

Revision of the faunal list and study of *Hipparion* (Equidae, Perissodactyla, Mammalia) of the Pliocene locality of La Gloria 4 (Spain)

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Abstract. An updated faunal list of La Gloria 4 (Ruscinian, Spain) and a description of the material referred to *H. cf. elegans* are presented. Comparisons with hipparions from Spain (Concud, El Arquillo, Venta del Moro, Layna), Greece (Dytiko), and Kazakhstan (Pavlodar, Kalmakpai) are provided. Possible parallelisms and problems of palaeoecological interpretations of anatomical characters of hipparions are discussed.

Key words: Vertebrata, *Hipparion*, Mio-Pliocene, Spain, Kazakhstan.

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I. INTRODUCTION

The fossil locality of La Gloria 4, discovered by R. ADROVER in 1982, is located 4 km east of Teruel at the end of a track providing access to the La Gloria estate. Along the same track are also located the fossil localities of La Gloria 6, La Gloria 3, and La Gloria 2. The localities of La Gloria 1 and La Gloria 5 are inside the property. The localities were numbered according to the sequence of discovery.

La Gloria 4 consists of grey beds of carbonated silts with dark intercalations, exposed on the side of a bank which is about 50 m long and reaches 1.5 m in height in its middle part.

The location of the site is given by MEIN et al. (1992, p. 123), together with a faunal list. The latter was slightly modified after review of the carnivores by ALCALA et al. (1992a, p. 62), the bovids by ALCALA et al. (1992b, p. 70), and the cervids by AZANZA & MENENDEZ (1992, p. 77). A palaeontological study of *Promimomys* has already been carried out (FEJFAR et al. 1990), and the rodent fauna as a whole was studied by ADROVER et al. (1995a). The present faunal list is:

Insectivora: *Erinaceus* sp.; *Galerix depereti* CROCHET, 1986; *Dibolia brailloni* RÜMKE, 1985; *Desmanella* sp.; *Talpa minor* FREUDENBERG, 1914; *Episoriculus gibberodon* (PÉTENYI, 1864); *Blarinella europea* REUMER, 1984; *Paenelimnoecus pannonicus* (KORMOS, 1934); ? *Myosorex* sp.

Chiroptera: *Eptesicus* sp.

Lagomorpha: *Prolagus michauxi* LOPEZ, 1975; *Prolagus crusafonti* LOPEZ, 1975; *Trischizolagus maritsae* BRUIJN, DAWSON & MEIN, 1970.

Rodentia: *Atlantoxerus margaritae* ADROVER, MEIN & MOISSENET, 1995; *Eliomys intermedius* (FRIANT, 1953); *Eliomys truci* MEIN et MICHAUX, 1970; *Promimomys moldavicus* (KORMOS, 1932); *Protatera* sp.; *Stephanomys dubari* AGUILAR, MICHAUX, BACHELET, CALVET & FAILLAT, 1991; *Occitanomys alcalai* ADROVER, MEIN & MOISSENET, 1992; *Castillomys gracilis* (VAN DE WEERD, 1976); *Huerzelerimys* aff. *turoliensis* (MICHAUX, 1969); *Apodemus* aff. *dominans* KRETZOI, 1959; *Apodemus gorafensis* RUIZ BUSTOS, SESE, DABRIO, PENA & PADIAL, 1984; *Rhagapodemus hautimagnensis* MEIN & MICHAUX, 1970; *Paraethomys meini* (MICHAUX, 1969); *Paraethomys abaigari* ADROVER, MEIN & MOISSENET, 1992.

Carnivora: *Nyctereutes donnezani* (DEPERET, 1890); *Plioviverrops faventinus* TORRE, 1989; *Hy-aena* cf. *pyrenaica* (DEPERET, 1890); *Felis issiodorensis* CROIZET & JOBERT, 1828.

Perissodactyla: *Hipparion* cf. *elegans* GROMOVA, 1952

Artiodactyla: *Croizetoceros* sp.; Giraffidae indet.; *Tragoreas* sp.; *Protoryx* sp.; *Gazella* sp.; Antilopini indet.

The site also yielded two kinds of coproliths, some belonging to Carnivora, and others, very small, to Muridae.

Among Gastropoda (identified by TRUC), there are 2 Planorbidae; 1 Helicidae of a rather dry type; 1 *Acmea*; 1 *Limnea*; 1 *Paleoglandina*.

