

Chapter 2

Nomenclatures and Taxonomy

Abstract In this chapter, we compare and redefine each species of horses from South America. We discussed different characters, nomenclature and measurements that used in fossil horses study. We used both morphological and morphometric characters on skulls, mandibles, teeth, and postcranial remains from different localities. Bivariate and multivariate analyses were performed to estimate variation and differences in size and proportions. We think that the cranial and dental morphology and this quantitative multivariate analysis support the recognized in *Hippidion* genus three valid species. We questioned the use of subgenus *Amerhippus*. The new molecular data increases the known phenotypic plasticity of horses and consequently casts doubt on the taxonomic validity of the subgenus *Amerhippus*. In the case of *Equus* genus, we recognized three valid species (*Equus neogeus*, *Equus andium*, and *Equus insulatus*). We included *Equus santaeelenae* into the *E. insulatus*. The status of *Equus lasallei* needs a revision, but there are small samples to make an evaluation.

Keywords Horses • South America • Taxonomy • Morphology • Systematic

2.1 Introduction

The fossil record of Equidae from South America is one of the best known of mammal's paleontology (Simpson 1951). This group arose in North America during the Eocene, where they had an exceptional adaptive radiation. As remarked before, the study of fossil horses in South America began in the nineteenth century when Darwin found one molar in Argentina (Owen 1840). Ever since, notes and articles grew rapidly, which in most cases do not express the global diversity of this group. The most recent papers of Equidae in South America (Alberdi 1987; Alberdi and Prado 1992, 1993, 2004; Prado and Alberdi 1994, 1996, 2012; Alberdi et al. 1989, 2001a, b, 2003; Prado et al. 1987, 1998, 2000, 2005, 2013a, b; among others) distinguish into two genera: *Equus* and *Hippidion*. Both genera share common

characteristics such as a large skull in comparison with body size. However, each genus has specific dental morphology, with a clear intraspecific variability. *Hippidion* has a more primitive morphology than *Equus*, and its body structure is the most robust (Prado 1984; Alberdi 1987; Alberdi et al. 1986, 1987; Prado and Alberdi 1994, 2014, 2016; Der Sarkissian et al. 2015, among others).

The *Hippidion* genus was defined by Owen (1869) based on a molar from the Lagoa Santa (Brazil) and figured by Lund (1846). Alberdi and Prado (1993) and Prado and Alberdi (1996) considered that this genus is endemic in South America, where it is recorded from the Pliocene to the late Pleistocene mainly in Argentina, Bolivia, Brazil, Chile, Colombia, Peru, and Uruguay. Alberdi and Prado (1993) reviewed this group and recognized three species: *Hippidion principale* (Lund), *Hippidion devillei* (Gervais), and *Hippidion saldiasii* (Roth).

The *Amerhippus* subgenus was created by Hoffstetter (1950) to include all different species of *Equus* genus from South America. Hoffstetter (1950, pp. 433–436, 1952, pp. 245–286) justified this subgenus based on only one characteristic: lack of infundibular marks in the lower incisor surface and consequent loss of surface enamel. Nevertheless, Eisenmann (1979a, b, c) analyzed the first characteristic in living and fossil equids and concluded that they show a high variability. In our opinion, this is a very variable feature because it is linked to the changes of the dental occlusal surfaces with wear (Alberdi 1974). Consequently, its systematic value is difficult to evaluate. Orlando et al. (2008, p. 533) suggest doubt on the taxonomic validity of the subgenus *Equus* (*Amerhippus*): they write ...“we show by retrieving new ancient mtDNA sequences that hippidions and *Equus* (*Amerhippus*) *neogeus* were members of two distinct lineages. Furthermore, using a rigorous phylogenetic approach, we demonstrate that while formerly the largest equid from Southern America, *Equus* (*Amerhippus*) was just a member of the species *Equus caballus*”. This new data strengthens the known phenotypic plasticity of horses and, therefore, we stopped using *Amerhippus* subgenus.

The earliest appearances of *Equus* in South America record correspond to the middle Pleistocene of Tarija (Bolivia), dated by MacFadden et al. (1983) and MacFadden (2013) around 1.0–0.8 Ma. Many articles have been published to arrange the knowledge of the *Equus* species in South America. Prado and Alberdi (1994) reviewed this group and recognized five species: *Equus andium* Branco, *Equus insulatus* Ameghino, *Equus neogeus* (Lund), *Equus santaeelenae* (Spillmann), and *Equus lasallei* (Daniel). This revision is based on the numerous remains from Argentina, Bolivia, Brazil, and Ecuador.

In order to characterize, compare, and redefine each species, we used both morphological and morphometric characters on skulls, mandibles, teeth, and postcranial remains from different localities of South America. Bivariate and multivariate analyses were performed to estimate variation and differences in size and proportions.

2.2 Morphometric Analysis

For character nomenclature and measurements in horses, we follow the recommendations of the “*Hipparion* Conference”, New York, (Eisenmann et al. 1988). All dimensions are expressed in millimeters (Figs. 2.1, 2.2, 2.3, and 2.4). We calculated the hypsodonty index on unworn or only slightly worn teeth (P3-4/p3-4, M1-2/m1-2) as H/L ratio, where H represents the maximal high of the tooth and L represents the maximal length of 1 cm from the base of the crown (Alberdi 1974). Two bivariate plots were achieved to analyze the robustness and slenderness of third metacarpals and metatarsal (MCIII, MTIII). We compare the maximum length (MCIII1 or MTIII1) with the minimal breadth at the middle of the bone (MCIII3 or MTIII3). Bivariate plots were also generated for first phalanx of the central digit (1PHIII) (Eisenmann et al. 1988).

We estimated the body masses using the third metacarpal MCIII, MCIII13 measurement ($r = 0.982$) and first phalanx of the central digit, PHIII5 measurement ($r = 0.991$), following Alberdi et al. (1995, see Chap. 6).

The most popular method for summarizing multivariate scatter, among linear metric methods, has been principal component analysis (PCA), a method that

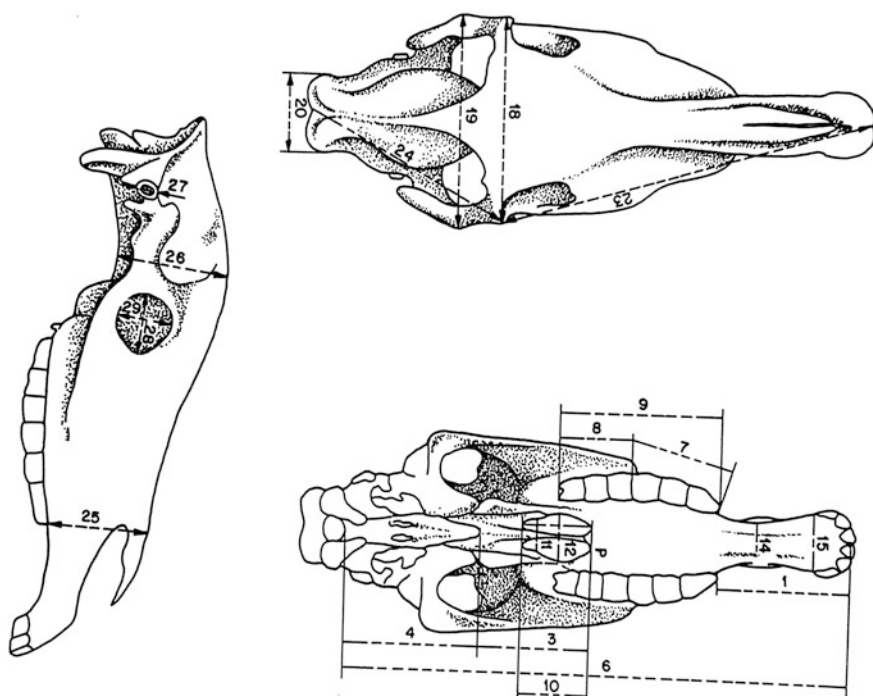


Fig. 2.1 The measurements and recommendations of the different character of skull following the “*Hipparion* Conference” (modified from Eisenmann et al. 1988)

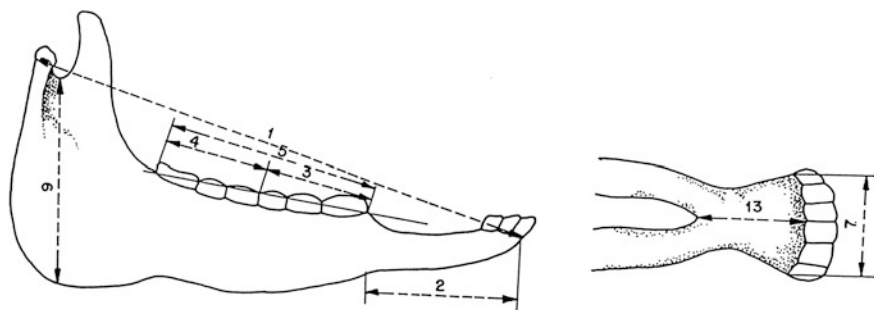
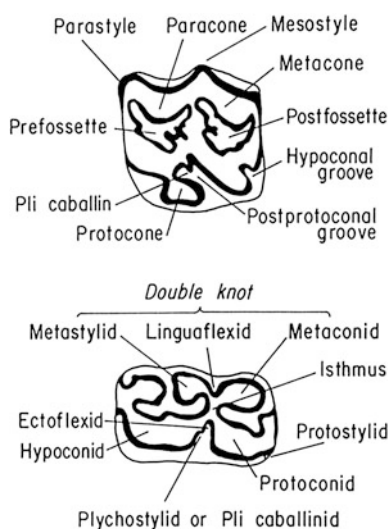


Fig. 2.2 The measurements and recommendations of the different character of mandible following the “*Hipparion* Conference” (modified from Eisenmann et al. 1988)

Fig. 2.3 The measurements and recommendations of the different character of teeth following the “*Hipparion* Conference” (modified from Eisenmann et al. 1988)



provides displays in the lowest possible dimension summarizing the maximum variance and covariance for multidimensional data. We use this method in metacarpals, metatarsals, astragali, and first phalanges to evaluate similarities and/or differences among the *Hippidion* and *Equus* remains, as to assess their relationship among the different localities. Then, discriminate analyses (DA) were performed by means of “variables in the block in a single step” method of groups previously identified by PCA. This is the aim of maximizing the separation between groups already recognized, as to evaluating whether the centroids differ significantly or not. The results of PCA enable us to group the remains by differences in size, while DA puts out how significant are the differences among them (Marcus 1990; Reymont 1991). In order to identify which character supported the best group discrimination, we terminated the characters that indicated maximal contribution values for the PCA (Table 2.1). Calculations were made using SPSS 15.0.

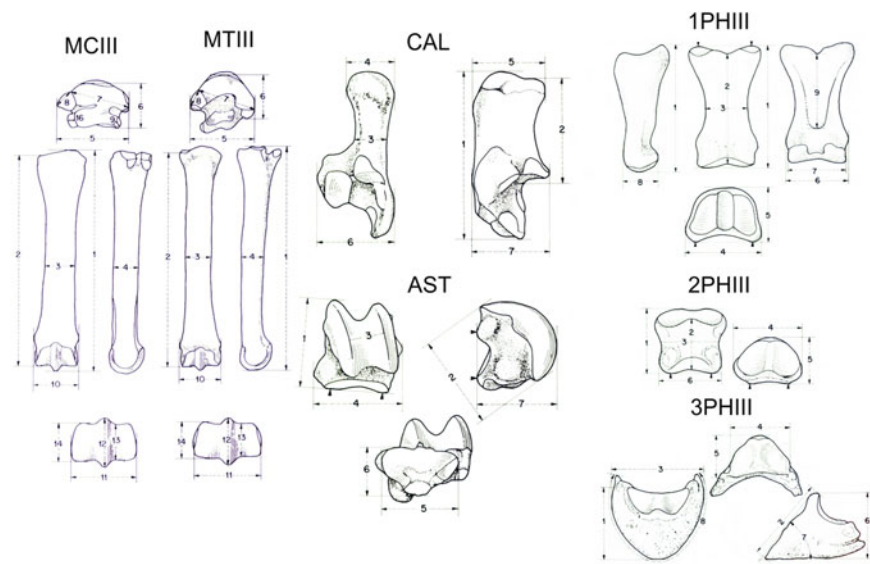


Fig. 2.4 The measurements and recommendations of the different character of appendicular skeleton following the “*Hipparion* Conference” (modified from Eisenmann et al. 1988)

Table 2.1 Character most important for Principal Component Analysis (PCA) 1, 2 and 3 components for *Hippidion* and *Equus* species. The numbers correspond to the measurements in Fig. 2.4 in this volume

<i>Hippidion</i>			<i>Equus</i>		
Principal component of limb bones	Number of character	Eigen value	Principal component of limb bones	Number of character	Eigen value
Third metacarpal			Third metacarpal		
First	13	0.945	First	13	0.962
	4	0.942		10	0.960
	5	0.936		11	0.958
	14	0.917		4	0.950
				5	0.947
Second	8	0.788	Second	8	0.727
Third	12	0.587	Third	6	0.497
Third metatarsal			Third metatarsal		
First	4	0.919	First	13	0.965
	5	0.919		10	0.964
	7	0.91		11	0.959
	12	0.909		14	0.955
				12	0.949
Second	8	0.642	Second	8	0.919
	10	-0.532			
Third	8	0.583	Third	8	0.37

(continued)

Table 2.1 (continued)

<i>Hippidion</i>			<i>Equus</i>		
Principal component of limb bones	Number of character	Eigen value	Principal component of limb bones	Number of character	Eigen value
Astragalus			Astragalus		
First	7	0.966	First	2	0.985
	2	0.956		1	0.978
	4	0.950		7	0.977
	1	0.944		5	0.972
Second	6	0.526	Second	3	0.346
Third	3	0.485	Third	4	0.206
Calcaneus			Calcaneus		
First	1	0.954	First	1	0.956
	5	0.849		7	0.949
	6	0.839		6	0.941
Second	2	0.684	Second	3	0.470
Third	7	-0.54	Third	5	-0.316
First phalanx			First phalanx		
First	5	0.905	First	6	0.965
	7	0.896		4	0.959
	8	0.872		7	0.958
	1	0.862		1	0.953
Second	9	0.656	Second	9	0.500
Third	9	0.522	Third	5	0.433
Second phalanx			Second phalanx		
First	4	0.967	First	4	0.957
	3	0.944		3	0.947
	5	0.917		1	0.937
Second	6	-0.412	Second	2	0.471
Third	5	-0.388	Third	5	-0.369

2.3 Data Set

Many of the South American remains do not have a precise stratigraphical position because they come from old collections where only mention the locality but many times the stratigraphic level or date is not indicated. The specimens studied here come from the following sites: Tarija (Bolivia) place at the middle Pleistocene by MacFadden et al. (1983) and MacFadden (2013) where are present *Hippidion* and *Equus* genera; Salinas Oil Fields and La Carolina in Santa Elena Peninsula and many sites in the Ecuadorian Andes and Río Chiche (Ecuador) only with *Equus* genus. Santa Elena site has data by 14C around 26,000 \pm 100 BP (Baldock 1982); Ecuadorian Andes sites (Punín, Chalán, Quebrada Colorada, Alangasí, Quebrada Grande, El Colegio, etc.) are dated between 40,000 and 4000 years BP by Dugas (1986);

and Río Chiche locality is considered as older than the others (Hoffstetter 1952). In Argentina, there are localities such as punta Vorohué, Miramar, Olivos, and La Plata, among others, from the early-middle Pleistocene in the Buenos Aires province; Barranco Negro in Jujuy, Río Salado, and Quequén Salado in the Pampean area and the archaeological sites in the Patagonian region from the latest Pleistocene (Alberdi et al. 1986, 1987; Prado and Alberdi 1999, 2010; Prado et al. 2013a, 2015; and references therein). The localities from Brazil, Chile, and Perú correspond to the late Pleistocene (Alberdi and Frassinetti 2000; Pujos and Salas 2002, 2004; Alberdi et al. 2003, 2004) (Fig. 2.5; Appendix A).

