SYSTEMATIC AND EVOLUTIONARY RELATIONSHIPS OF THE HIPPARIONINE HORSES FROM MARAGHEH, IRAN (LATE MIOCENE, TUROLIAN AGE)

by

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SUMMARY

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Key-words : HIPPARIONINE HORSES, TUROLIAN, IRAN, SYSTEMATIC, EVOLUTION.
Mots-clés : HIPPARIONS, TUROLIEN, IRAN, SYSTÉMATIQUE, ÉVOLUTION.

Palaeovertebrata, Montpellier, 15 (4) : 173-269, 19 fig., 20 tabl.
(Reçu le 3 Octobre 1985, accepté le 14 Novembre 1985, publié le 30 Décembre 1985)

ABSTRACT

A systematic analysis of an hipparionine horse assemblage from Maragheh, Iran is made. A brief orientation to systematic philosophy and informal superspecific characterizations of some Old World hipparionines is given as a background to this work. A character state analysis of skulls is made, and has revealed five distinct species. A character state and stratigraphic trend analysis of isolated cheek tooth and postcranial remains, with known provenance, is also made. These two combined analyses reveal that the most resolute discrimination of hipparionine species and their evolutionary relationships occurs when multiple character complexes of associated skulls, maxillary and mandibular dentitions are made. When this is not possible, skulls have provided the best basis for discriminating species and their evolutionary relationships. Traditional characters of isolated cheek teeth and postcranial remains are shown here to offer limited information content for hipparionine phylogenetic systematics. The systematic portion of this study includes a comprehensive description of cranial and postcranial remains, and has further corroborated the distinction of five species which belong to at least three superspecific groups including: «*Hipparion*» *gettyi* sp. nov., Group 1; *Hipparion prostylum* (*s.l.*), and *Hipparion campbelli* sp. nov., Group 3; «*Hipparion*» aff. *moldavicum* and «*Hipparion ?matthewi*, Group 2. These species stratigraphic ranges and evolutionary relationships are also given here and argued to be important for establishing future hipparionine geochronologic correlations between a number of Eurasian late Miocene provinces.

RÉSUMÉ

Cette étude a permis d'effectuer une analyse systématique des associations d'Hipparions récoltées à Maragheh en Iran. Une orientation brève vers la philosophie systématique et une définition informelle des groupes supraspécifiques pour les Hipparions de l'Ancien Monde apparaissent comme une toile de fond de ce travail. L'analyse de caractères crâniens a révélé la présence de cinq espèces différentes à Maragheh. L'analyse des caractéristiques morphologiques et des tendances stratigraphiques sur les dents isolées et sur les restes postcrâniens, de provenance connue, a également été faite. Ces deux analyses combinées ont révélé que le meilleur moyen de distinguer les espèces du groupe des Hipparions et d'identifier leurs rapports évolutifs est de réunir les caractéristiques du crâne et de la dentition, inférieure et supérieure. Lorsque cela n'est pas possible, les crânes fournissent les meilleures bases pour la distinction des espèces et pour la compréhension de leurs rapports évolutifs. Les caractères classiques de dents isolées et des restes postcrâniens offrent, comme il a été démontré dans ce travail, une information limitée pour la systématique phylogénétique des Hipparions. La partie systématique de ce travail comprend une description claire des restes crâniens et postcrâniens et permet de distinguer cinq espèces appartenant au moins à trois groupes supraspécifiques: «*Hipparion*» *gettyi* n. sp. dans le Groupe 1; «*Hipparion*» aff. *moldavicum* et «*Hipparion*» *?matthewi* dans le Groupe 2; *Hipparion prostylum* (*s.l.*), et *Hipparion campbelli* n. sp. dans le Groupe 3. L'étendue stratigraphique de ces espèces et leurs rapports évolutifs ont été également discutés afin de fournir des bases documentées pour des corrélations géochronologiques futures, avec les Hipparions des provinces du Miocène supérieur d'Eurasie.

INTRODUCTION

The Maragheh district, Azerbaijan, Iran, has been renowned for over a century for its classical «Pontian» (late Miocène) large mammal fauna. In the late 19th century several investigators collected or studied the Maragheh fauna including Abich (1858), Brandt (1870), Grewingk (1881), Pohlig (1886 a, b), Kittl (1885, 1887), Rodler (1890), Rodler and Weithofer (1890), Forsyth Major (1893). In 1904, a group of French paleontologists under the direction of M. Boule made an extensive exploration and collection of the Maragheh district which eventually culminated in a monographic study by de Mecquenem (1924-25).

Work on the Maragheh fauna virtually ceased until 1956 when Takai, Tokyo University, reinitiated studies there (Takai, 1958). In 1966 Tobien, Johannes-Gutenberg University, Mainz, followed making some small but important collections from the middle portion of the Maragheh section (Tobien, 1968). A Dutch and German group led by Erdbrink (Erdbrink *et al.*, 1976) and another Japanese group led by Kamei (Kamei *et*

al., 1977) made further fossil collections from Maragheh's middle and upper stratigraphic intervals and independently collected rock samples for paleomagnetic and radiometric dating.

