A CLADISTIC ANALYSIS OF THE HORSES OF THE TRIBE EQUINI

by JOSÉ L. PRADO *and* MARÍA T. ALBERDI

ABSTRACT. The Equini tribe with seven genera forms a monophyletic group defined by one synapomorphy: protocone connected to the protoloph. Fourteen species are considered as the terminal taxa: *Protohippus* (two species), *Calippus* (two), *Pliohippus* (one), *Hippidion* (three), *Dinohippus* (three), *Astrohippus* (one) and *Equus* (two). A cladistic analysis was performed using 20 characters from cranial morphology, upper and lower teeth, and appendicular skeletons. Polarity of characters was based on outgroup criterion using the Hippotheriini tribe. For some characters, apomorphic states were identified using *Merychippus*, which was the sister group of both tribes. One parsimonious cladogram of 31 steps and a consistency index of 0·77 was produced, from which a classification of the tribe Equini was constructed. We recognize two subtribes: Protohippina (*Protohippus* and *Calippus*) and Pliohippina subtrib. nov. (*Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*). *Pliohippus* was the sister group to the rest of the subtribe. The species of *Hippidion* form a monophyletic group and there is no evidence of a relationship between '*Onohippidium*' *galushai*, from North America, and the *Hippidion* group, from South America. *Astrohippus stocki* was the sister species of the *Equus*-group, which includes '*Dinohippus*' *mexicanus*. The analysis shows that characters mostly from the cranial morphology and upper teeth characterize the suprageneric taxa. High congruence between the stratigraphical record and the phylogenetic hypothesis is observed.

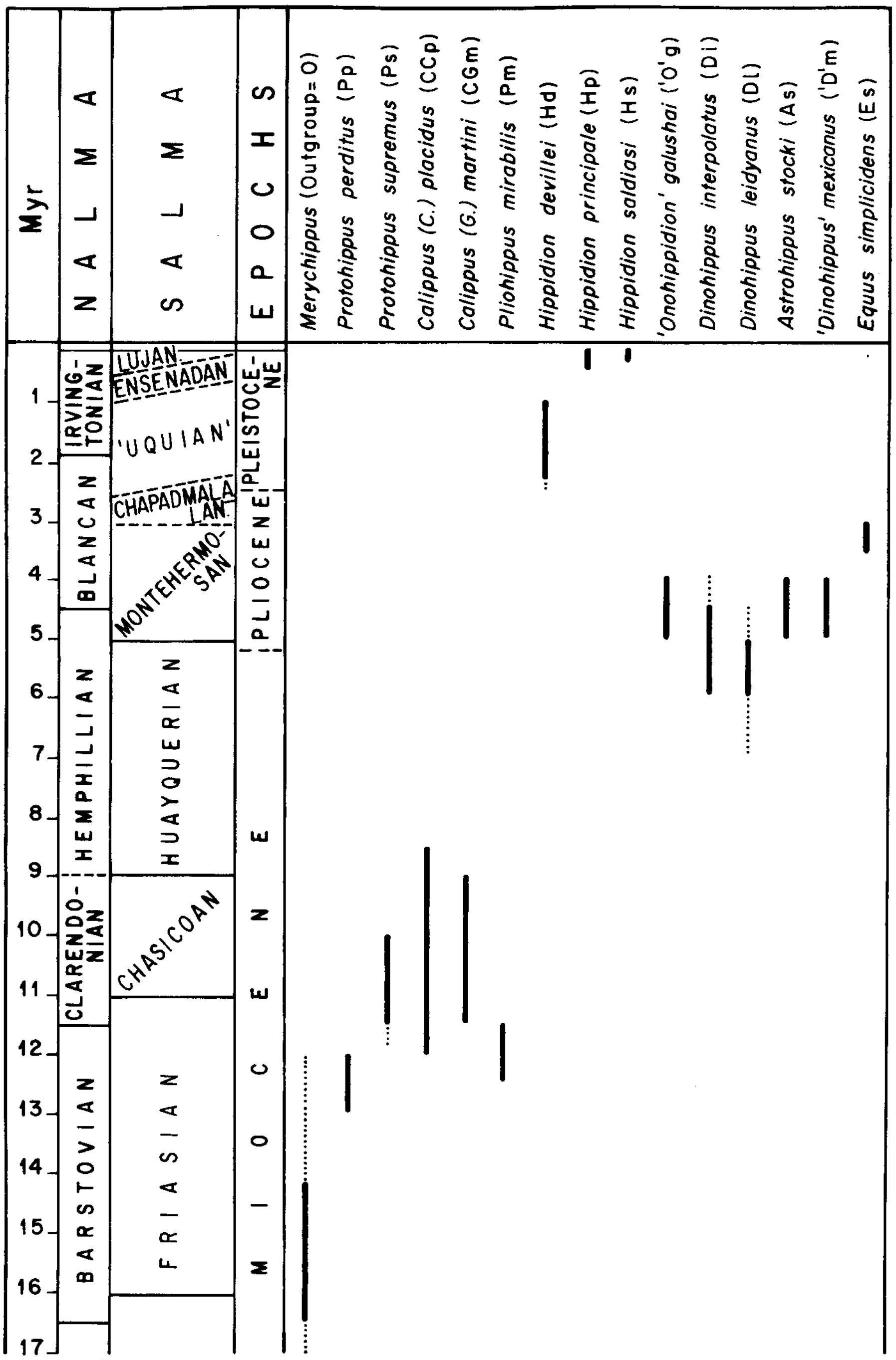
THE subfamily Equinae Gray is clearly recognizable as a monophyletic group on the basis of at least five major shared-derived character states of the cheek teeth: (1) cement formed on deciduous and permanent cheek teeth; (2) presence of the pli caballin on premolars and molars; (3) presence of the pli linguaflexid; (4) moderately deep ectoflexid on p2; (5) unworn M1-M2 crown heights greater than 23–28 mm (Hulbert 1988*a*; Hulbert and MacFadden 1991; MacFadden 1992). This clade represents the major adaptive radiation of hypsodont horses and includes Equini and Hippotheriini (*sensu* Prothero and Schoch 1989, p. 532; = Hipparionini Quinn, 1955).

The Equini tribe comprises eight genera, one widespread throughout the world (*Equus*), six endemic to North America: *Protohippus*, *Calippus*, *Pliohippus*, *Dinohippus*, '*Onohippidium*' and *Astrohippus* (Evander 1989; Hulbert 1989; Prothero and Schoch 1989) and one endemic to South America: *Hippidion* (Alberdi 1987; Alberdi and Prado 1993). The Equini lineage is well-known from the middle Miocene until the upper Pliocene in North America (Text-fig. 1). In South America, the first record of this lineage comes from the upper Pliocene–lower Pleistocene (Marshall *et al.* 1984; Alberdi and Prado 1993). The lineage became extinct during the late Pleistocene (Alberdi and Prado 1993; Martin and Klein 1984; Prado and Alberdi 1994; Politis *et al.* 1995).

Equini is a monophyletic group of genera distinguished from the tribe Hippotheriini (Prothero and Schoch 1989) by at least one apomorphic character state: protocone connected to the protoloph (Hulbert 1988*a*; Hulbert and MacFadden 1991; MacFadden 1992).

Different phylogenies of equids have been proposed. Some authors (Stirton 1940; Lance 1950; Simpson 1951; Quinn 1955) considered, based on phylogenetic systematics, '*Merychippus*' (*Protohippus*) as an ancestor of *Calippus* and *Pliohippus* and *Pliohippus* to be the ancestor of all *Hippidion*, *Astrohippus* and *Equus* species. On the other hand, Hulbert (1989) and MacFadden (1992) suggested, based on cladistics analysis, *Merychippus* as a sister group of Equini and Hippotheriini tribes (hipparionines and protohippines). *Protohippus* and *Calippus* form a

[Palaeontology, Vol. 39, Part 3, 1996, pp. 663–680]



TEXT-FIG. 1. Chronological distribution of Equini species. Myr = million years; NALMA = North America Land Mammal Ages; SALMA = South America Land Mammal Ages. The stratigraphical framework was taken from Marshall *et al.* (1983, 1984), Tedford *et al.* (1987) and Alberdi *et al.* (1995).

monophyletic group and are set apart from the other genera: *Astrohippus*, *Hippidion*, '*Onohippidium*', *Dinohippus*, *Equus* and *Pliohippus*.