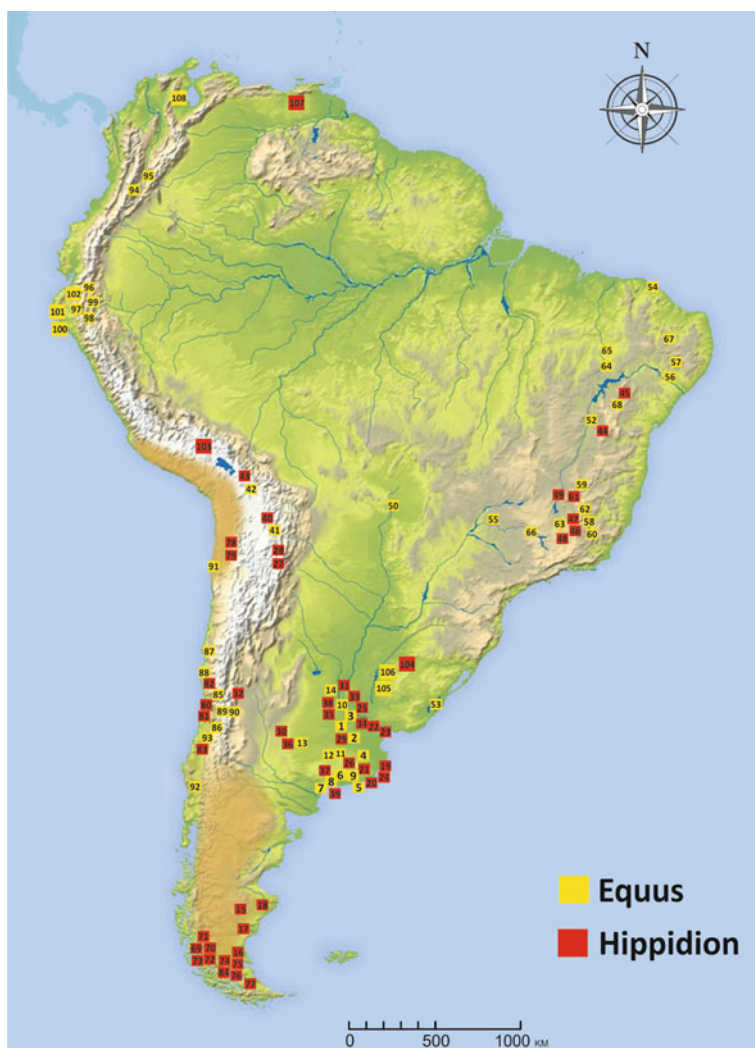


Fig. 2.5 Geographic distribution of different taxa of *Hippidion* and *Equus* from South America

PCA and DA were performed on 68 third metacarpals (MCIII) of *Equus* and 39 of *Hippidion*, 77 third metatarsals (MTIII) of *Equus* and 34 of *Hippidion*, 64 astragali (AST) of *Equus* and 31 of *Hippidion*, 60 calcanei (CAL) of *Equus* and 22 of *Hippidion*, 144 first phalanges (1PHIII) of *Equus* and 65 of *Hippidion*, and 102 s phalanges (2PHIII) of *Equus* and 66 of *Hippidion* from many sites of different South American populations.

2.4 Bivariate Analyses

The bivariate analyses performed by contrasting length versus width of the upper and lower cheek teeth (P3-4/p3-4 and M1-2/m1-2), as well as considering length/protocone length ratio in upper teeth and length/double-knot ratio and length/postflexid ratio in lower teeth permit us a first discriminations (Figs. 2.6 and 2.7).

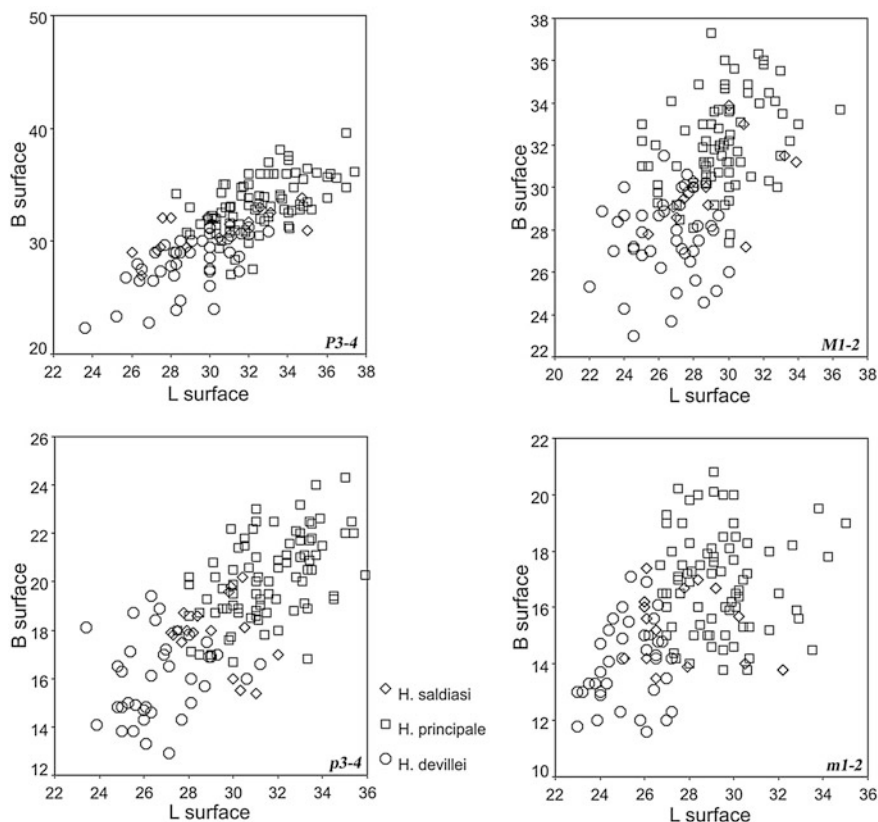


Fig. 2.6 Bivariate diagrams of teeth from the South American *Hippidion* species. Abbreviations: *L* length; *B* at 1 cm base of tooth

The majority of teeth that we measure are located in complete maxilla and mandibles (this is the case of *E. andium* from the Andean localities), and in consequence, we take up only the occlusal measurements. Other problems to measure are different ages of specimens. Those bring along a major distribution of points in the different plots. Concretely, in the bivariate plots of *Hippidion* teeth, P3-4/p3-4 y M1-2/m12, we would find two groups that overlap between them: *H. principale* (larger in size) and *H. devillei* (smaller in size). The spatial distribution of the small-sized *H. saldiassi* teeth overlaps the area where *H. devillei* and *H. principale* come together (Fig. 2.6). In the *Equus* teeth, P3-4/p3-4 and M1-2/m1-2) plots likewise we would find two groups that overlap between them: one small in size, *E. andium* and another larger in size that grouped *E. neogeus*, *E. insulatus*, and *E. santaeelenae* that overlap among them (Fig. 2.7). The bivariate diagram of metapodials: MCIII1 and MTIII versus MCIII3 and MTIII3 and 1PHIII1 versus 1PHIII3 gives us a vision of its proportions (Fig. 2.8). In *Equus* species, we observe a similar distribution that we described with the teeth, where the small species, *E. andium*, have a clear discrimination. The other species of *Equus* (*E. neogeus*,

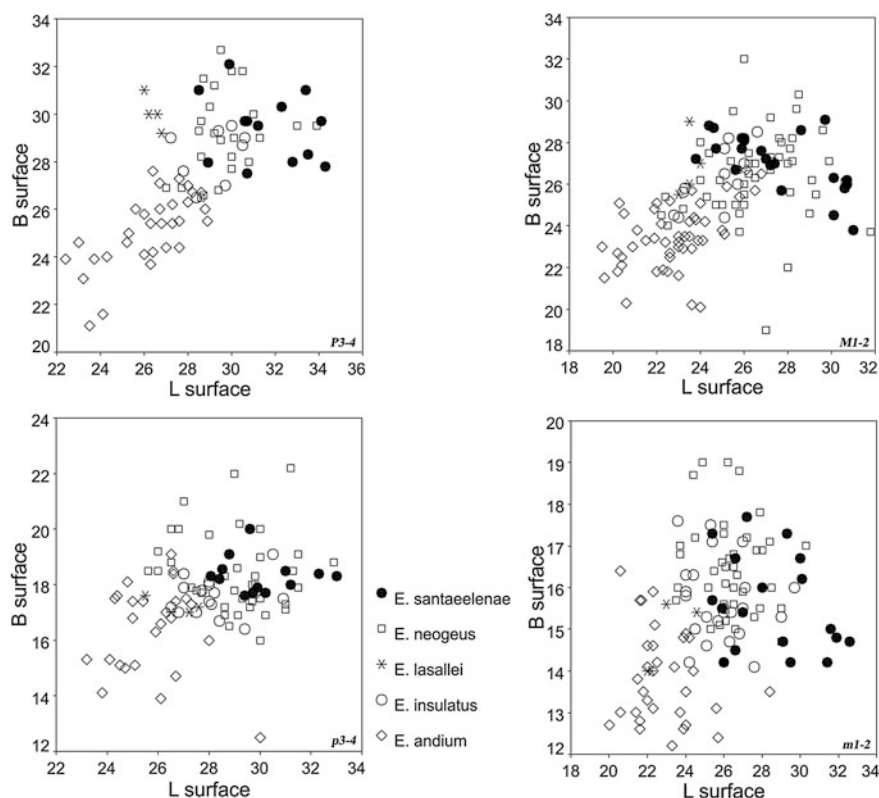


Fig. 2.7 Bivariate diagrams of teeth from the South American *Equus* species. Abbreviations as in Fig. 2.6

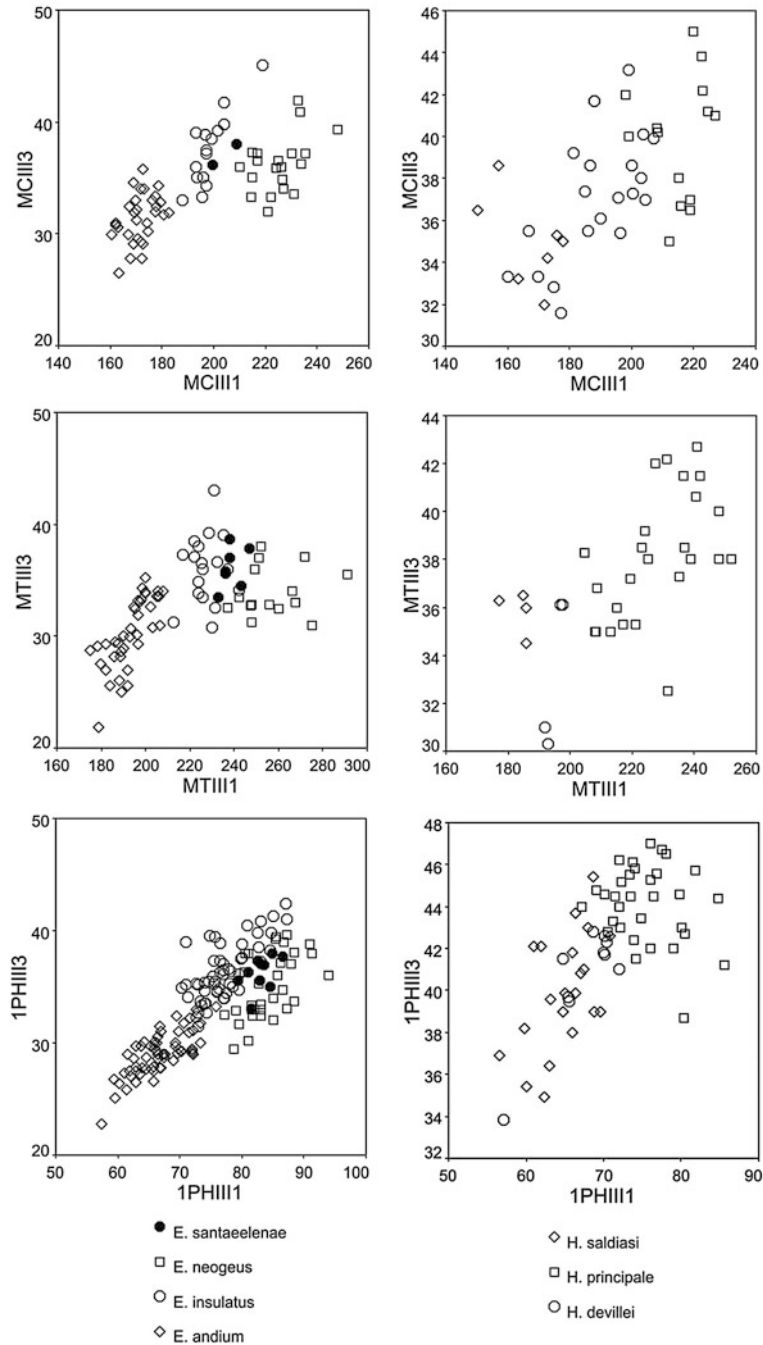


Fig. 2.8 Bivariate diagrams of MCIII1/MTIII1/1PHIII1 versus MCIII3/MTIII3/1PHIII3 bones of *Equus* and *Hippidion* species

E. insulatus and *E. santaeeleae*) overlapping among them (Fig. 2.8). Among *Hippidion* species, the distribution is not so clear because *H. saldiasi* and *H. devillei* overlapping between them, while *H. principale* have a clear distribution (Fig. 2.8).

2.5 Multivariate Analyses

The multivariate analyses were performed on the measurements of limb bones to identify groups in equids (MCIII, MTIII, AST, CAL, 1PHIII, and 2PHIII). PCA of *Hippidion* skeletal measurements is based on 41 MCIII, 34 MTIII, 33 AST, 23 CAL, 67 1PHIII, and 66 2PHIII. These PCAs are distinguished into two main groups, one is small in size and another is large in size, between them there exists an intermediate size overlapping in different degree. Concretely, in the PCA of MCIII result, there are three groups in size, the smaller remains of the intermediate group overlap with the small group in size; the accumulate variance for the first three components reached 85.54%, and the most important characters for the first component are MCIII13, MCIII4, MCIII5, and MCIII14, for the second component is MCIII8, and for third component is MCIII12 (see Fig. 2.9; Table 2.1). In the PCA of MTIII result there are two groups which differ in size, the small-sized group is divided into two groups one slender than the other; the variance accumulated by the first three components reached 86.29%, and the characters that are most important for the first component are MTIII4, MTIII5, MTIII7, and MTIII12, for the second component are MTIII8 and MTIII10, and for the third is MTIII8 (Fig. 2.9; Table 2.1). In the PCA of AST result there are three groups which differ in size, the variance accumulated by the first three components reached 94.48%, and the characters that are most important for the first component are AST7, AST2, AST4, AST1, and AST5, for the second component it is AST6, and for the third component it is AST3 (Fig. 2.9; Table 2.1). In the PCA of CAL (small sample, most of the remains are broken) result there are three groups which differ in size; the variance accumulated by the first three components reached 86.56%, and the characters that are most important for the first component are CAL1, CAL5, and CAL6, for the second component it is CAL2, and for the third component it is CAL7 (Table 2.1). In the PCA of 1PHIII result two groups, the small group includes overlapping of the groups which have intermediate size; the variance accumulated by the first three components reached 87.81%, and the characters that are most important for the first component are 1PHIII5, 1PHIII7, 1PHIII8, and 1PHIII1 for the second component it is 1PHIII9, and for the third component it is 1PHIII9 (Fig. 2.9; Table 2.1). In the PCA of 2PHIII result two clear groups and two alone specimens between them. The variance accumulated by the first three components reached 97%, and the characters that are most important for the first component are 2PHIII4, 2PHIII3, 2PHIII5, and 2PHIII1, for the second component is 2PHIII6, and for the third component is 2PHIII5 (Table 2.1). It is important to note that both first and second phalanges of third digit are highly variables because they include the differences between anterior and posterior ones.