The latest paleontologic study at Maragheh was made by the Lake Rezaiyeh Expedition during the Spring of 1974 and Summers of 1975 and 1976. This project initiated a broad range of paleontological studies including mammalian systematics, physical stratigraphy, sedimentology, biostratigraphy, mammalian biochronology, paleoecology and radiometric dating. Thus far some preliminary studies of these various facets of the Lake Rezaiyeh Expedition have been published (Bernor *et al.*, 1979; Bernor *et al.*, 1980; Campbell *et al.*, 1980).

This manuscript presents the first detailed systematic study specifically focussed on the Maragheh hipparionines. The Maragheh hipparionines have been used extensively for biostratigraphic characterization and definition as well as geochronologic correlation of the locality with other Eurasian late Miocene faunas (Bernor, 1978; Bernor *et al.*, 1980). Therefore, a detailed systematics, including an investigation of the evolutionary relationships and biogeographic distribution of species related to the Maragheh hipparionines is important for refining, corroborating and elaborating upon earlier work. Furthermore, this work stabilizes, for the first time, our knowledge of the species present at Maragheh, and provides the basis for more resolute paleontologic and geologic comparisons. A recent comprehensive geological, mammalian biostratigraphic and zoogeographic study has preceeded this work, (Bernor, 1986), and should be referred to for further details about these aspects of the Maragheh fauna.

Forsten (1968) provided the first modern interpretation of the diversity of species at Maragheh by identifying three species: *Hipparion primigenium, Hipparion matthewi* and *Hipparion mediterraneus dietrichi.* Her species designations were largely based on size and proportional comparisons of cheek teeth and postcrania to other Old World species. Bernor *et al.* (1979), Woodburne and Bernor (1980), and Bernor *et al.* (1980) followed employing discrete morphologic characters and identified five species ranging some 2.5 million years in age: *Hipparion* sp. Kopran, «*Hipparion*» cf. *mediterraneum, Hipparion* cf. *prostylum, Hipparion* cf. *dietrichi*, and *Hipparion matthewi.* The authors found that Forsten's analysis was biased by her combining specimens from mixed stratigraphic intervals. This had the effect of underestimating the diversity of species; her method distinguished mostly size groups, not distinct morphospecies. In their revision of the Siwalik hipparionines, Bernor and Hussain (1985) further validated the Maragheh hipparionine species clusters based on morphologic attributes and expanding the number of skull, dental and postcranial characters used in their analysis. However, their work was not intended to, and did not stabilize the Maragheh hipparionine alpha systematics.

A number of studies of relevant Greek localities have been pursued during the last 20 years. The Samos assemblage was studied by Sondaar (1971) who recognized four species on morphologic bases: *Hipparion matthewi, Hipparion dietrichi, Hipparion proboscideum*, and *Hipparion* sp. large. Woodburne and Bernor (1980) and Bernor *et al.* (1980) also employed morphologic characters in identifying as many as five species of Samos hipparions belonging to four superspecific groups. In addition to Sondaar's four species, they suggested that a second small hipparion species occurred at Samos (their «*Hipparion*» *minus*). Bernor and Hussain (1985) revised the earlier referral of Samos hipparionines to four superspecific groups, arguing that only three of these groups were actually valid. They did however retain the species recognized by Woodburne and Bernor (1980) and Bernor *et al.* 1980). Most recently (Koufos 1984) has published a new Vallesian age dwarf species, *Hipparion macedoniensis*, from Ravin de la Pluie, Thessalo-

niki, Greece. The systematics of this taxon will be discussed in more detail as a comparison to the Maragheh species « *Hipparion* » *?matthewi.*

Recent work on Turkish hipparionines has been published by Sondaar and Staesche (1975), Sen *et al.* (1978) and Staesche and Sondaar (1979). Evidently, very little complete or partial skull material was available for study, making their analyses dependant largely on isolated cheek tooth and postcranial materials. The authors chose to employ a statistical methodology which characterized phena by size and proportions. The lack of morphologic details in their analysis largely excludes any possibility for comparisons with other such work. Bernor and Hussain (1985) and Bernor (here) have demonstrated that when care is taken to use morphology at comparable ontogenetic stages, accurate species identification and phylogenetic comparisons can be made.

This study further develops character state analyses of discrete skull, cheek tooth and postcranial characters, describes their variability, and records relevant measurements. The measurements adhere to procedures recommended at the 1982 American Museum of Natural History conference on *Hipparion* systematics, New York. Furthermore, this study endeavors to study specimens from discrete stratigraphic intervals, avoiding the pitfalls of combining samples for statistical evaluation from mixed stratigraphic levels.

The Maragheh hipparionine horses have a particular importance for local biostratigraphic subdivision, geochronologic correlations and understanding biogeographic relationships. Biostratigraphic subdivision of the Maragheh Formation has been made on the basis of a potential hipparionine clade including the species « *Hipparion* » *gettyi* n. sp., *Hipparion prostylum* and *Hipparion campbelli* n. sp. which are described in detail here for the first time. In turn, the relatively large sample of hipparionines from Maragheh allows the opportunity to reveal the relative stability of various skull morphological characters that the author and other recent students of the group have endeavored to develop for systematic use. The Maragheh hipparionine biostratigraphy is calibrated (Bernor, 1986 and here, Section D) and together with the improving phylogenetic framework for various clades, provides the basis for future correlations of the fauna with others in a number of Eurasian provinces.