There are also corpuscles of *Limax* and *Lumbric*, fruits of *Celtis lacunosa* (identified by MACGREGOR), fragments of one big ratite egg, tubular algal concretions, a few vertebrae and pharyngeal teeth of *Leuciscus*, a few osteoderms of Anguidae, dentals of Lacertidae, fangs and vertebrae of snakes, and 1 small passeriform bird.

The rich micromammal fauna indicates a lower Pliocene age, in the middle of MN 14 (zone with two *Paraethomys* and *Promimomys*). Among the macromammals, a large primitive Giraffidae and a *Gazella* are good evidence of dry conditions.

II. HIPPARION FROM LA GLORIA 4

Hipparion cf. *elegans* GROMOVA, 1952

Description

The genus *Hipparion* is represented by two upper cheek teeth and a lower cheek tooth series, both very worn (the crown heights are between 15 and 19 mm), a fragment of mandibular symphysis, a complete third metatarsal (MT III), a distal MT III of another individual, and a few other bones. The complete metatarsal (Fig. 1-a, Table I) is very slender. The ratio diagram (Fig. 2), using an already slender form, *H. mediterraneum*, as the basis for comparison, shows this marked slenderness in the line uniting measurements 1 (length) and 3 (width at mid-diaphysis). Slenderness is a good indicator of dry environments (GROMOVA 1949). The depth of the bone at mid-diaphysis (4), at the proximal end (6), and at the distal end (12, 14), the development of the facet for the cuboid (8), the effacement of the supra-articular tuberosities (10), and the constriction near the keel (13) are characters indicating strong cursorial adaptations and a tendency towards functional monodactyly. The fragmentary MT III is larger (Table I), but has similar proportions.

As the upper cheek teeth (Fig. 1-c, d) seem to belong to an old animal, one could object to the discussion of their morphology. But wear of upper cheek teeth usually results in small and rounded protocones, whereas these are long and oval (8.5 by 5 on the P3, for an occlusal length of 24 mm;

Table I

Measurements (mm) of third metatarsals (MT III) of hipparions. n = number of specimens. Venta M = Venta del Moro. Kalmak = Kalmakpai

MT III	Gloria4	Gloria4	Venta M	Concud	El Arquillo	Layna
			n=2-14	n=6-30	n=1-12	IPS 2104
1: Maximal length	277.0		235.0	237.8	203.0	288.0
3: Minimal breadth	25.0	27.5	22.1	27.1	21.5	30.0
4: Depth at level of 3	27.5		24.2	26.4	22.0	30.0
5: Proximal articular breadth	38.0		34.4	38.8	31.9	37.0
6: Proximal depth	31.0		29.0	31.9	26.2	30.5
10: Distal max. supra-art. breadth	34.0	36.2	31.2	35.4	28.2	39.0
11: Dist. max. art. breadth	34.0	35.0	30.3	34.2	27.7	33.7
12: Dist. max. depth of keel	30.0	33.0	26.6	29.3	24.2	30.0
13: Dist. min. depth of medial condyle	24.0	27.0	21.1	23.5	19.8	25.0
14: Dist. max. depth of medial condyle	26.5	29.0	23.4	25.8	21.5	27.5
7: Max. diameter facet 3rd tarsal	34.1		32.5	36.2	29.4	34.5
8: Diam. facet 2nd tarsal	10.0		8.3	9.2	8.3	10.0
MT III	Kalmak	Kalmak	Kalmak	Dytiko	Pavlodar	Layna
	243-290			n=3-13	n=11-12	
1: Maximal length	275.0	256.0	256.0	238.3	230.7	
3: Minimal breadth	26.0	23.0	23.5	22.1	22.5	29.0
4: Depth at level of 3	27.7	25.0		24.4	23.6	31.0
5: Proximal articular breadth	40.0		35.7	34.1	34.8	40.0
6: Proximal depth	32.0	28.0		28.9	28.7	33.0
10: Distal max. supra-art. breadth	33.1		31.0	30.7	30.5	38.0
11: Dist. max. art. breadth	34.0		33.0	29.5	28.6	33.5
12: Dist. max. depth of keel	30.0			26.6	26.3	31.8
13: Dist. min. depth of medial condyle	25.0	23.0	25.0	21.2	20.8	25.5
14: Dist. max. depth of medial condyle	28.0	27.0	27.0	23.5	27.0	28.0
7: Max. diameter facet 3rd tarsal	36.0			30.9	31.5	35.0
8: Diam. facet 2nd tarsal		10.0		7.8	8.4	11.0

8 by 4 on the M3 for an occlusal length of 23); moreover, the enamel plication is moderate (15 plis fossette on the P3, 7 on the M3), not rudimentary as in overworn teeth. Elongated protocones and reduction of enamel plication are believed to represent an adaptation to abrasive food (GROMOVA 1949, 1952). Thus, both the metapodials and the upper cheek teeth show evolved features that can be interpreted as evidence of a dry climate, an open landscape, and a tough vegetation.