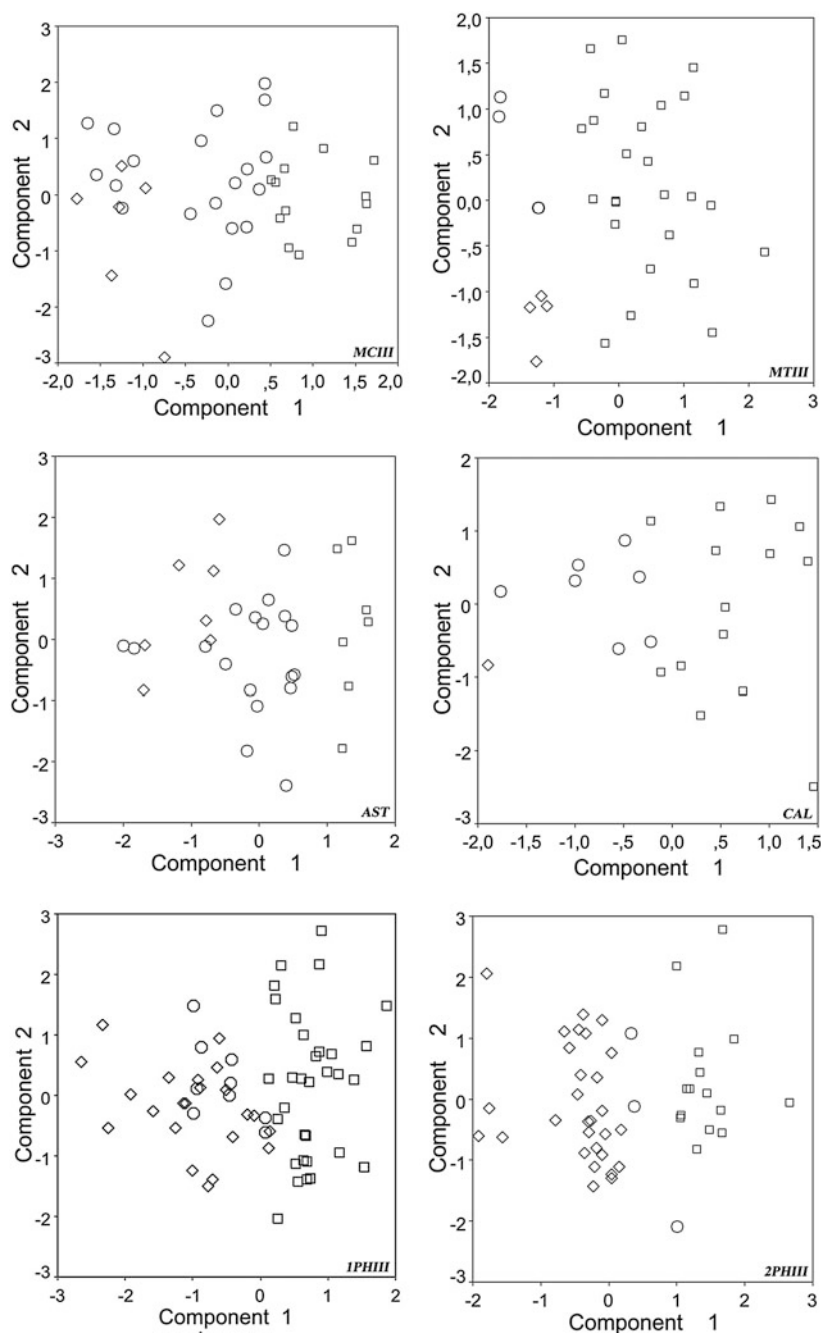


Fig. 2.9 PCA diagrams of MCIII, MTIII, AST, CAL, 1PHIII and 2PHIII bones from South American *Hippidion* species. Symbols as in Figs. 2.6 and 2.8

The DA analyses based on the PCA groups can provide a correct identification and a significance degree. Results of DA indicate that among the analyzed specimens MCIII (41) were correctly identified in 97.6% of cases originally classified, only one specimen of *H. devillei* is grouped with *H. saldiasi* (4.8%). In case of MTIII (34) were correctly identified in 100% of cases originally classified (Fig. 2.10; Table 2.2). In case of AST (33) were correctly identified in 87.9% of cases originally classified, three specimens of *H. devillei* were associated with *H. saldiasi* (15.8%), and one of *H. saldiasi* with *H. devillei* (14.3%). In case of CAL (23) were correctly identified in 100% of cases originally classified. Both astragalus and calcaneus are more variables than other bones of the extremities. In case of 1PHIII (67) were correctly identified in 95.5% of cases originally classified, two specimens of *H. principale* were grouped one with *H. devillei* (2.8%) and other with *H. saldiasi* (2.8%), and one specimen of *H. saldiasi* was associated with *H. devillei* (4.5%). The phalanges, in general, are more variables than other bones because we analyse together anterior and posterior phalanges (Fig. 2.10; Table 2.2). In the case of 2PHIII (66) were correctly identified in 98.5% of cases originally classified, one specimen of *H. devillei* was grouped with *H. principale* (33.3%). The second phalanges, in general, are less significant than other bones because this bone is very uniform with little variation in size.

PCA of *Equus* genus skeletal measurements is based in 70 MCIII, 78 MTIII, 74 AST, 60 CAL, 158 1PHIII, and 102 2PHIII. These PCAs are distinguished into two main groups, one small in size and another large in size and between them an intermediate size overlapping in different degree. Concretely, in the PCA of MCIII result there are three groups which differ in size, the small group in size is clear and the large group in size (intermediate + large) overlaps the majority of remains large in size; the variance accumulated by the first three components reached 90.18%, and characters that are most important for the first component are MCIII13, MCIII10, MCIII11, MCIII4, and MCIII5, for the second component it is MCIII8, and for third component it is MCIII6 (Fig. 2.11; Table 2.1). In the PCA of MTIII result there are two groups that differ in size, the small group in size is also clear, and the large group in size has three different species; the variance accumulated by the first three components reached 91.62%, and the characters that are most important for the first component are MTIII13, MTIII10, MTIII11, MTIII14, and MTIII12, for the second component it is MTIII8 and for the third it is MTIII8 (Fig. 2.11; Table 2.1). In the PCA of astragalus result there are two groups that differ in size, in the same way that MTIII the small size is clear and the large size group has three different species; the variance accumulated by the first three components reached 97.24%, and the characters that are most important for the first component are practically all but more important are AST2, AST1, AST7, and AST5, for the second component it is AST3, and for the third component it is AST4 (Fig. 2.11; Table 2.1). In the PCA of calcaneus result there are two groups that differ in size in the same way of MTIII; the variance accumulated by the first three components reached 94.7%, and the characters that are most important for the first component are practically all but more important are CAL1, CAL7, and CAL6, for the second component it is CAL3, and for the third component it is CAL5 (Table 2.1). In the PCA of 1PHIII result there are

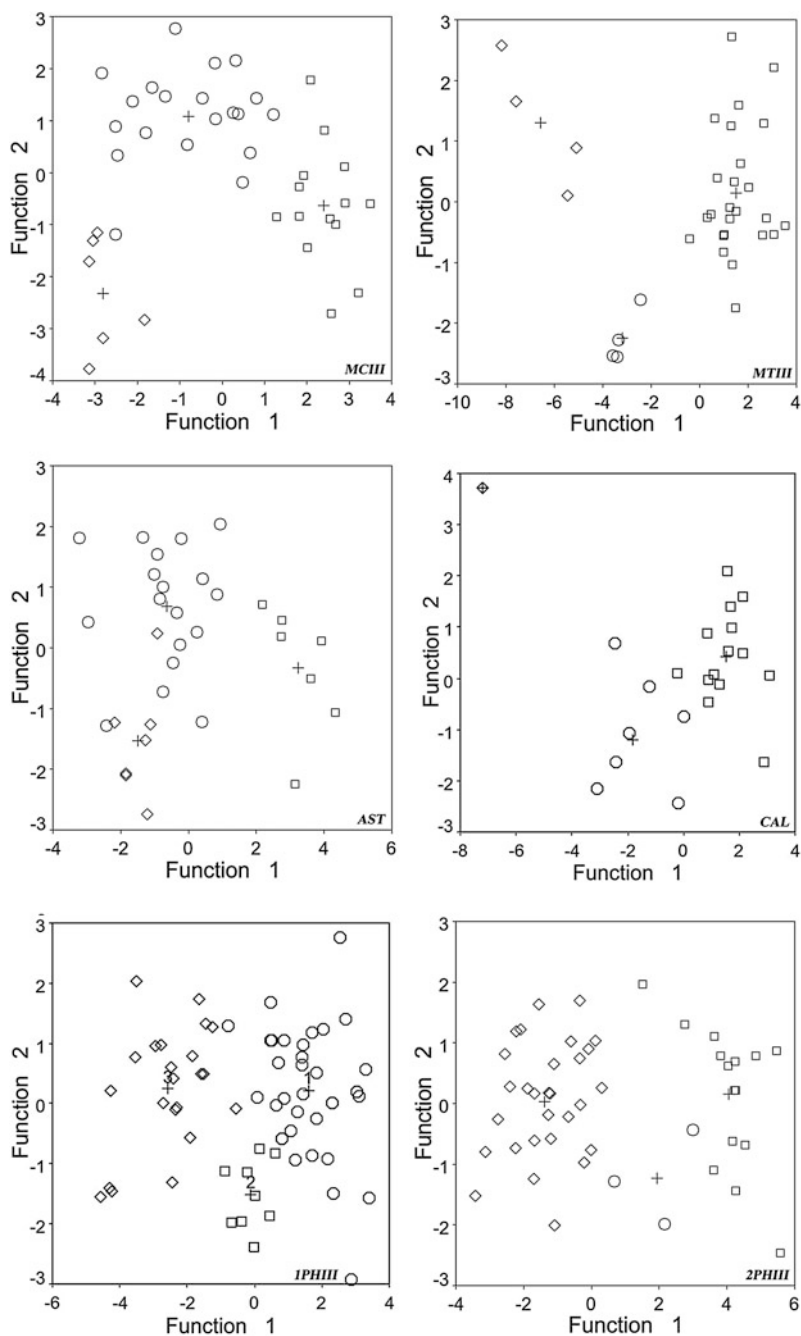


Fig. 2.10 DA diagrams of MCH, MT, AST, CAL, 1PH, and 2PH bones from South America *Hippidion* species. Symbols as in Figs. 2.6 and 2.8

Table 2.2 Percentage of correct classification by cross-validation techniques of DA analysis of *Hippidion* and *Equus* species. 1, 2 and 3 = *Hippidion principale*, *Hippidion devillei* and *Hippidion saldiasi* respectively; and 1, 2, 3 and 4 = *Equus neogaeus*, *Equus insulanus*, *Equus “santaeelenae”* and *Equus andium* respectively. N = sample number

<i>Hippidion</i>		<i>Equus</i>									
	Original	N	1 (%)	2 (%)	3 (%)	Original	N	1 (%)	2 (%)	3 (%)	4 (%)
McIII	1	14	100	0	0	1	22	100	0	0	0
	2	21	0	95.2	0	2	15	0	100	0	0
	3	6	0	0	100	3	2	0	50	50	0
MdIII						4	31	0	0	0	100
	1	26	100	0	0	1	15	93.3	0	6.7	0
	2	4	0	100	0	2	17	0	94.1	5.9	0
Astragalus	3	4	0	0	100.0	3	7	0	0	100	0
						4	39	0	0	0	100
	1	7	100	0	0	1	4	75	0	25	0
Calcaneus	2	19	0	84.2	15.8	2	20	10	80	10	0
	3	7	0	14.3	85.7	3	5	0	0	100	0
						4	45	0	0	2.2	97.8
First phalanx	1	14	100	0	0	1	8	62.5	37.5	0	0
	2	8	0	100	0	2	18	27.8	66.7	5.6	0
	3	1	0	0	100	3	4	0	0	100	0
Second phalanx						4	30	0	3.2	0	96.8
	1	36	94.4	2.8	2.8	1	32	78.1	6.3	15.6	0
	2	9	0	100	0	2	54	1.9	88.9	7.4	1.9
	3	22	0	4.5	95.5	3	10	10	10	80	0
						4	62	0	1.6	0	98.4
	1	15	100	0	0	1	22	81.8	4.5	9.1	4.5
	2	3	33.3	66.7	0	2	20	15	75	10	0
	3	48	0	0	100	3	14	21.4	21.4	57.1	0
						4	43	0	7	0	93

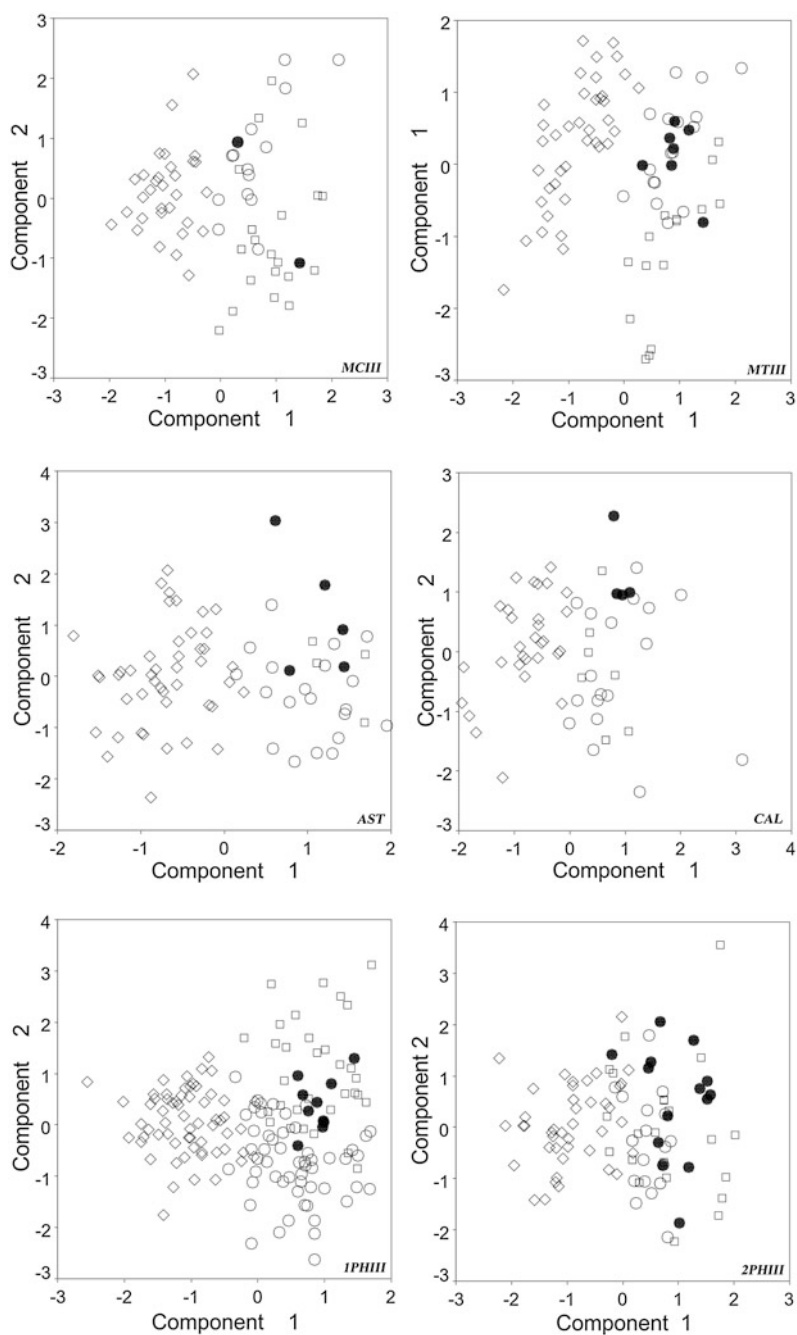


Fig. 2.11 PCA diagrams of MCIII, MTIII, AST, CAL, 1PHIII, and 2PHIII bones from South America *Equus* species. Symbols as in Figs. 2.7 and 2.8

three groups, the intermediate and large groups in size overlap between them; the variance accumulated by the first three components reached 94.66%, and the characters that are most important for the first component are 1PHIII6, 1PHIII4, 1PHIII7, and 1PHIII1 for the second component it is 1PHIII9, and for the third component it is 1PHIII5 (Fig. 2.11; Table 2.1). In the PCA of 2PHIII result there are two clear groups and two specimens between them, corresponding to intermediate remain in size; the variance accumulated by the first three components reached 95.03%, and the characters that are most important for the first component are practically all but more important are 2PHIII4, 2PHIII3, and 2PHIII1, for the second component it is 2PHIII2, and for the third component it is 2PHIII5 (Table 2.1). It is important to note that both first and second phalanges of third digit are highly variables because both include differences between anterior and posterior phalanges.

