Materials and Methods" sections, except the remains belonging to *Hipparion matthewi* and *Hipparion* sp. cf. *H. longipes* (see below).

Diagnosis. Robust *Hipparion* species, with a significantly larger body mass than *H. primigenium*; well-developed DPOF; large upper and lower cheek teeth, with characteristic "wrinkled" enamel plications whose number decreases with wear. Robust metapodials, more slender than those of other Vallesian populations.

Description. The protocone shape is lenticular on premolars and an elongated-oval on molars. Sometimes connected to the protoloph in advanced stage of wear (less than 2 cm high) (two P2 and three P3-4). Premolar parastyle and mesostyle larger than those on molars, and without groove. Marked fossette folds, showing deep-medium folding (varying from 0-9 at Apre/2-10 at Dpre/2-9 at Apof/0-3 at DPOF; mode as follows: 1/6/5/1, respectively). Pli caballin varies between 1 and 3, while the mode for both premolars and molars is 1. Hypsodonty index is 2.4 in P3-4 and 2.6 in M1-2 (Pl. 1, Table 1).

Lower cheek teeth are also of large size. Occlusal morphology is not complicated, with rounded oval double-knot. Wide linguaflexid, which is shallow on premolars and deeper on molars. Ectoflexids slightly developed in premolars, well developed in molars, where it crosses the isthmus, between the preflexid and postflexid, and reaches the linguaflexid in worn teeth. Molars with a protostylid isolated on occlusal surface in unworn teeth, only joined to protoconid in advanced stages of wear. The hypsodonty index is 2.5 in p3-4 and 2.6 in m1-2 (Pl. 1, Table 1).

Well preserved remains of the appendicular skeleton, characterizing an animal of large size with robust extremities.

Metapodials long, wide, and robust. In McIII proximal articulation, the angle between the magnum and unciform facets varies from 128º to 139º (two specimens). Unciform facet (McIII8 and McIII16) consists of two isolated subfacets. Two facets for McIV: one dorsally placed, subtriangular in shape and other placed posteriorly, which is more or less rounded. Magnum facet subtriangular in shape with a not very well-developed muscular insertion area. The gracility index of McIII1 versus McIII3 varies from 11.2 to11.7 (X = 11.5); that of McIII1 versus McIII11 varies from 15.3 to 15.6 (X = 15.5) (Pl. 2, Table 2).

Proximal articulations surface of MtIII with well-delimited facets. Cuboid facet well developed and quadrangular in shape. In four measured samples the angle formed between the cuboid facet and the large cuneiform was, on average 142º. Small cuneiform facet subquadrangular in shape and curved in proximal direction. MtIV, has two facets variable in size; the anterior facet is triangular and posterior facet is rounded. MtII has two well-developed subtriangular facets. Supra-articular fossette well marked, more than in metacarpals. Gracility index is 11.4 (one specimen), (X = 10.4) for MtIII1 versus MtIII3, and 14.4 for MtIII1 versus MtIII11 (Table 2).

Calcanea and astragali are large. Calcaneus facet C of astragali (nomenclature from Eisenmann *et al.*, 1988) is generally proximo-distally elongated, large and variable in size. This facet is in contact with the posterior part of the large condyle of the pulley in several specimens (PM-7, PM-18, PM-330), but in some cases with a small groove between them (PM-516, PM-781, PM-845, PM-878). Calcaneus facet B situated in two planes; it is continuous in six specimens, isolated in one specimen and absent in three specimens. Navicular facet subtriangular, with a well-developed area for muscular insertion. Cuboid facet is subtriangular and forms an angle with the navicular facet (X=108º). In calcaneus, internal facet of sustentaculum tali is more or less elongated, isolated, and variable in size, and articulates with astragalus facet C. Tuber calcis strongly developed.

1PhIII, 2PhIII, and 3PhIII wide and robust, anterior and posterior 1PhIII can be easily distinguished following Prat (1957). Proximal part of anterior 1PhIII rounded and deeply grooved; posterior 1PhIII shorter than anterior and more robust, with a quadrangular and wide proximal facet. Anterior and posterior 2PhIII are more difficult to distinguish than 1PhIII. The 3PhIII are incomplete.

Hipparion matthewi (Abel 1926)

(or *Cremohipparion matthewi*, sensu Bernor *et al*. 1996)

Plates 1-2

Synonymies. In Pesquero *et al*. 2007

1989-90 *Hipparion gromovae* Villata and Crusafont; Alberdi and Alcalá p. 107.

1994 *Hipparion gromovae* Villata and Crusafont; Alcalá, p. 268-269.

Holotype. Skull OK-557 Geological Institute, Budapest. This specimen was first described by Abel (1926). Following Forsten (1968) it was referred to *H. elegans* by Gromova (1952).

Type locality. Unknown locality of Samos (Greece).

Stratigraphic distribution: Late Turolian of Samos. The new remains indicate that this taxon was present as early as the Turolian, thus extending its stratigraphic range.

Geographic distribution. This species has been found in several localities from the Eastern Mediterranean area, including Salonike, Maragha and Quarry 5 of Samos. It is also found in Pavlodar (Kazahkstan, Asia). In Spain it is found in the Teruel, Cabriel and Granada Basins.

Material. One right upper dental series, P2-M3 (PM-1350-2/PM-1350-7), four upper P3-4 (PM-114, PM-464, PM-304, PM-1350-1), one M1-2 (PM-581), one p3-4 (PM-1070), three m1-2 (PM-155, PM-470, PM-731); one distal radial fragment (PM-735); one distal tibial fragment (PM-909); two astragali (PM-708, PM-1205), two calcanea (PM-375, PM-796); three MtIII (PM-791, PM-883, PM-960), two 1PhIII (PM-771, PM-898), three first lateral phalanges (PM-947, PM-849, PM-993), four 2PhIII (PM-719, PM-737, PM-787, PM-788), one second lateral phalanx (PM-809); one ectocuneiform, one navicular and one cuboid.

Diagnosis. Slender, medium to small-sized *Hipparion*. Molars are hypsodont and the pattern of enamel of the occlusal surface is moderately complex on both the upper and lower cheek teeth. Small oval protocone that only merges with loph in cases of advanced wear, and pli caballin single in the majority. The protostylid is weakly developed in the lower molars and absent in the premolars. Ectostylid absent. Postcranial bones are slender and the metapodials are elongated and slender.

Description. Upper cheek teeth characterized by their small size and uncomplicated enamel plications. Protocone lenticular in shape and connected to the protoloph in advanced stages of wear. The fossette pattern is simple (Apref.: 0-1; Dpref.: 2-4; Aposf.: 0-2 ; Dposf.: 1. The caballine fold is absent (Pl. 1).

In the lower cheek teeth the enamel is smooth with a rounded double-knot. Linguaflexid well-developed and deep. Ectoflexid slightly developed in the premolar and very developed in the molars, where it crosses the isthmus, between the preflexid and the postflexid, reaching the linguaflexid in all cases; protostylid very well developed and joined to the protoconid in a advanced state of wear.

Postcranial remains medium to small in size (Pl. 2). Proximal articulations of MtIII include a well developed, subquadrangular cuboid facet, which forms a wide angle (150º), with the facet of the big cuneiform. Small cuneiform facet very reduced and subtriangular. There are two facets for MtIV: a triangular anterior facet and a rounded posterior facet.

Calcanea and astragali medium in size. Calcaneus facet C of astragali elongated in both specimens. Calcaneus facet B lacks a small facet beside it. Navicular facet subtriangular in shape with the area for muscular insertion moderately developed. Cuboid facet is elongated and forms an angle of 96º with the navicular facet. Internal facet of the sustentaculum tali of the calcaneus oval in shape. Cuboid facet elongated and well developed. Tuber calcis moderately developed. Posterior 1PhIII with wide and quadrangular proximal facet. Trigonium phalangis not well defined.

Hipparion sp. cf. *H. longipes* Gromova, 1952

(or ¿*Plesiohipparion longipes*, sensu Bernor *et al*. 1996).

Plates 1-2

Holotype. MtIII stored at The Institut Paléontologique de l'Académie des Sciences de l' Ancient URSS (PIN, 2413/5030, pl.X, Fig. 3 Gromova 1952).

Type locality. Pavlodar (Irtych, Kazakhstan)

Stratigraphic distribution. Upper Miocene or Lower Pliocene

Geographic distribution. Çalta (Turkish, Heintz *et al.* 1975), referred to MN15 by Sen *et al.* (1978). This species has also been recognized from the MN15 locality of Megalo Emvolon (Koufos *et al.* 1991) (Macedonia, Greece) by Steffens *et al.* (1979); Pavlodar, Kazakhstan by Gromova (1952), Alberdi (1989) and Forsten (1997), among others; and Akkasdagi, Turkey by Scott and Maga (2005) and Koufos and Vlachou (2005).

Material. Four m1-2 (PM-556, PM-728, PM-1219, PM-1284), two McIII (PM-780, PM-958) and two MtIII (PM-776, PM991).

Diagnosis. Gromova (1952) characterized *Hipparion longipes* as being of large body size, with moderately complex enamel plications in the upper cheek teeth, a short and wide protocone, very long and slender extremities, and long metapodials.

Description. Lower cheek teeth are characterized by their large size. Occlusal morphology not complex with rounded double-knot and shallow linguaflexid. Ectoflexid well developed but it does not cross the isthmus (Pl. 1). Metapodials very elongated and large in size. In the proximal articulation of McIII, the angle between the magnum and unciform facets varies from 129º to 130º (two specimens). Magnum facet subtriangular in shape. Area for muscular insertion not well developed. Unciform facet with two isolated subfacets and two facets for McIV. The gracility index varies from 11.3 to 11.4 (X = 11.4) for McIII1 versus McIII3, and from 14.3 to 14.5 (X = 14.4) for McIII1 versus McIII11 (Table 2). Proximal articulation of MtIII with a cuboid facet very well-developed and the angle formed with large cuneiform is 140º in one measured sample. Gracility index varies between 9.8 and 10 (X = 9.9) for MtIII1 versus MtIII3, and from 13.4 to 13.6 (X = 13.5) for MtIII1 versus MtIII11 (Table 2).

RESULTS

Morphological and univariate analysis

The results suggest the presence of three forms of *Hipparion* in the Puente Minero locality. The largest of these forms [form 'A' = *Hipparion* sp. cf. *H. longipes*] is poorly represented whilst the other two forms are well represented.

Of the latter, one of the forms [form 'B' = *Hipparion laromae*] is well represented; this form is large, while the other [form 'C' = *Hipparion matthewi*] is small.

Morphological analysis of *H. laromae* reveals similarities in skeletal structure among the Spanish sample grouped as "*H. primigenium*" morphotype 1 by Alberdi (1989). There are some morphological and size differences among dental samples. Equids from Puente Minero and La Roma 2 have similar occlusal tooth morphology. This differs from the morphology found in *H. primigenium* from other localities (Nombrevilla, Los Valles de Fuentidueña, and Masía del Barbo in Spain, included the Turolian localities from Greece and Turkey and Höwenegg and Vienna Basin in central Europe) (Pesquero *et al*. 2006). Equids from these latter localities tend to have a more complicated enamel pattern on the occlusal surface (Alberdi 1974). The dental morphology of the [form 'B'] *Hipparion* from Puente Minero is moderately complicated and it is simpler in the lower cheek teeth than in the upper ones. Prefossette and postfossette folds, which show moderately deep folding, are similar to those from La Roma 2 sample. The protocone is an elongated oval in all the Spanish specimens. The occlusal morphology of the lower dentition from the [form ‘B’] *Hipparion* from Puente Minero lacks complexity. The ectoflexid is slightly developed in the premolars and is very developed in the molars from Puente Minero, and thus bear a similarity to La Roma 2 sample.

The hypsodonty index of the [form ‘B’] *Hipparion* from Puente Minero was calculated from two P3-4, two M1-2, two p3-4 and two m1-2. The hypsodonty index is higher in the Puente Minero remains than in those from La Roma 2 (Table 1). Puente Minero [form ‘B’] is the most hypsodont of all the studied large sized forms (*H. primigenium* from Nombrevilla and Los Valles de Fuentidueña and *H. laromae* from La Roma 2).