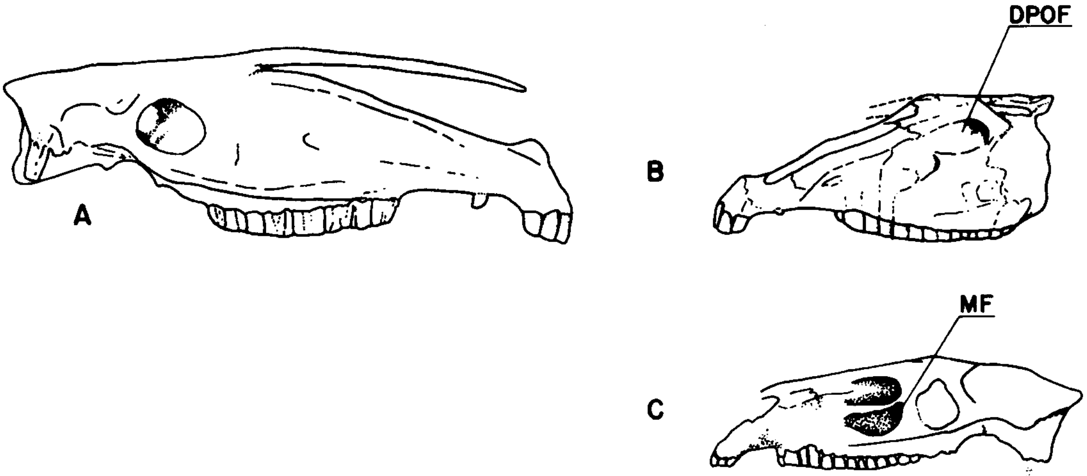
The phylogenetic relationships within the tribe Equini are a matter for debate (e.g. Matthew 1926; Stirton 1940; Quinn 1955; Evander 1989; Hulbert 1989; Prothero and Schoch 1989). This paper comprises a cladistic analysis for this tribe, with special attention to the relation of South American horses, based on data obtained from the cranial and appendicular skeleton morphology. In addition, we examined its congruence with the fossil record.

MATERIAL AND METHODS

We examined 14 species of Equini (Text-fig. 1). Since many species of fossil Equini are very poorly known, we decided to include only the best-known species of each recognized genus (as defined by Evander 1989 and Prothero and Schoch 1989). Specimens of *Protohippus perditus* (FAM 126623, 125626, 60351, and 126759; from Devils Gulch Member, Nebraska, upper Barstovian), *Protohippus supremus* (FAM 12631, 125258 and 111728, from Mac Adams Quarry, Texas, lower Clarendonian), *Pliohippus mirabilis* after Evander (1989), MacFadden (1992), among others (FAM 60810 (skull, mandible and complete skeleton), from Devils Gulch Member, Nebraskă, upper Barstovian), *Dinohippus interpolatus* (FAM 87201 and 18972, from Edson Quarry, Kansas, upper Hemphillian), *Dinohippus leidyanus* (FAM 116191, 116194, from Guymon quarries, Texas, upper Hemphillian), *Astrohippus stocki* (FAM 74290, 74291 and 74283, from Ogallala Formation, Texas, upper Hemphillian and from Yepómera, Mexico, uppermost Hemphillian in Lance 1950), '*Onohippidium*' *galushai* (FAM 116136, 31938, 11872, Wikieup Fauna, Arizona, upper Hemphillian, and MacFadden and Skinner 1979) and *Equus simplicidens* (FAM 32550, 32551, 32553, 32535 and 20077, from Hagerman Horse Quarry, Idaho and Crosby Co., Texas, middle Blancan) came from the Frick Collection of the American Museum of Natural History. Data for *Calippus* (*Calippus*) *placidus* and *Calippus* (*Grammohippus*) *martini* were taken from Hulbert (1988*a*), '*Dinohippus*' *mexicanus* from Lance (1950) and *Hippidion* species from Alberdi and Prado (1993). The review of late Oligocene to early Pliocene mammalian biochronology by Tedford *et al.* 1987 and the recent review of Plio-Pleistocene biochronology from Argentina by Alberdi *et al.* 1995 provided a chronological framework for the analysis.

Character polarity was determined by outgroup comparison methods (Eldredge and Cracraft 1980; Watrous and Wheeler 1981; Humphries and Funk 1984; Maddison *et al.* 1984), collectively using the other tribe (Hippotheriini) of the subfamily Equinae as the outgroup. For some characters, apomorphic states were identified using *Merychippus* (*sensu* Evander 1989; Hulbert 1989; Hulbert and MacFadden 1991), which was the sister group of both tribes. The '*Merychippus*-group' has traditionally been a large polyphyletic assemblage with many species. Recent studies have separated the merychippine grade into a monophyletic clade (MacFadden 1992). The Hippotheriini data were taken from Simpson (1951), Gromova (1952), Forsten (1968), Alberdi (1974) and Watabe (1992).

In current cladistic analysis, missing entries in data matrices represent information that is unknown. This is the case for *Hippidion saldiasi* and '*Dinohippus*' *mexicanus* which are known only from a few remains. The selection of characters is based on a critical review of specimens and the previous literature about cladistic analyses on horses (Bennett 1980; Hulbert 1988*a*, 1988*b*; Evander 1989; Hulbert 1989; Hulbert and MacFadden 1991; MacFadden 1992; Watabe 1992). In order to get one parsimony tree we used, where possible, the characters which present the fewest missing data. Consequently, our data matrix has more cranial characters than appendicular skeleton ones. Twenty characters were used: five from the cranial morphology (characters 1–5), six from the upper teeth (characters 6–11), four from the lower teeth (characters 12–15), three from the mandible (characters 16–18), and two from the appendicular skeleton (characters 19–20).



TEXT-FIG. 2. Skull characteristics. A, *Hippidion principale* with nasal notch posterior to M1 (character 1) and long muzzle (character 4); B, '*Onohippidion*' *galushai*; C, *Astrohippus stocki*. DPOF = dorsal preorbital fossa; MF = malar fossa.

Character definition and codification

1. Depth of nasal notch (Text-fig. 2A). Some living mammals, such as tapirs, have retracted nasal bones, which have an adaptation to the presence of a proboscis. This feature, however, is rare in fossil horses, although some *Hipparion* from Eurasia apparently possessed a tapir-like proboscis (Studer 1911; Sefve 1927).

Outgroup comparison. All *Merychippus* species and the primitive group of Hippotheriini (morphotype 1 *sensu* Alberdi 1989) have a nasal notch level with, or anterior to P2 (Hulbert 1988*b*, 1989; Hulbert and MacFadden 1991; Watabe 1992), which is regarded as primitive.

States. 0 = anterior to P2; 1 = between P2-M1; 2 = posterior to M1.

2. Malar fossa (Text-fig. 2C). The malar fossa of Hulbert (1988*b*) is the same as the facial fossa of Gregory (1920) and the infracranial fossa of Gromova (1952).

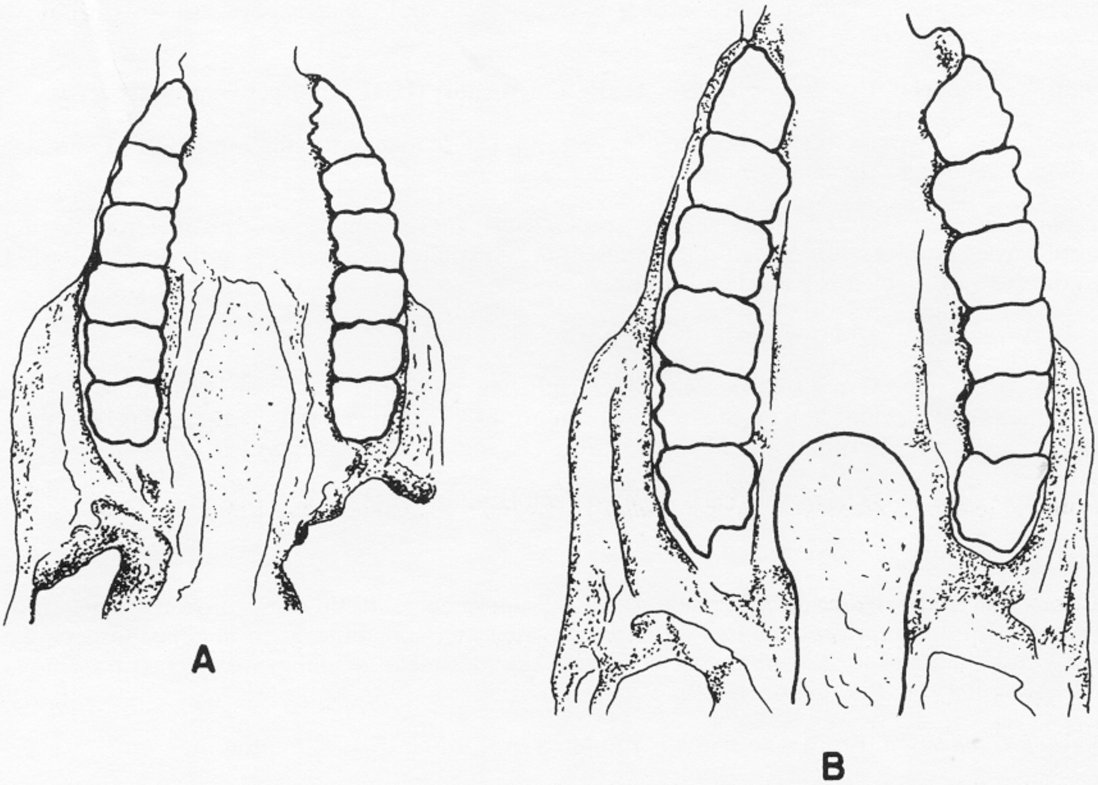
Outgroup comparison. All Hippotheriini species have an absent or shallow malar fossa.

States. 0 = absent or shallow; 1 = present.