In case of *Equus* DA analyses based on the PCA groups can provide a correct identification and the significance degree. Results of DA indicate that among the analyzed specimens MCIII (70) were correctly identified in 98.6% of cases originally classified, two specimens are attributed to *E. santaeeleae*, one specimen is grouped with *E. insulatus* (50%). In case of MTIII (78) were correctly identified in 97.4% of cases originally classified, one specimen of *E. neogeus* and other specimen of *E. insulatus* was grouped with *E. santaeeleae* (6.7 and 5.9%, respectively) (Fig. 2.12; Table 2.2). In case of AST (74) were correctly identified in 91.9% of cases originally classified, one specimen of *E. neogeus* was associated with *E. santaeeleae* (25%), two of *E. insulatus* with *E. neogeus* (10%) and two with *E. santaeeleae* (10%), and one of *E. andium* with *E. santaeeleae* (2.2%). In case of CAL (60) were correctly identified in 83.3% of cases originally classified, three specimens of *E. neogeus* were identified with *E. insulatus* (37.5%), five specimens of *E. insulatus* with *E. neogeus* (27.8%), and one with *E. santaeeleae* (5.6%), and one of *E. andium* with *E. insulatus* (3.2%). As in *Hippidion* both astragalus and calcaneus are more variables than other bones of the extremities. In case of 1PHIII (158) were correctly identified in 89.9% of cases originally classified, two specimens of *E. neogeus* were grouped with *E. insulatus* (6.3%) and five to *E. santaeeleae* (15.6%), one specimen of *E. insulatus* was associated with *E. neogeus* (1.9%), four with *E. santaeeleae*, and one with *E. andium* (1.9%), two specimens of *E. santaeeleae* one with *E. neogeus* (10%) and other *E. insulatus* (10%), and one specimen of *E. andium* with *E. insulatus* (1.6%). The phalanges, in general, are more variables than other bones because we must add the differences between anterior and posterior phalanges (Fig. 2.12 and Table 2.2). In case of 2PHIII (102) were correctly identified in 81.8% of cases originally classified, four specimens of *E. neogeus* were associated one specimen with *E. insulatus* (4.5%), two with *E. santaeeleae* (9.1%) and one with *E. andium* (4.5%). Five specimens of *E. insulatus* were grouped three with *E. neogeus* (15%) and two with *E. santaeeleae* (10%). Six specimens of *E. santaeeleae* were associated three with *E. neogeus* (21.4%) and three with *E. insulatus* (21.4%). Three specimens of

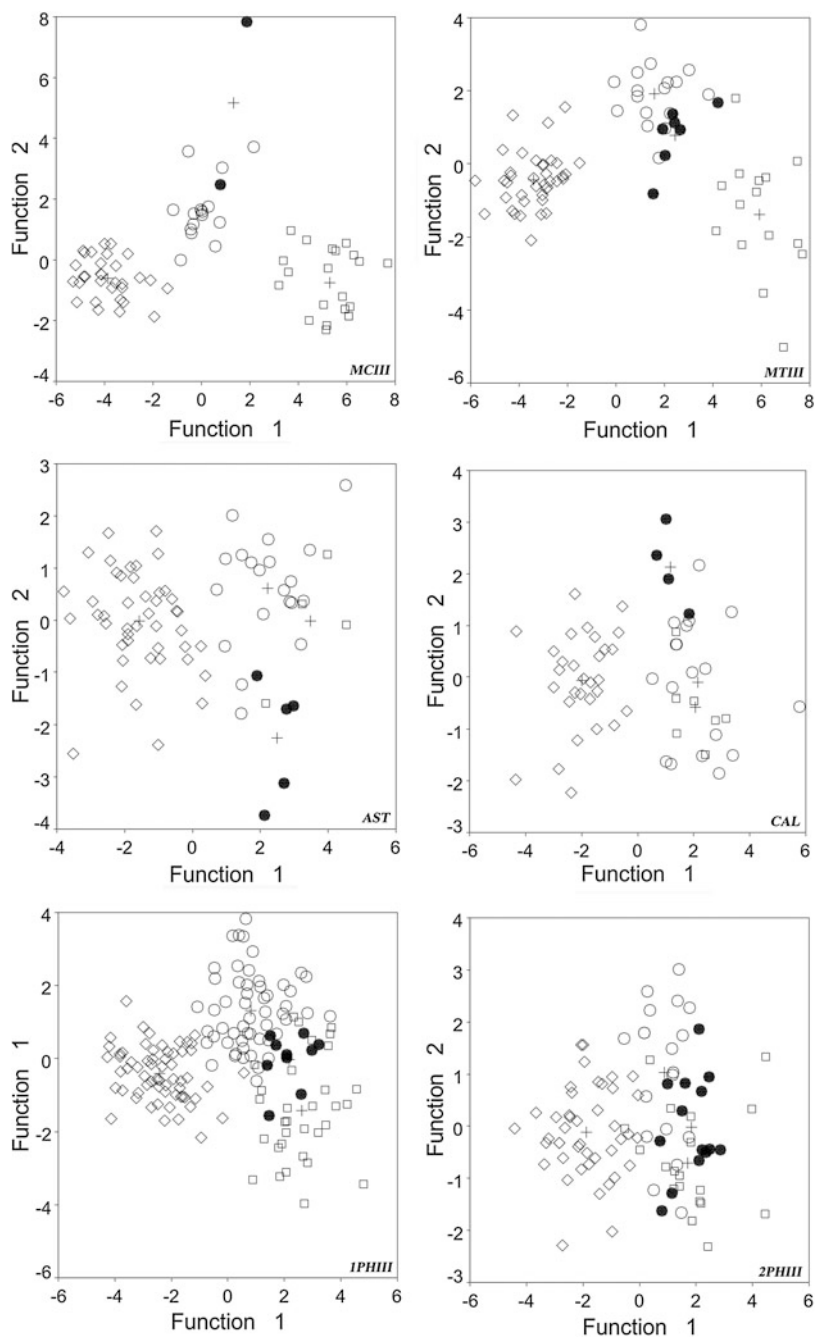


Fig. 2.12 DA diagrams of MCH, MT, AST, CAL, 1PH, and 2PH bones from South America *Equus* species. Symbols as in Figs. 2.7 and 2.8

E. andium were grouped with *E. insulatus* (7%). The second phalanges, as in *Hippidion*, are less significant than other bones because this bone is very uniform with little variation in size.

2.6 Morphology

There are numerous remains of *Hippidion* genus from different localities of South America, but scarce specimens with complete skulls. The skulls are characterized by a retracted nasal notch at the level of M2 or behind M3. The preorbital fossa is sometimes present with different state of developed. The nasal bone is narrow, long, and stylet-shaped. Dentition is primitive, comparable to the *Pliohippus* type, with the oval protocone more or less rounded oval and with the anterior and posterior hypoconal groove with assorted development. Lower teeth present protoconid and hypoconulid walls rounded and the double-knot of the metaconid-metastylid reduced with linguaflexid smaller, similar to the *Pliohippus-Dinohippus* horses. Dental morphology varies in relation with the degree of wear (age). The hypsodonty index (HI) indicates that *Equus* species are more hypsodont than *Hippidion* species. Among the *Equus* species, *E. andium* is the most hypsodont, while *H. devillei* is the most hypsodont between the *Hippidion* species (Table 2.3). The limbs are monodactyls and robust, the second and fourth metapodials, sometimes, reduced to less than half the length of the third metapodial. In general, the metapodials of *Equus* are robust, but not so robust as in *Hippidion*. The most slender are *E. neogeus* and *H. principale*, and the most robustness is *H. saldiasi* (Table 2.4). Concerning to the body mass *H. principale* is the much weight among the different species of *Hippidion* and *H. saldiasi*

Table 2.3 Hypsodonty index of the South America *Hippidion* and *Equus* species. Abbreviations: N = specimen number; Min = minimum; Max = maximum; X = mean

	P3-4			M1-2			p3-4			m1-2		
	Min	X	Max	Min	X	Max	Min	X	Max	Min	X	Max
<i>Hippidion devillei</i> (N)		3			3			3			5	
	2.71	2.87	2.94	2.94	3.11	3.36	2.38	2.63	3.1	2.68	3.14	3.43
<i>Hippidion principale</i> (N)		3			4			3			3	
	2.34	2.53	2.64	2.23	2.62	2.88	1.96	2.05	2.13	2.37	3.05	3.43
<i>Hippidion saldiasi</i> (N)								4			2	
							2.56	2.74	2.89	2.52	2.94	3.36
<i>Equus neogeus</i> (N)		3			10			7			4	
	2.73	2.24	2.85	2.93	3.27	3.67	2.86	3.12	3.35	2.8	3.04	3.38
<i>Equus andium</i> (N)					8			1			3	
				2.95	3.5	3.94		3.91		3.53	3.00	3.66
<i>Equus insulatus</i> (N)		8			8			4			8	
	2.80	2.91	3.02	2.88	3.17	3.49	2.84	3.23	3.64	2.81	3.23	3.44

Table 2.4 Gracility index of South America *Hippidion* and *Equus* species. Abbreviations as in Table 2.3

	MCIII			MTIII				
	N	Min	X	Max	N	Min	X	Max
<i>Equus neogeus</i>	22	14.48	16.16	18.2	15	11.27	12.33	15.08
<i>Equus insulatus</i>	17	17.3	18.83	20.59	22	13.39	17.78	18.61
<i>Equus andium</i>	31	15.21	18.28	20.75	39	12.34	15.62	17.6
<i>Hippidion devillei</i>	21	17.83	19.79	22.18	4	15.7	17.11	18.32
<i>Hippidion principale</i>	14	16.51	18.59	21.21	26	14.04	16.82	18.72
<i>Hippidion saldiasi</i>	7	18.6	21.04	24.59	4	18.55	19.54	20.51

is the lightweight (Tables 2.5 and 6.2). The first phalanx of the third digit is very characteristic and has wide breadth, with two lateral scars that are well developed and the V-scar (typical to *Equus*) very reduced. Morphologically is difficult identified the *Hippidion* species because the biggest differences can be found in size more than in morphology. The sum of quantitative multivariate analysis plus cranial and dental morphology permits us to decode the taxonomy of this group.

Concerning to *Equus* genus from different localities of South America, there is a similar history. There are many remains but scarce specimens of skulls, except the localities from Ecuador. The skull is large, in relation to the postcranial skeleton, with sharp and marked supraoccipital crest. They present a reduced nasal notch retracted at the level of P2 or anterior to it and some specimens presented a narrow and slightly excavated preorbital nasal area. Sometimes, the occipital condyles can be joined ventrally. The vomer reaches the palatal processes of the maxillary anterior to the palatine. Dentition is very similar to recent horses. The upper cheek teeth present triangular protocone and the upper shows the distal part longer than the mesial in lower. Most of them presented enamel plication. Prefossettes and postfossettes have developed folds. The mandible is robust and the lower cheek

Table 2.5 The predicted body mass (kg) for fossil species of *Hippidion* and *Equus* from South America. Abbreviations as in Table 2.3, plus MCIII13 and PHIII 5 measurements: the best measurements for estimate body mass following Alberdi et al. (1995)

	MCIII 13			PHIII 5				
	N	Min	X	Max	N	Min	X	Max
<i>Equus neogeus</i>	22	282.5	338.2	532.8	36	266.3	362.8	554.3
<i>Equus insulatus</i>	13	275.9	359.3	455.7	41	167.4	354.2	578.5
<i>Equus "santaeelenae"</i>	2	317.1	366.3	415.6	10	301.8	355.8	420.3
<i>Equus andium</i>	31	162.6	220.6	302.9	62	133.7	214.6	397.3
<i>Hippidion devillei</i>	16	221.2	330.1	428.6	7	272	329.9	389.9
<i>Hippidion principale</i>	12	437.5	513.8	618.6	29	375.2	452.9	554.3
<i>Hippidion saldiasi</i>	7	194.2	252.3	299.5	22	188.6	286.6	393.6

teeth with protoconid and hypoconulid walls straight, and the double-knot, the metaconid and metastylid, are rounded and angular, respectively. The linguaflexid is, in general, shallow and more angular in p3-4 and more open in m1-2. The ectoflexid varies from shallow (in premolars) and deep (in molars), in general, is not connected with linguaflexid. Dental morphology varies in relation to the degree of wear (age). All species of *Equus* have hypsodonty teeth (Table 2.3). The limbs are monodactyls and robust, the second and fourth metapodials are longer, in relation with the length of the third metapodial, than in *Hippidion* genus. The metapodial slenderness corresponds to *E. neogeus*, while the other three species are similar in gracility but not in body mass: *E. insulatus* and *E. santaeelenae* have a very similar body mass, while *E. andium* is smaller in body mass (Tables 2.5 and 6.2). *Equus* species are difficult to identified only with morphologic character. In the same way as the *Hippidion* species, quantitative multivariate analyses permit us to decode the taxonomy of this group.

2.7 Discussion

The skull of *Hippidion* presents specimens with dorsal preorbital fossa (DPOF) or without it. We observe in several specimens of *H. principale* skulls with and without DPOF, but with the same size skulls, only found variations in the area of the insertion of the nasal notch and DPOF; in *H. devillei* we know a skull with DPOF from Tarija and another without DPOF from Santana (Brazil) perhaps with a small depression (Alberdi et al. 2003), but both skull are incomplete; and we know only one skull of *H. saldiasi* also is incomplete from Calama (Chile; see Alberdi et al. 2007) (Fig. 2.13; Table 2.6). The morphology of teeth is close to the three species of *Hippidion* and only is different in size. In the bivariate diagrams length versus breadth in occlusal surface, we observe two groups in size: one small corresponding to *H. devillei* another large in size corresponding to *H. principale* with an area overlapping between them where are place the teeth of *H. saldiasi*. It is important to note that dimensions in occlusal surface are more variable than the measurement taken at 1 cm from the base of the teeth, but the majority of the remains are included in the maxilla or mandible and cannot get the dimensions at this level (Fig. 2.14). Concerning to the appendicular skeleton the differences are also in size, with robust and a marked shortening of the metapodials more strong in *H. saldiasi* and in several specimens of *H. devillei* from Tarija, not from the Pampean area (Fig. 2.15). These differences in size are clearly reflected in the bivariate plots of teeth and several bones and as it indicates Alberdi and Prado (1993) the shortening and widening of metapodials and phalanges are mostly marked in extreme environmental conditions as in Patagonia (*H. saldiasi*) and Tarija (*H. devillei*). The multivariate analyses results permit us for a better characterization of the species of *Hippidion* from South America already identified morphologically.