The bivariate plot of the dental measurements indicates that the remains of the [form ‘B’] from Puente Minero clearly fall within the distribution of the La Roma 2 remains (Text-fig. 3). In both forms the length of the lower cheek teeth is similar, but in Puente Minero the breadth is wider than in La Roma 2 samples. Nevertheless, there are four m1-2 (PM-556, PM-728, PM-1219, PM-1284) from Puente Minero that are larger than the general distribution. Both upper cheek teeth in La Roma 2 and [form ‘B’] from Puente Minero have a similar distribution, but those from La Roma 2 are slightly larger. The Student’s t-test indicates that there are significant differences between the remains of [form ‘B’] from Puente Minero and those teeth that are larger in size. The measures are significantly different ($t = 0.05$) for most of the remains of the [form ‘B’] from Puente Minero (Table 3). The specimens of the [form ‘B’] *Hipparion* from Puente Minero and La Roma 2 are larger than the specimens of *H. primigenium* from Nombrevilla, Los Valles de Fuentidueña, Masía del Barbo, Höwenegg and the Vienna Basin (Pesquero *et al.* 2006).

The bivariate plots for the McIII and MtIII indicate differences among the [form 'B'] *Hipparion* from Puente Minero and the La Roma 2 samples and those from other localities analysed in this paper (Text-fig. 4). The bones from Puente Minero and La Roma 2 are larger than those from Höwenegg and Concud. There are two McIII (PM-780 and PM-958) and two MtIII (PM-776 and PM991) that are very much longer than those from La Roma 2 with a similar breadth. These MtIIIs reach a length of more than 300 mm and the McIIIs are longer than 250 mm (they correspond to [form 'A']).
The gracility index indicates that the largest Puente Minero form [form 'A'] is slightly more slender than *Hipparion longipes* from Akkaşdaği. And the [form 'B'] from Puente Minero is more slender than those from La Roma 2 and Höwenegg (Table 2).
Morphological analyses of the remains of the small form from Puente Minero [form 'C'] indicates that the upper and lower cheek teeth are characterized by their small size and uncomplicated enamel plication. The postcranial remains are medium to small in size.

The bivariate plot for dental measurements indicates that small teeth from [form 'C'] from Puente Minero are intermediate in size between those of *H. matthewi* and *H. periafricanum* (Text-fig. 3). The lower cheek teeth (PM-470, PM-731, PM-1070) fall between *H. periafricanum* from Las Casiones and *H. matthewi* from Milagros in size. In the case of the upper cheek teeth, one of the P3-4 is placed between the largest *H. periafricanum* from Las Casiones and the smallest *H. matthewi* from Milagros and the other two are distributed among the sample of *H. matthewi* from Las Casiones and Venta del Moro. The M1-2 is placed within the distribution of *H. matthewi*. The Student's t-tests of the lower cheek teeth show that several samples have more similarities with *H. periafricanum* while another samples shows more similarities with

H. matthewi. In relation to the upper cheek teeth one tooth shows more similarity with *H. periafricanum* whilst the others show more similarity with *H. matthewi* (Table 3).

In the bivariate plot for the metapodials only two MtIII from the [form 'C'] from Puente Minero are represented (Text-fig. 4). These are placed between the distributions of *H. periafricanum* and that of *H. matthewi* from Las Casiones and Venta del Moro. The Student's t-tests indicate that the MtIII from Puente Minero are significantly different both from *H. matthewi* ($t = 0.001$) and from *H. periafricanum* ($t = 0.05$) (Table 3).

The gracility index indicates that the [form 'C'] *Hipparion* from Puente Minero is more robust than *H. periafricanum* from las Casiones and *H. matthewi* from Milagros, Venta del Moro and Pavlodar, and similar to *H. matthewi* from Las Casiones (Table 2). Moreover, several small isolated teeth and postcranial fragments are recorded from Los Aljezares and Cerro de la Garita (Concud) (MN12). The dental remains consist of two p3-4 and three m1-2 from Los Aljezares and one M1-2 from Cerro de la Garita. In the bivariate diagrams, the teeth from Los Aljezares are located within distribution of *H. matthewi*, whereas the M1-2 from Cerro de la Garita is situated within the distribution of the largest *H. periafricanum* from Las Casiones.

Multivariate analysis

Principal component analysis (PCA). Principal component analysis allows us to explore the similarities and/or differences in size and length between the remains from Puente Minero and the samples from the other localities included for comparison. PCA based on skeletal measurements permits us to indentify five main groups on the basis of size (Text-fig. 5). The first group includes the specimens of *H. longipes* from Pavlodar, Çalta and Akkaşdaği, and the [form 'A'] from Puente Minero. The second group clusters the specimens belonging to the [form 'B'] from Puente Minero and La Roma 2, as they are larger in size, while the third one contains the specimens from Höwenegg and Concud. The fourth group includes the relatively smaller specimens of *H. matthewi* from Venta del Moro, Las Casiones, Milagros, *H. elegans* from Pavlodar, *H. moldavicum* from Akkaşdaği, and the [form 'C'] from Puente Minero. The fifth group includes only *H. periafricanum* from Las Casiones.

In the PCA of the McIII all characteristics influence the first component; therefore, skeletal size carries the most weight for this component (Text-fig. 5A). The most influential characters are the proximal articular breadth (McIII5), maximal distal depth of the medial condyle (McIII14) and maximal distal supra-articular breadth (McIII10). This component separates clearly the McIII of the [form 'B'] from Puente Minero and La Roma 2 from the rest from Concud. The McIII of Höwenegg falls between the two previous groups. The second component is mainly influenced by the maximal length (McIII1) and depth of the diaphysis (McIII4).

The results of the MtIII PCA are similar to those of the McIII (Text-fig. 5B); here, too, in the first component the most influential character is size. The most influential variables are the maximal distal supra-articular breadth and maximal distal articular breadth (MtIII10 and MtIII11), while in the second component the most important variables is the maximal length (MtIII1). This PCA differentiates five groups: the first includes the [form 'A'] from Puente Minero and the specimens of *H. longipes* from Çalta and Pavlodar; the second includes La Roma 2, [form 'B'] from Puente Minero and specimens of *H. longipes* and *H. dietrichi* from Akkaşdaği; the third comprises all remains from Höwenegg and Concud; the fourth includes Venta del Moro and Pavlodar (both small in size); and the fifth includes only *H. periafricanum* from Las Casiones. In the second component we observe two MtIII from Puente Minero much longer that those from La Roma 2 and the [form 'B'] from Puente Minero. For this analysis, we included specimens of *H. longipes* from Pavlodar, Akkaşdaği and Çalta as comparative material. The results indicate that these remains are well distinguished from all the other material analysed here. The results also indicate that the MtIII of the [form 'C'] from Puente Minero are situated between the specimens of *H. matthewi* from Pavlodar and Venta del Moro and the remains of *H. periafricanum* from Las Casiones.

PCA for the astragali differentiates four groups (Text-fig. 5C). The first includes La Roma 2, the [form 'B'] from Puente Minero and Höwenegg remains, the second includes Concud remains, the third comprises all remains of *H. matthewi* analyzed from Venta del Moro, Las Casiones, Milagros and *H. elegans* from Pavlodar, and the fourth includes only *H. periafricanum* from Las Casiones. In this analysis, all characteristics influence the first component; therefore, this component emphasizes the size of the different specimens. Breadth of the trochlea (AS3) carries most of the weight in the second component. In this analysis the two specimens of the [form 'C'] from Puente Minero are rather isolated from each other: one overlaps with the distribution of *H. matthewi* and the other is closer to *H. periafricanum* from Las Casiones.

PCA for calcanea differentiates only three groups because there are no specimens of *H. periafricanum* from Las Casiones (Text-fig. 5D), and only three specimens are assigned to the [form 'B'] from Puente Minero. These are located inside the Höwenegg distribution. There is also a small calcaneus from Concud, slightly smaller than those of *H. matthewi*.

For the first phalanx, the most influential character in the first component is again skeletal size (Text-fig. 5E). Maximal length and anterior length are the most important variables (1PhIII1 and 1PhIII2) for the second component. In this diagram the [form 'B'] from Puente Minero overlaps those from La Roma 2 and is close to Höwenegg.

The small size remains from PM and CD analysed here are located between the distributions of *H. matthewi* and *H. periafricanum*.

Discriminant analysis (DA). Discriminant analysis was carried out on the results obtained from the PCA, in order to maximize the separation among the identified groups. DA was performed using the five main groups that had been established by PCA. The first group includes the largest remains divided into two subgroups: 1) Puente Minero [form 'A']; and 2) *H. longipes* from Akkaşdaği, Çalta and Pavlodar. The second group includes: 1) Puente Minero [form 'B']; and 2) La Roma 2. The third group, with the relatively large sized remains, was divided into two subgroups: 1) Höwenegg; and 2) Concud. The fourth group consists of the relatively small-sized remains from Venta del Moro, Las Casiones, Milagros and Pavlodar and the fifth group includes: 1) Puente Minero [form 'C']; 2) Concud small size; and 3) the smallest remains of *H. periafricanum* from Las Casiones. The McIII DA clearly separates the [form 'A'] from Puente Minero and *H. longipes* from Akkaşdaği from the samples of La Roma 2 group and *H. primigenium* (or *Hippotherium primigenium* sensu Bernor *et al*., 1996) from Höwenegg (Text-fig. 6A). The groups analyzed were correctly identified in 100% of cases. The MtIII DA also reproduces these results, but confirms the separation observed in the PCA of the two specimens [form 'A'] that are longer than the rest of specimens of the [form 'B'] from Puente Minero (Text-fig. 6B). These two specimens overlap with some specimens of *H. longipes* from Akkaşdaği , Pavlodar and Çalta. Remains of the small form from PM are between *H. periafricanum* from Las Casiones and *H. matthewi* more close to latter.

DA for astragali DA confirms the separation observed in the PCA (Text-fig. 6C). The remains of the form 'B' from Puente Minero overlap with those from La Roma 2. The two small Puente Minero [form 'C'] specimens are clearly separated from each other.

The first is located within the distribution of *H. matthewi* from Venta del Moro, Las Casiones, Milagros and Pavlodar, and the second is closer to the distribution of *H. periafricanum* from Las Casiones. In the DA for the calcanea, the remains of the [form 'B'] from Puente Minero overlap with those from Höwenegg (Text-fig. 6D). The small calcaneus from Puente Minero clusters with those of *H. matthewi* from Venta del Moro, Las Casiones, Milagros and Pavlodar, but the small calcaneus from Concud, which is smaller, is separated from this group.

The DA for the 1PhIII also reproduces these results, but some specimens from Höwenegg overlap the distribution of the [form 'B'] from Puente Minero (Text-fig. 6E). The remains of the [form 'C'] from Puente Minero and the small 1PhIII from Concud form are placed between the *H. periafricanum* distribution and the distribution of *H. matthewi* from Venta del Moro, Las Casiones, Milagros and Pavlodar.

DISCUSSION

Morphological comparison and bivariate and multivariate analyses show that the remains from La Roma 2 and those of the large form from Puente Minero [form 'B'] have similarities that clearly differentiate them from the specimens from the other localities studied. Affinities between the large Puente Minero specimens are detected in the overall dental and postcranial morphology. These forms from those two localities are clearly distinguished from the medium-sized forms from Höwenegg and Concud. It is important to note the differences in body mass of the Spanish *Hipparion* (Ortiz-Jaureguizar and Alberdi 2003). The [form 'B'] *Hipparion* from Puente Minero has a mean estimated weight of 331 Kg. This is close to the mean weight of 349 Kg for the La Roma 2 equids that was estimated using the methodology of Alberdi *et al*. (1995) (Table 2). Additionally, comparison of gracility indices reveals that the postcranial skeletons from Puente Minero more closely resemble those from La Roma 2 than those of *H. primigenium* from Höwenegg (Table 2). Some of the largest specimens of this group are the large *Hipparion* from Puente Minero [from 'B'] and those from La Roma 2. The forms with the largest body mass were recorded in MN10 and MN16, while throughout their biochron *Hipparion* remains fundamentally within the 100-200 Kg range (Pesquero *et al*. 2006). Therefore, the similarities in weight, morphological characters, and the results of the bivariate and multivariate analyses between the Puente Minero and La Roma 2 remains inclines us to include the large PM *Hipparion* [form 'B'] within *H. laromae* from La Roma 2.