3. Dorsal preorbital fossa (DPOF; Text-fig. 2B). This fossa is the same as the lacrimal fossa of Gregory (1920), the supracranial fossa of Gromova (1952), the preorbital fossa of Pirlot (1953) and the nasomaxillary fossa of Skinner and MacFadden (1977). Many authors use the morphology of the DPOF as a taxonomic character in fossil horses. We believe, however, that this is an unstable character (Forsten 1983; Eisenmann *et al.* 1987; Alberdi 1989). According to Gromova (1952) its morphology varies among the ontogenetic states. We used only the presence/absence of this feature but did not consider the morphology.

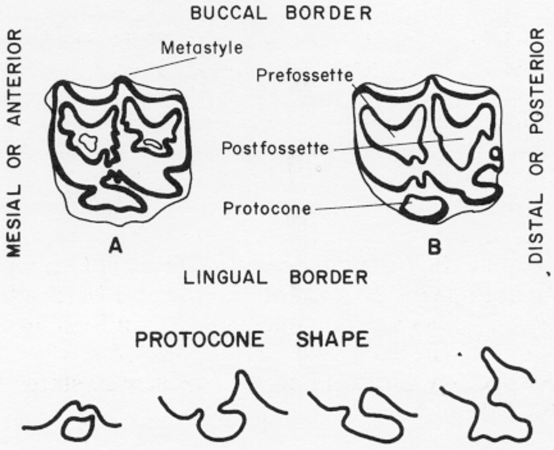
Outgroup comparison. The most derived Hippotheriini species (morphotype 6 *sensu* Alberdi 1989) lost the DPOF (Hulbert 1988*b*; Watabe 1992). A very well-developed DPOF is regarded as primitive.

States. 0 = present; 1 = absent.



TEXT-FIG. 3. Position of choanae anterior border: A, at the level of P4-M1 of *Merychippus* (drawing from FAM 12793); B, posterior to P4-M1 of *Equus* (redrawn from Eisenmann *et al.* 1988; fig. 6).

TEXT-FIG. 4. Upper teeth characteristics. A, *Equus*; B, *Merychippus*. Redrawn from Eisenmann *et al.* (1988).



4. Muzzle length (Text-fig. 2). This character is determined by comparing I3-P2 diastema length (UDL) and upper tooth-row length (UTRL). Hulbert (1988*b*) recognized five character states. In our case we considered two character states because we analysed a different group of horses.

Outgroup comparison. Hippotheriini horses have a long muzzle, which is regarded as primitive (character state 0).

States. 0 = long (UDL > 40 per cent. of UTRL); 1 = short (UDL < 40 per cent of UTRL).

5. Position of choanae anterior border (Text-fig. 3). The tendency for the retraction of choanae position is related to the lengthening of the face.

Outgroup comparison. All *Merychippus* species and the primitive group of Hippotheriini (morphotypes 1 and 2 *sensu* Alberdi 1989) present the choanal anterior border at the level of P4-M1 or more forward, which is considered primitive.

States. 0 = to level P4-M1 or forward; 1 = posterior to P4-M1.

6. Protocone connection (Text-fig. 4). The protocone condition has been used to subdivide mesodont and hypsodont horses (Stirton 1940). In most recent papers, this character has been used to distinguish the Hippotheriini and Equini tribes (Evander 1989; MacFadden 1992).

Outgroup comparison. The protocone is isolated in all Hippotheriini species (Eisenmann *et al.* 1988).

States. 0 = isolated; 1 = connected.

7. Protocone shape on P3-M2 (Text-fig. 4). In the upper cheek teeth, the protocone varies from rounded, with an anterior spur, to oval and elongated and sometimes with angular borders. To employ this character for taxonomy, we compared the specimens at similar wear stages (Gromova 1952; Alberdi 1974; Eisenmann 1980).

Outgroup comparison. Protocone shape is round to oval in the tribe Hippotheriini.

States. 0 = round; 1 = oval; 2 = elongate-oval; 3 = triangular.

8. Internal postfossette plication (Text-fig. 4). Enamel plication is development in the anterior and posterior walls of prefossettes and postfossettes respectively. The plication decreases during ontogeny (Alberdi 1974). To employ this character for taxonomy we chose anterior postfossette plication because it is more stable. Nevertheless, specimens at similar wear stage were used.

Outgroup comparison. All *Merychippus* species and the most primitive groups of Hippotheriini have simple plication, which is regarded as primitive.

States. 0 = simple; 1 = multiple.

9. Metastyle development (Text-fig. 4). This is observed especially on P3-P4 at middle wear stages.

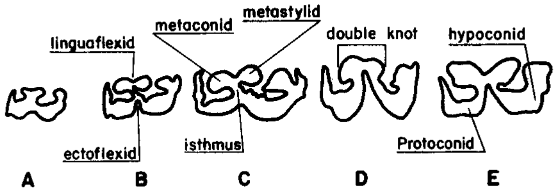
Outgroup comparison. Most Hippotheriini have a simple metastyle; the derived species have some developed but not to the degree of the Equini tribe (Hulbert 1988*b*).

States. 0 = simple; 1 = well-developed.

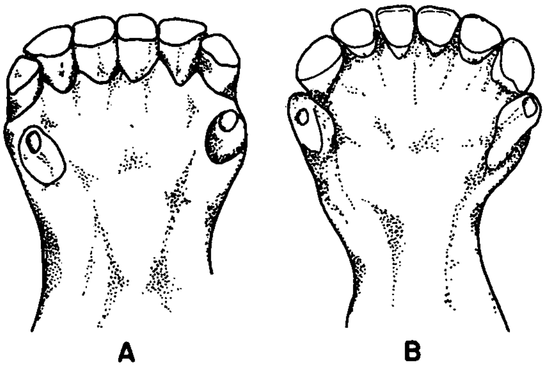
10. Protocone lingual border. This is observed especially on P3-M2 at middle wear stages. Text-figure 4 illustrates a sample of protocone lingual border.

Outgroup comparison. The most derived Hippotheriini species (morphotype 6 *sensu* Alberdi 1989) have a straight or concave lingual border to the protocone (Hulbert 1988*b*). A round or convex state is regarded as primitive.

States. 0 = round or convex; 1 = straight or concave.



TEXT-FIG. 5. Lower teeth characteristics. A, *Merychippus*; B, *Protohippus*; C, *Pliohippus*; D, *Hippidion*; E, *Equus*.



TEXT-FIG. 6. Lower symphysial dentitions. A, *Calippus*, with diastema i3-c and linear arcade; B, *Pliohippus*, without diastema i3-c and arcuate arcade.

11. Molar crown height. The increase in height of the tooth crowns was classically related with the change from browsing (brachydont) to grazing (hypsodont) horses (Simpson 1951). The height is taken from the crown bottom to the parastyle top in M1-M2, only in unworn specimens. In the Equini tribe, we think it is important to mark the state of character that reflects the change from browsing to grazing. The molar crown height of more than 28 mm indicates hypsodont horses.

Outgroup comparison. All *Merychippus* species have molar crown heights of about 25 mm (Hulbert 1988*a*, 1988*b*; Hulbert and MacFadden 1991). A molar crown height of less than 28 mm is regarded as primitive.

States. 0 = < 28 mm; 1 = ⩾ 28 mm.

12. Depth of linguaflexid. Shape and depth of the linguaflexid varies with wear. The depth is taken on p3-p4 with middle wear (Text-fig. 5). This character seems more variable because the size of double-knots can be small or very big in relation to the tooth size (character 14).

Outgroup comparison. Merychippus has a shallow linguaflexid, which is regarded as primitive (see Text-fig. 5A).

States. 0 = shallow, as in Text-figure 5A morphology; 1 = middle, as in Text-figure 5B and 5D morphologies; 2 = deep, as in Text-figure 5C and 5E morphologies.

13. Depth of the ectoflexid (Text-fig. 5). This character varies with wear. The ectoflexid grooves from the buccal side continue inside and sometimes divide the isthmus into an anterior and a posterior part. The depth is taken on p3-p4 (Alberdi 1974; Hulbert 1988*b*; Watabe 1992).

Outgroup comparison. All Hippotheriini have a shallow ectoflexid, which is regarded as primitive.

States. 0 = shallow, as in Text-figure 5A morphology; 1 = moderate, without penetrating the isthmus, as in Text-figure 5B and 5D morphologies; 2 = deep, penetrating the isthmus, as in Text-figure 5C and 5E morphologies.

14. Sizes and shapes of the metaconid and the metastylid (Text-fig. 5). The metaconid and metastylid shape on the lower cheek was considered by Gromova (1952), who recognized two morphological types: hipparionid and caballoid. The linguaflexid affects this feature, classically named the double-knot. In the Equini tribe the size and shape of the linguaflexid give the peculiar morphology to the double-knot.

Outgroup comparison. Merychippus has small metaconid and metastylid, which is regarded as primitive.

States. 0 = small, as in Text-figure 5A; 1 = of medium size, as in Text-figure 5B–D; 2 = large, as in Text-figure 5E.

15. Buccal borders of the protoconid and the hypoconid (Text-fig. 5). There is no variation during ontogeny (Alberdi 1974; Hulbert 1988*b*; Watabe 1992).