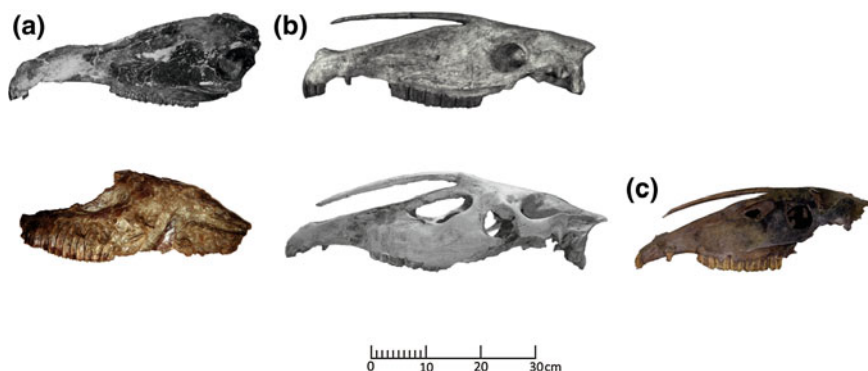


Fig. 2.13 Skull of different *Hippidion* species: with POF below and without POF above. **a** *Hippidion devillei* from Santana and Tarija, respectively; **b** *Hippidion principale* from Mercedes and Mar del Plata, respectively; **c** *Hippidion saldiasi* (only with POF) from Calama

Concerning to *Equus* species, the differences in the appendicular skeleton are also in size, one species is larger with slender metapodials (*E. neogeus*), and two species are large with more robust metapodials (*E. insulatus* and *E. santaeleenae*) and one species is small with metapodials marked shortening (*E. andium*) (Figs. 2.16, 2.17 and 2.18). These differences in size are clearly reflected in the bivariate plots of teeth and several bones as indicated by Prado and Alberdi (1994).

We think that the cranial and dental morphology and this quantitative multivariate analysis support the recognized in *Hippidion* genus three valid species. In the case of *Equus* genus, we recognized three valid species (*E. neogeus*, *E. andium*, and *E. insulatus*). We included *E. santaeleenae* into the *E. insulatus*. The status of *E. lasallei* needs a revision, but there are small samples to make an evaluation.

2.8 Systematic Paleontology

Order	Perissodactyla Owen 1848
Family	Equidae Gray 1821
Subfamily	Equinae Gray 1821
Tribe	Equini Gray 1821
Subtribe	Pliohippina Prado and Alberdi 1996
Genus	<i>Hippidion</i> Owen 1869

Synonyms:

- 1846 *Equus* Lund, pp. 33–35, Tab. XLIX, Figs. 2 and 4.
- 1891 *Onohippidium* Moreno, pp. 66–71.
- 1904 *Parahippidion* C. Ameghino, pp. 273–274.
- 1910 *Hyperhippidion* Sefve, pp. 1–43, Plate 1–6.

Table 2.6 Measurements in millimeters of *Hippidion* species skull from different South American localities, following the nomenclature and recommendations of the “Hippurion Conference” (Eisenmann et al. 1988). Codes following the “Hippurion Conference”; ca = approximated measure

Col. number	Locality	Species	Fossa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
MLP c-2 r	Loberia, Buenos Aires	<i>Hippidion principale</i>	With POF	162	102	169	121	290	556	103.5	85	185	132	44	43	83.5	56		126	192	211	215
MLP c-2 i	Buenos Aires	<i>Hippidion principale</i>	With POF	148	134	149	123	270	558	105	86	187	111.5	44.5	48.5	84			104	188	191	222.5
MNCN-1289	Tarija, Bolivia	<i>Hippidion principale</i>	Without POF	187	145.5	105 ca			>550	128	104	218				87.5	40.5	53.5	75.5			
MNCN_13763	Villa Ballestar	<i>Hippidion principale</i>	With POF	128	133	145 ca	109 ca	233 ca	494	109			96.5	31	43	87.5	42.5	67	86	164	210	211
ULP-TAR-1242	Tarija	<i>Hippidion principale</i>	With POF	150	157.5	126ca	172ca	290	532.5	106	94.2	192	111ca	35.9	37	71.3	37	65	126	241.5		
GEOBOL-LPV-0080 i	Tarija	<i>Hippidion devillei</i>								88.7	78.2	166.3										
GEOBOL-LPV-0080 r	Tarija	<i>Hippidion devillei</i>									77											
MACN 4102	Buenos Aires	<i>Hippidion principale</i>	Without POF	181.3	154	154	123	270	600	104	91.2	188.5	102.5	44	40	70	42.5	63.7	114	210.5		225
MMP 381	Vorohué	<i>Hippidion principale</i>	With POF		150	146	129	274		101	86.5	187.5	115	40.5	48.5	79			137	214	215	219
MACN 401 r	Mercedes	<i>Hippidion principale</i>	With POF	162.5	136	126	132	253	560	99	83.4	180.7	101	40.1	44.4	79.5	40.5	60.8	96	191	205	213
MACN 401 i	Mercedes	<i>Hippidion principale</i>	Without POF							97.4	84.1	177.6										
MMP2600 r	Mar del Plata	<i>Hippidion principale</i>	With POF	165	144	149	143	290	601	104	90	193	117	34	42	77	44	65	93.5	205.5	201	213
MMP2600 i	Mar del Plata	<i>Hippidion principale</i>	With POF							106	91	191.5										
MPH-P067 i	Miramar	<i>Hippidion principale</i>	With POF		162	134.5	110	251		100	81	183.5	99.5	35	51	89			87.6	181	218	201
MPH-P067 r	Miramar	<i>Hippidion principale</i>	With POF		152.5					99	83.5	181							85	187		
MHM-P54 r	Río Salado d	<i>Hippidion principale</i>	Without POF			142	116	258			90	154 +P2	110 ca	43	>	87.5			>	190 ca	216	220
MHM-P54 i	Río Salado i	<i>Hippidion principale</i>	Without POF								91	151.7 +P2										

(continued)

Table 2.6 (continued)

Col. number	Locality	Species	Fossa	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Remark
MLP 6-2 r	Lobería, Buenos Aires	<i>Hippidion principale</i>	With POF	72	136.5	81	435	225	150	158	164	66.9	57.1	360	18	11	124	54	46	73	29.5		
MLP 6-2 l	Buenos Aires	<i>Hippidion principale</i>	With POF	77.5	128.5	79	445	231	145	131	70.5	57.6	369	13	11	124		54.5	77				
MNCN-1289	Tarija, Bolivia	<i>Hippidion principale</i>	Without POF				463.5	212 ca	140 ca	160 ca	62	51	>335	88									
MNCN_13763	Villa Ballestar	<i>Hippidion principale</i>	With POF	78 ca	115 ca	90 ca	387	219.5 ca	81 ca	138	62	54.2	324			9.5			37	57.5			Young
ULP-TAR-1242	Tarija	<i>Hippidion principale</i>	With POF		125	87	495	280 ca	134 ca	145 ca	15.9	63.5	47	400	28 ca								
GEOBOL-LPV-0080 I	Tarija	<i>Hippidion devilei</i>																					
GEOBOL-LPV-0080 r	Tarija	<i>Hippidion devilei</i>																					
MACN 4102	Buenos Aires	<i>Hippidion principale</i>	Without POF	77	135.5	77	450	235		130	10	63.6	58.7	370	30	93							
MMP 381	Vorohué	<i>Hippidion principale</i>	With POF	61	140	82		223		139	70	58.5			13	19	123			68			
MACN 401 r	Mercedes	<i>Hippidion principale</i>	With POF	72.5	133	78	432	218	130.5	155	19.7	67.5	53.1	334	50						60		
MACN 401 l	Mercedes	<i>Hippidion principale</i>	Without POF																				
MMP2600 r	Mar del Plata	<i>Hippidion principale</i>	With POF	67	136	77	457	228	133.5		13.4	68	60	378	23	33	127	105	55	54.5	80.5	130	
MMP2600 l	Mar del Plata	<i>Hippidion principale</i>	With POF				460	225.5	140	116	65	54.5	380	23	23	33.5	117	89	45	67	82	130	
MPH-p067 l	Miramar	<i>Hippidion principale</i>	With POF	94	123	77.5		231.5		137	17.5	59.5	52		41.5	41	89.4	111	49	67	67	131	
MPH-p067 r	Miramar	<i>Hippidion principale</i>	With POF					230.6	126.5		13	58	56.5		31.6	36	92.5	99.5		69.2	81.8	131.6	
MHM-P54 r	Rio Salado d	<i>Hippidion principale</i>	Without POF	79	> 86	77		242		>99.8	17.4	63.5	55.6										
MHM-P54 l	Rio Salado i	<i>Hippidion principale</i>	Without POF								61	58											
MLP-1.1.III.9.1 r	Quequén Grande	<i>Hippidion principale</i>	With POF																				
MLP-1.1.III.9.1 l	Quequén Grande	<i>Hippidion principale</i>	With POF														76.7	85.1	33.8 ca	78.3	77.7	116	

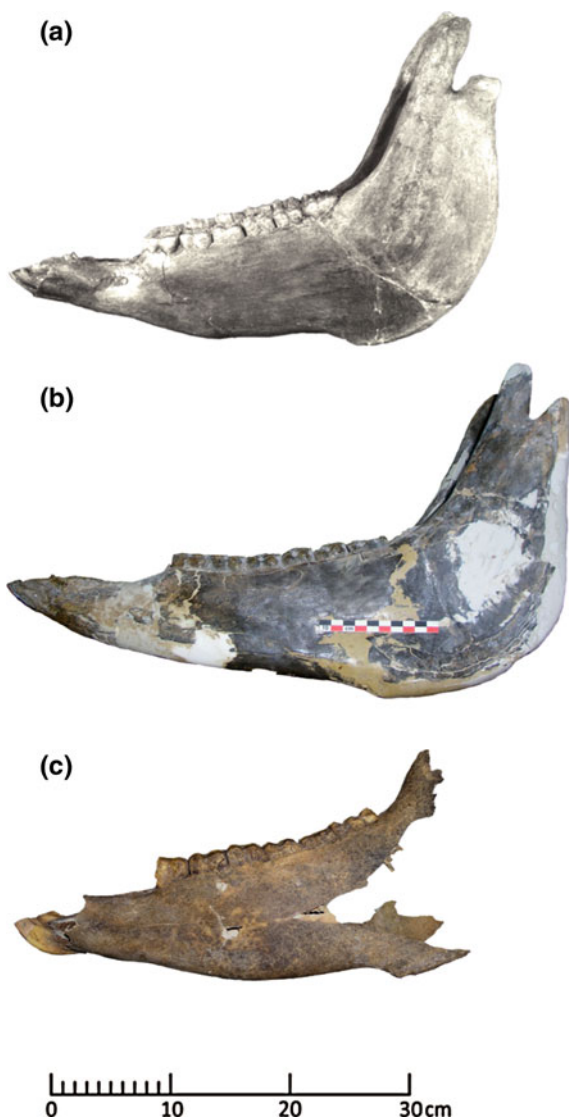
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Table 2.6 (continued)

Col. number	Locality	Species	Fossa	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Remark
MCL-6277 l	Santana (Bahia)	<i>Hippidon devillei</i>	Without POF				470							418							70		
MCL-6278 r	Santana (Bahia)	<i>Hippidon devillei</i>	Without POF																				
MMH-08.03.3 r	Montehermoso	<i>Hippidon principale</i>	With POF				379		125 ca	141		56	49.5	317		35	84	80.5	37	66	62.5	104	
MMH-08.03.3 l	Montehermoso	<i>Hippidon principale</i>	With POF																				
MCL-6112 r	Toca dos Osos (Bahia)	<i>Hippidon principale</i>																					
MCL-6195 l	Toca dos Osos (Bahia)	<i>Hippidon principale</i>																					
TAR-795 l	Tarija, Bolivia	<i>Hippidon devillei</i>	With POF	80.7	69.4	149											84.4	42					
TAR-795 r	Tarija, Bolivia	<i>Hippidon devillei</i>	With POF	82.8																			
TAR-691	Tarija, Bolivia	<i>Hippidon devillei</i>																					
TAR-856	Tarija, Bolivia	<i>Hippidon principale</i>																					
TAR-856 l	Tarija, Bolivia	<i>Hippidon principale</i>																					
TAR-780 r	Tarija, Bolivia	<i>Hippidon devillei</i>																					
TAR-780 l	Tarija, Bolivia	<i>Hippidon devillei</i>																					
SEK- r	Batessa, Calama	<i>Hippidon sudasi</i>	With POF	45 ca			370	215 ca	111			55	50.5	30			75	68	41	85		117.5ca	
SEK- l	Batessa, Calama	<i>Hippidon sudasi</i>	With POF						106			51	49			28.5	76	60	41	63	86	109.5	

Fig. 2.14 Mandible of different *Hippidion* species.

a *Hippidion devillei* from Barro Negro; **b** *Hippidion principale* from Monte Hermoso; **c** *Hippidion saldiasi* from Calama



Type species: not designated, but there is consensus on considering it as *H. principale* (Lund 1846; Tab. XLIX, Figs. 1, 3, and 5).

Geographic distribution: The *Hippidion* genus is known only in South America, specifically from Argentina, Bolivia, Brazil, Chile, Ecuador (without an exact localization, Hoffstetter 1952), Perú, and Uruguay (Fig. 2.5).

Stratigraphic distribution: The *Hippidion* remains come from different levels of the South American Pleistocene. Specimens from Uquia (Kraglievich 1934), the

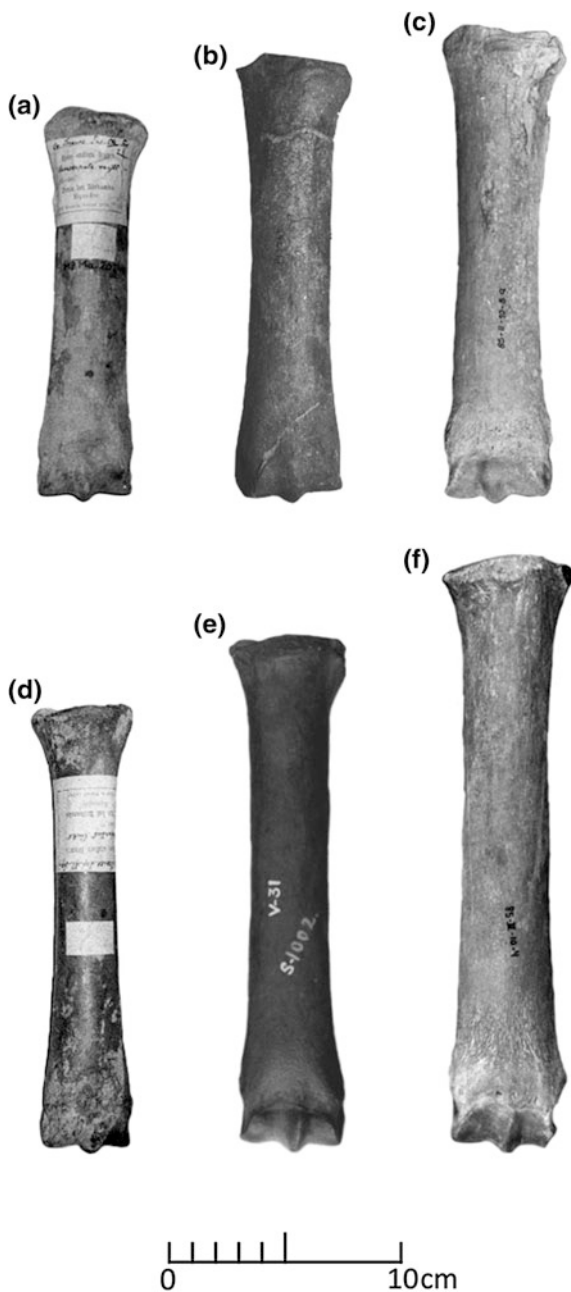
Upper Pliocene–Lower Pleistocene, are the oldest known, and the more recent come from the late Pleistocene (Alberdi et al. 2001a, b).

Diagnosis: (taken from Alberdi and Prado 1993). *Hippidion* is characterized by the retracted nasal notch at the level of M2 or behind M3 (Fig. 2.13; Table 2.6). The nasal bone is narrow and long, stylet-shaped. Primitive dentition, similar to the *Pliohippus* type, with the oval protocone more or less rounded and with the anterior and posterior hypoconal groove with varied development with wears. Double-knot with metaconid and metastylid reduced and a small linguaflexid. Dental pattern varies in relation with the wear degree (age) like the *Pliohippus-Dinohippus* horses. Monodactyl and robust limbs, with the second and fourth metapodials, reduced overpass half the length of the third metapodial.