SYSTEMATICS

A. SYSTEMATIC PERSPECTIVE

The last 150 years of systematic and evolutionary research on Old World hipparionines has produced a staggering body of literature. During the last several years, two apparent schools of systematic perspective have surfaced. One, a traditional school, has concerned itself largely with defining species statistically. The other, fostered by a few American workers, has endeavored to reemphasize morphological attributes of the skull and dentition for species definition, and seek their evolutionary, biochronologic and zoogeographic relationships. A review of this literature has been recently given by Bernor and Hussain (1985).

Bernor and Hussain (1985) have attempted to bridge the obvious hiatus between these two schools of thought by combining studies of cranial and postcranial morphology with an extensive suite of measurements in a systematic, evolutionary and biogeographic analysis of Siwalik hipparionines. Theirs, and other recent analyses of Old and New World hipparionine cranial and dental morphology (Woodburne and Bernor,

1980; MacFadden and Woodburne, 1982), have demonstrated that taxonomic groups of specific and superspecific rank can be erected and used for a variety of geological and paleobiological studies (Bernor *et al.*, 1980; Woodburne *et al.*, 1981; Bernor, 1984).

This work follows earlier morphologic investigations by identifying character states which have proven to be reasonably consistent at comparable ontogenetic stages (*i.e.* middle wear stage adults). The analysis of morphospecies character state distributions allows the most resolute means of identifying evolutionary transformation series, and thus determining phylogenetic relationships. I depart from the use of statistical analyses alone to discover species relatedness because such analyses use distance measurements, not shared-derived characters. Morphologic distance studies are phenetic by definition, not phylogenetic, and as such, they confuse evolutionary relationships. Hipparionine horses are a particularly diverse group and display extensive convergence in the numerical characteristics commonly used. The only means of identifying homoplasies in this group is by comparing character states of multiples morphological complexes. My intention here is to further use morphologic character states to identify species and their evolutionary relationships. This presentation follows the earlier work cited above in recongnizing the validity of several superspecific groups of Old World hipparionines. Presently, I characterize them as follows:

Group 1 hipparionines:

This group contains the first species to appear in the Old World, and has a chronologic range spanning the early Vallesian through the medial Turolian (*ca.* 12-7 ma.). Woodburne *et al.* (1981) have given a compelling argument for this group's origin from a New World late Barstovian species of *Cormohipparion, C. sphenodus.* While fundamentally agreeing with their interpretation, Bernor and Hussain (1985) questioned some salient details of the authors' argument. Group 1 hipparionines are the most primitive group of Old World hipparionines. Species of this group range from being medium to large sized species; preorbital bar is always long; the facial fossa is anteroposteriorly long, its dorsoventral height is usually significantly greater than the distance from its ventral border to the facial-maxillary crest, it is deeply pocketed posteriorly, oriented variably anteroposteriorly or anteroventrally, medial depth is usually great, the anterior rim may be prominent or faint, but is always present; the lacrimal bone is always placed well posterior to the fossa. The nasal notch is either anterior to or above P2/. The cheek teeth in a middle adult wear stage have complex plications of the pre- and postfossettes; the pli caballin is bifid or complex; the hypoglyph is usually rather deeply incised; the protocone is primitively either elongate or flattened lingually and rounded labially; the P2/ anterostyle is elongate. The metapodials of Group 1 species demonstrate great interspecific variability with regards to length and robusticity. Species included in this group may very well prove to be paraphyletic, containing sister taxa of species in other recognized, and yet to be recognized superspecific groups.

Group 2 hipparionines :

This group contains a number of Turolian-?Ruscinian age (*ca.* 10-4 ma.) eastern European, southwest Asian, western U.S.S.R. and Chinese hipparionines (Bernor and Qiu, in progress). Woodburne *et al.* (1981) have suggested an origin of this group which is independent of Old World Group 1 horses, citing the morphology of late Barstovian/ early Clarendonian North American species *Cormohipparion sphenodus* as being potentially ancestral to both lineages. Alternatively, Bernor and Hussain (1985) have suggested that since the earliest known record of these horses is Turolian age, and Group 1

shares synapomorphies with Group 2 hipparionines, that an Old World Group 1 origin is more plausible.

Presently, Group 2 hipparionines are characterized as being large to small sized species. The preorbital bar is short to very short; the facial region may have one to three or four distinct fossae; the preorbital fossa is usually long, the dorsoventral height dimension is always much greater than the distance between the fossa's ventral border and the facial-maxillary crest, it is only slightly pocketed posteriorly and oriented anteroventrally; medial depth varies from deep to shallow, the anterior rim may be prominent or faint. The lacrimal bone is always placed close-to or invades the posterior edge of the fossa. The nasal notch reveals a species transformation polarity from slightly retracted (over the anterior border of P2/) to strongly retracted (above P4/). In middle adult wear, the cheek teeth of some species have a complex plication amplitude, while others have a more simple plication amplitude of the pre- and postfossettes; the pli caballins may be double or single, the hypoglyph is usually moderately to slightly incised, the protocone is lingually flattened in some species, and rounded in others. P2/ anterostyle may be short and rounded in some species, but is usually elongate. Postcranial morphology is not known by direct, unequivocal quarry associations, and like Group 1 may include a diversity of morphologies.