Outgroup comparison. Hippotheriini has a rounded condition; only the most derived species (morphotype 6 *sensu* Alberdi, 1989) show a tendency to straight protoconid and hypoconid labial borders.

States. 0 = rounded; 1 = straight.

16. Diastema i3-c (Text-fig. 6). Many horses possess a characteristic diastema between i3 and c. This character is mentioned by Bennett (1980).

Outgroup comparison. All *Merychippus* species do not present diastema between i3 and c. An absent diastema i3-c is regarded as primitive.

States. 0 = absent; 1 = present.

17. Incisor arcade (Text-fig. 6). The first and second incisors are arranged in a straight line or in an arcuate line. This feature is mentioned by Hulbert (1988*a*). Several papers have examined the muzzle and incisor morphologies in relation to dietary preference (e.g. Owen-Smith 1985; Janis and Ehrhardt 1988). These studies have shown that horses adapted to browsing habits had a relatively narrow muzzle and a strongly curved incisor arcade. At the other end of the morphological spectrum, most grazing species had a very broad muzzle, wide symphysis and a linear arrangement of incisors (MacFadden 1992, p. 241). Within fossil *Equus*, several different incisor and muzzle morphologies evolved, but *Equus simplicidens*, considered here, presents the arcuate state.

Outgroup comparison. Hippotheriini has an arcuate arcade, which is regarded as primitive.

States. 0 = arcuate; 1 = linear.

18. Muzzle width relative to upper tooth-row length at moderate wear-stage. This character is mentioned by Hulbert (1988*a*, 1989). The grazing ungulates have relatively broader muzzles in contrast with browsers. In general, dietary selectivity is related to muzzle width (MacFadden 1992). This character distinguishes *Protohippus* and *Calippus* from the other Equini horses.

Outgroup comparison. Hippotheriini has a narrow muzzle (Hulbert 1989), which is regarded as primitive.

States. 0 = moderate or narrow; 1 = broad (> 36 per cent.).

19. Number of digits. The pentadactyl limb has traditionally been recognized as the tetrapod archetype. Reduction of lateral metapodials in the evolution of horses has been mentioned by several authors (e.g. Matthew 1926; Simpson 1951) in relation to the development of the monodactyl limb.

Outgroup comparison. Hippotheriini species have a tridactyl condition. Loss of digits is derived. Classical ontogenetic studies on the development of the carpus of horses support this polarity (Ewart 1894*a*, 1894*b*).

States. 0 = tridactyl; 1 = monodactyl.

20. Gracility of metapodials. The morphological characters in metapodials are closely associated with body weight and functional locomotion and their modifications throughout the evolutionary lineages of horses have been mentioned (Camp and Smith 1942; Sondaar 1968; Alberdi 1974; Hussain 1975; Alberdi and Prado 1993; Prado and Alberdi 1994). The slenderness index was defined by Gromova (1952) as the ratio percentage of the minimum breadth (near the middle of the bone) and the maximum length.

Outgroup comparison. All *Merychippus* species have slender metapodials, which are regarded as primitive.

States. 0 = slender, when the slenderness index is < 15; 1 = robust, when the slenderness is > 15.

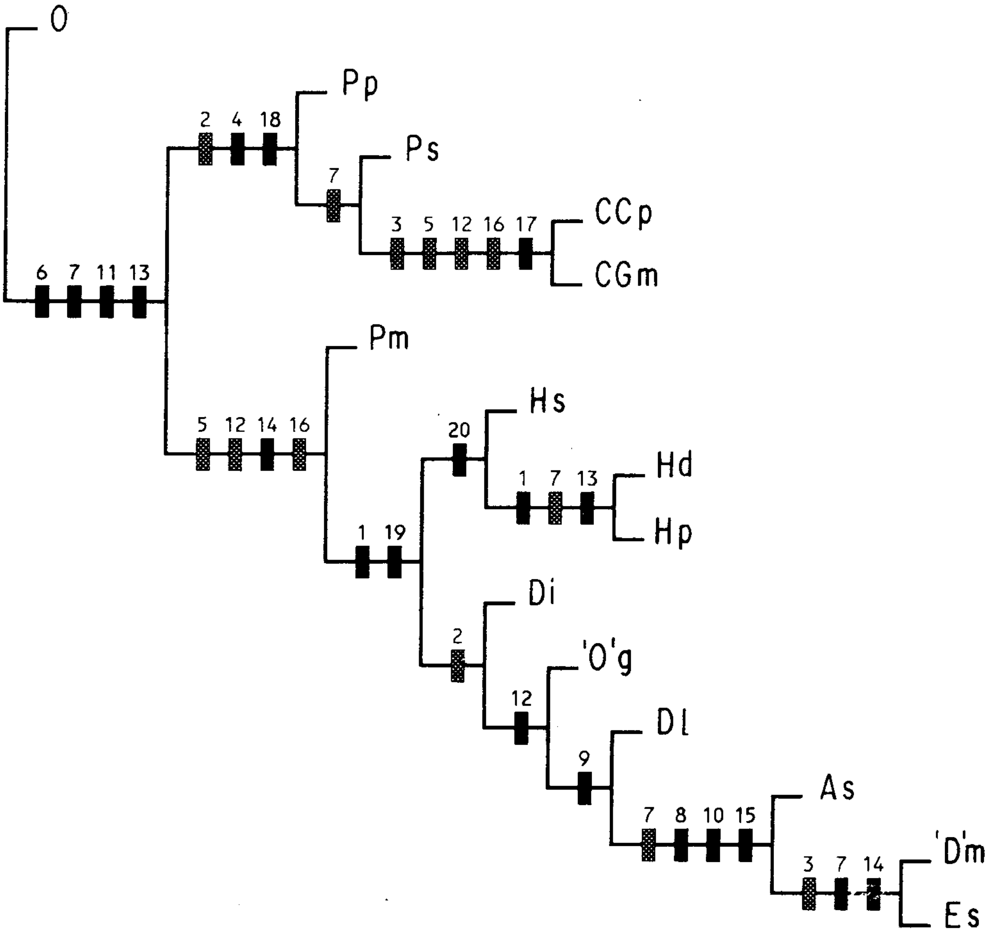
Methods

We have used the method of phylogenetic systematics developed by Hennig (1966). All characters are treated as additive, i.e. the transformation sequences are considered to be linear. Table 1 contains the data matrix used in this analysis. The data were analysed using Hennig86 version 1.5 (Farris 1988) for parsimony analysis and CLADOS version 0.9 (Nixon 1991) for examining the character distribution and production of publishing figures. Hennig86 was run with the implicit enumeration option ('ie') for calculating trees.

TABLE 1. Data matrix.

	Characters																			
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protohippus supremus	0	1	0	1	0	1	2	0	0	0	1	0	1	0	0	0	0	1	0	0
Protohippus perditus	0	1	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0
Pliohippus mirabilis	0	0	0	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	0	0
Hippidion devillei	2	0	0	0	1	1	2	0	0	0	1	1	2	1	0	1	0	0	1	1
Hippidion principale	2	0	0	0	1	1	2	0	0	0	1	1	2	1	0	1	0	0	1	1
Hippidion saldiasi	?	?	?	?	?	1	?	?	0	0	1	1	1	1	0	?	0	?	1	1
'*Onohippidium*' *galushai*	1	1	0	0	1	1	1	0	0	0	1	2	1	1	0	1	0	0	1	0
Dinohippus interpolatus	1	1	0	0	1	1	1	0	0	0	1	1	1	1	0	1	0	0	1	0
Dinohippus leidyanus	1	1	0	0	1	1	1	0	1	0	1	2	1	1	0	1	0	0	1	0
'*Dinohippus*' *mexicanus*	?	1	1	0	1	1	3	1	1	1	1	2	1	2	1	1	0	0	1	0
Astrohippus stocki	1	1	0	0	1	1	2	1	1	1	1	2	1	1	1	1	0	0	1	0
Calippus (*Calippus*) *placidus*	0	1	1	1	1	1	2	0	0	0	1	1	1	0	0	1	1	1	0	0
Calippus (*Grammohippus*) *martini*	0	1	1	1	1	1	2	0	0	0	1	1	1	0	0	1	1	1	0	0
Equus simplicidens	1	1	1	0	1	1	3	1	1	1	1	2	1	2	1	1	0	0	1	0

We rank a fossil's stratigraphical position based on the radiometric dates of the first occurrence following the method proposed by Norell and Novacek (1992*a*, 1992*b*) to analyse the consensus between the fossil record and cladistic results. This method is based on that of Gauthier *et al.* (1988). We used the Spearman rank correlation coefficient (Hollander and Wolfe 1973) to measure the fit



TEXT-FIG. 7. Cladogram resulting from analysis of the character matrix in Table 1. Character numbers above the hashmarks correspond to the variables explained in the text. Filled hashmarks indicate non-homoplastic steps; grey patterned hashmarks denote convergences.