Discussion: There is a disagreement important in this taxonomic group, (1) recognition of two genera *Hippidion* and “*Onohippidium*” by MacFadden (1997) by absence or presence DPOF, respectively; and (2) recognition of one only genus *Hippidion* with or without DPOF by Alberdi and Prado (1998). Some specimens of *H. principale* have a very developed DPOF, but not always, since different degrees of development are observed. Their importance at a specific level is doubtful. Sefve (1912) and Boule and Thevenin (1920) think the DPOF is a primitive character and that “*Onohippidium*” (with DPOF) is more primitive than *Hippidion* (without DPOF). Lydekker (1884), Gaudry (1862), and Sefve (1927) pointed out that the DPOF could have served as the location of glands that were important in the social life of the animal. Pirlot (1953) reported that it is a character with little physiological importance for the individual, and most likely unstable. Forsten (1982, 1983) criticized the use of the DPOF in horse systematics, claiming that the function of this character is unknown. Eisenmann (1981, 1982) stated that its shape is not enough to define trends of evolution and to obtain concrete points on which to build a wide scale chronology. Alberdi (1987) reported that the DPOF had possibly evolved as a sexual character. Evander (1989, p. 113) explained clearly the problem of using facial fossae as a taxonomic characteristic. The only argument used by MacFadden and Skinner (1979) to support the differences between *Hippidion* and *Onohippidium* was the presence or absence of the DPOF. The lack of agreement in the literature about the taxonomical importance of this character makes us to consider *Hippidion* as the only valid genus in South America. Recently, Avilla et al. (2015) are in agreement with MacFadden and Skinner (1979) about the presence of hippidiforms in North America and created a new genus, *Boreohippidion*, where including “*Onohippidium*” *galushai*. In our opinion, the comparative analysis is incomplete because they compared only with *Hippidion* from South America and its comparison with *Dinohippus* genus is pending and we think it is necessary. Additionally, they considered a slight depression preorbital as a type of DPOF and we considered it as absence of DPOF.

The identification of the *Hippidion* species was a difficult task, and the great quantity of specific names present in literature was probably a consequence of this. Alberdi and Prado (1993) revised this genus. Posteriorly, they studied the new findings, which they have been included here (Alberdi and Frassinetti 2000; Alberdi and Prieto 2000; Alberdi et al. 2001a, b, 2003, 2006, 2007; Cerdeño et al. 2008;

Fig. 2.15 Metapodials, MCIII and MTIII, of different *Equus* species. **a** MCIII *Equus andium* from Riobamba; **b** MCIII *Equus insulatus* from Tarija; **c** MCIII *Equus neogeus* from Quequén Salado-Indio Rico; **d** MTIII *Equus andium* from Riobamba; **e** MTIII *Equus insulatus* from Santa Elena Peninsula; **f** *Equus neogeus* from Quequén Salado-Indio Rico



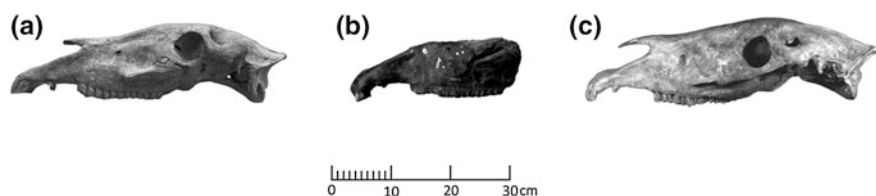


Fig. 2.16 Skull of different *Equus* species. **a** *Equus andium* from Chalan Punín (Ecuador); **b** *Equus insulatus* from La Carolina, Santa Elena Peninsula (Ecuador); **c** *Equus neogeus* stored at Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN-15149)

Fig. 2.17 Mandible of different *Equus* species. **a** *Equus andium* from Ecuador; **b** *Equus neogeus* from Monte Hermoso



Paunero et al. 2008; Prado et al. 1998, 2012, 2013a; Prado and Alberdi 2008, 2012; Rincón et al. 2009). However, the quantitative multivariate analysis together with the cranial and dental morphology supports the division of this genus into three different valid species.

H. principale (Lund) 1846

Fig. 2.18 Metapodials, MCIII and MTIII, of different *Hippidion* species: **a** MCIII *Hippidion devillei* from Tarija; **b** MCIII *Hippidion principale* from Tarija; **c** MCIII *Hippidion salsiasi* from Última Esperanza; **d** MTIII *Hippidion principale* from Tarija; **e** MTIII *Hippidion devillei* from Tarija; **f** *Hippidion salsiasi* from Última Esperanza



Synonyms:

1846 *Equus principalis* Lund, p. 93, pl.XLIX, Fig. 1.

1846 *Equus neogaeus* Lund, p. 76, pl. XLIX, Fig. 3.

1869 *Equus arcidens* Owen, p. 565, pl.LXII, Figs. 1 to 3.

1888 *Onohippidium compressidens* F. Ameghino, in Ameghino 1889, p. 517, pl. XXVII, Figs. 5, 6 and 7.

1889 *Hippidium angulatum* F. Ameghino, p. 520, pl. XXVII, Figs. 2 and 3.

1891 *Onohippidium munizi* Moreno, pp. 65–71, not figured.

1907 *Hippidium bonaerense* C. Ameghino, pp. 35–43.

Holotype: upper right M2 from the older breccia of the Lagoa Santa cave (Brazil), figured by Lund (1846, plate XLIX, Fig. 1). Peter W. Lund Collection (ZMK).

Type locality: Lagoa Santa, Minas Gerais State, Brazil.

Geographic distribution: South America, from several localities of the Buenos Aires and Santa Fé provinces (Argentina), Tarija (Bolivia), Artigas Department (Uruguay) and Toca dos Ossos and Lagoa Santa (Brazil) (Fig. 2.5).

Stratigraphic distribution: Upper Pleistocene, Lujanian Land Mammal Age (see Chap. 5).

Studied material: In Alberdi and Prado (1993) we include the material from Tarija (Bolivia) that which Boule and Thevenin (1920) recognized as *Hippidium principale* and *Hippidium neogeum*, as well as the material called by Burmeister (1875) *H. neogeum* from the Buenos Aires province (Argentina). Another material from this province is referred to as *H. principale* and *Hippidion compressidens* (Ameghino 1889). The material of *O. munizi* Moreno 1891 and *Hippidion bonaerensis* C. Ameghino 1907 is also from the same province. It also included one skull from Vorohué formation (Buenos Aires province) cited by Reig (1957) as *Onohippidium* and material assigned to *Hippidion* from Sopas Formation (Upper Pleistocene, Uruguay; Ubilla and Alberdi 1990). The material from Toca dos Ossos (Bahia, Brazil) stored at Museo de Ciências Naturais and Pontificia Universidad Catolica de Minas Gerais (MCN).

In this revision, we also included all remains that we studied since 1993 to the present.

Diagnosis: (taken from Alberdi and Prado 1993). The nasal notch is quite retracted (Fig. 2.13b). In general, in the skulls without the DPOF, the nasal notch is placed at the M2 mesostyle level, and in the skulls, with DPOF it is placed at the upper M3 level or behind it. In lateral view, the dorsal profile shows an anterior convexity followed by a frontal-nasal inflection, which in occipital-dorsal view is narrow. The upper cheek teeth are relatively curved in the linguo-ventral sense. The skeleton is large and bulky, and the extremities are robust, mainly the metapodials and phalanges (Fig. 2.16b, e). It is the largest and strongest among the South American hippidiforms.

Discussion: The skeletal is large and heavy, and the extremities are robust. The multivariate analysis presents little differences among the distinct localities with *H. principale*. The samples from the Buenos Aires province are more varied than that from Tarija concerning dentition and postcranial skeleton. The postcranial elements of the Tarija locality are larger than that of the Buenos Aires province sites. The gracility of both samples is similar.

H. devillei (Gervais) 1855

Synonyms:

1855 *Equus devillei* Gervais, p. 35, pl. VII, Figs. 11 and 12.

1889 *Hippidium nanum* Burmeister, p. 10, pl. XI, Fig. 6.

1893 *Hippidium bolivianum* Philippi, p. 88, not figured.

1908 *Onohippidium peruanum* Nordenskiöld, p. 16, Figs. 5, 6 and 7.

1912 *Parahipparion burmeisteri* Sefve, p. 109, pl. I Figure 10 and pl. II Fig. 19.

1934 *Hippidium uquiense* Kraglievich, p. 403, not figured. It is figured by Fernández de Álvarez 1957.

1957 *Hypohippidium humahuaguense* Fernández de Álvarez, pp. 85–95, Figs. 1–53.

Holotype: The material figured by Gervais (1855) in Plate VII, Figs. 11 and 12 (the left P2-M3 row and fragment and right astragalus). Institut de Paléontologie IPMNH, Paris (France).

Type locality: Uquía, Jujuy, Argentina.

Geographic distribution: Esquina Blanca en Uquía and Barro Negro in Jujuy, San Luis, Uspallata en Mendoza (Cerdeño et al. 2008) and several localities of the Buenos Aires province (Argentina). In Santana and Toca dos Ossos in the Bahia State and possibly in the Lagoa Santa área in Minas Gerais State in Brazil (Alberdi et al. 2003). Tarija and Ulloma in Bolivia, and Tirapata in Perú (Fig. 2.5).

Stratigraphic distribution: Pleistocene sensu lato. The remains from Barro Negro are dated as the late Pleistocene (Alberdi et al. 1987). The Uquia remains (Kraglievich 1934) refer to the Upper Pliocene–Lower Pleistocene. Remains from Tarija and the Buenos Aires province refer to the Middle Pleistocene (Ensenadan Land Mammal Age) to Late Pleistocene (Lujanian Land Mammal Age) in Buenos Aires province (see Prado et al. 2013a; see Chap. 5).

Studied material: This group includes the material of *Onohippidium devillei* cited by Boule and Thevenin (1920) from Tarija (Bolivia). *H. bolivianum* from Ulloma, Bolivia (Philippi 1893). *Onohippidion peruanum* (Nordenskiöld 1908) from Perú and several remains cited by different authors from the Buenos Aires province. *Hippidion* sp. from Jujuy (Argentina) described by Alberdi et al. (1986), and the material described by Fernández de Álvarez (1957) as *H. humahuaguense*, and the remains from Barro Negro (Jujuy) and Patagonia described by Alberdi et al. (1987) and named them *Hippidion* sp. is included in *H. devillei*, and possibly *Hippidion* sp. from Breal de Orocal in Venezuela (Rincón et al. 2009). And also all remains studied posteriorly to Alberdi and Prado (1993) described in several papers (Alberdi et al. 2003; Cerdeño et al. 2008; Prado et al. 1998, 2012, 2013a).

Diagnosis: (taken from Alberdi and Prado 1993). The skull is bigger compared to the postcranial skeleton (Fig. 2.13a). The nasal notch is retracted to the M2 mesostyle level. In lateral view, the skull is convex, without frontal-nasal inflection. The molar series shows the diagnostic characters of the genus, being quite shorter than that of *H. principale* and shorter than that *H. saldiasi*. The skeleton is short and strong, and the extremities are robust, mainly the metapodials and phalanges. The metapodial strength index in Tarija is greater than in the Buenos Aires province

sample (Fig. 2.15a, d). Slender middle-sized *Hippidion*, intermediate between *H. principale* and *H. saldiasi* in several remains, another more similar to *H. saldiasi*.

Discussion: According to the International Code of Zoological Nomenclature, *H. devillei* is a priority over *Hippidion neogaeus*. Burmeister (1875, p. 5) considered *E. devillei* to be similar to *E. neogaeus*, and Boule and Thevenin (1920) designated *H. devillei* as *O. devillei*. There is only one incomplete skull from Tarija (see plate 13, Fig. 1 in Boule and Thevenin 1920, and stored at Institut de Paléontologie MNHN), which is included in this species. It shows a somewhat reduced DPOF in comparison with *H. principale*, but the area is broken. There is another incomplete skull from Santana (Bahia, Brazil) without DPOF (see Fig. 5: A, B in Alberdi et al. 2003), and stored at Museo de Ciências Naturais and Pontificia Universidad Catolica de Minas Gerais (MCN).

In the bivariate analyses of the upper and lower teeth, length versus breadth in the surface, how we have seen above, the teeth of *H. devillei* are the smallest among the hippidifoms (Fig. 2.6). This indicates that the teeth of *H. devillei* are smaller in size than of *H. saldiasi* while the skeletal remains are larger in size than latter. The teeth are more hypsodont and less more curved than *H. principale* (Table 2.3). In the PCA based on the skeletal elements, how we have seen before, these remains are intermediate between the other two with a certain overlap only among the 1PHIII (Fig. 2.9). The multivariate analysis shows little differences among the distinct localities with *H. devillei*. The samples from the Buenos Aires province are some larger than those from Tarija in both dentition and postcranial skeleton. But nevertheless, the size of 1PHIII and astragalii is larger in Tarija than in Buenos Aires localities. The gracility is slightly more marked in Tarija than in the latter localities.

H. saldiasi (Roth) 1899

Synonyms:

1899 *Onhippidium saldiasi* Roth, p. 448, pl. V, Fig. 6.

Holotype: A p2 described by Roth (1899) and figured by Roth (1902, Plate II, Fig. 4). LPM, La Plata (Argentina).

Type locality: Cueva del *Myloodon* (= Eberhardt = Ultima Esperanza), Magallanes, Chile.

Geographic distribution: Patagonia region (Fig. 2.5). Localities from Argentina and Chile are specified by Alberdi et al. (1987). In Chile, there are three localities more to the North with *H. saldiasi* as they are Santa Rosa de Chena and Chacabuco described by Alberdi and Frassinetti (2000) and Calama by Alberdi et al. (2007).

Stratigraphic distribution: late Pleistocene. Remains from Patagonia were dated between 13.000 and 10.000 years BP (Alberdi et al. 1987; Barnosky et al. 2015; Villavicencio et al. 2016). The specimen from Calama was dated 21.070 ± 100 BP (GrA-29389, a tooth) and 21.380 ± 100 BP (GrA-29388, bone) by 14C AMS at Centrum voor Isotopen Onderzoek of Groningen (Alberdi et al. 2007) (see Chap. 5).

Studied material: This group includes the remains collected by Hauthal (1899) in the *Myodon* Cave which were studied by Roth (1899, 1902) and Lehmann Nistche (1899, 1902), who consider them as *O. saldiasi*; the material collected in Los Toldos II (Menghin 1952, 1965) which Mengoni Goñalons (1980) considers to be *Onohippidium* (*Parahipparion*) *saldiasi*; the material from Los Toldos III which Hoffstetter cites as *Onohippidium* (*Parahipparion*) sp. (in Cardich et al. 1973); the material from Las Buitreras Cave which Borrero (1997) consider to be *Hippidion*, and the remains coming from the Pali Aike Cave and Cerro Soto sites, which Bird (1938) consider to be *Onohippidium*. Alberdi and Prieto (2000) revised all material from the several caves of the Patagonia region. More recently, we revised a new remain from Chile (Alberdi and Frassenetti 2000; Alberdi et al. 2007), and from Argentina (Alberdi et al. 2001a; Paunero et al. 2008).

Diagnosis: small-sized, *Hippidion* with the relatively large skull (Fig. 2.13c, Table 2.7). The only two skulls that we have are very old and both are present with the nasal notch retracted to the distal part of M3 (Fig. 2.13c). The molar series shows the diagnostic characters of the genus, being something minor than *H. devillei*. Metapodials and phalanges show a characteristic shortness and enlarged articular surfaces.

Discussion: In the bivariate analyses of the upper and lower teeth, length versus breadth in surface, how we have seen above, the teeth of *H. saldiasi* are intermediate between *H. principale* and *H. devillei* (Fig. 2.6). This indicates that the teeth of *H. saldiasi* are not the smallest size of the hippidiforms, while the skeletal remains (distal part of the extremities) are the smallest of this group of equids (Fig. 2.15c, f). The teeth are a hypsodont intermediate and straighter than *H. principale* (Table 2.3). In the PCA based on the skeletal elements, how we have seen before, these remains are the smallest of this group and present a difference in slenderness with *H. devillei* on MCIII and MTIII, where the remains of *H. saldiasi* are more robust than the *H. devillei* (Fig. 2.9). The multivariate analysis of the limb bones indicates that there is a clear distinction of *H. saldiasi* from the other species of *Hippidion* (Fig. 2.10; Table 2.2). The dental remains are scarce and do not allow us to evaluate exactly the differences between *H. devillei* and *H. saldiasi*. This latter species possibly presents a close anatomical adaptation to the environmental factors, reflected in the metapodial shortness and enlarged articular surfaces (Alberdi et al. 1987, 2001a, 2007; Alberdi and Prieto 2000; Paunero et al. 2008; among others).