The lower cheek tooth series (Fig. 1-e) is 143 mm long. It exhibits a pattern usually considered as primitive for all equids: a deep vestibular valley not only on the molars, but on the P3 and P4 also. The vestibular groove is considered as a weak point in the structure of the lower cheek teeth (GROMOVA 1952), and its depth in the La Gloria 4 material is in functional contradiction to the elongated protocone of the upper cheek teeth. If grass is tougher than leaves, the upper cheek teeth

would rather belong to a grazer, and the lower to a browser. The morphology of the lower cheek teeth also does not seem to be the result of overwear: the teeth do not look excessively worn, and in lower premolars, even when very worn, the vestibular grooves are not usually as deep as they are here.

Moreover, the mandibular symphysis, although very fragmentary (Fig. 1-b), shows that the muzzle was probably narrow, rounded, and deep. In grazing forms one expects to find a flattened, broad pattern, with the I1 and I2 on the same line, as in some advanced African hipparions of the

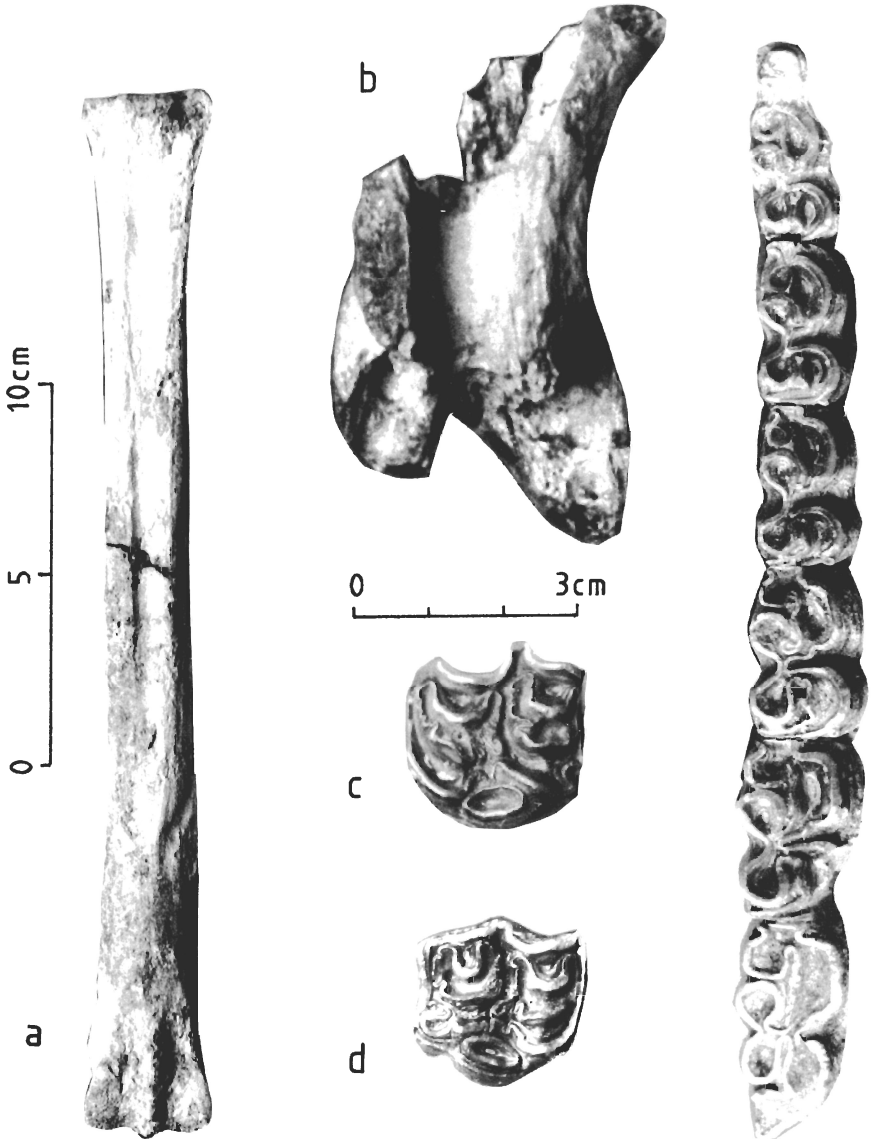


Fig. 1. *Hipparion cf elegans*. a. Third metatarsal, volar view. b. Fragmentary mandibular symphysis, occlusal view. c. Left upper P3, occlusal view. d. Right upper M3, occlusal view. e. Left lower cheek tooth series, occlusal view.

"*Eurygnathohippus*" type. We stress these discrepancies to show how difficult it may be to infer one character from another and correctly associate different parts of the body of a species of hipparion.