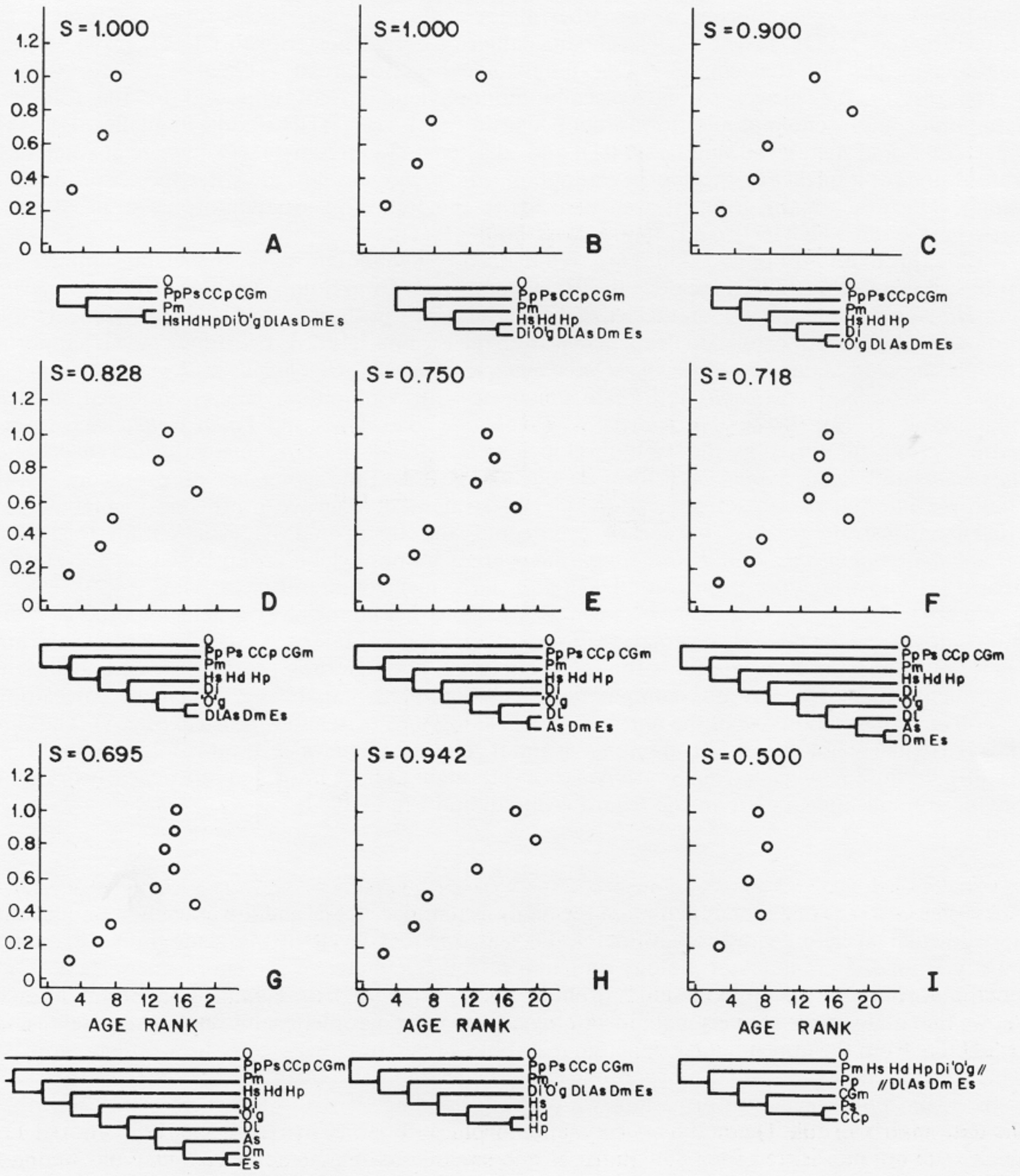
between the fossil record and rank clade in the cladograms (order of branching, with the first branch off of the main spine having the lowest clade rank). This coefficient was calculated using STATGRAPHICS version 5.0 (1991).

RESULTS

The data matrix (Table 1) contains two synapomorphies for the entire tribe (characters 6 and 11) which were not considered for calculations of tree length and consistency index. One parsimonius cladogram of 31 steps and a consistency index of 0·77 was obtained (Text-fig. 7). The cladogram shows that characters from cranial morphology (2, 3 and 5) reflect more parallel evolution.

The tribe Equini presents four synapomorphies: 'protocone connection' [6]; 'shape of protocone' [7]; 'height of molar crown' [11]; and 'depth of ectoflexid' [13]. Two of the four transformation series (7 and 13) present further changes in the cladogram.

The basal node shows two major clades. *Protohippus perditus*, *Protohippus supremus*, *Calippus* (*Calippus*) *placidus* and *Calippus* (*Grammohippus*) *martini* form a first monophyletic group supported by the following synapomorphies: 'short muzzle' [4(1)]; and 'broad muzzle' [18(1)]. There is another character state that supports this group: 'presence of malar fossa' [2(1)], which is



TEXT-FIG. 8. Simple pectinate phylogeny of Equini taxa and plots of age rank versus clade rank for pectinate cladograms (*sensu* Norell and Novacek 1992*a*, 1992*b*). Clade ranks are rescaled from 0 to 1. S, Spearman coefficient; O, outgroup; Pp, *Protohippus perditus*; Ps, *Protohippus supremus*; CCp, *Calippus* (*Calippus*) *placidus*; CGm, *C.* (*Grammohippus*) *martini*; Pm, *Pliohippus mirabilis*; Hs, *Hippidion saldiasi*; Hd, *Hippidion devillei*; Hp, *Hippidion principale*; Di, *Dinohippus interpolatus*; 'O'g, '*Onohippidion*' *galushai*; Dl, *Dinohippus leidyanus*; As, *Astrohippus stocki*; Dm, '*Dinohippus*' *mexicanus*; Es, *Equus simplicidens*.

also found as a synapomorphy in the other major clade. *Calippus* species form a natural group defined by the 'DPOF absent' [3(1)], 'choanae anterior border posterior to P4-M1' [5(1)], 'middle linguaflexid' [12(1)], 'diastema i3-c' [16(1)] and 'linear incisor arcade' [17(1)].

The rest of the species forms a second monophyletic group supported by the following synapomorphies: 'choanae anterior border posterior to P4-M1' [5(1)], 'middle linguaflexid' [12(1)], 'metaconid and metastylid middle' [14(1)] and 'diastema i3-c present' [16(1)] where characters 12 and 14 present a further change in the cladogram. *Pliohippus mirabilis* are sister species of the main group. The other main group is well defined by the following synapomorphies: 'nasal notch between P2 and M1' [1(1)]; and 'monodactyl limb' [19(1)].

Inside this main group, two clades are well defined by synapomorphies. One clade supported by 'robust metapodials' [20(1)] includes the *Hippidion* species from South America. *Hippidion devillei* and *Hippidion principale* are characterized by 'nasal notch posterior to M1' [1(2)], 'elongate-oval protocone' [7(2)] and 'ectoflexid deep, penetrating the isthmus' [13(2)]. The other clade is supported by 'presence of malar fossa' [2(1)]. '*Onohippidium*' *galushai*, *Dinohippus leidyanus*, *Astrohippus stocki*, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a monophyletic group based on 'deep linguaflexid' [12(2)]. *Dinohippus leidyanus*, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a natural group supported by the 'well-developed metastyle' [9(1)]. *Astrohippus stocki*, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a clade characterized by 'elongate-oval protocone' [7(2)], 'multiple internal postfossette plication' [8(1)], 'straight or concave protocone lingual border' [10(1)] and 'straight labial border of protoconid and hypoconid' [15(1)]. Within this clade, '*Dinohippus*' *mexicanus* and *Equus simplicidens* are a monophyletic group based on the 'DPOF absent' [3(1)], 'triangular protocone' [7(3)] and 'large metaconid and metastylid' [14(2)].

We observed a good congruence between the fossil record and the phylogenetic hypothesis. Using our cladogram, nine possible pectinate cladograms have been obtained. Text-figure 8 shows the nine cladograms and the bivariate plots for each clade rank and age rank (A–I). Spearman coefficients are calculated and the results compared in Text-figure 8. Statistically significant correlations ($P < 0{\cdot}05$) are found in five of the nine examined cladograms (A–B and F–H in Text-fig. 8). The close fit is particularly notable in Text-figure 8A–B and H. The last includes one non-resolved point (Text-fig. 8H), because *Hippidion* from South America is thought to have branched off very early in Equini phylogeny, but appears late in the record (Alberdi and Prado 1993).

DISCUSSION

The different kinds of characters used in the analysis (cranial, upper and lower teeth, mandible and appendicular skeleton morphology) define taxa at different levels in the cladogram. Characters mostly from the cranial morphology and upper teeth characterize the suprageneric taxa. Only synapomorphies of the upper dental morphology supported the tribe Equini. In addition, analysis shows that characters from cranial morphology suffer more parallel evolution and reversals, while characters from the appendicular skeleton, mandible, upper and lower teeth show little homoplasy. This suggests that the cranial morphology could be less conservative than the other features.