After Prado and Alberdi (1994), the multivariate analyses permit to distinguish four different groups of *Equus*, which can correspond to different species. But it is true that the species of *E. insulatus* and *E. santaeelenae* are very similar in several features.

Genus *Equus* Linnaeus 1758

E. andium Branco 1883 ex Wagner 1860

Table 2.7 Measurements in millimeters of *Equus* species skull from different South American localities, following the nomenclature and recommendations of the “Hipparion Conference” (Eisenmann et al. 1988). Codes following the “Hipparion Conference”; ca = approximated measure

Col. Number	Locality	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
MACN-15149	(6.1 La Plata)	<i>Equus neogaeus</i>	134	132.5	111	134.7	242	512	89	73	158.5	90.5	34	45.5	74	47.5	65.2	81.5	78.5	208 ca	209 ca	75
MLP-6.1	Luján (AR)	<i>Equus neogaeus</i>	137			133		510	92	73.5	159		49.5		75	47.5	65.5	110	191	203	213	76
MACN-1115	Pampa (AR)	<i>Equus neogaeus</i>		110	119	120	240		105			82 ca	28	34.5	62.5			88	167	172 ca	182 ca	84
MLP-6.4	Luján (AR)	<i>Equus neogaeus</i>			121 ca	125	246			76			41	50	73.5			108 ca	193			61
MLP-6.3	Buenos Aires (AR)	<i>Equus neogaeus</i>	129	87	150 ca	131	269.5	489	93		157ca		37	39	70	41	58 ca	118	195	205 ca	204	69
MACN-11721 r	Pro S Martín, Santa Fe	<i>Equus neogaeus</i>							86.5	75	161											
MACN-11721 i	Pro S Martín, Santa Fe	<i>Equus neogaeus</i>							85.6	75.1	161											
MCL-0200010203 r	Tecón dos Ossos (BR)	<i>Equus neogaeus</i>	135	138 ca					94.5	>47.2	>165				92	51	74.8					62.5
MCL-0200010203 i	Tecón dos Ossos (BR)	<i>Equus neogaeus</i>							95	>50.6	165-170											
MHN-P-70 r	Confins, Lapa do Galinheiro (BR)	<i>Equus neogaeus</i>	137	155					95	91	170				72	44	72.2					
MHN-P-70 i	Confins, Lapa do Galinheiro (BR)	<i>Equus neogaeus</i>							93	80	171											
3784-V (Cunha 1981) i	Corumbá, Matogrosso do Sul (BR)	<i>Equus neogaeus</i>		116	115	126	236		91	79	165	82.5	33.3	43.2	70			76.5	160	186	196	68
3784-V (Cunha 1981) d	Corumbá, Matogrosso do Sul (BR)	<i>Equus neogaeus</i>		114					93	80	165	83										
MMH-87.6.10d	Montehermoso (AR)	<i>Equus neogaeus</i>							105.8	82.2	185											
MMH-98.9.95	Montehermoso (AR)	<i>Equus neogaeus</i>																				
MB Ma-24675	Punín (ECU)	<i>Equus andium</i>	118						84.7	69.2	153.5				60 ca	48	61 ca					
MB Ma-24676	Punín (ECU)	<i>Equus andium</i>										87.5 ca	34.5	38	65							

(continued)

Table 2.7 (continued)

Cat. Number	Locality	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
EPN-V-73 (S-131) I	Chalán, Punín (ECU)	<i>Equus andium</i>	102.5						83	66.4	154.3				62.5	54	76					
EPN-V-73 (S-131) r	Chalán, Punín (ECU)	<i>Equus andium</i>							83.4													
EPN-V-2152 r	Chalán, Punín (ECU)	<i>Equus andium</i>	120.5	119					90						74	51.5	73					
EPN-V-2152 I	Chalán, Punín (ECU)	<i>Equus andium</i>							89.6	68.2	155											
EPN-V-76 r	Chalán, Punín (ECU)	<i>Equus andium</i>	100.5	95	105	112	215	405	77.7	62.4	138	69	30.6	32.5	61.8	57.2	83.4	93	160	183	176	
EPN-V-76 I	Chalán, Punín (ECU)	<i>Equus andium</i>							78.3	61.7	138											
EPN-V-2161 r	Chalán, Punín (ECU)	<i>Equus andium</i>	121.5	120.5	97.5	118	211	445	87.5	68.7	154.2	64	35.7	40	68	52.5	77.4	90	163	192	184	78.4
EPN-V-2161 I	Chalán, Punín (ECU)	<i>Equus andium</i>							88	66.2	153.3											
EPN-V-2160 r	Chalán, Punín (ECU)	<i>Equus andium</i>	102	116	90	116	201	420	80	70 ca	150 ca	50.6	37	38	65	51.5	>67	85	153	179	177	71
V-2159-CR2159 r	Chalán, Punín (ECU)	<i>Equus andium</i>	135	117 ca	120 ca	113	228 ca	247 (427?)	93	70.8	162		35	40	73.2	64.5	75	96.5	173	188.5	194	73.3
V-2159-CR2159 I	Chalán, Punín (ECU)	<i>Equus andium</i>							92	71	159											
MNCN-1288	Turija, Bolivia	<i>Equus insulanus</i>	149.5	138	118.5	147.5	264	549	104.5	83.5	185.2	100.5	57.5	52.5	80.5	52.5	76.2	94	180.5	194	209	73
MNHN-BOL-V-400693 r	Turija, Bolivia	<i>Equus insulanus</i>							98	80.4	176											
MNHN-BOL-V-400922 r	Turija, Bolivia	<i>Equus insulanus</i>							100.8	90.8	178.2											
MNHN-BOL-V-401432 I	Turija, Bolivia	<i>Equus insulanus</i>							99.1	77.5	177.6											
MNHN-BOL-V-without number I	Turija, Bolivia	<i>Equus insulanus</i>							99.2	81.4	178											
TAR-997 r	Turija, Bolivia	<i>Equus insulanus</i>							97	78	177											
UF90551 (M & A 1987)	Turija, Bolivia	<i>Equus insulanus</i>					226	496			176						71.5				198	

(continued)

Table 2.7 (continued)

Col. Number	Locality	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
TAR-783	Tarija, Bolivia	<i>Equus insulanus</i>		141.5 ca					97	81.7	179		43 ca	47	81							
EPN-V-3037 r	La Carolina (ECU)	<i>Equus insulanus</i>	124	135					102.5	80.5	178.5	67			72	50.6	70					
MUSM-1 r	Saeco, Arequipa, Perú	<i>Equus insulanus</i>	129.2	122.1	126 ca	128.7	251	487	93.6	81.6	166	82 ca	22.4 ca	27.8 ca	66.8	45.8	63.5	81.9	180	184	194	73.2
MUSM-17 r	Aguada de Lomas, Arequipa, Perú	<i>Equus insulanus</i>	119	132	129	124	247 ca	489	102	80.5	179.5	90 ca	15	31.4	>60	41.5	64	74	176 ca		77 ca	
MUSM-17 l	Aguada de Lomas, Arequipa, Perú	<i>Equus insulanus</i>							101	83	179.6											
MUSM-sn-1 l	Aguada de Lomas, Arequipa, Perú	<i>Equus insulanus</i>							103.5	80	180					46.2	73					
MUSM-sn-2 l	Aguada de Lomas, Arequipa, Perú	<i>Equus insulanus</i>							108	87.9	194.5											
MUSM-7 (Lima) r	Aguada de Lomas, Arequipa, Perú	<i>Equus insulanus</i>	132	117	109 ca	126.5 ca	227 ca	482	90.3	76.9	166	90	>15		>14	42.5	63.5	66	143 ca	>150	>162 ca	75 ca
MUSM-7 (Lima) l	Aguada de Lomas, Arequipa, Perú	<i>Equus insulanus</i>							89.4	76.9	166											
Lasalle 5 right	Bosú, Condinamarca, Colombia	<i>Equus neogaeus</i>	140	136			267	639ca	90.6	79.2	172				80.6		71.4		231ca			
Lasalle 5 left	Bosú, Condinamarca, Colombia	<i>Equus neogaeus</i>							91	75.9	171											
Col. Number	Locality	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Remark	
MACN-15149	(6.1 La Plata?)	<i>Equus neogaeus</i>	120	72	408.5	232	115	128 ca	11.5	59.2	54	171	195.5	115.7							Old	
MLP-6.1	Luján (AR)	<i>Equus neogaeus</i>	105 ca	69	406	235	119	146.5	13.5	60.5	59	169.5	193	113.5								
MACN-1115	Pampa (AR)	<i>Equus neogaeus</i>	>108	79.5		214	98	125 ca	14	49	42		174.5	101							Young	

(continued)

Table 2.7 (continued)

Col. Number	Locality	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Remark
MLP-6.4	Luján (AR)	<i>Equus neogeus</i>	114	70		151			13 ca												
MLP-6.3	Buenos Aires (AR)	<i>Equus neogeus</i>	110	>72	354	226	96	135	14.5	60	48.1	158	156	102.5				43.3			
MACN-11721 r	Pro S Martín, Santa Fe	<i>Equus neogeus</i>																			
MACN-11721 l	Pro S Martín, Santa Fe	<i>Equus neogeus</i>																			
MCL-62000/10203 r	Toca dos Ossos (BR)	<i>Equus neogeus</i>	122.5	76				114	15			166							63		Very old
MCL-62000/10203 l	Toca dos Ossos (BR)	<i>Equus neogeus</i>							16.2										67.2		
MHN-P-70 r	Confins, Lapa do Galinheiro (BR)	<i>Equus neogeus</i>					83					175									
MHN-P-70 l	Confins, Lapa do Galinheiro (BR)	<i>Equus neogeus</i>																			
3784-V (Cunha 1981) i	Corumbá, Matogrosso do Sul (BR)	<i>Equus neogeus</i>	98	70	195	100	105	10	64.7	50.8	>167										
3784-V (Cunha 1981) d	Corumbá, Matogrosso do Sul (BR)	<i>Equus neogeus</i>						11	61	49											
MMH-87.6.10l	Montehermoso (AR)	<i>Equus neogeus</i>																			
MMH-98.9.95	Montehermoso (AR)	<i>Equus neogeus</i>								176											
MB-Ma-24675	Punín (ECU)	<i>Equus andium</i>					90 ca				136							46.3			
MB-Ma-24676	Punín (ECU)	<i>Equus andium</i>																			
EPN-V-73 (S-131) l	Chalán, Punín (ECU)	<i>Equus andium</i>					67.4				123.3								56		
EPN-V-73 (S-131) r	Chalán, Punín (ECU)	<i>Equus andium</i>																			
EPN-V-2152 r	Chalán, Punín (ECU)	<i>Equus andium</i>					77.5					147							62.5 ca		
EPN-V-2152 l	Chalán, Punín (ECU)	<i>Equus andium</i>																			

(continued)

Table 2.7 (continued)

Cat. Number	Locality	Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Remark
EPN-V-76 r	Chalán, Punín (ECU)	<i>Equus andium</i>		61	320	195	75	100	11.4	53.4	44.4	124	54.8						52.2		
EPN-V-76 l	Chalán, Punín (ECU)	<i>Equus andium</i>																			
EPN-V-2161 r	Chalán, Punín (ECU)	<i>Equus andium</i>		75	354	196.5	89	110	12.5	52	29.6	138	173						63.4		
EPN-V-2161 l	Chalán, Punín (ECU)	<i>Equus andium</i>																			
EPN-V-2160 r	Chalán, Punín (ECU)	<i>Equus andium</i>	97.5	72	337 ca	190	95.5	120	13	55	49	130	164						59		
V-2159-CR2159 r	Chalán, Punín (ECU)	<i>Equus andium</i>		75	378	200	107.5	130	13	59.3	45	152	179	100							
V-2159-CR2159 l	Chalán, Punín (ECU)	<i>Equus andium</i>																			
MNCN-1288	Tarija, Bolivia	<i>Equus insulans</i>	135	81.2	398	236	113	120 ca	10.5	61.5	56	170.5	198	116.5							
MNHN-BOL-V-400693 r	Tarija, Bolivia	<i>Equus insulans</i>																			
MNHN-BOL-V-400922 r	Tarija, Bolivia	<i>Equus insulans</i>																			
MNHN-BOL-V-401432 l	Tarija, Bolivia	<i>Equus insulans</i>																			
MNHN-BOL-V-without number l	Tarija, Bolivia	<i>Equus insulans</i>																			
TAR-997 r	Tarija, Bolivia	<i>Equus insulans</i>																			
UF90551 (M & A 1987)	Tarija, Bolivia	<i>Equus insulans</i>	113																		From MacFadden abd Azzaroli 1987
TAR-783	Tarija, Bolivia	<i>Equus insulans</i>																			
EPN-V-3087 r	La Carolina (ECU)	<i>Equus insulans</i>										157									
MUSM-1 r	Sacaco, Arequipa, Perú	<i>Equus insulans</i>	>126	75.5	380	213	71.7 ca	86.5	13.3	62	41.8	148.6	177								
MUSM-17 r	Aguada de Lomas, Arequipa, Perú	<i>Equus insulans</i>	97 ca	75	403	182	81		15.2			161									Deform

(continued)

Synonymy:

1860 *Equus fossilis andium* Wagner, pp. 336–338. Nomen nudum after Mones (1986).

1875 *Equus quitensis* Wolf, p. 155. Nomen nudum after Mones (1986).

1931 *Hippidium jijoni* Spillmann, pp. 50–52.

1938 *Neohippus rivadeneira* Spillmann, pp. 386–388, Fig. 1C.

1938 *Neohippus postremus* Spillmann, pp. 389–391, Fig. 1E.

1992 *E. andium* Branco 1883; nec Wagner-Branco, Azzaroli p. 134, Fig. 3b.

Lectotype: Hoffstetter (1952, p. 247) stated that the material described by Spillmann was lost, and proposed two lectotypes, one for *N. rivadeneira*, specimen V-78 stored in EPN (Quito), and another for *N. postremus*, specimen V-430, also in EPN. We think it is best to consider the first as the Lectotype (V-78) and the second as the Paralectotype (V-430).

Type locality: Punín, near Riobamba, Ecuador.

Geographic distribution: Recorded from Otón in the North to Punín in the South of Ecuadorian Andes (Ecuador). And possibly a site in the upper Pleistocene of Chile: Valle de Elqui and Calera, Lo Aguirre (Alberdi and Frassinetti 2000) (Fig. 2.5).

Stratigraphic distribution: The Cancagua Formation (Sauer 1965) from Ecuador. Cited as Upper Pleistocene after Hoffstetter (1952). MacFadden and Azzaroli (1987) placed it between Middle–Upper Pleistocene. Recently, Dugas (1986) described it between 40,000 and 4000 years. Azzaroli (1992) referred it to Late Pleistocene (see Chap. 5).

Type level: “Puninian” (Hoffstetter 1952, p. 248).

Studied material: Material studied by Hoffstetter (1952) from several localities of the Ecuadorian Andes, stored in the EPN Museum (Quito), Naturkunde of Berlin (Germany), IPMNH (Paris), and the material deposited in the American Museum of Natural History (Frick Collection). And the material stored at the Museo Nacional de Historia Natural (MNH), Santiago de Chile.

Diagnosis: (taken from Prado and Alberdi 1994). Skull is large with sharp and marked supraoccipital crest (Fig. 2.16a). It is large in relation to the postcranial skeleton, and shows a narrow and lightly excavated preorbital and nasal region. This species shows the orbit as wider and situated more lateral and lower (Table 2.7). Short and robust limbs characterize the skeleton of *E. andium*, most significantly in the radius and metapodials thus producing unusual proportions between these (Fig. 2.18a and d). It corresponds to a morphotype easily distinguishable from the others by the multivariate analysis of the dental and limb bones (Figs. 2.7, 2.11, and 2.12).