The results obtained from frequency analyses, as well as those from PCA, indicate the presence of another, much scarcer group of remains that are significantly smaller in size. Due to the scarcity of these remains, an exhaustive morphological description cannot be carried out. Bivariate and multivariate analyses placed this form between the smallest remains of *H. matthewi* and the largest of *H. periafricanum*. To discriminate these teeth we used the Simpson analysis. The results of this suggest that, for both lower (PM-470, PM-731, PM-1071) and upper (PM-114, PM-464) cheek teeth, some measurements are more similar to *H. periafricanum* whilst others are more similar to *H. matthewi* (Table 3). With respect to the postcranial remains, these are similar in size to those of *H. matthewi* from ML, although there are two MtIII that are more similar in length to those of *H. periafricanum*.

Those remains that are smaller than *H. matthewi*, and larger than *H. periafricanum*, come from an older stratigraphic level (MN11) than the remains of *H. matthewi* and *H. periafricanum* from the late Turolian (MN13). These species from the late Turolian could represent the forms that evolved from the more primitive forms from PM. The scarce remains incline us to include the smaller forms from PM in *H. matthewi*.

Among the remains from PM there are some larger individuals than those included in *H. laromae* (one M1-2, four m1-2, two McIII and two MtIII). The metapodials are larger than those from *H. laromae* and the Simpson analysis indicates significant differences between them. The presence of a larger form in PM required a comparasion with *H. longipes* from Akkaşdaği, Çalta and Pavlodar. The Puente Minero metapodial [form 'A'] gracility indices are slightly slenderer than the Akkaşdaği' *H. longipes*. Following Scott and Magga (2005), this could indicate that [form 'A'] was adaptated to more open habitats compared with Höwenegg' *Hipparion primigenium*, whose gracility index indicates a better adaptation to forested conditions. The PCA and DA results indicate a high similarity existing between *H. longipes* and the biggest remains from PM.

The presence of these species, *H. longipes* and *H. matthewi*, in the Teruel basin suggests that they could have arrived there as a part of an Asiatic faunal dispersal (Villata and Crusafont 1957; Alberdi 1974).

From a stratigraphic point of view, Pavlodar was assigned to the Upper Miocene or Lower Pliocene by Gromova (1952), Vangengein and Pevzner (1993) placed it in the Maeotian, and Forsten (1997: 15) indicate a late Turolian age. Çalta was assigned to the Lower Pliocene by Heintz *et al*. (1975) and to the MN 15 by Sen *et al.* (1978).

Among the Concud remains we found some specimens corresponding to a small *Hipparion*. These consist of one M1-2, one calcaneus and one 1PhIII (MNCN-15898, MNCN-15900 and MNCN-15899, respectively). The results of the multivariate analysis show several remains to be intermediate between those from *H. periafricanum* and *H. matthewi*, these being closest to *H. periafricanum* from Las Casiones. One could consider that *H. matthewi* was present in Concud (MN12), although the remains are slightly smaller than the small-sized *Hipparion* found in PM (MN11). This suggests the possibility that the small remains found in PM, ALJ and CD are more primitive than the smallest forms found in the more recent MN13 sites. It also suggests that the forms in the Teruel Basin are Eurasiatic immigrants instead of Spanish endemisms (Villalta and Crusafont 1957; Alberdi 1974). As the remains from Concud are smaller in size than the small form from PM [from 'C'] it might indicate that size has decreased through time, leading to the late Turolian forms (MN13) being the smallest. Overall, the later period of *Hipparion* diversification was characterized by a progressive overall decrease in size, at least in the Turolian Basin.

CONCLUSIONS

Three different forms of *Hipparion* are identified in the Puente Minero assemblage (early Turolian, MN 11). The [form 'B'], which is the predominant form in PM, is assigned to *Hipparion laromae* by their similarity in size and estimated body weight with those from La Roma 2 locality. The [form 'C'] corresponds to a small *Hipparion* that we assigned to *Hipparion matthewi* (or *Cremohipparion matthewi*, *sensu* Bernor *et al*. 1996). The [form 'A'] includes the largest remains, which are attributed to *Hipparion* sp. cf. *H. longipes* (or *¿Plesiohipparion longipes*, sensu Bernor *et al*. 1996). The material assigned to *Hipparion matthewi* is scarce. Nevertheless, it shows a size and some morphological features that are similar to those of *H. matthewi* from Spain and other European localities. It is the first time that the presence of a small *Hipparion* has been detected in Spain in the early Turolian. Whilst this form is scarce in the early-middle Turolian of Spain smaller *Hipparion* forms are well known in several Greek and Euroasiatic localities during this time. We consider these forms in the Teruel Basin and Southern Spain as immigrants.

The presence of intermediate characters in *H. matthewi* and *H. periafricanum* could indicate an evolutionary trend of a progressive decrease in size. It could also indicate that there were certain differences in the ecological environments.

The occurrence of some longer specimens than those from *H. laromae* could indicate that *H. longipes*, from Akkaşdaği, Çalta and Pavlodar were immigrants to the Teruel Basin and Southern Spain, although this dispersal event had little success.

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EXPLANATIONS OF PLATES, TEXT-FIGURES, AND TABLES

EXPLANATION OF PLATE 1

Figs. 1-7. *Hipparion* from Puente Minero (Teruel, Spain). 1-2, *Hipparion laromae* (Pesquero et al. 2006). 1, PM-881, left upper series P2-M3 in occlusal view. 2,. PM-512, right hemimandible in occlusal view. 3, *Hipparion matthewi* (Abel 1926), PM-1350, left upper series P2-M3 in occlusal view. 4-7, *Hipparion* cf. *H. longipes* Gromova, 1952. 4, PM-1284, right m1-2. 5, PM-1219, right m1-2. 6, PM-556, left m1-2. 7, PM-728, left m1-2.

EXPLANATION OF PLATE 2

Figs. 1-13. *Hipparion* from Puente Minero (Teruel, Spain). 1-2, *Hipparion* sp. cf. *H. longipes* Gromova, 1952. 1, PM-991, right MtIII. 2, PM-780, right McIII. 3, *Hipparion laromae* Pesquero *et al*., 2006, PM-648, right MtIII. 4, *Hipparion matthewi* (Abel 1926), PM-960, right MtIII. 5, *Hipparion laromae* Pesquero *et a*l., 2006, PM-717, right calcaneus. 6, *Hipparion matthewi* (Abel, 1926), PM-375, right calcaneus. 7, *Hipparion laromae* Pesquero *et al*., 2006, PM-845, right astragalus. 8, *Hipparion matthewi* (Abel, 1926), PM-708, right astragalus. 9-10, *Hipparion laromae* Pesquero *et al*., 2006. 9, PM-514, anterior 1PhIII. 10, PM-515, posterior 1PhIII. 11, *Hipparion matthewi* (Abel, 1926), PM-771, posterior 1PhIII. 12, *Hipparion laromae* Pesquero *et al*., 2006, PM-39, 2PhIII. 13, *Hipparion matthewi* (Abel, 1926), PM-714, 2PhIII.

TEXT-FIG. 1. Geographic distribution of the localities cited in the text. 1, Teruel area: La Roma 2 (RO2), Puente Minero (PM), Concud (CD), Milagros (ML), and Las Casiones (KS); 2, Venta del Moro (VM); 3, Los Valles de Fuentidueña (LVF); 4, Höwenegg (HO); 5, Çalta (ÇA); 6, Pavlodar (PAV).

TEXT-FIG. 2. Nomenclature of upper (top) and lower (bottom) cheek teeth of *Hipparion* following "*Hipparion* Conference" recommendations (Eisenman *et al*. 1988).

TEXT-FIG. 3. Occlusal length vs. occlusal breadth plotted for upper and lower cheek teeth (P3-4, M1-2, p3-4, m1-2) of Spanish, central European and Asiatic *Hipparion* localities.

TEXT-FIG. 4. Scatter diagram of McIII and MtIII (dimension 1 vs. dimension 3, and dimension 1 vs. dimension 11) of Spanish, central European and Asiatic *Hipparion* localities.

TEXT-FIG. 5. Principal component analysis of the distribution of Spanish, central European and Asiatic *Hipparion* localities using McIII, MtIII, astragalus, calcaneus and the first phalanx III.

TEXT-FIG. 6. Discriminant analysis based on PCA results (see Fig. 5) for the McIII MtIII, astragalus, calcaneus and the first phalanx III from Spanish, central European and Asiatic *Hipparion* localities.

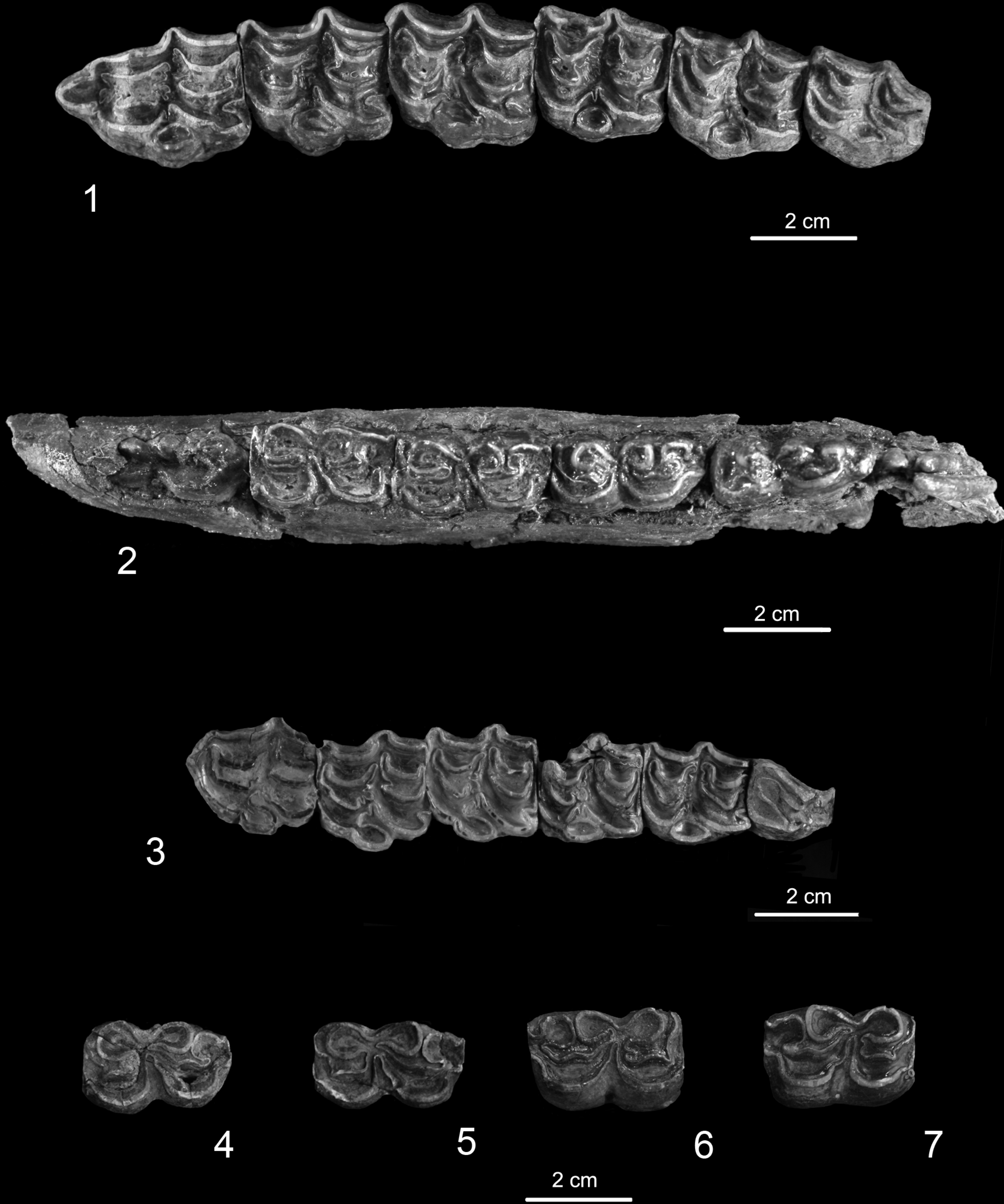
TABLE 1. Hypsodonty index of the Spanish *Hipparion*. N = number of specimens; Sd = standard deviation; X = mean.