Group 3 hipparionines:

This group contains a number of Turolian age species (*ca.* 9-6 ma.) from western and eastern Europe, southwest and south Asia, and possibly North Asia. MacFadden (1980) and Woodburne *et al.* (1981) have suggested that the origin of this group is from a North American late Miocene species. Bernor and Hussain (1985) have argued for this group's Old World origin from a Group 1 species.

Group 3 hipparionines are characterized as being medium sized species. The preorbital bar is moderately long. The preorbital fossa shows a distinct tendency to be reduced in size, and becomes absent in some species; when present, it is usually moderate to short in length, the dorsoventral height dimension is usually equal to the distance between the fossa's ventral border and the facial-maxillary crest, it is only slightly pocketed posteriorly, usually anteroposteriorly oriented, the anterior rim may be faint or absent. The lacrimal bone is always placed somewhat posterior to the posterior rim of the fossa, never invading the latter. The nasal notch is usually only slightly retracted (above some part of P2/). The cheek teeth in middle adult wear show reduced complexity and banding thickness of the pre- and postfossettes; the pli caballins also become simplified, being variably double or single, to persistently single in more advanced forms; the hypoglyph is usually only moderately deeply incised; the protocone is usually slightly elongate to rounded, but some primitive species may have lingually flattened and labially rounded protocones; P2/ anterostyle is always elongate. Postcranial morphology is always elongate and gracile when known.

Group 4 hipparionines:

Bernor and Hussain (1985) have recently reevaluated this « lineage » of dwarf hipparionines and concluded that they are undoubtedly a polyphyletic group. They have identified one small hipparionine species as being a Group 2 derivative which shares the characteristic short preorbital bar, typical dimensions, orientation, and slight postrior pocketing of the fossa, position of the lacrimal and length of the preorbital bar. This species is a derived Group 2 hipparionine in its reduced body size, lesser facial fossa medial depth, reduced cheek tooth complexity, single pli caballin and shallowly incised

hypoglyph in middle adult wear. The metapodials are believed to be long and slender in proportion (based on unassociated postcrania in several museums).

« Cormohipparion » (Sivalhippus) group:

Bernor and Hussain (1985) further identified a distinct evolutionary group of hipparionines from the Siwaliks of « Nagri » and « Dhok Pathan » age (*ca.* 9.5-5.2 ma.; Barry *et al.*, 1982; MacFadden and Woodburne, 1982; Bernor and Hussain, 1985). This group would appear to share phyletic relationships with a Chinese species, and perhaps some more derived East african species. The « *Cormohipparion* » (*Sivalhippus*) lineage is characterized as containing species which are medium to very large sized. The preorbital bar is long to very long anteroposteriorly. The preorbital fossa is large in anteroposterior and dorsoventral dimensions of two species, significantly smaller in two others where it becomes placed high and far anteriorly on the face. An apparent advanced species of this lineage, « *C*« (*S.*) *turkanense*, reduces the fossa to a vestigial depression. Orientation of the fossa evolves from a primitive anteroventral to a more anteroposteriorly aligned state in advanced species. Concommitantly, the fossa peripheral and anterior rims become progressively reduced in the transformation series. The lacrimal bone becomes placed progressively farther posterior to the posterior rim of the fossa as a consequence to the fossa's more anterior placement on the face. The nasal notch, when known, is never more than slightly retracted (above some portion of P2/). The cheek teeth are remarkably uniform amongst known species of this lineage, having complex and thickly banded plications of the pre- and postfossettes; pli caballins are double or complex; hypoglyphs are deeply incised; protocones are flattened lingually and rounded labially; P2/ anterostyles are elongate. There are no reported cranial-postcranial skeletal associations of these species, but Bernor and Hussain (1985) have cited the probability that at least some Siwalik species of this group had very robust metapodials and a relatively primitive postcranial morphology when compared to Group 3 hipparionines.

The above information on Old World hipparionine superspecific groups is summarized here in Tables 1a and 1b, with an explanation for character coding given in the methods section. The reader is referred to Bernor and Hussain (1985), Woorburne and Bernor (1980); Bernor *et al.* (1980), Woodburne *et al.* (1981), Woodburne and MacFadden (1982) for details leading to our current understanding of Old World hipparionine evolutionary relationships, and Bernor and Hussain (1985), and Bernor (1984), concerning their zoogeographic relationships.

Abbreviations and Definitions:

AMNH ..... Department of Vertebrate Paleontology, The American Museum of Natural History, New York.
BMNH ..... Department of Paleontology, British Museum (Natural History), London.
GIU ..... Geological Institute Utrecht.
JGUM ..... Institute of Paleontology, Johannes-Gutenberg Universitat, Mainz.
KNHM ..... Naturhistorisches Museum, Vienna.
MNHN ..... Museum National d'Histoire Naturelle, Paris.
MMTT ..... National Museum of Natural History, Tehran, Iran.
Hipparionine ..... An informal taxonomic rank referring to equid species belonging to any of the following genera: *Hipparion, Neohipparion, Nannippus, Cormohipparion, Proboscidipparion, Stylohipparion,* « *Cormohipparion* », (*Sivalhippus*).

«*Hipparion*» ..... following MacFadden and Woodburne (1982) and Bernor and Hussain (1985) Old World hipparion horses with facial morphologies that differ from either *Hipparion* or *Cormohipparion* (includes Groups 1, 2, 3, and 4 of Woodburne and Bernor, 1980).