The diaphysis of a distal tibia measures 36 mm in minimal width and 27 mm in minimal antero-posterior diameter (APD). The distal width and APD of this tibia and a second one are 53 by 40 mm and 61 by 43. An astragalus is 55 mm high; the distal articular facet is 41 by 33 mm.

C o m p a r i s o n s

1. Venta del Moro

From Venta del Moro (MN 13 according to MEIN 1990) we know an MT III (Table 1; Fig. 2) which is very similar to those from La Gloria 4, although smaller and possibly a little more primitive judging by the small cuboid facet (8) and the less developed keel (12). Elongated protocones also occur at Venta del Moro (ALBERDI 1972, Fig. 114). Thus, in our opinion, the hipparion from La Gloria 4 is probably a descendant of the hipparion from Venta del Moro, although no deep vestibular groove appears on the lower premolars of the latter (ALBERDI 1972, Fig. 114).

The metacarpals from Venta del Moro belong to the "*H. dietrichi*" morphotype together with metacarpals from Le Ravin des Zouaves, Vathylakkos, Andrianos Quarry of Samos, Maragheh, Lubéron, Saloniki, Pikermi, Dytiko, Pavlodar, and Kalmakpai (EISENMANN in press). The metatarsals from Venta del Moro have the size and proportions of the middle-sized MT III of Dytiko (Fig. 2), MN 13, Greece (referred to *H. matthewi* by KOUFOS 1988 a,b), of some MT III from Lubéron (MN 12, France), of the small MT III from Maragheh (MN 11, Iran) and of the small MT III from Pavlodar (MN 13, Kazakhstan) (Fig. 2) described under the name of *H. elegans* by GROMOVA (1952).

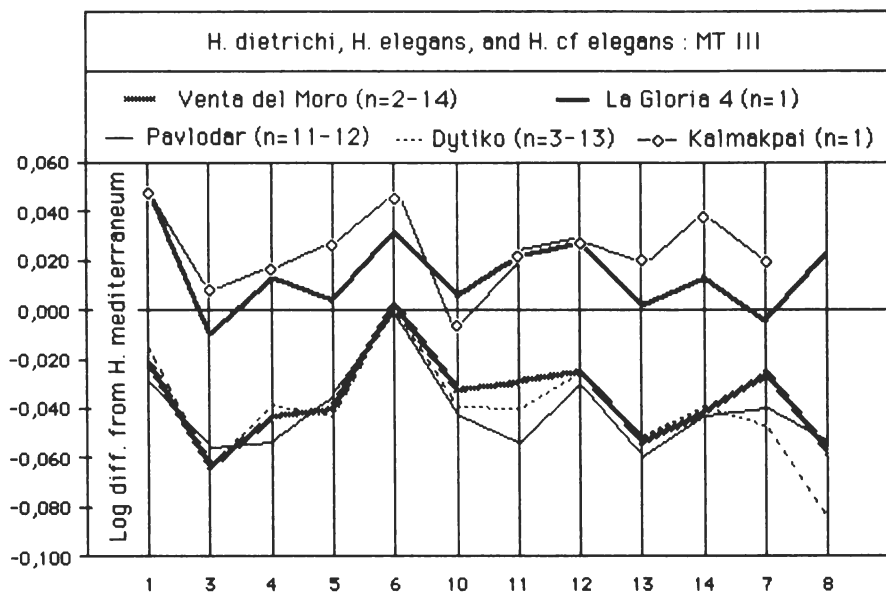


Fig. 2. Ratio diagrams of third metatarsals of *Hipparion elegans* (Pavlodar), *H. cf elegans* (Venta del Moro, La Gloria 4, Kalmakpai), and *H. dietrichi* (Dytiko). n = number of specimens. 1, 2, 3, etc. = Measurements. See Table I for their definition.