TABLE 2. Gracility index of Spanish, European and Asian *Hipparion*. Abbreviations as in Table 1.

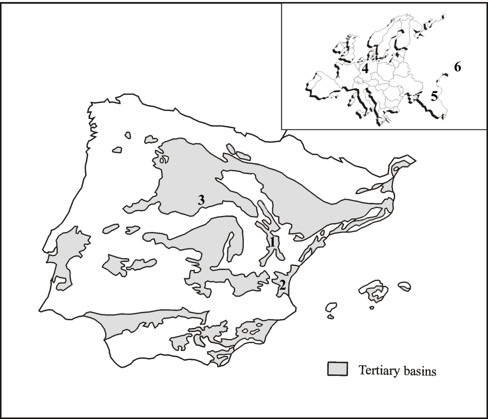
TABLE 3. Homogeneous subsets calculated by t-test following Simpson et al. (1963) showing significant differences among McIII, MtIII, Ast., Calc., and 1PhIII from PM, VM, KS, ML and PAV. Abbreviations explained in text. Probability: * = <0.05; ** = < 0.001.

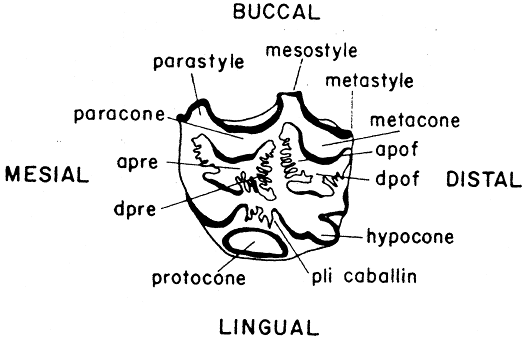
TABLE 4. Most influential characters for component 1 (corresponds to size) and component 2 in Principal Component Analysis (PCA).

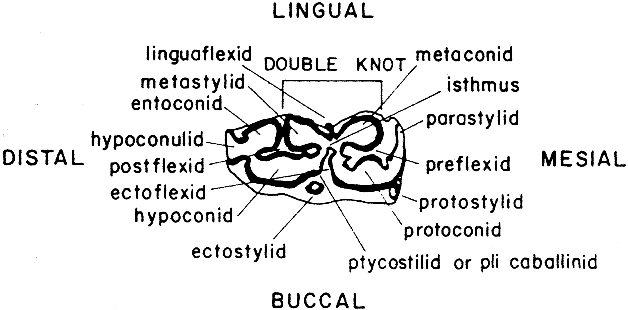
TABLE 5. Percentage of correct classification by cross-validation techniques. 1: largest form from PM [form ‘B’] 2: *Hipparion longipes* (AK+PAV+CA); 3: *Hipparion laromae* (RO2); 4: large *Hipparion* from PM [form ‘B’]; 5: *Hipparion primigenium* (HO); 6: *Hipparion concudense* (CD); 7: *Hipparion matthewi* (VM+KS+ML+PAV); 8: small-size *Hipparion* from CD; 9: small-size *Hipparion* from PM [form ‘C’]; 10: *Hipparion periafricanum* (KS)