Hipparion s.s. ..... I follow MacFadden (1980), Woodburne and Bernor (1980), Woodburne *et al.* (1980), MacFadden and Woodburne (1982), and Bernor and Hussain (1985) in restricting this nomen to a specific lineage of horses which have a facial fossa positioned high on the face; the posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne and Bernor, 1980). I differ with some of the previous authors in the specific referrals of *Hipparion s.s.*; this has been the subject of considerable discussion in the specific referrals of *Hipparion s.s.* (Bernor and Hussain, 1985), and will be further developed here.

Measurements ..... all measurements are in millimeters.

B. METHODS

Crania

Bernor and Hussain (1985) have outlined methods for measuring fossil hipparionine skulls and for doing a character state analysis on skulls. That methodology is followed and expanded here so that the standard measurements recently formulated at the American Museum Conference on Equid Systematics (Woodburne, Sondaar and others, in progress) may be applied. The measurements made on the skulls and associated maxillary and mandibular dentitions are given below (Figures 1-5). Measurements and character state analysis of maxillae, mandibles, and isolated cheek teeth are given in Sections II. B. 1., II. B. 2, and Tables 2 and 3. A description of character states used follows Bernor and Hussain (1985).

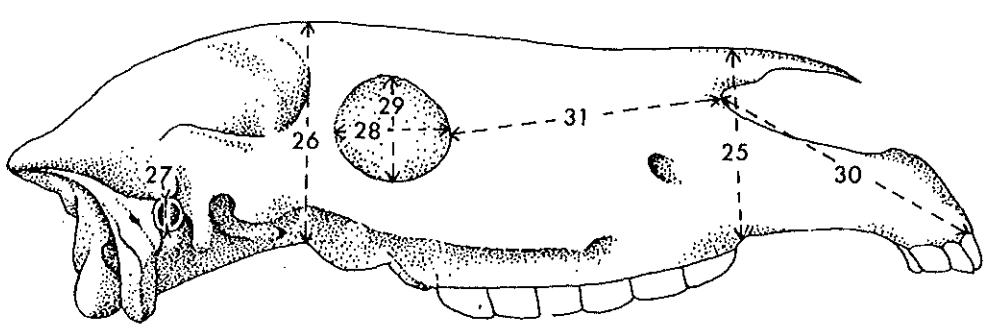


Fig. 1. — Measurements taken on *Hipparion* skulls; lateral view.

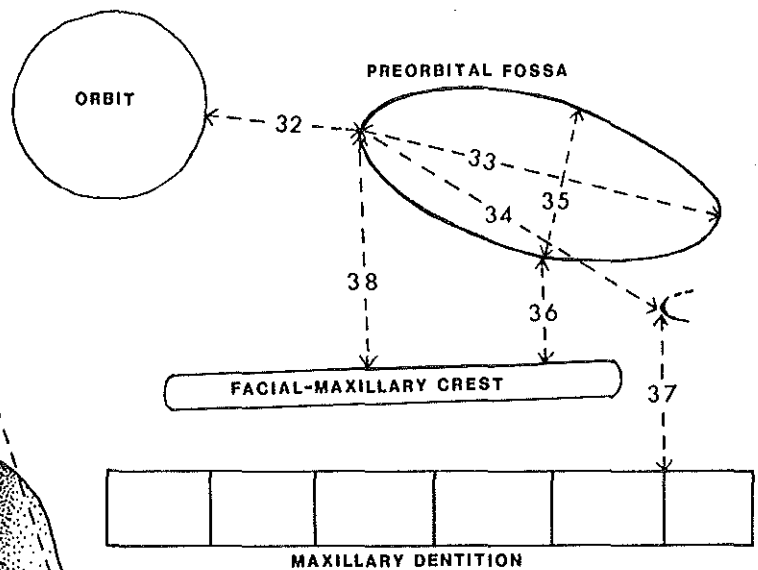


Fig. 2. — Measurements taken on *Hipparion* skulls; preorbital fossa and adjacent structures.

Fig. 3. — Measurements taken on *Hipparion* skulls; a: dorsal view; b: occipital view.