2. El Arquillo

ALBERDI (1974, p. 109) considered that the Venta del Moro hipparion was close to *H. gromovae* (El Arquillo, MN 13, MEIN 1990). Careful comparisons show that the Venta del Moro metatarsals are slenderer and larger than those from El Arquillo. The latter (i.e., *H. gromovae*) look like diminutive MT III of *H. concudense* (Fig. 3).

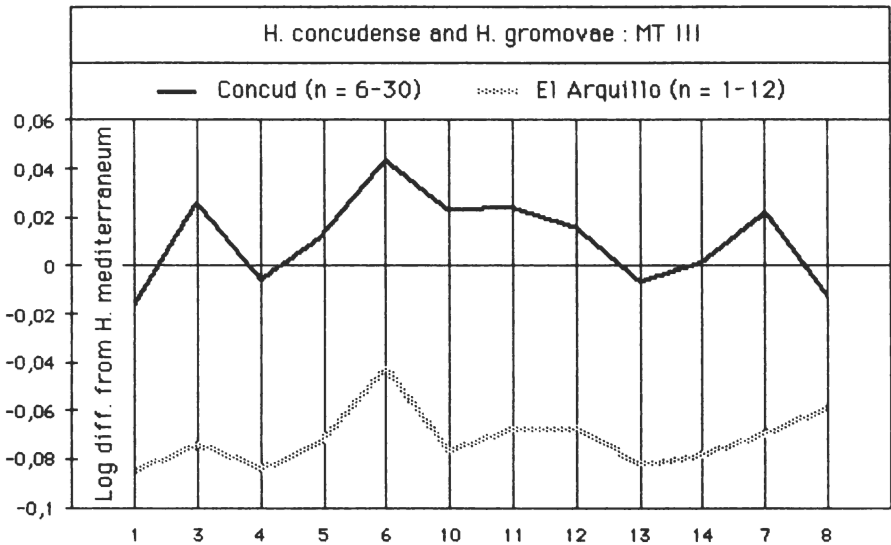


Fig. 3. Ratio diagrams of third metatarsals of *Hipparion concudense* (Concud) and *H. gromovae* (El Arquillo). n = number of specimens. 1, 2, 3, etc. = Measurements. See Table I for their definition.

3. Layna

ALBERDI (1974, p. 109) also believed that the Venta del Moro hipparion was close to *H. fissurae* (Layna, top of MN 15, MEIN 1990). Later, (ALBERDI & ALCALA 1992), she referred the hipparion from La Gloria 4 to *H. fissurae*.

The MT III of *H. fissurae* from Layna are less slender at the level of the diaphysis and have more developed supra-articular distal widths than those from La Gloria 4 (Fig. 4). EISENMANN & SONDAAR (1989) have already noted the similarities between the MT III of Layna, Karaburun, and Çalta; observations on another specimen from Layna confirm these similarities.

The single lower premolar from Layna (sectioned at mid-crown at the Laboratory of Paleontology, Paris) has a shallow ectoflexid. On five upper cheek teeth (also sectioned at mid-crown), the protocones are small and rounded. Thus, the morphologies of the metatarsals, the upper cheek teeth, and the lower cheek teeth of Layna are not similar to those of La Gloria 4. Admittedly, the material is poor, and it would be simpler to accept a local evolution from Venta del Moro (not El Arquillo!) to Layna through La Gloria 4, but there is no obvious evidence for this. The only evidence lies in the similarities between the hipparions from Venta del Moro and La Gloria 4, not between either of them and *H. fissurae* from Layna.