Based on phylogenetic information, we propose dividing the tribe Equini into two subtribes: Protohippina *sensu* Hulbert (1988*a*) and Pliohippina (= Equinae *sensu* Gidley 1907 and Equina *sensu* Hulbert and MacFadden 1991). The former includes two genera: *Protohippus* and *Calippus*, and the latter includes five genera: *Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. Text-figure 7 shows the synapomorphies of cranial and upper teeth morphology that support these subtribes. In the latter subtribe, our analysis differentiated between two lineages, one that gave rise to *Hippidion* and the other to *Equus*.

Protohippus, previously placed as a subgenus of *Merychippus* (Stirton 1940), is now considered to be a valid genus, closely related to *Calippus*. These two genera form a monophyletic group (Hulbert 1988*a*). Several authors (Stirton 1940; Simpson 1951), have suggested *Protohippus* to be the ancestor of *Pliohippus* and *Equus*; however, our analysis does not support this relationship. *Protohippus supremus* is the sister taxon of *Calippus* species.

The subtribe Protohippina forms the sister group to a second monophyletic group, the subtribe Pliohippina. Different phylogenetic relationships have been proposed between the genera *Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. Stirton (1940) proposed *Astrohippus* as a subgenus of *Pliohippus*. This author recognized two distinct lineages within *Pliohippus s.l.* based on dental characters: *Pliohippus s.s.*, closely related to South American horses; and *Astrohippus*, that gave rise to the *Equus* group species. Quinn (1955) showed that neither *Astrohippus* nor *Dinohippus* could be considered as ancestors of *Equus* based on facial and dental morphology. Quinn derived *Equus* separately from his new genus '*Eoequus*'. Sondaar (1968), in his study of the equid manus, found that '*Dinohippus*' *mexicanus* from Yepómera (Lance 1950) was closely related to *Equus* and generally more advanced in monodactyly than *Astrohippus stocki*. Dalquest (1978) suggested a polyphyletic origin of *Equus* based on dental morphology. Bennett (1980) and MacFadden (1984) showed close affinities between '*Dinohippus*' *mexicanus* and *Equus*. Azzaroli (1982, 1988) considered *Dinohippus leidyanus* to be the ancestor of *Equus*.

Based on our phylogenetic analysis, we consider *Pliohippus* to be the sister taxon to *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. The three species of *Hippidion*, *sensu* Alberdi and Prado (1993), form a monophyletic group, which is geographically restricted to South America and became extinct late in the Pleistocene. Alberdi and Prado (1993) did not find evidence of a relationship between '*Onohippidium*' *galushai* and the *Hippidion* group, as suggested by MacFadden and Skinner (1979), and consequently regarded the former species as belonging within the *Dinohippus*-group. Our phylogenetic analysis supports this hypothesis. Within the *Hippidion* clade, *Hippidion saldiasi* is a sister species of *Hippidion devillei* and *Hippidion principale*. This phylogenetic hypothesis does not fit with the biochronology because the most derived *Hippidion* species appeared first in the South America fossil record.

Astrohippus stocki, '*Dinohippus*' *mexicanus* and *Equus simplicidens* form a monophyletic group. Our analysis shows *Astrohippus stocki* to be the sister group of *Equus*-group. We consider '*Dinohippus*' *mexicanus* as belonging within *Equus*-group.

Both subtribes delimited in the analysis show little overlap in their stratigraphical range (Text-fig. 1). Species of *Protohippus* and *Calippus* are frequently encountered across wide areas of North America east of the Rocky Mountains, ranging from Florida to Texas, and south to Honduras (Hulbert 1988*a*). The extinction of this subtribe at the end of the early Hemphilian (Text-fig. 1) occurred at a time of major reduction in Mio-Pliocene equid diversity (Webb 1977). The shift from tip-toed tridactyl to a monodactyl foot may have taken place at this time, accompanied by the evolution of a special ligamental pattern of the distal foot (Camp and Smith 1942). In the genus *Pliohippus* the side-toes were finally lost. This one-toed condition was, of course, retained in the various descendants of *Pliohippus*, including *Equus* (Simpson 1951). The Pliohippina subtribe represented a second monophyletic radiation of hypsodont equids. This radiation occurred in North America when aridity reached its peak in the Hemphillian and late Pliocene Blancan with the spread of open grassland in the Great Plains, Great Basin, and in the south-west (Shotwell 1961; Webb 1977). Southern members of this clade (*Hippidion*) dispersed into South America after the Great American Biotic Interchange that occurred about 3 Ma (*sensu* Webb 1985) through the isthmus of Panamá (Alberdi and Prado 1993). On the other hand, *Equus* dispersed throughout Eurasia and Africa during the late Pliocene and, also throughout South America at about the mid Pleistocene (Azzaroli 1982, 1992; Bonadonna and Alberdi 1987; Alberdi and Bonadonna 1988; Alberdi *et al.* 1991; Prado and Alberdi 1994). Before the Great American Biotic Interchange both lineages were represented in North America which would be the locus of origin of *Hippidion* and *Equus*. Nevertheless, *Hippidion* remains occur in the South American record stratigraphically below *Equus* remains. The former appeared during the upper Pliocene–lower Pleistocene and the latter in the middle Pleistocene (Alberdi and Prado 1993; Prado and Alberdi 1994). This can be correlated with the existence of two inter-American savannah corridors through South America (Webb 1985). The first was the high-level Andean route, while the second one corresponds to the low-level Eastern route. The existence of these different routes could be a consequence of the different climatic conditions and possibly was also related to shifts in the pasture photosynthesis cycle of carbon (from C3 to C4 plants) that occurred in grassland communities (Cerling *et al.* 1991, 1993; Cerling 1992). MacFadden *et al.* (1994) pointed out the possibility of a relationship between fossil horse diet and the type of carbon grasses (C3 or C4). Nowadays, the high grassland has C3 plants while lower elevations have C4 plants.

This cladistic analysis is developed independently of biostratigraphical relationships, although this information is implicit in some character polarities. Nevertheless, there exists a high congruence between our cladistic analysis and the fossil record, especially in Text-figure 8H. This confirms (following Norell and Novacek 1992*a*, 1992*b*) the correspondence between age and cladistic information in most vertebrate examples. But, in our case, as we noted above, there is one unresolved point. This surely is a consequence of the fact that, in the phylogenetic tree, *Hippidion* occurred earlier than in the fossil record. Consequently, the pectinate cladogram shows a close fit with the fossil record, and cladogram H (Text-fig. 8) may represent the best preliminary hypothesis of Equini tribe history throughout geological time.

TABLE 2. Systematic palaeontology: classification of family Equidae *sensu* Prothero and Schoch (1989, p. 531) and the tribe Equini based on Text-figure 7. We detail only genera and species dealt with in our cladistic analysis. '*Onohippidium*' appears in inverted commas because we do not consider this genus to be valid (Alberdi and Prado 1993).

- Family Equidae Gray, 1821
  - Subfamily Anchitheriinae Leidy, 1869
  - Subfamily Equinae Gray, 1821
    - Genus *Kalobatippus* Osborn *in* Cope-Matthew, 1915
    - Genus *Archaeohippus* Gidley, 1906
    - Genus *Parahippus* Leidy, 1858
    - Genus *Merychippus sensu stricto* Leidy, 1857
  - Tribe Hippotheriini Bonaparte, 1850
  - Tribe Equini Gray, 1821
    - Subtribe Protohippina Hulbert, 1988*a*
      - Genus *Protohippus* Leidy, 1858
        - *Protohippus perditus* (Leidy, 1858)
        - *Protohippus supremus* Leidy, 1869
      - Genus *Calippus* Matthew and Stirton, 1930
        - subgenus *Calippus* Matthew and Stirton, 1930
          - *Calippus* (*Calippus*) *placidus* (Leidy, 1858)
        - subgenus *Grammohippus* Hulbert, 1988*a*
          - *Calippus* (*Grammohippus*) *martini* Hesse, 1936
    - Subtribe Pliohippina subtrib. nov.
      - Genus *Pliohippus* Marsh, 1874
        - *Pliohippus mirabilis* Leidy, 1858
      - Genus *Hippidion* Owen, 1869
        - *Hippidion saldiasi* (Roth, 1899)
        - *Hippidion devillei* (Gervais, 1855)
        - *Hippidion principale* (Lund, 1845)
      - Genus *Dinohippus*-group Quinn, 1955
        - *Dinohippus interpolatus* (Matthew and Stirton, 1930)
        - '*Onohippidium*' *galushai* MacFadden and Skinner, 1979
        - *Dinohippus leidyanus* (Osborn, 1918)
      - Genus *Astrohippus* Stirton, 1940
        - *Astrohippus stocki* Lance, 1950
      - Genus *Equus*-group Linnaeus, 1858
        - '*Dinohippus*' *mexicanus* (Lance, 1950)
        - *Equus simplicidens* Cope, 1892

CONCLUSIONS

One parsimonious cladogram of 31 steps with a consistency index of 0·77 was produced, from which a classification of the tribe Equini was constructed. The analysis shows that characters mostly from the cranial morphology and upper teeth characterized the suprageneric taxa. As a result of this phylogenetic analysis, we propose the classification of family Equidae shown in Table 2.

We recognize two subtribes: Protohippina and Pliohippina. The first includes two genera: *Protohippus* and *Calippus*; and the second, five genera: *Pliohippus*, *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus* (Text-fig. 7). *Protohippus supremus* is the sister-taxon of *Calippus* species.