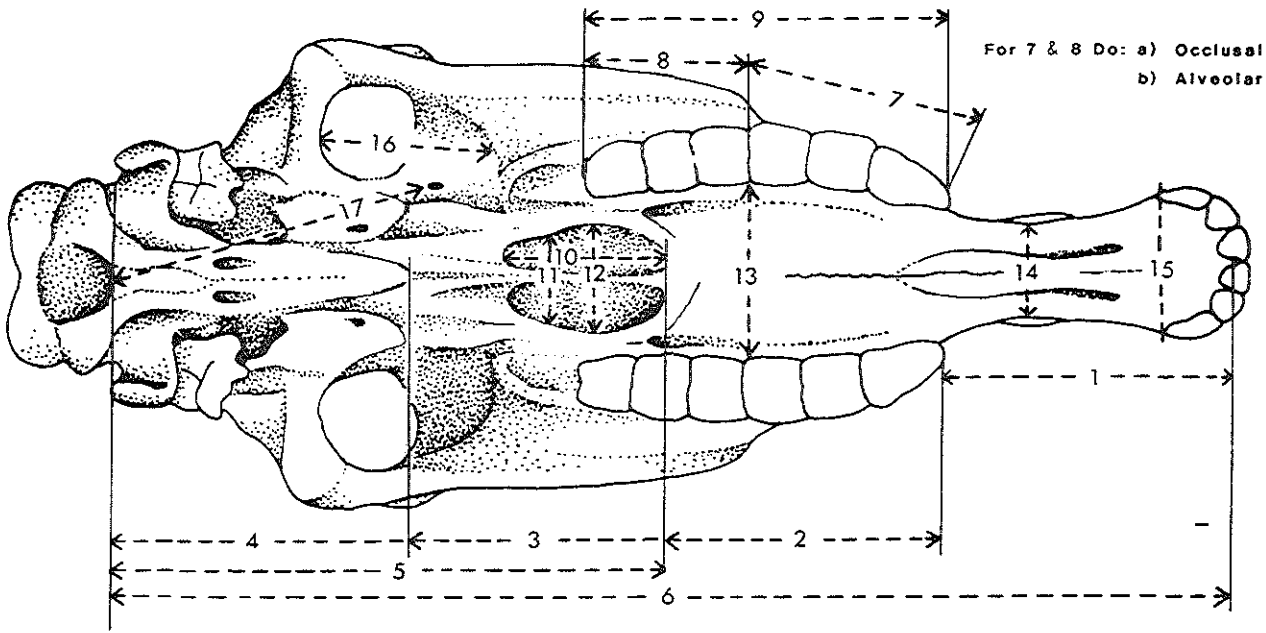


Fig. 4. — Measurements taken on *Hipparion* skulls; ventral view.

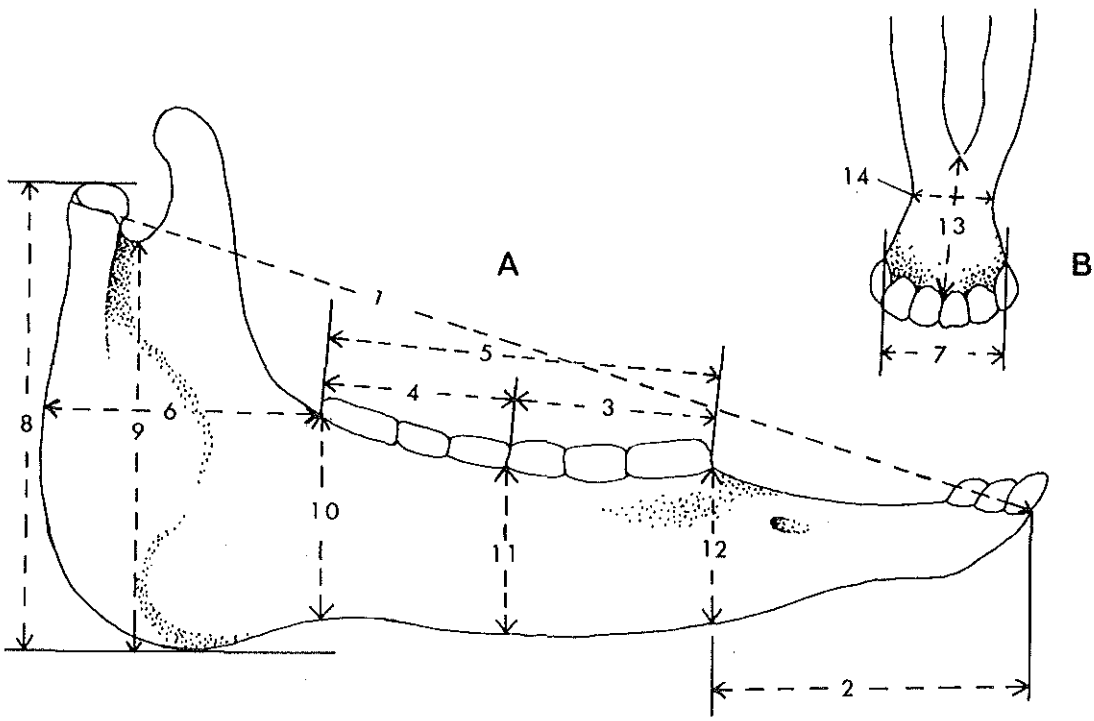


Fig. 5. — Measurements taken on *Hipparion* mandibles; a: lateral view; b: anteroventral view.

Postcrania

The methods of measuring postcrania follow the American Museum Conference on Equid Systematics (Woodburne, Sondaar and others, in progress). In addition, some character states of the metapodials are included following Bernor and Hussain (1985). Description, measurement (Figures 6-8) and character state analysis of postcrania collected by the Lake Rezaiyeh expedition are given in Section II. D. 3. The measurements and character states are listed in Table 4. Their description is given in Section III. D. 3.