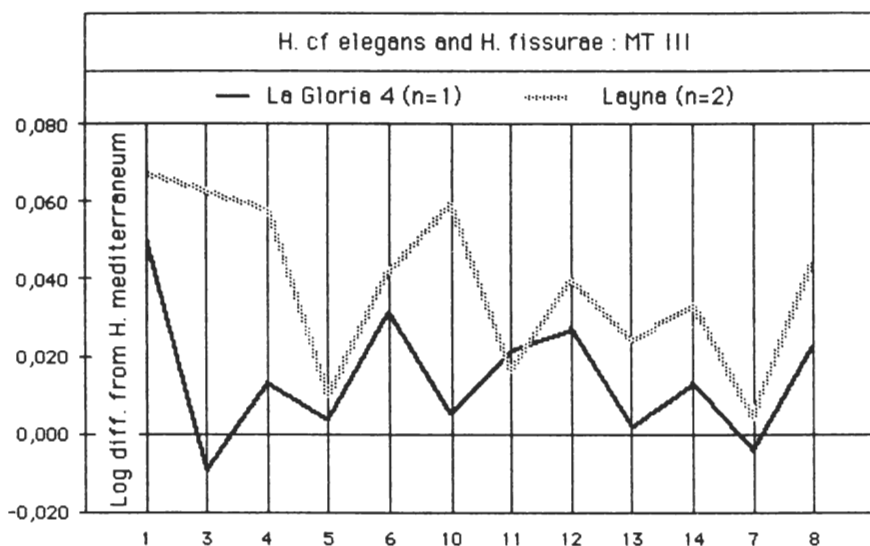


Fig. 4. Ratio diagrams of third metatarsals of *Hipparion* cf. *elegans* (La Gloria 4) and *H. fissurae* (Layna). n = number of specimens. 1, 2, 3, etc. = Measurements. See Table I for their definition.

III. DISCUSSION

Third metatarsals from La Gloria 4 and Venta del Moro are morphologically very close to those referred to *H. dietrichi* from the base of MN 11 at Ravin des Zouaves and Vathylakkos (KOUFOS 1987, 1988). The referral to *H. dietrichi* was made because of the coexistence of skulls or mandibles having a short and wide muzzle where the four central incisors tend to be set in a single line; this sort of muzzle is characteristic of *H. dietrichi* from Samos 1-4 (top of MN 11) and exists also at Dytko, Lubéron, and Maragheh. At Pavlodar, however, the small *H. elegans* to which are referred the small metapodials seems to have a narrow and round muzzle, as probably did the hipparion of La Gloria 4.

On morphological grounds, the metatarsals from Venta del Moro and La Gloria 4 may just as well be referred to *H. dietrichi* as to *H. elegans*. On geographical grounds, *H. dietrichi* would be the natural choice. But assuming that metapodials of this type are really associated with *H. dietrichi* skulls, the muzzle from La Gloria 4 obliges us to refer this form to *H. cf. elegans*. Incidentally, this shows that nearly identical metapodials may be associated with very different muzzles.

Parallelism or conspecificity with hipparions from Kazakhstan

We have already noted the similarities between *H. elegans* from Kazakhstan and the hipparion from Venta del Moro. Another hipparion from Kazakhstan (Kalmakpai) has a metatarsal that is similar in shape and in size to those of La Gloria 4 (Fig. 2).

According to VANGENGEIM et al. (1993), Kalmakpai, like Pavlodar, belongs in MN 13 and indicates a dry environment (*Gazella*), but Kalmakpai is closer to the Mio-Pliocene boundary and bears evidence of drier conditions.

At Kalmakpai the sample is poor, but a few specimens have basically the same proportions as *H. elegans*, although they are larger and possibly more evolved. Thus, in both Spain and Kazakhstan it seems that a small slender species evolved by augmenting its size and improving its cursorial adaptations. The result is that the MT III from Kalmakpai and La Gloria 4 are rather similar (Fig. 2). Are these resemblances evidence of conspecificity or of a parallelism restricted to the metapodials? Comparisons of the teeth should help to answer this question. The upper cheek teeth from Kalmakpai, including one series belonging to a well preserved skull, are bigger than those from La Gloria, more plicated, and have shorter and rather more rounded protocones. On the lower premolars the vestibular groove is shallow. If the MT III are associated with the skull, the hipparion of Kalmakpai is not the same as the one from La Gloria 4, and we have again (as between *H. dietrichi* and *H. elegans*) a case of parallelism.