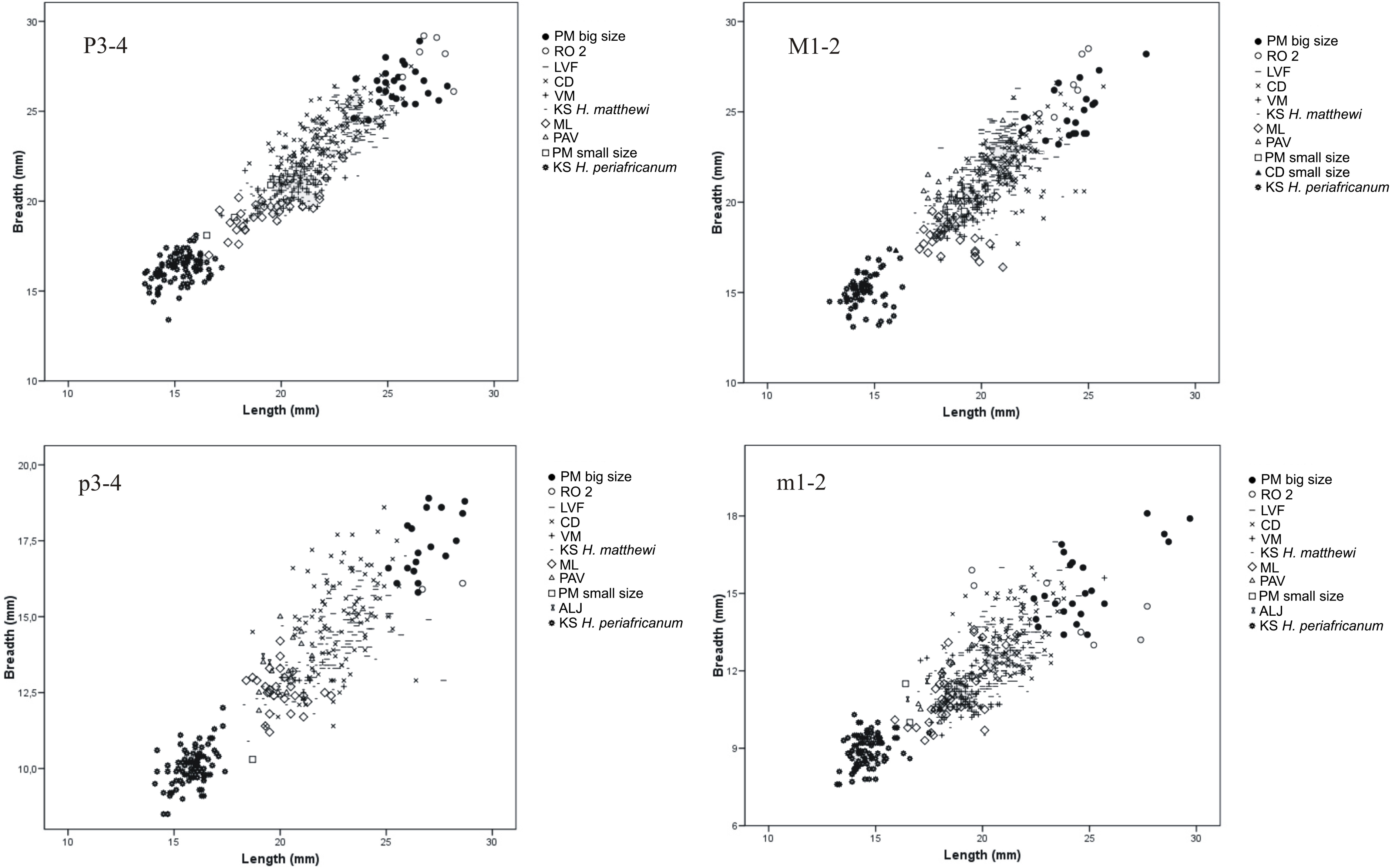

1
2 cm
2
2 cm
3
2 cm
4
5
6
7
2 cm


1
2
3
4
5
6
2 cm
9
10
11
7
8
12
13

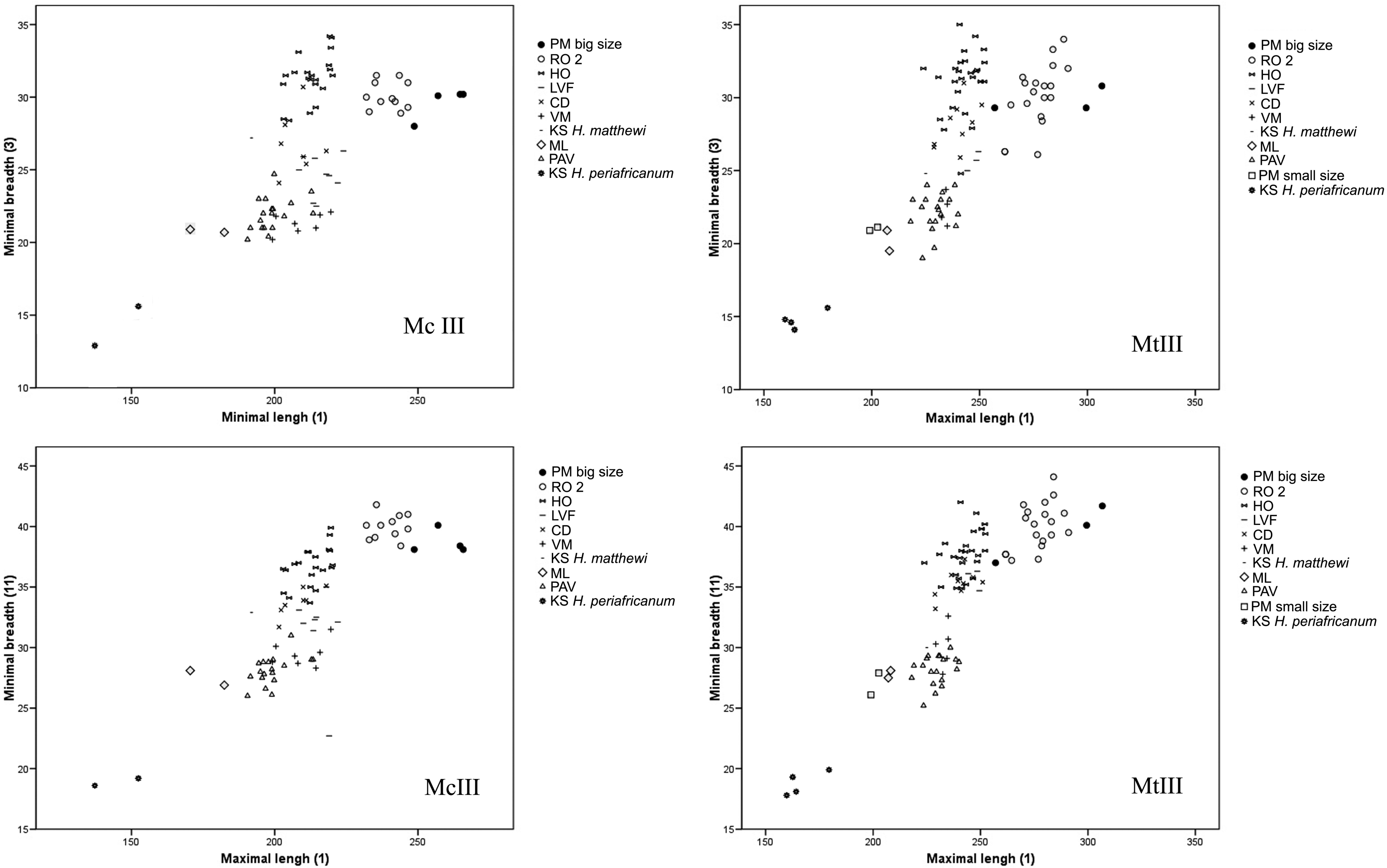

1
2
3
4
5
6
Tertiary basins

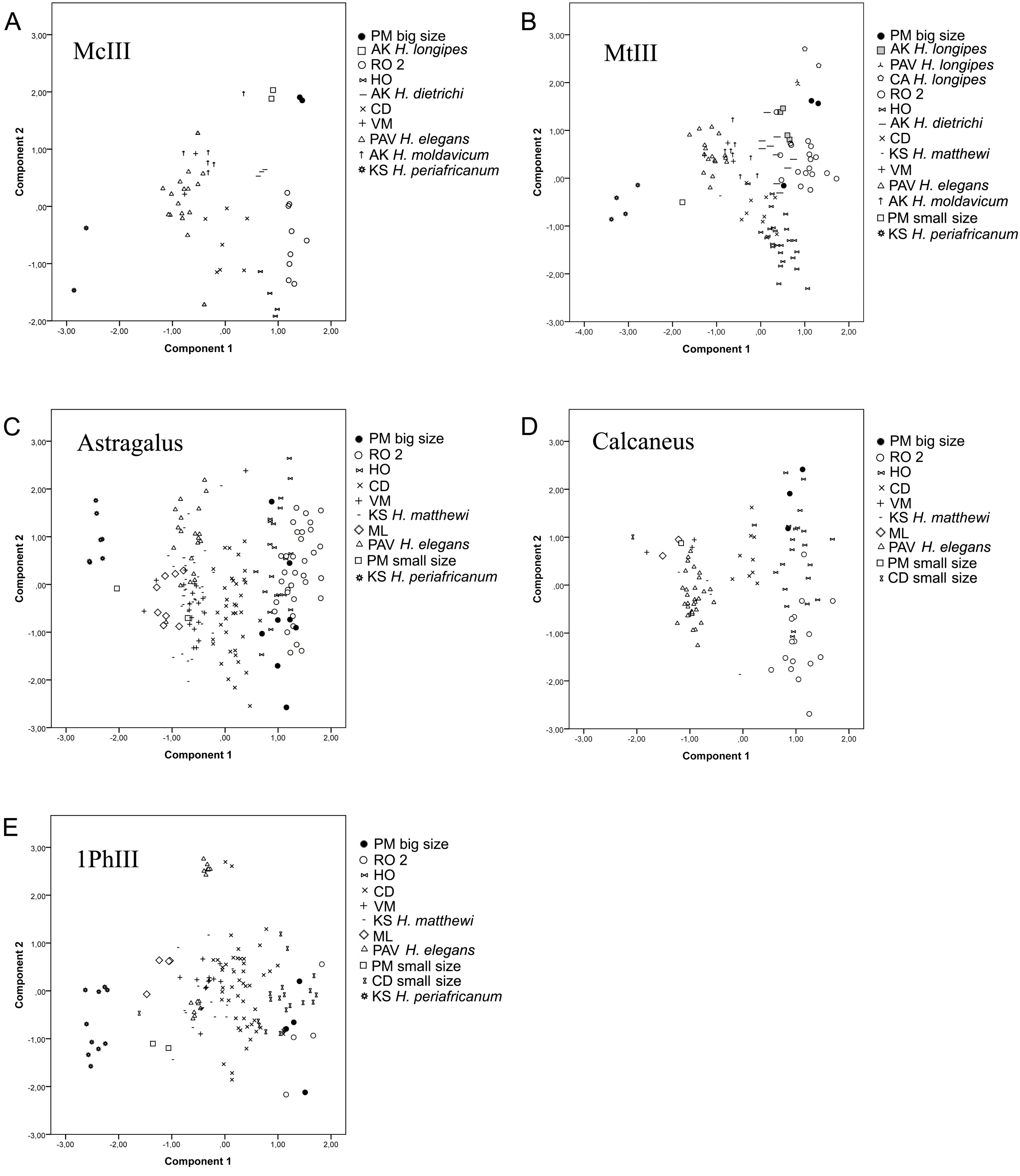

BUCCAL
parastyle
mesostyle
metastyle
paracone
metacone
apof
MESIAL
apre
dpof
DISTAL
dpre
hypocone
protocone
pli caballin
LINGUAL

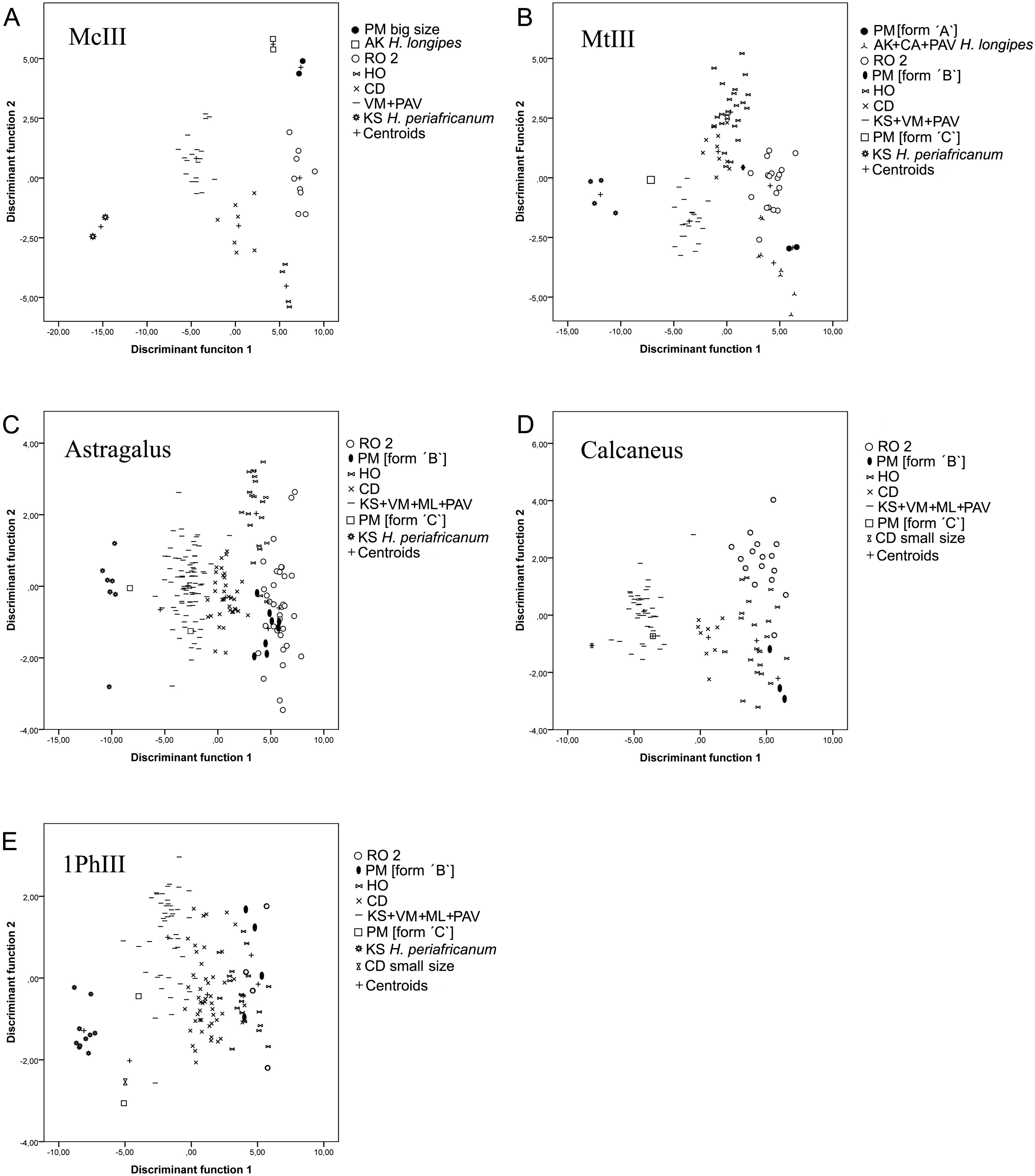

LINGUAL
linguaflexid
DOUBLE KNOT
metaconid
metastylid
isthmus
entoconid
parastylid
hypoconulid
DISTAL
postflexid
preflexid
MESIAL
ectoflexid
protostylid
hypoconid
protoconid
ectostylid
ptycostilid or pli caballinid
BUCCAL

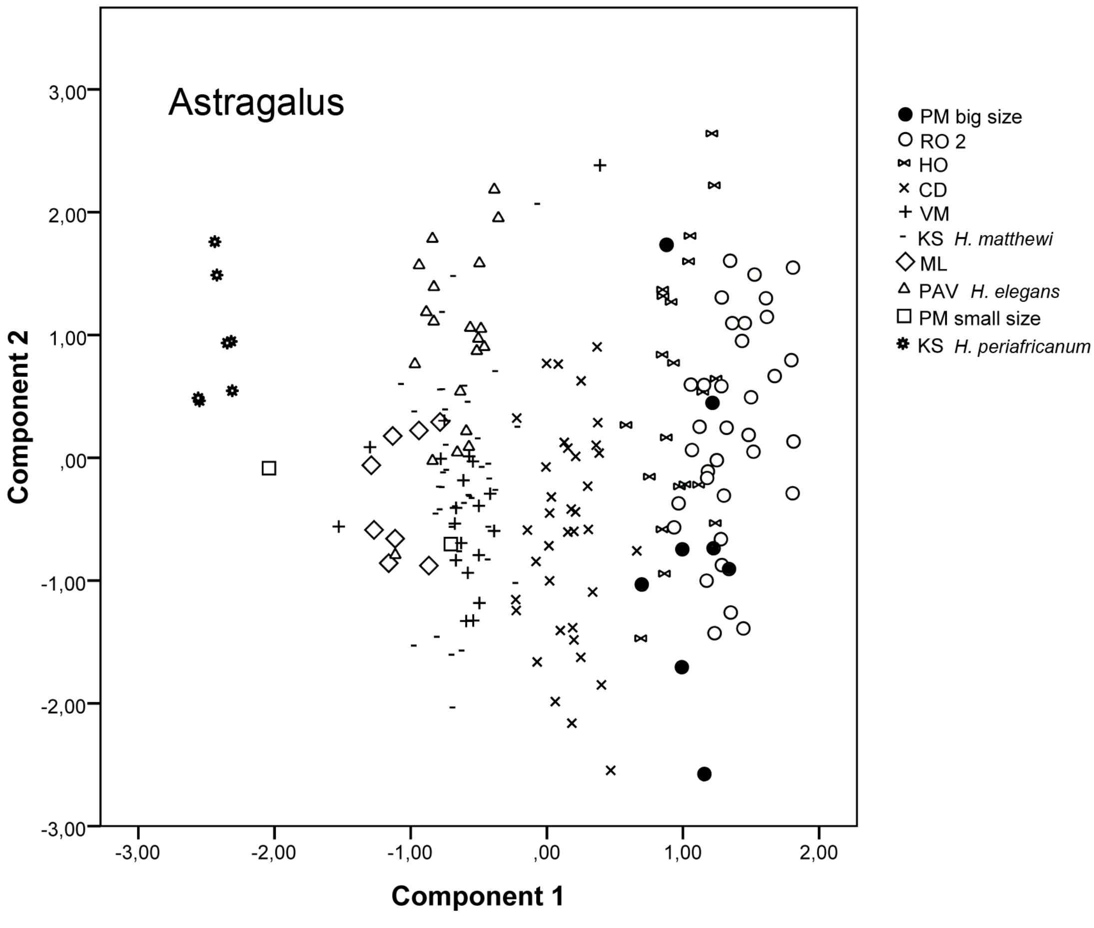


P3-4
Breadth (mm)
Length (mm)
PM big size
RO 2
LVF
CD
VM
KS *H. matthewi*
ML
PAV
PM small size
KS *H. periafricanum*
M1-2
Breadth (mm)
Length (mm)
PM big size
RO 2
LVF
CD
VM
KS *H. matthewi*
ML
PAV
PM small size
CD small size
KS *H. periafricanum*
p3-4
Breadth (mm)
Length (mm)
PM big size
RO 2
LVF
CD
VM
KS *H. matthewi*
ML
PAV
PM small size
ALJ
KS *H. periafricanum*
m1-2
Breadth (mm)
Length (mm)
PM big size
RO 2
LVF
CD
VM
KS *H. matthewi*
ML
PAV
PM small size
ALJ
KS *H. periafricanum*