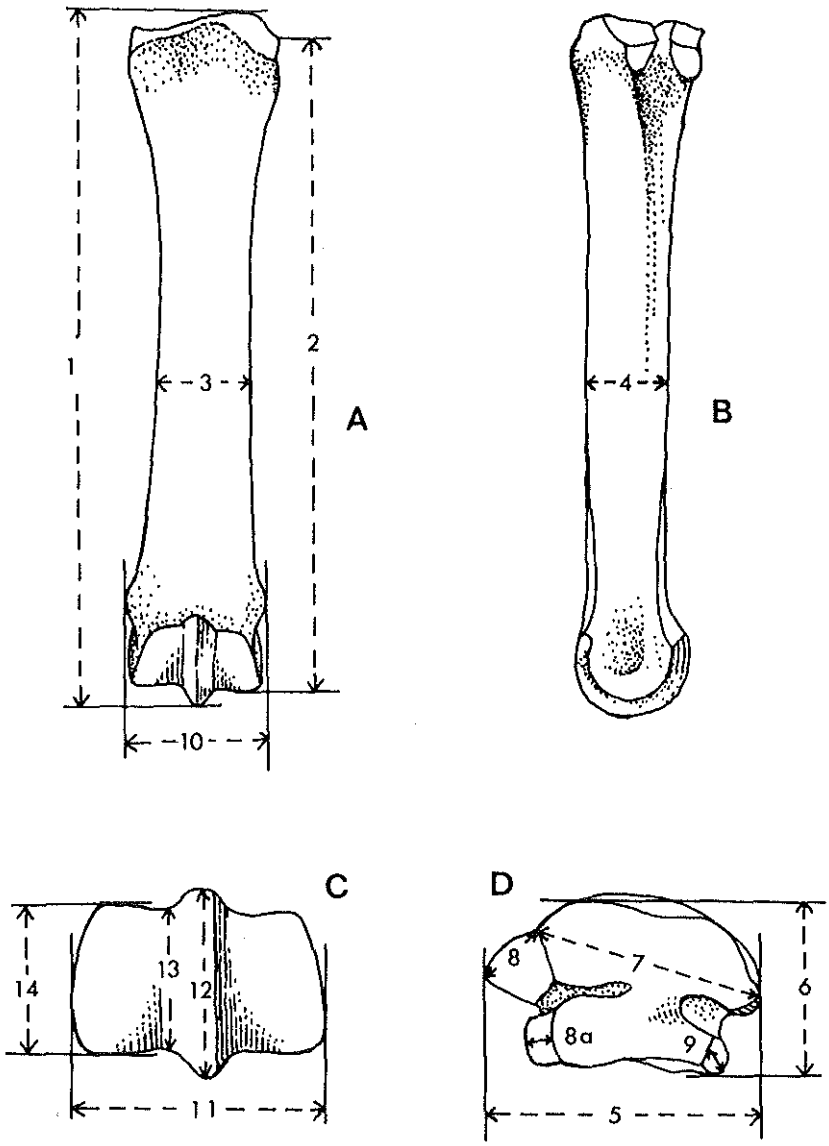


Fig. 6. — Measurements on metacarpals; a: anterior view; b: lateral view; c: distal view; d: proximal view.