There may, however, remain some doubt as to the association between the skull and the slender metapodials of Kalmakpai: 1. The size (transverse diameter) of the slender Kalmakpai MT III and MC III seems too small for the skull. 2. There is one fragmentary MC III at Kalmakpai (2432-61) whose size would fit better with the skull; its diaphysis is flat, which usually is correlated with relative robustness. 3. The skull of *H. elegans* from Pavlodar has a preorbital fossa, while the skull from Kalmakpai has none. Thus, the material from Kalmakpai could be assigned to two hipparion species: one with a big skull without fossa, plicated upper cheek teeth with rather rounded protocones, and probably flat and robust metapodials; the other, deriving from the Pavlodar *H. elegans*, smaller, with slender metapodials, probably a preorbital fossa, and moderately plicated upper cheek teeth with elongated and narrow protocones. In that case, conspecificity between the hipparions of Kazakhstan and Spain could be possible.

IV. CONCLUSIONS

Both reviewers of this paper have expressed their scepticism concerning the possible conspecificity of Spanish and Kazak hipparions. One of the reviewers states that "A safer bet is that the La Gloria hipparion is a local form and related to the one from Layna (as strongly indicated by Table I) in spite of Fig. 4". In the draft of this paper, we had noted the differences between the metatarsals from Layna and La Gloria 4. In answer to the reviewer's remark, we have added in this version a few notes on the morphologies of the cheek teeth from Layna, which differ from cheek teeth found at La Gloria 4. But above all, we disagree with the philosophy of "a safer bet" in referring new material to locally described species. In our opinion, specific attributions should be made on the basis of morphological similarities. We may be proven wrong, and the risk is great since all these hipparions are poorly known (let us stress that we have not referred the hipparion from La Gloria 4 to *H. elegans*, but only noted its similarities by using the indicator "cf"); we feel, however, obliged to say what resemblances we see, even if they lead to risky or surprising references. Moreover, we would like to point out that at least one other geographically surprising affinity does exist in Spain during the Ruscianian: *Celadensia nicolae* from the Teruel Basin resembles *Microtodon* from Mongolia (MEIN et al. 1992).

The discussions in this paper show also, that all too often we are unable to predict what kind of skulls, upper cheek teeth, lower cheek teeth, and metapodials are associated within a species of hipparion, partly because of the lack of good reference material (complete skeletons), partly because our functional interpretation of characters leads to contradictions (e. g., *H. cf. elegans* of La Gloria 4), partly because of the possibility of parallelisms such as those we have seen in the metapodials of two, and possibly three, different lineages: *H. dietrichi* s. l. of Iran, Greece, and France, *H. elegans* of Pavlodar and Kalmakpai, *H. cf. elegans* of Venta del Moro and La Gloria 4.

The paleoecological inferences that may be drawn from hipparion anatomy and in particular the metapodials, are discussed elsewhere (EISENMANN in press). Let us just stress that the presence of "a hipparion" is not enough to infer a particular environment. Anatomical characters must be interpreted in order to decide, for instance, whether this particular hipparion was a forest or a savanna dweller. Thus, using "Late Miocene Equidae" without distinction in a multivariate analysis of mammalian faunas (BONIS et al. 1992) may rather blur the picture than make it more precise. At any rate, the contribution of "Equidae" to one or the other factorial axis will depend on whether the number of hipparions adapted to arid or to humid conditions was predominant in the samples used for the analyses.

Moreover, species seeming to indicate arid, dry, and humid conditions or forest and open environments may be found together at the same site. During MN 13 this is the case at Pavlodar (GROMOVA 1952), Samos 5, Dytiko, Sahabi (EISENMANN in press), and probably Kalmakpai. During the Ruscinian, it is true at Çalta and Karaburun, during the Villafranchian, at Beregovaja (ZHEGALLO 1978). It remains to be seen if these apparently contradictory associations result from taphonomy, or the inadequacy of our paleoecological interpretations.