Discussion: This species has been widely described as much by Branco (1883) as by Hoffstetter (1952). This form possibly presents an anatomical adaptation to environmental factors, reflected in the metapodial shortness (mean slenderness index: MCIII = 18.27; MTIII = 15.81). Hoffstetter (1952) has doubts about this relation because he thinks the shortness of the extremities is differential.

Alberdi et al. (1995) considered that this species, adapted to the Ecuadorian Andes, evolved from a larger form such as *E. insulatus*. It is the smallest form of all *Equus* from South America (Fig. 2.18a, d). Although Hoffstetter (1952) considered this species restricted to the Andes Ecuadorian, there are some localities in Chile where Alberdi and Frassinetti (2000) cited the presence of *E. andium*. In the bivariate analyses of the upper and lower teeth, length versus breadth in surface, we identified two main groups (Fig. 2.7). The smaller group in size corresponds to *E. andium*, and the other group larger in size presents overlapping specimens of *E. insulatus*, *E. neogeus*, *Equus* “*santaeelenae*” and *Equus* “*lasallei*”. *E. andium* is a morphotype characterized by a small size adapted to a mountain habitat, well separated by the skeletal elements from others species (Figs. 2.8 and 2.18). The PCA based on the skeletal elements permits us to identify two groups, one small in size clearly, characterized by its adaptation to mountain habitat that corresponds to *E. andium*, and another large in size that shows overlapping and grouped *E. insulatus*, *E. neogeus* and “*E. santaeelenae*” (Fig. 2.11). The DA based on skeletal elements permit us to identify two clear groups, smaller and larger (*E. andium* and *E. neogeus*, respectively), and one-third intermediate group where there are overlapping specimens of *E. insulatus* and *Equus* “*santaeelenae*” (Fig. 2.12).

E. insulatus C. Ameghino in F. Ameghino 1904

Synonymy:

1851 *Equus macrognathus* Weddell, p. 204.

1855 *E. neogaeus* Lund; Gervais (1855, pp. 33–39 Pl. 7, Figs. 2 and 3.

1904 *E. insulatus* C. Ameghino unpublished; published by F. Ameghino, Fig. 250.

1938 *Neohippus martinei* Spillmann, pp. 382–384, Fig. 1B.

1938 *Neohippus santaeelenae* Spillmann, pp. 384–386, Fig. 1D.

1952 *Equus (Amerhippus) martinei* (Spillmann 1938); Hoffstetter, p. 301.

1992 *Equus martinei* Spillmann 1938; Azzaroli, pp. 137–138.

1994 *Equus (Amerhippus) santaeelenae* (Spillman) 1938, in Prado and Alberdi, pp. 475–476

Holotype: Upper cheek teeth (M3 not M2) figured in F. Ameghino (1904, p.190, Fig. 250), stored in MACN, number 1703. It is not lost as suggested by Mones (1986).

Geographic distribution: Tarija (Bolivia), Rio Chiche in the Ecuadorian Andes and La Carolina and Salinas Oil Fields localities in Santa Elena peninsula (Ecuador), and in Inciarte site, Zulia State, Venezuela (Rincón et al. 2006) (Fig. 2.5).

Stratigraphic distribution: The Tarija locality (MacFadden et al. 1983) as well as the Rio Chiche locality (Sauer 1965) is referred to Middle Pleistocene. Hoffstetter (1952) referred *E. martinei* to be the oldest *Equus* material from Ecuador. Clapperton and Vera (1986) in Azzaroli (1992) assigned this locality to the Late Pleistocene. The remains from Ecuador are from the Upper Pleistocene. Material was recovered from Pichilingue Formation, dated by 14C in 26,000 ± 100 BP (Baldock 1982), and the late Pleistocene of Inciarte, Venezuela (Rincón et al. 2006) (see Chap. 5).

Type level: Ensenadan and Lujanian Land Mammal Ages.

Studied material: Includes material studied by Boule and Thevenin (1920), and MacFadden and Azzaroli (1987) from Tarija (Bolivia) and that from Rio Chiche, Ecuador (Hoffstetter 1952). It also includes material from the Frick collection, American Museum of Natural History (New York); material studied by Spillmann (1938) and Hoffstetter (1952) from the EPN Museum (Quito) and MNHN (Paris); and material from the Sección de Paleontología del Museo de Biología de la Universidad del Zulia, Maracaibo, state of Zulia, Venezuela (MBLUZ-P) (Fig. 2.17).

Comparative diagnosis: This species has a bigger skull than *E. andium*, but is similar in general morphology (see MacFadden and Azzaroli 1987; Fig. 2.16b). It has a prominent cranial flexion between face and braincase. Nuchal crest extends posteriorly to occipital condyles. External auditory meatus located close to glenoid fossa. The preorbital region is also narrow but less excavated (Table 2.7). The mandible is deep and massive (Fig. 2.15). The upper dental pattern is a characteristic of *Equus* but larger in size. Protocones are moderately elongated and fossettes from moderately plicated to more wrinkles than in *E. andium* while in the lower cheek teeth the wrinkling is more complex. The ectoflexids is relatively shallow in the premolars and relatively deep in molars. The postcranial skeleton is larger and stronger than in *E. andium*, but similar in morphology despite living in a different environment (Fig. 2.18b, e). He has a wider and heavier skeleton. The body size is intermediate between *E. andium* and *E. neogeus*.

Discussion: The skulls of *E. insulatus* and *E. santaeelenae* (not complete) are similar in size to those of *E. neogeus*, but this is more dolichocephalic with a relatively high and narrow rostrum (Table 2.7). The protocone is longer, elongated at the distal part, with a certain enamel complication and the lingual groove. In the bivariate analyses of the upper and lower teeth, length versus breadth in the surface shows an overlapping of these species: *E. insulatus*, *E. santaeelenae*, and *E. neogeus* (Fig. 2.7). The bivariate analyses of the MCIII, MTIII, and IPIII; the remains of *Equus* “*santaeelenae*” on place between *E. insulatus* and *E. neogeus*, more close to the first. These two species, *E. insulatus* and *Equus* “*santaeelenae*”, correspond to a robust horse, with moderate slenderness index of metapodials: MCIII = 18.16 and MTIII = 16.01 in the first and MCIII (18.18) and MTIII (15.11) in the second, very close between them. In the PCA based on the skeletal elements, the remains from *Equus* “*santaeelenae*” overlap amply with the remains of *E. insulatus* and something with *E. neogeus* (Fig. 2.11); while DA based on the four groups identified in the PCA permits us observed a marked overlap between *E. insulatus* and *E. santaeelenae* in MCIII and MTIII, the most significant bones (Fig. 2.12; Table 2.2).

E. neogeus Lund 1840

Synonymy:

1840 *E. neogeus* (not *neogaeus*) Lund, p. 319.

1840 *Equus* Owen, pp.108–109, figured Pl. XXXII Figs. 13 and 14.

- 1845 *Equus curvidens* Owen, p. 235.
1875 *Equus argentinus* Burmeister, pp. 55–56, pl. IV, Fig. 6.
1880 *Equus rectidens* Gervais and Ameghino, pp. 92–93.
1881 *Equus lundii* Boas, pp. 307–319, Pl. I and II (Fig. 10–20) grouped all equidiform material from the Lagoa Santa.
1905 *Equus haasei* Reche, pp. 225–241, figured Pl. XXII.
1912 *E. neogaeus* Lund 1840; Sefve pp. 138–143.
1948 *E. lasallei* Daniel, pp. 278–279, Fig. 66.
1960 *Equus (Amerhippus) lasallei* Daniel; Porta, p. 53, Figs. 3–8, Pl. I to II.
1981 *Equus (Amerhippus) vandonii* Cunha, pp. 5–6, Pl. I, II and III.
1987 *Equus (Amerhippus) curvidens* Owen; MacFadden and Azzaroli p. 331.
1992 *E. curvidens* Owen; Azzaroli p. 134, Fig. 1b.
1992 *E. neogaeus* Lund; Azzaroli, p. 134, as uncertain species.
1994 *Equus (Amerhippus) lasallei* Daniel, in Prado and Alberdi, pp.476–477.

Holotype: Right metacarpal III, number 866, stored in Zoologisk Museum, Peter W. Lund Collection, Copenhagen, Denmark.

Geographic distribution: Main remains came from the Pampean region, Argentina (see studied material); others from Lagoa Santa (Lund 1840), Corumba (Cunha 1981), Sao Raimundo Nonato, Piaui (Guérin 1991), Chique-Chique and Aguas do Araxa (Paula Couto 1979), and Cota dos Ossos (Alberdi et al. 2003) in Brazil; and Arapey Grande creek and Sopas Creek in the Sopas Formation, Uruguay; Cerro Gordo (Porta 1960) and Tibitó (Correal Urrego 1981), Colombia (Fig. 2.5).

Stratigraphic distribution: Upper Pleistocene of Buenos Aires province, Argentina, Brazil, Colombia, and Uruguay. Porta (1960) correlated Cerro Gordo (Colombia) with the Punian in Ecuador (sensu Hoffstetter 1952). Tibitó site was dated by 14C between 28,000 and 4000 years BP (Carbonari et al. 1992) (see Chap. 5)

Type level: Lujanian Land Mammal Age.

Studied material: Includes the material studied by Sefve (1912) such as *E. neogaeus* and *E. curvidens* from Mercedes (Luján), Ayacucho, Necochea, Río Quequén Salado, Paso Otero, Arroyo Tapalqué, Montehermoso, among others, in the Buenos Aires province. The material from the Brazilian localities, Toca dos Ossos in the Bahia State and Lagoa Santa area in Minas Gerais State (Alberdi et al. 2003) stored at Museo de Ciências Naturais and Pontificia Universidad Catolica de Minas Gerais (MCN). And material from Sopas Formation stored at the Universidad Nacional de la República de Uruguay (Montevideo). A complete skull collected by Brother Daniel (Porta 1960) and a few remains from Tibitó (Correal Urrego 1981) from the Museo de la Universidad de Lasalle (MCLU) and Instituto de Ciencias Naturales (ICN), Bogotá, Colombia.

Comparative diagnosis: This is largest species of South American horses. The skulls are large and show an enlarged preorbital and nasal region (Fig. 2.16c and Table 2.7). The skull from Cerrogordo, which belongs to old animal, has the largest basilar length of skull among the South American horses, but the other

measurements are comparable with other equids except *E. andium*. The presence of the fore lobes of the occipital condyles joint, observed also in *E. haasei* described by Reche (1905), may be related to the age of the animal. Upper cheek teeth contain widely developed fossettes and the enamel line is something wrinkled. The length of upper and lower row is intermediate among *E. andium* on one side and another *E. insulatus* and *E. santaeelenae*, and close to *E. neogeus*. Its morphology is similar to *E. neogeus* but possibly something larger in size. But, it is important to note that these teeth correspond to a very old animal and therefore its dimensions are a little smaller.

Discussion: From the nomenclatorial point of view, Lund (1840) described *E. neogaeus* from a third metatarsal found at Lagoa Santa. Later, the same author (1846) described new remains from the same place. He referred two molars to *E. neogaeus*, one molar to *E. principalis* and the rest to *Equus aff. caballus*. Gervais (1855) assigned part of this material to *E. neogaeus* and another part to *E. devillei*. In 1869, Owen created a new genus: *Hippidion*, which 1870 included *E. neogaeus*, *E. principalis* and *E. arcidens*. Boas (1881) considered the metatarsal described by Lund (1840) as a metacarpal, and he created a new species: *E. lundii*, based on this material and the molars referred by Lund (1846) as *Equus aff. caballus*. Winge (1906) considered all material from Lagoa Santa as *E. curvidens*. Later, Sefve (1912) referred to *E. neogaeus* as all the material from Lagoa Santa and to *E. curvidens* as the material from the Pampean Region. In 1971 Cunha explained in detail that only the teeth referred by Lund (1846) to *E. neogaeus* and *E. principalis*, correspond to *Hippidion*, while the remaining teeth and metacarpal correspond to *Equus*. Owen (1840) mentioned and figured one horse, which he later (1845) named *E. curvidens*. Based on the rules of Principle of Priority (ICZN 2000), we consider that *E. neogeus* (not *neogaeus*) should have priority over *E. curvidens* (Prado and Alberdi 1994, p. 475). We include in this species the skull high and long, with a longer diastema and relatively slender rostrum that corresponds to a very old animal from Cerro Gordo: *E. lasallei*, because it is very similar to skull of *E. neogeus* in morphology and measurements. In 1994, we suggested continue to use the name *lasallei*, pending to found new remains to enlarge it diagnosis, but until now we don't know about new finding. The slenderness is greater (MCIII = 16.16; MTIII = 12.33). Sefve (1912) thinks it is very difficult to separate this species if we do not consider its dimensions. He also explained that *E. neogeus* is both the largest and the most slender species in comparison with all other South American *Equus* (Fig. 2.16c; Table 2.4). Winge (1906) synonymized *E. neogeus* under *E. curvidens*, but we consider priority corresponds to *E. neogeus* (see above). The PCA based on the skeletal elements shows overlapping morphological patterns of *E. neogeus* grouped with *E. insulatus* and *E. santaeelenae* (Fig. 2.11). But the DA of the multivariate analysis underlines this species from the rest and grouped all specimens from Buenos Aires province sites as well as Brazilian localities with a good discrimination among them concretely 98.6% in MCIII, 97.4% in MTIII, 91.9% in AST, 83.3% in CAL, 89.9% in 1PHIII, and 81.8% in 2PHIII of the cases properly grouped previously (Fig. 2.12; Table 2.2).

2.9 Conclusions

The results of the morphological study of skulls, mandibles and teeth agree with those from the bivariate and multivariate analysis of the skeletal remains in hippidiforms and equidiforms. The bivariate analyses of the upper and lower teeth of *Hippidion* genus are clearly distinct between *H. devillei* (smaller teeth) and *H. principale* (largest teeth), and the teeth of *H. saldiasi* are intermediate between both species. While in the DA of the appendicular skeleton there is a clear difference among them, and *H. saldiasi* is the smallest and *H. principale* is the largest and *H. devillei* is the intermediate. The conclusions for hippidiforms can be summarized as follows:

The genus *Hippidion* Owen, 1869 in South America has the priority according to the principle of priority (Alberdi 1987), and has three valid species following Alberdi and Prado (1993): *H. principale* (Lund), 1846, *H. devillei* (Gervais), 1855 and *H. saldiasi* (Roth), 1899.

In the equids group, we questioned the use of subgenus *Amerhippus*. The new molecular data increases the known phenotypic plasticity of horses and consequently casts doubt on the taxonomic validity of the subgenus *Amerhippus*. We reduce the valid species of *Equus* to: *E. andium* Branco 1883, ex Wagner (1860), *E. insulatus* Ameghino 1904, and *E. neogeus* Lund 1840. Our morphological and statistical analysis does not permit us to get a clear differentiation between *E. santaeelenae* and *E. insulatus*, consequently; we considered *E. santaeelenae* a synonymous of *E. insulatus* according to the International Code of Zoological Nomenclature, because *E. insulatus* is considered as a priority over *E. santaeelenae*. The differences between them are due more to the intraspecific variation in the samples than different specifics.

We now question the validity of the species *E. lasallei* Daniel 1948. The only skull and mandible assigned to this species are very similar to skull and mandible to *E. neogeus*, only the basilar length is larger (Table 2.7). The upper and lower rows are close to those for *E. neogeus* while premolar and molar rows are very similar to *E. neogeus*. On the other hand, this skull is restored and possible modifications are not so clear. Consequently, we consider this skull how an insufficient material to support this species and we considered, based on cranial morphology and its measurements, this material as synonymous of *E. neogeus*. According to the International Code of Zoological Nomenclature *E. neogeus* is a priority over *E. lasallei*. Only future findings may confirm or reject these agreements.

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