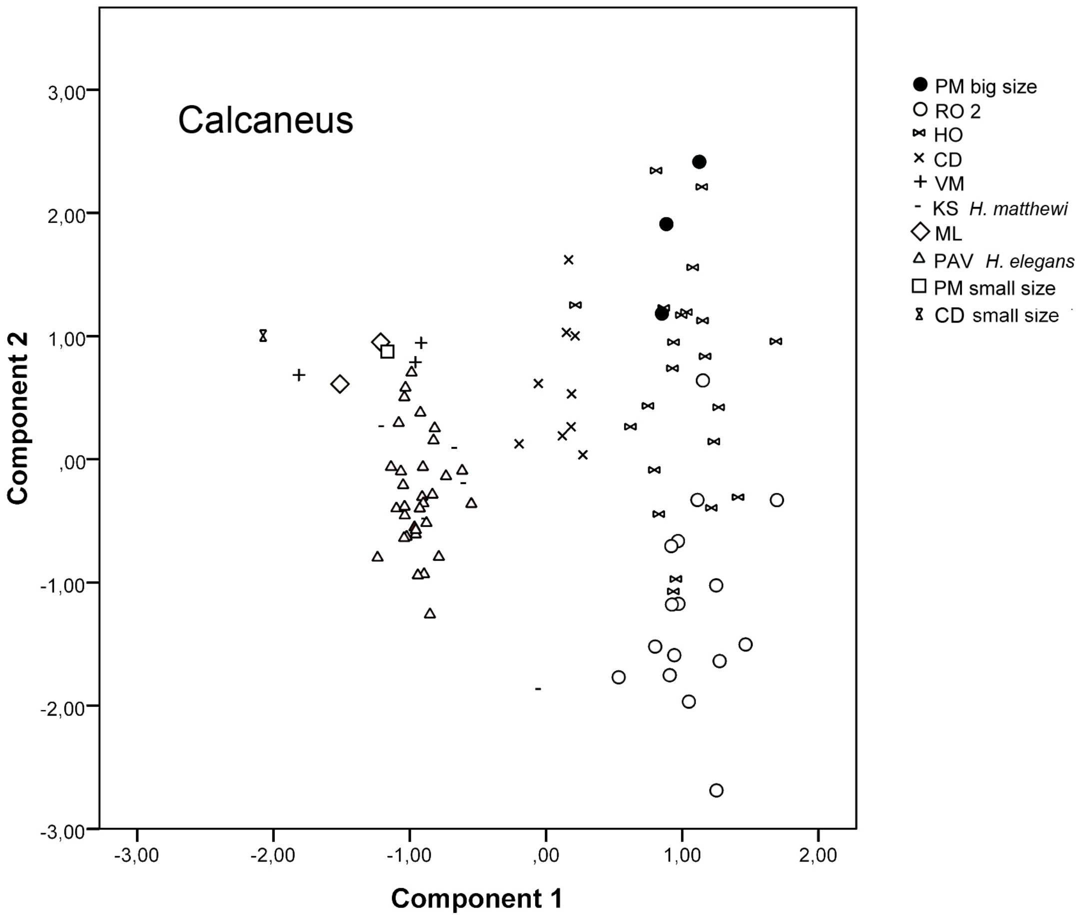

Mc III
Minimal breadth (3)
Minimal lengh (1)
PM big size
RO 2
HO
LVF
CD
VM
KS H. matthewi
ML
PAV
KS H. periafricanum
MtIII
Minimal breadth (3)
Maximal lengh (1)
PM big size
RO 2
HO
LVF
CD
VM
KS H. matthewi
ML
PAV
PM small size
KS H. periafricanum
McIII
Minimal breadth (11)
Maximal lengh (1)
PM big size
RO 2
HO
LVF
CD
VM
KS H. matthewi
ML
PAV
KS H. periafricanum
MtIII
Minimal breadth (11)
Maximal lengh (1)
PM big size
RO 2
HO
LVF
CD
VM
KS H. matthewi
ML
PAV
PM small size
KS H. periafricanum

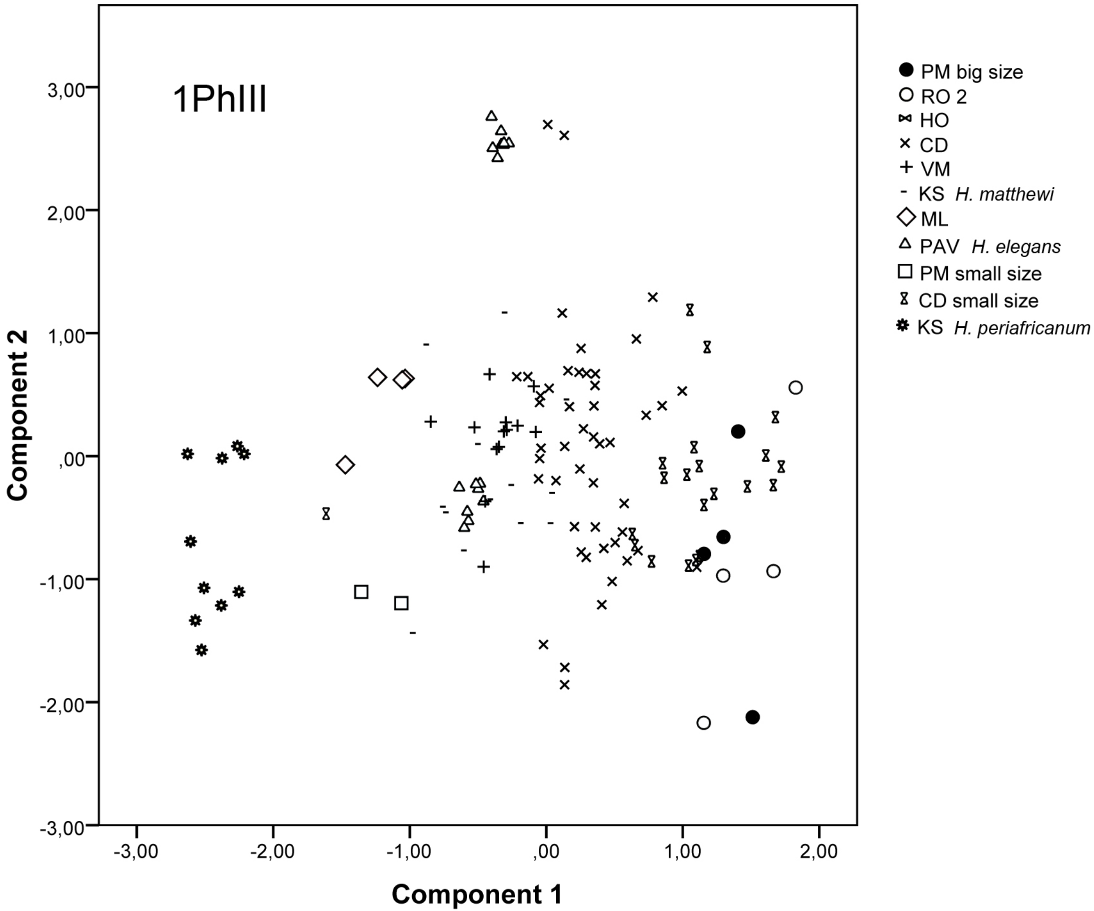

A
McIII
PM big size
AK H. longipes
RO 2
HO
AK H. dietrichi
CD
VM
PAV H. elegans
AK H. moldavicum
KS H. periafricanum
Component 1
Component 2
B
MtIII
PM big size
AK H. longipes
PAV H. longipes
CA H. longipes
RO 2
HO
AK H. dietrichi
CD
KS H. matthewi
VM
PAV H. elegans
AK H. moldavicum
PM small size
KS H. periafricanum
C
Astragalus
PM big size
RO 2
HO
CD
VM
KS H. matthewi
ML
PAV H. elegans
PM small size
KS H. periafricanum
D
Calcaneus
PM big size
RO 2
HO
CD
VM
KS H. matthewi
ML
PAV H. elegans
PM small size
CD small size
E
1PhIII
PM big size
RO 2
HO
CD
VM
KS H. matthewi
ML
PAV H. elegans
PM small size
CD small size
KS H. periafricanum

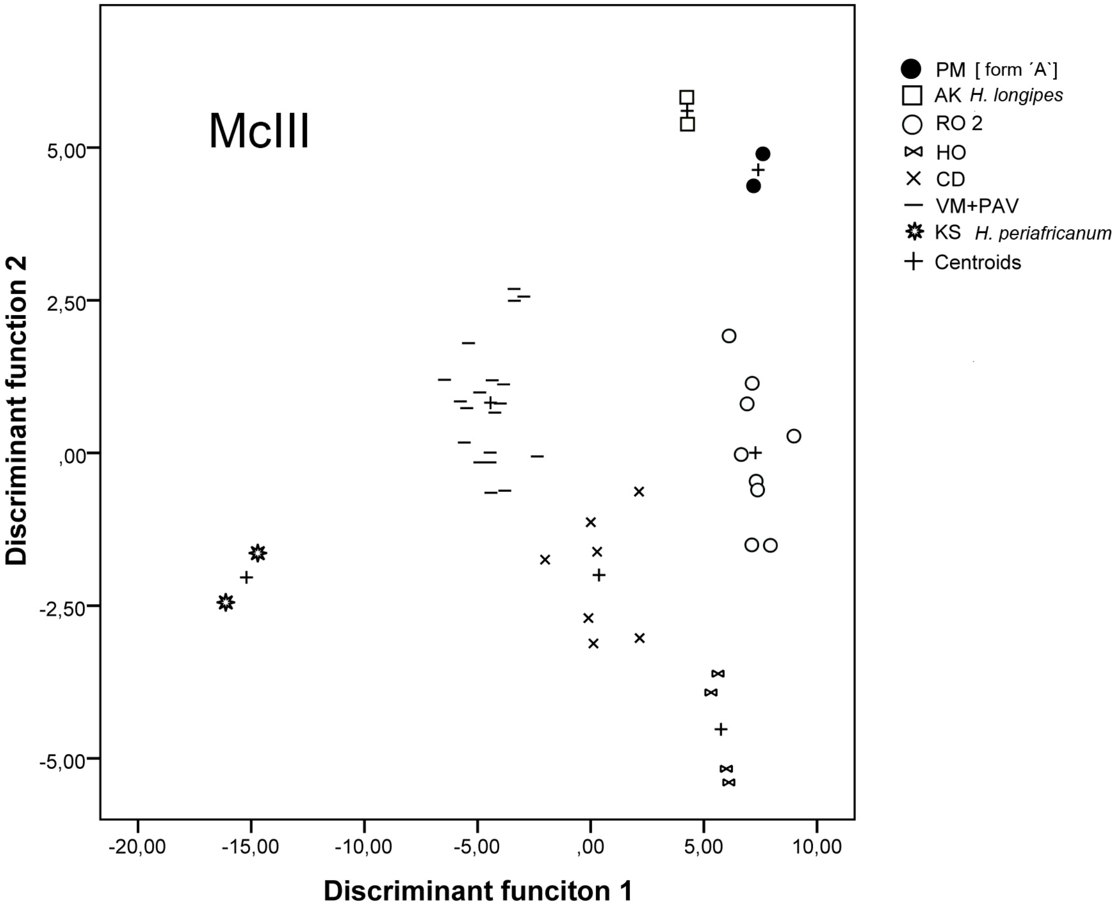

A
McIII
PM big size
AK H. longipes
RO 2
HO
CD
VM+PAV
KS H. periafricanum
Centroids
Discriminant function 2
Discriminant funciton 1
B
MtIII
PM [form ´A`]
AK+CA+PAV H. longipes
RO 2
PM [form ´B`]
HO
CD
KS+VM+PAV
PM [form ´C`]
KS H. periafricanum
Centroids
Discriminant Función 2
Discriminant function 1
C
Astragalus
RO 2
PM [form ´B`]
HO
CD
KS+VM+ML+PAV
PM [form ´C`]
KS H. periafricanum
Centroids
Discriminant function 2
Discriminant function 1
D
Calcaneus
RO 2
PM [form ´B`]
HO
CD
KS+VM+ML+PAV
PM [form ´C`]
CD small size
Centroids
Discriminant function 2
Discriminant function 1
E
1PhIII
RO 2
PM [form ´B`]
HO
CD
KS+VM+ML+PAV
PM [form ´C`]
KS H. periafricanum
CD small size
Centroids
Discriminant function 2
Discriminant function 1