The subtribe Protohippina forms the sister-group to a second monophyletic group, the subtribe Pliohippina. The latter represents a second monophyletic radiation of hypsodont equids. Possibly this was as a result of the more arid conditions and the spread of open grassland in North America.

We consider *Pliohippus* to be the sister-group to *Hippidion*, *Dinohippus*, *Astrohippus* and *Equus*. The three species of *Hippidion* form a monophyletic group, which are geographically restricted to South America. In this clade, *Hippidion saldiasi* is a sister-species of *Hippidion devillei* and *Hippidion principale*. However, *H. devillei* appeared first in the South American fossil record. There is no evidence of a relationship between '*Onohippidium*' *galushai*, from North America, and the *Hippidion* group, from South America. We include '*O.*' *galushai* in the *Dinohippus*-group. *Astrohippus stocki* was the sister-species of the *Equus*-group, which includes '*Dinohippus*' *mexicanus*.

This cladistic analysis has a high congruence between the stratigraphical record and the phylogenetic hypothesis. The pectinate cladogram H (Text-fig. 8) is a good hypothesis of Equini tribe history throughout geological time.

Acknowledgements. We thank Dr Tedford for kindly allowing us to study the Frick Collection (AMNH). The authors also thank Drs J. V. Crisci, J. J. Morrone, B. Sánchiz and E. Ortiz-Jaureguizar for their critical revision of the manuscript and valuable comments. We also thank Dr A. R. Milner and two anonymous referees for their criticism, comments and suggestions. The drawings were prepared by J. Arroyo. The present work was made possible through a research grant CE num. CI1*-CT90-0862, Bilateral Convention CSIC-CONICET and Spanish DGICYT PB91-0082, and grants from the Universidad Nacional del Centro, Argentina (to JLP).

REFERENCES

ALBERDI, M. T. 1974. El genero *Hipparion* en España. Nuevas formas de Castilla y Andalucía, revisión y historia evolutiva. *Trabajos sobre Néogeno-Cuaternario*, **1**, 1–146.

—— 1987. La familia Equidae, Gray 1821 (Perissodactyla, Mammalia) en el Pleistoceno de Sudamérica. *IV Congreso Latinoamericano de Paleontología, Bolivia*, **1**, 484–499.

—— 1989. A review of old world hipparionine horses. 234–261. *In* PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.

—— and BONADONNA, F. P. 1988. Equidae (Perissodactyla, Mammalia): extinctions subsequent to climatic changes. *Revista Española Paleontología*, **3**, 39–43.

—— CALOI, L. and PALOMBO, M. R. 1991. Pleistocene equids from Western Europe: their biostratigraphic and palaeoecological characteristics. '*Ongulés/Ungulates 91*', *Paleontology*, 31–35.

—— and PRADO, J. L. 1993. Review of the genus *Hippidion* Owen, 1869 (Mammalia: Perissodactyla) from the Pleistocene of South America. *Zoological Journal of the Linnean Society*, **108**, 1–22.

—— LEONE, G. and TONNI, E. P. 1995. *Evolución biológica y climática de la Región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental.* Monografías del Museo Nacional de Ciencias Naturales, 12, 423 pp.

AZZAROLI, A. 1982. On Villafranchian Palaearctic equids and their allies. *Paleontographica Italica*, **72**, 74–97.

—— 1988. On the equid genera *Dinohippus* Quinn 1955 and *Pliohippus* Marsh 1874. *Bolletino della Società Paleontologica Italiana*, **27**, 61–72.

—— 1992. The present status of knowledge of the Ecuadorian species of the genus *Equus*. *Bolletino della Società Paleontologica Italiana*, **31**, 133–139.

BENNETT, D. K. 1980. Stripes do not a zebra make, Part I: a cladistic analysis of *Equus*. *Systematic Zoology*, **29**, 272–287.

BONADONNA, F. P. and ALBERDI, M. T. 1987. *Equus stenonis* Cocchi as a biostratigraphical marker in the Neogene-Quaternary of the western Mediterranean basin: consequence on Galerian–Villafranchian chronostratigraphy. *Quaternary Science Reviews*, **6**, 55–66.

BONAPARTE, C. L. 1850. *Conspectus systematics. Mastozoologiae.* Lugduni Batavorum. Editio altera reformata, E. J. Brill, Batavia, 1 p.

CAMP, C. and SMITH, N. 1942. Phylogeny and functions of the digital ligaments of the horse. *Memoirs of the University of California*, **13**, 69–124.

CERLING, T. E. 1992. Development of grassland and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **97**, 241–247.

—— QUADE, J., AMBROSE, S. H. and SIKES, N. E. 1991. Fossil soils, grasses, and carbon isotopes from Fort Ternan, Kenya: grassland or woodland? *Journal of Human Evolution*, **21**, 295–306.

—— WANG YANG and QUADE, J. 1993. Global ecological change in the late Miocene: expansion of C4 ecosystems. *Nature*, **361**, 344–345.

COPE, E. D. 1892. A contribution to the vertebrate paleontology of Texas. *Proceedings of the American Philosophy Society*, **30**, 123–131.

—— and MATTHEW, W. D. 1915. Tertiary Mammalia and Permian Vertebrata. *Monograph of the American Museum of Natural History*, **2**, 145–151.

DALQUEST, W. W. 1978. Phylogeny of American horses of Blancan and Pleistocene age. *Annales Zoologici Fennici*, **15**, 191–199.

EISENMANN, V. 1980. *Les chevaux* (Equus sensu lato) *fossiles et actuels: crânes dents jugales supérieures.* Cahiers de paléontologie, Editions du CNRS, Paris, 186 pp.

—— ALBERDI, M. T., GIULI, C. de and STAECHES, U. 1988. *Studying fossil horses.* E. J. Brill, Leiden, 72 pp.

—— SONDAAR, P. Y., ALBERDI, M. T. and GIULI, C. de 1987. Is horse phylogeny becoming a playfield in the game of theoretical evolution? Essay review. *Journal of Vertebrate Paleontology*, **7**, 224–229.

ELDREDGE, N. and CRACRAFT, J. 1980. *Phylogenetic patterns and the evolutionary process. Method and theory in comparative biology.* Columbia University Press, New York, 349 pp.

EVANDER, R. L. 1989. Phylogeny of the family Equidae. 107–127. *In* PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls.* Oxford University Press, New York, 537 pp.

EWART, J. C. 1894*a*. The second and fourth digits in the horse: their development and subsequent degeneration. *Proceedings of the Royal Society of Edinburgh*, **1894**, 185–191.

—— 1894*b*. Development of the skeleton of the limbs of the horse, with observations on polydactyly. *Journal of Anatomic Physiology*, **28**, 236–256.

FARRIS, J. S. 1988. *Hennig86. Program and documentation.* Port Jefferson Station, New York, 18 pp.

FORSTEN, A. 1968. Revision of the Palearctic *Hipparion*. *Acta Zoologica Fennica*, **119**, 1–134.

—— 1983. The preorbital fossa as a taxonomic character in some Old World *Hipparion*. *Journal of Paleontology*, **57**, 686–704.

GAUTHIER, J., KLUGE, A. G. and ROWE, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, **4**, 105–209.

GERVAIS, P. 1855. *Recherches sur les Mammifères fossiles de l'Amérique méridionale.* P. Bertrend, Libraire-Editeur, Paris, 63 pp.

GIDLEY, J. W. 1906. New or little known mammals from the Miocene of South Dakota. Part N. Equidae. *Bulletin of the American Museum of Natural History*, **22**, 135–153.

—— 1907. Revision of the Miocene and Pliocene Equidae of North America. *Bulletin of the American Museum of Natural History*, **23**, 865–934.

GRAY, J. E. 1821. On the natural arrangement of vertebrate animals. *London Medical Reposition Review*, **15**, 296–310.

GREGORY, W. K. 1920. Studies of comparative myology and osteology. V. On the anatomy of the preorbital fossae of Equidae and other ungulates. *Bulletin of the American Museum of Natural History*, **42**, 265–283.

GROMOVA, V. 1952. Le genre *Hipparion* (translated from Russian by St Aubin). *Bureau Recherche Géologique Minera*, **12**, 1–288.

HENNIG, W. 1966. *Phylogenetic systematics.* University of Illinois Press, Urbana, 263 pp.

HESSE, C. J. 1936. Lower Pliocene vertebrate fossils from the Ogallala Formation (Lavern Zone) of Beaver County, Oklahoma. *Publications of the Carnegie Institute of Washington*, **476**, 47–72.

HOLLANDER M. and WOLFE, D. A. 1973. *Nonparametric statistical methods.* John Wiley and Sons, Inc., New York, 503 pp.

HULBERT, R. C. Jr 1988*a*. *Calippus* and *Protohippus* (Mammalia, Perissodactyla, Equidae) from the Miocene

(Barstovian–Early Hemphillian) of the Gulf Coastal Plain. *Bulletin of the Florida State Museum, Biological Science*, **32**, 221–340.