REFERENCES

- ADROVER R., MEIN P., MOISSENET E. 1992. Contribucion al conocimiento de la fauna de Roedores del Plioceno de la region de Teruel. *Revista Teruel, Seccion de Ciencias*, 1988, **79**(1): 91-151.
- ADROVER R., MEIN P., MOISSENET E. 1995a. Los Sciuiridae de la transition del Turolense superior, Rusciniense y Villanyense de la region de Teruel. *Paleontologia i Evolucio*, **26-27**(1993): 85-106.
- ADROVER R., MEIN P., MOISSENET E. 1995b. Roedores de la transicion Mio-Plioceno de la cuenca de Teruel. *Paleontologia i Evolucio*, **26-27**(1993): 47-84.
- ALBERDI M.-T. 1972. El genero *Hipparion* en España. Vol.1: Texto, 368p.; Vol.2: Tablas y figuras, 235 tabl., 79 fig., 47 pl.
- ALBERDI M.-T. 1974. El genero *Hipparion* en España. Nuevas formas de Castilla y Andalucia, revision e historia evolutiva. *Trabajos sobre Neogeno-Cuaternario*, **1**: 1-146.
- ALBERDI M.-T., ALCALA L. 1992. El genero *Hipparion* en la fossa de Alfambra-Teruel. *Paleontologia i Evolucio*, **23**: 105-109.
- ALCALA L., MORALES J., SORIA D. 1992. El registro fossil neogeno de los carnivoros (Creodonta y Carnivora, Mammalia) de España. *Paleontologia i Evolucio*, **23**: 55-66.
- ALCALA L., MORALES J., MOYA-SOLA S. 1992. El registro fossil neogeno de los bovidos (Artiodactila, Mammalia) de España. *Paleontologia i Evolucio*, **23**: 67-73.
- AZANZA B., MENENDEZ E. 1992. Los ciervos fosiles del neogeno español. *Paleontologia i Evolucio*, **23**: 75-82.
- BONIS DE L., BOUVRAIN G., GERAADS D., KOUFOS G. 1992. Multivariate study of late Cenozoic mammalian faunal compositions and paleoecology. *Paleontologia i Evolucio*, **24-25**: 93-101.
- EISENMANN V., SONDAAR P. Y. 1989. Hipparions and the Mio-Pliocene boundary. *Bolletino della Societa Paleontologica Italiana*, **28**(2-3): 217-226.
- EISENMANN V. in press. What metapodial morphometry has to say about some Miocene Hipparions. [In:] E. S. VRBA (ed.) – Palaeoclimate and Evolution, with emphasis on Human origins. Yale University Press.
- FEJFAR O., MEIN P., MOISSENET E. 1990. Early arvicolidids from the Ruscinian (Early Pliocene) of the Teruel Basin, Spain. [In:] O. FEJFAR, W.-D. HEINRICH (eds.) – International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolidids, Ruhanov (Czechoslovakia) 1987. Geological Survey, Prague: 133-164.
- GROMOVA V. I. 1949. Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 2. Evoljutsija i klassifikatsija roda. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **17**(2), 162p. (In Russian).
- GROMOVA V. I. 1952. Gippariony (rod *Hipparion*) po materialam Taraklii, Pavlodara i drugim. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **36**: 1-475. (In Russian).
- KOUFOS G. D. 1987. Study of the Turolian Hipparions of the Lower Axios Valley (Macedonia, Greece). 1. Locality "Ravin des Zouaves-5" (RZO). *Géobios*, **20**(3): 293-312.

- KOUFOS G. D. 1988a. Study of the Turolian Hipparions of the Lower Axios Valley (Macedonia, Greece). 3. Localities of Vathylakkos. *Paleontologia i Evolucio*, **22**: 15-39.
- KOUFOS G. D. 1988b. Study of the Turolian Hipparions of the Lower Axios Valley (Macedonia, Greece). 4. Localities of Dytiko. *Palaevertebrata*, **18**(4): 187-239.
- MEIN P. 1990. Updating of MN zones. [In:] E. H. LINDSAY, V. FAHLBUSCH, P. MEIN (eds.) – European Neogene Mammal Chronology, Plenum Press, New York: 73-90.
- MEIN P., MOISSENET E., ADROVER R. 1992. Biostratigraphie du Néogène supérieur du Bassin de Teruel. *Paleontologia i Evolucio*, **23**: 121-139.
- VANGENGEIM E. A., VISLOBOKOVA I. A., GODINA A. YA., DMITRIEVA E. L., ZHEGALLO V. I., SOTNIKOVA M. V., TLEUBERDINA P. A. 1993. O vozraste fauny mlekopitajushchikh iz karabulakskoi svity na r. Kalmakpai (Zaisanskaya vpadina, vostochnyi Kazakstan). *Stratigrafia. Geologicheskaya Korrelatsiya*, **1**(2): 37-44. (In Russian).
- ZHEGALLO V. I. 1978. Gippariony Tsentral'noj Azii. *Sovmestnaya Sovetsko-Mongol'skaya paleontologicheskaya Ehkspeditsiya, Trudy*, **7**: 152p, 80 fig. (In Russian).