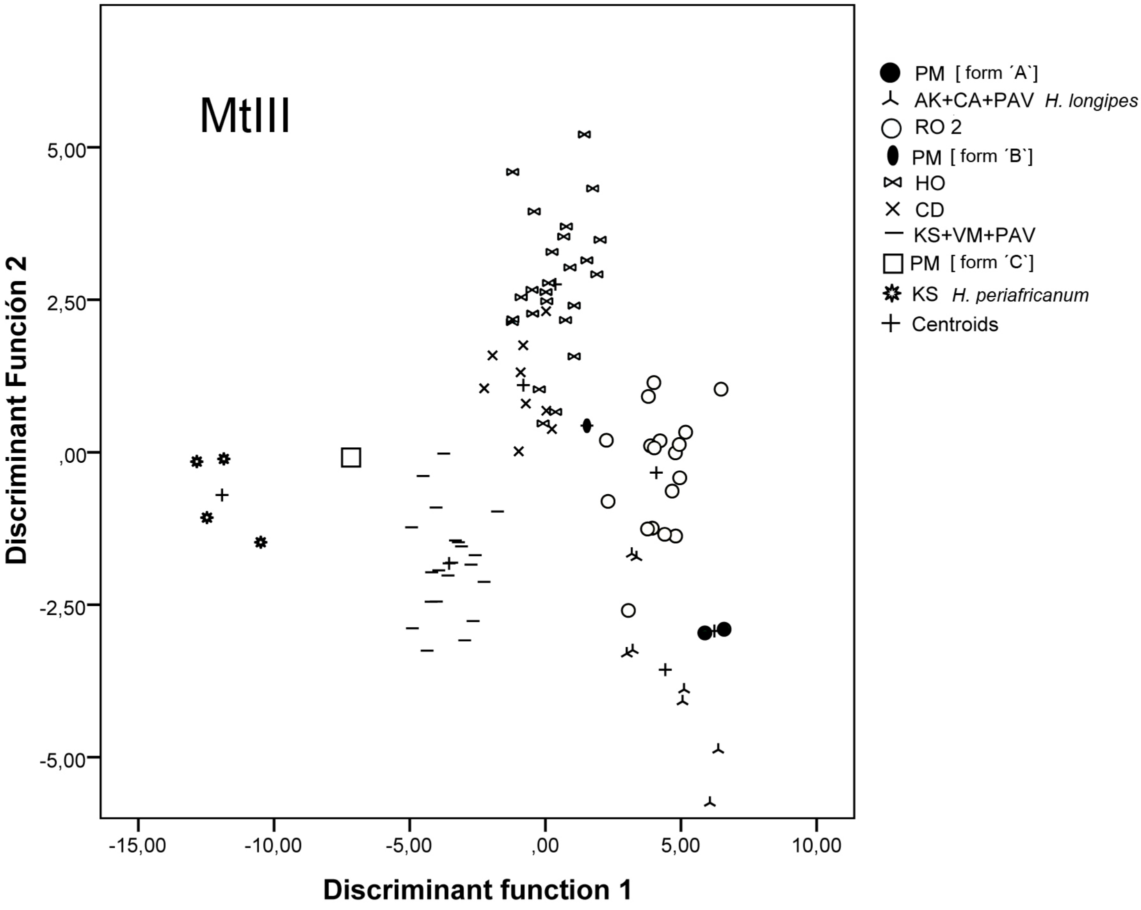


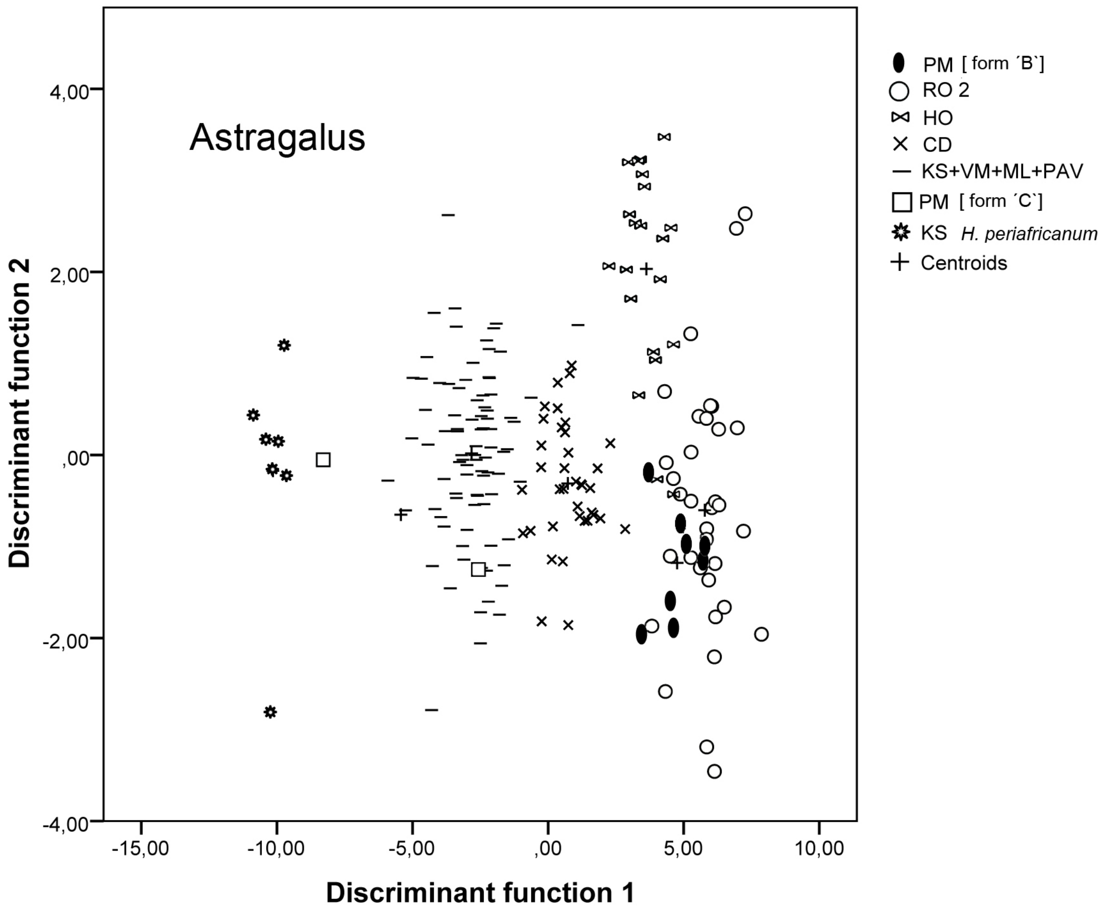
Astragalus
Component 2
Component 1
3,00
2,00
1,00
,00
-1,00
-2,00
-3,00
-3,00
-2,00
-1,00
,00
1,00
2,00
PM big size
RO 2
HO
CD
VM
KS H. matthewi
ML
PAV H. elegans
PM small size
KS H. periafricanum

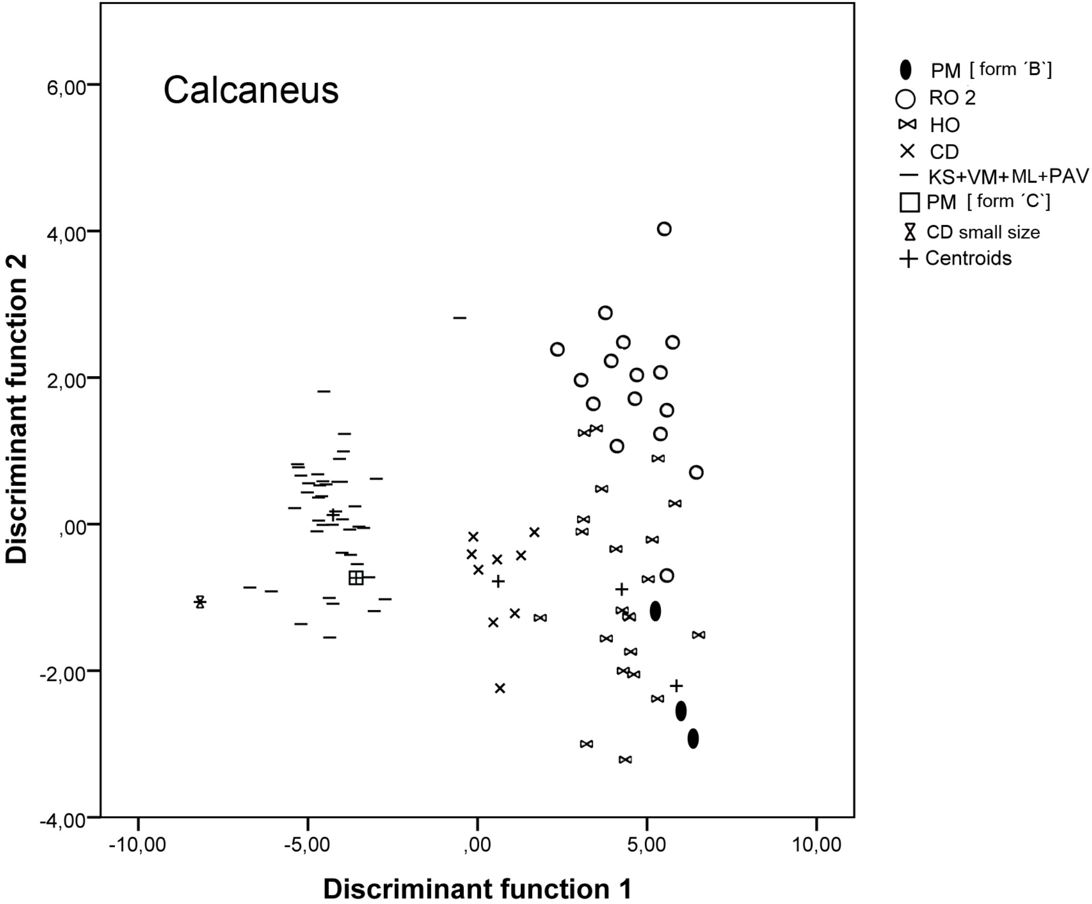

Calcaneus
Component 1
Component 2
3,00
2,00
1,00
,00
-1,00
-2,00
-3,00
-3,00
-2,00
-1,00
,00
1,00
2,00
PM big size
RO 2
HO
CD
VM
KS H. matthewi
ML
PAV H. elegans
PM small size
CD small size


1PhIII
Component 2
Component 1
3,00
2,00
1,00
,00
-1,00
-2,00
-3,00
-3,00
-2,00
-1,00
,00
1,00
2,00
PM big size
RO 2
HO
CD
VM
KS *H. matthewi*
ML
PAV *H. elegans*
PM small size
CD small size
KS *H. periafricanum*