—— 1988*b*. *Cormohipparion* and *Hipparion* (Mammalia, Perissodactyla, Equidae) from the late Neogene of Florida. *Bulletin of the Florida State Museum, Biological Science*, **33**, 229–338.

—— 1989. Phylogenetic interrelationships and evolution of North American late Neogene Equinae. 176–196. *In* PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.

—— and MACFADDEN, B. J. 1991. Morphological transformation and cladogenesis at the base of the adaptive radiation of Miocene hypsodont horses. *American Museum Novitates*, **3000**, 1–61.

HUMPHRIES, C. J. and FUNK, V. A. 1984. Cladistic methodology. 323–362. *In* HEYWOOD, V. H. and MOORE, D. M. (eds.) *Current concepts in plant taxonomy*. Academic Press, London, 432 pp.

HUSSAIN, S. T. 1975. Evolutionary and functional anatomy of the pelvic limb in fossil and Recent Equidae (Perissodactyla, Mammalia). *Anatomy, Histology, Embryology*, **4**, 179–222.

JANIS, C. M. and EHRHARDT, D. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, **92**, 267–284.

LANCE, J. F. 1950. Paleontología y Estratigrafía del Plioceno de Yepómera, Estado de Chihuahua. 1ª Parte: Equidos, excepto *Neohipparion*. *Boletín de la Universidad Autónoma de Mexico*, **54**, 1–81.

LEIDY, J. 1857. Notices of extinct vertebrates discovered by F. V. Hayden, during the expedition to the Sioux County under the Command Lieut. G. K. Warren. *Proceedings of the Academy of Natural Science, Philadelphia*, **1856**, 311.

—— 1858. Notice of remains of extinct Vertebrata from the valley of the Niobrara River. *Proceedings of the Academy of Natural Science, Philadelphia*, **10**, 20–29.

—— 1869. The extinct mammalian fauna of Dakota and Nebraska. *Journal of the Academy of Natural Science, Philadelphia*, ser. 2, **7**, 1–472.

LINNAEUS, C. 1858. *Systema naturae per regna tri naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Stockholm, Laurentii Salvii, vol. 1, 824 pp.

LUND, P. W. 1845. Meddlelse af det Udbytte de I 1844 undersögte Knoglehuler Have avgivet til hundskaben om Brasiliens Dyreverden för sidste Jordomvaeltning. *Det Köngelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandlinger*, **12**, 57–94.

MACFADDEN, B. J. 1984. *Astrohippus* and *Dinohippus* from the Yepómera Local Fauna (Hemphillian, Mexico) and implications for the phylogeny of one-toed horses. *Journal of Vertebrate Paleontology*, **4**, 273–283.

—— 1992. *Fossil horses, systematics, paleobiology, and evolution of the family Equidae*. Cambridge University Press, New York, 369 pp.

—— and SKINNER, M. F. 1979. Diversification and biogeography of the one-toed horses *Onohippidium* and *Hippidion*. *Postilla*, **175**, 1–10.

—— WANG YANG, CERLING, T. E. and ANAYA, F. 1994. South American fossil mammals and carbon isotopes: a 25 million-year sequence from the Bolivian Andes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **107**, 257–268.

MADDISON, W. P., DONOGHUE, M. J. and MADDISON, D. R. 1984. Outgroup analysis and parsimony. *Systematic Zoology*, **33**, 83–103.

MARSH, O. C. 1874. Fossil horses in America. *American Naturalist*, **8**, 288–294.

MARSHALL, L. G., BERTA, A., HOFFSTETTER, R., PASCUAL, R., REIG, O. A., BOMBIN, M. and MONES, A. 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. *Palaeovertebrata. Mémoire Extraordinaire*, 1–76.

—— HOFFSTETTER, R. and PASCUAL, R. 1983. Geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertebrata, Mémoire Extraordinaire*, 1–93.

MARTIN, P. S. and KLEIN, R. G. 1984. *Quaternary extinctions. A prehistoric revolution*. University of Arizona Press, Tucson, 892 pp.

MATTHEW, W. D. 1926. The evolution of the horses: a record and its interpretation. *Quarterly Review of Biology*, **1**, 139–185.

—— and STIRTON, R. A. 1930. Equidae from the Pliocene of Texas. *University of California, Publications of Geological Science*, **19**, 349–396.

NIXON, K. C. 1991. *CLADOS version 0.9. IBM PC compatible character analysis program*. Documentation published by author, 41 pp.

NORELL, M. A. and NOVACEK, M. J. 1992*a*. The fossil record and evolution: comparing cladistic and paleontologic evidence for vertebrate history. *Science*, **255**, 1690–1693.

—— —— 1992*b*. Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics*, **8**, 319–337.

OSBORN, H. F. 1918. Equidae of the Oligocene, Miocene and Pliocene of North America, iconographic type revision. *Memoirs of the American Museum of Natural History, New Series*, **2**, 1–217.

OWEN, R. 1869. On fossil teeth of equines from Central and South America, referable to *Equus conversidens*, *Equus tau*, and *Equus arcidens*. *Proceedings of the Royal Society of London*, **17**, 267–268.

OWEN-SMITH, N. 1985. Niche separation among African ungulates. 167–171. *In* VRBA, E. S. (ed.). *Species and speciation*. Transvaal Museum Monograph 4, Pretoria, 176 pp.

PIRLOT, P. R. 1953. The preorbital fossa of *Hipparion*. *American Journal of Science*, **251**, 309–312.

POLITIS, G. G., PRADO, J. L. and BEUKENS, R. P. 1995. The human impact in Pleistocene–Holocene extinctions in South America. The Pampean case. 187–205. *In* JOHNSON, E. (ed.). *Ancient peoples and landscapes*. Museum of Texas Tech University, Lubbock, Texas, 425 pp.

PRADO, J. L. and ALBERDI, M. T. 1994. A quantitative review of the horse genus *Equus* from South America. *Palaeontology*, **37**, 459–481.

PROTHERO, D. R. and SCHOCH, R. M. 1989. Classification of the Perissodactyla. 530–537. *In* PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.

QUINN, J. H. 1955. Miocene Equidae of the Texas Gulf Coastal Plain. *University of Texas Publications of the Bureau of Economic Geology*, **5516**, 1–102.

ROTH, S. 1899. Descripción de los restos encontrados en la Caverna de Ultima Esperanza. *Revista del Museo de la Plata*, **9**, 421–453.

SEFVE, I. 1927. Die Hipparionen Nord-Chinas. *Palaeontologia Sinica*, **4**, 1–93.

SHOTWELL, J. A. 1961. Late Tertiary biogeography of horses in the northern Great Basin. *Journal of Paleontology*, **35**, 203–217.

SIMPSON, G. G. 1951. *Horses: the story of the horse family in the Modern World and through sixty million years of history*. Oxford University Press, New York, 247 pp.

SKINNER, M. F. and MACFADDEN, B. J. 1977. *Cormohipparion* n. gen. (Mammalia, Equidae) from the North America Miocene (Barstovian–Clarendonian). *Journal of Paleontology*, **51**, 912–926.

SONDAAR, P. Y. 1968. The osteology of the manus of fossil and Recent Equidae. *Koninklijke Nederlandse Akademie van Wetenschappen, Natuurkunde*, **25**, 1–76.

STATGRAPHICS, 1991. *Version 5.0*. Statistical Graphic Corporation, 1450 pp.

STIRTON, R. A. 1940. Phylogeny of North American Equidae. *University of California Publication, Bulletin of the Department of Geological Science*, **25**, 165–198.

STUDER, T. 1911. Eine neue Equidenform aus dem Obermiocän von Samos. *Mitteilungen der naturforschenden Gesellschaft in Bern*, 192–200.

TEDFORD, R. H., GALUSHA, T., SKINNER, M. F., TAYLOR, B. E., FIELDS, R. W., MACDONALD, J. R., RENSBERGER, J. M., WEBB, S. D. and WHISTLER, D. P. 1987. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene Epochs) in North America. 153–210. *In* WOODBURNE, M. O. (ed.). *Cenozoic mammals of North America. Geochronology and biostratigraphy*. University of California Press, Berkeley, 336 pp.

WATABE, M. 1992. Evolution of Late Miocene *Hipparion* (Equidae, Perissodactyla) in Eurasia: its pattern and process. Unpublished PhD thesis, 150 pp.

WATROUS, L. E. and WHEELER, Q. D. 1981. The outgroup comparison method of character analysis. *Systematic Zoology*, **30**, 1–11.

WEBB, S. D. 1977. A history of savanna vertebrates in the New World. Part I. North America. *Annual Reviews of Ecology and Systematics*, **8**, 355–380.

—— 1985. Late Cenozoic mammal dispersals between the Americas. 357–386. *In* STEHLI, G. and WEBB, S. D. (eds). *The Great American Biotic Interchange*. Plenum Press, New York and London, 532 pp.

JOSÉ L. PRADO

INCUAPA. Fac. Cs. Soc. UNC.
San Matín 306 – 7400-Olavarría,
Argentina

MARÍA T. ALBERDI

Museo Nacional de Ciencias Naturales, CSIC
José Gutierrez Abascal 2,
28006 Madrid, Spain

Typescript received 12 December 1994
Revised typescript received 13 December 1995