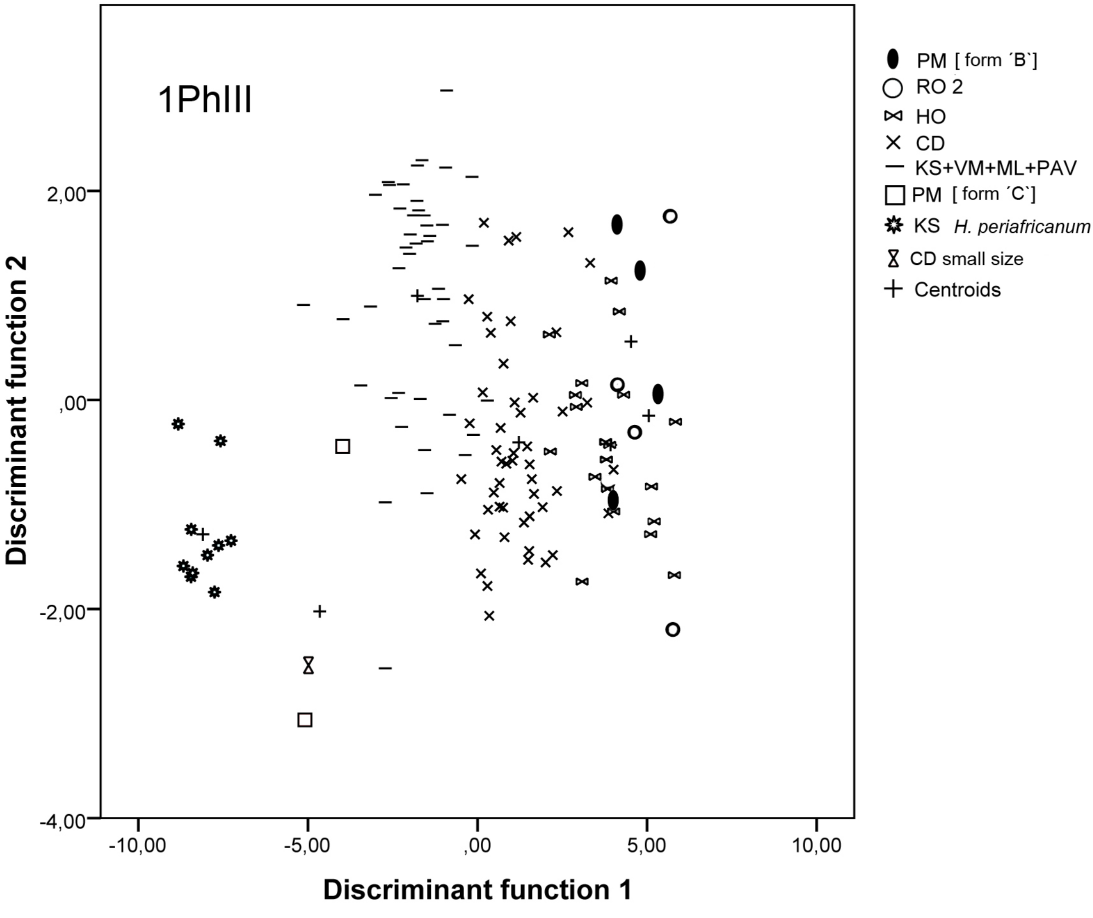

McIII
PM [form ´A`]
AK H. longipes
RO 2
HO
CD
VM+PAV
KS H. periafricanum
Centroids
Discriminant function 2
5,00
2,50
,00
-2,50
-5,00
-20,00
-15,00
-10,00
-5,00
,00
5,00
10,00
Discriminant funciton 1


MtIII
Discriminant Función 2
Discriminant function 1
5,00
2,50
,00
-2,50
-5,00
-15,00
-10,00
-5,00
,00
5,00
10,00
PM [form ´A`]
AK+CA+PAV H. longipes
RO 2
PM [form ´B`]
HO
CD
KS+VM+PAV
PM [form ´C`]
KS H. periafricanum
Centroids


Astragalus
Discriminant function 2
Discriminant function 1
4,00
2,00
,00
-2,00
-4,00
-15,00
-10,00
-5,00
,00
5,00
10,00
PM [form ´B`]
RO 2
HO
CD
KS+VM+ML+PAV
PM [form ´C`]
KS H. periafricanum
Centroids



Calcaneus
PM [form ´B`]
RO 2
HO
CD
KS+VM+ML+PAV
PM [form ´C`]
CD small size
Centroids
Discriminant function 2
Discriminant function 1
6,00
4,00
2,00
,00
-2,00
-4,00
-10,00
-5,00
,00
5,00
10,00


1PhIII
PM [form ´B`]
RO 2
HO
CD
KS+VM+ML+PAV
PM [form ´C`]
KS H. periafricanum
CD small size
Centroids
2,00
,00
-2,00
-4,00
-10,00
-5,00
,00
5,00
10,00
Discriminant function 2
Discriminant function 1

HYPSODONTY INDEX

	H. laromae (RO2)			*H.* [form 'B'] (PM)			*H. primigenium* (NO)			*H. concudense* (CD)		
	N	**Sd**	**X**	**N**	**Sd**	**X**	**N**	**Sd**	**X**	**N**	**Sd**	**X**
P3-4	-	-	-	(2)	0.13	2.4	(6)	0.14	1.8	(13)	0.13	2.5
M1-2	-	-	-	(2)	0.08	2.6	(6)	0.14	2.5	(19)	0.12	2.6
p3-4	(1)	-	2	(2)	0.09	2.5	(2)	0.11	2.1	(16)	0.09	2.4
m1-2	(1)	-	2.2	(2)	0.04	2.6	(3)	0.1	2.4	(19)	0.12	2.6

	H. matthewi (VM)			*H. matthewi* (KS)			*H. matthewi* (ARQ)			*H. periafricanum* (KS)		
	N	**Sd**	**X**	**N**	**Sd**	**X**	**N**	**Sd**	**X**	**N**	**Sd**	**X**
P3-4	(1)	-	2.5	(3)	0.11	2.5	(3)	0.1	2.7	(2)	0.13	2.9
M1-2	(9)	0.04	2.4	(17)	0.16	2.7	(10)	0.11	2.8	(7)	0.14	3.2
p3-4	(1)	-	2.5	(2)	0.16	2.3	(1)	-	2.7	(2)	0.02	2.8
m1-2	(5)	0.16	2.7	(14)	0.18	2.7	(3)	0.05	2.8	(5)	0.04	3.1

	MtIII1/MtIII3			McIII1/McIII3			MtIII1/MtIII11			McIII1/McIII11			Body mass
	(min.)	X	(máx.)	(min.)	X	(máx.)	(min.)	X	(máx.)	(min.)	X	(máx.)	Kg.
Puente Minero (*H.* cf. *H. longipes*)	9.8	9.9	10	11.3	11.4	11.4	13.4	13.5	13.6	14.3	14.4	14.5	-
Puente Minero (*H. laromae*)	-	11.4	-	11.3	11.5	11.7	-	14.4	-	15.3	15.5	15.6	331
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
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
Nombrevilla (*H. primigenium*)	-	12.6	-	-	13.8	-	-	-	-	-	-	-	178
L.V.F. (*H. primigenium*)	9.4	10.3	10.8	10.6	11.3	12.3	13.9	14.4	14.8	-	15.2	-	170
Concud (*H. concudense*)	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
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
Las Casiones (*H. matthewi*)	-	11	-	-	14.2	-	-	13.3	-	-	17.1	-	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
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	231
Puente Minero (*H. matthewi*)	10.4	10.5	10.5	-	-	-	13.1	13.4	13.8	-	-	-	89
Las Casiones (*H. periafricanum*)	8.7	9	9.3	9.4	9.8	10.2	11.1	11.4	11.9	12.6	13.1	13.6	29

		H. periafricanum (KS)		*H. matthewi* (ML, KS, VM, PAV)	
		Length	Breadth	Length	Breadth
p3-4	**Puente Minero** small size				
	(PM-1070)	3.76**	0.497	1.78	3.23*
m1-2	**Puente Minero** small size				
	(PM-731)	2.406	1.694*	2.168*	1.499
	(PM-470)	2.159*	4.023**	2.328*	0.142
P3-4	**Puente Minero** small size				
	(PM-464)	1.51	2.367	3.06*	2.688*
	(PM-114)	3.031*	3.627*	1.129	1.774
MtIII	**Puente Minero** small size				
	(PM-960)	3.847*		7.13**	
	Puente Minero small size				
	(PM-883)	3.459*		8.05**	

Probability: * = < 0.05; ** = < 0.001

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	0.979	First component	2	0.983
	14	0.972		5	0.98
	10	0.971		4	0.979
Second component	8	0.38	Second component	3	0.295
	3	0.165		4	0.03
	11	0.158	**Calcaneus**		
			First component	5	0.962
MtIII				4	0.956
First component	10	0.962	Second component	3	0.372
	11	0.962		4	0.116
	4	0.955	**First phalanx**		
Second component	2	0.461	First component	7	0.983
	1	0.438		4	0.982
	14	-0.009		6	0.982
			Second component	8	0.391
				3	0.046

	Original	N	0	1	2	3	4	5	6	7	8
McIII	1	8	-	100% (8)	0%	0%	0%	0%	-	-	0%
	2	2	-	0%	100% (2)	0%	0%	0%	-	-	0%
	3	3	-	0%	0%	100% (3)	0%	0%	-	-	0%
	4	12	-	0%	0%	0%	100% (12)	0%	-	-	0%
	5	19	-	0%	0%	0%	0%	100% (19)	-	-	0%
	8	1	-	0%	0%	0%	0%	0%	-	-	100% (8)
MtIII	0	4	100% (4)	0%	0%	0%	0%	0%	0%	-	0%
	1	19	0%	94.7% (18)	5.3% (1)	0%	0%	0%	0%	-	0%
	2	1	0%	100% (1)	0%	0%	0%	0%	0%	-	0%
	3	22	0%	0%	13.6% (3)	86.4% (19)	0%	0%	0%	-	0%
	4	17	0%	0%	0%	5.9% (1)	88.2% (15)	5.9% (1)	0%	-	0%
	5	20	0%	0%	0%	0%	5% (1)	95% (19)	0%	-	0%
	6	1	0%	0%	0%	0%	0%	0%	100% (1)	-	0%
	8	2	0%	0%	0%	0%	0%	0%	0%	-	100% (2)
Astragalus	1	34	-	73.5% (25)	23.5% (8)	2.9% (1)	0%	0%	0%	-	0%
	2	8	-	37.5% (3)	62.5% (5)	0%	0%	0%	0%	-	0%
	3	24	-	0%	12.5% (3)	87.5% (21)	0%	0%	0%	-	0%
	4	59	-	0%	5.1% (3)	0%	91.5% (54)	3.2% (2)	0%	-	0%
	5	85	-	0%	0%	0%	2.4% (2)	88.2% (75)	9.4% (8)	-	0%
	6	2	-	0%	0%	0%	0%	50% (1)	0%	-	50% (1)
	8	8	-	0%	0%	0%	0%	0%	0%	-	100% (8)
Calcaneus	1	16	-	87.5% (14)	6.3% (1)	0%	6.3% (1)	0%	0%	0%	-
	2	3	-	0%	100% (3)	0%	0%	0%	0%	0%	-
	3	22	-	18.2% (4)	0%	81.8% (18)	0%	0%	0%	0%	-
	4	16	-	6.3% (1)	0%	0%	93.8% (15)	0%	0%	0%	-
	5	42	-	0%	0%	0%	2.4% (1)	92.9% (39)	2.4% (1)	2.4% (1)	-
	6	1	-	0%	0%	0%	0%	0%	100% (1)	0%	-
	7	1	-	0%	0%	0%	0%	0%	0%	100% (1)	-
First phalanx	1	4	-	50% (2)	50% (2)	0%	0%	0%	0%	0%	0%
	2	4	-	25% (1)	50% (2)	0%	25% (1)	0%	0%	0%	0%
	3	22	-	22.7% (5)	9.1% (2)	50% (11)	18.2% (4)	0%	0%	0%	0%
	4	84	-	1.2% (1)	1.2% (1)	3.6% (3)	90.5% (76)	3.6% (3)	0%	0%	0%
	5	46	-	0%	0%	0%	6.5% (3)	89.1% (41)	4.3% (2)	0%	0%
	6	2	-	0%	0%	0%	0%	0%	100% (2)	0%	0%

7	1	-	0%	0%	0%	0%	0%	0%	100% (1)	0%	
8	10	-	0%	0%	0%	0%	0%	0%	0%	100% (10)	