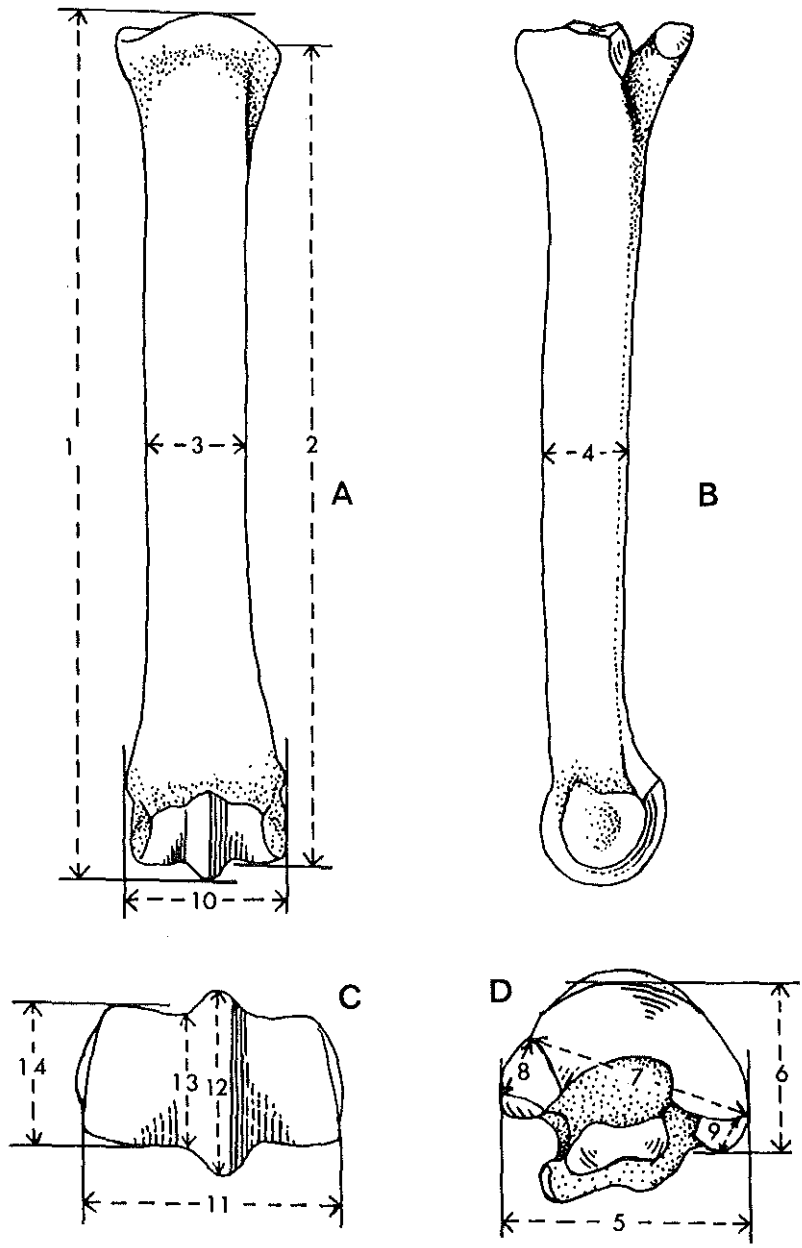


Fig. 7. — Measurements on metatarsals; a: anterior view; b: lateral view; c: distal view; d: proximal view.

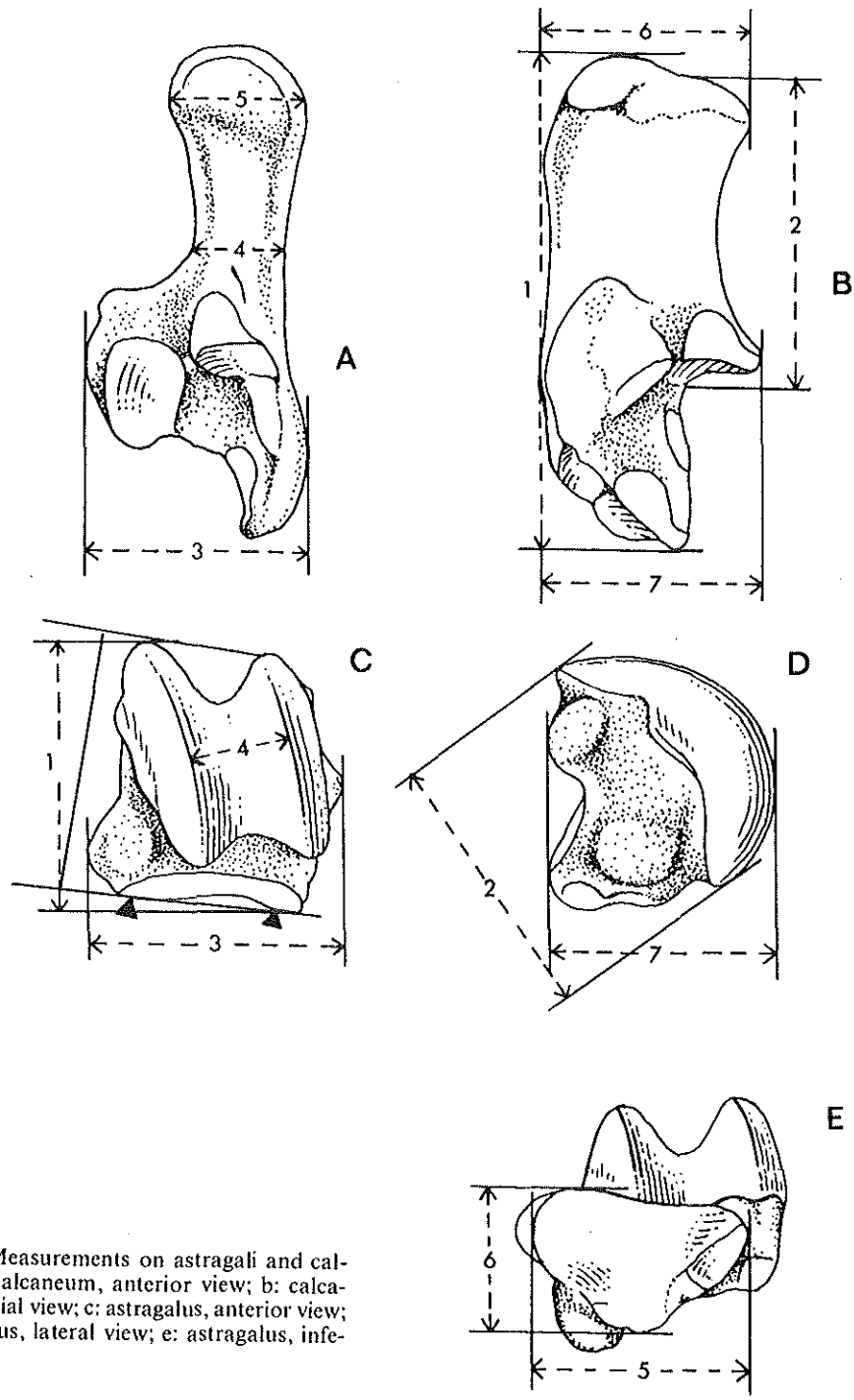


Fig. 8. — Measurements on astragali and calcanea; a: calcaneum, anterior view; b: calcaneum, medial view; c: astragalus, anterior view; d: astragalus, lateral view; e: astragalus, inferior view.

C. CHARACTER STATE ANALYSIS OF MARAGHEH HIPPARIONINE SKULLS

The Maragheh hipparionine assemblage is good both from the standpoints of sample size and stratigraphic provenance. Bernor (1986) has shown that the UCR-MMTT, KNHM and JGUM collections all have close to relatively close stratigraphic control. The MNHN assemblage is believed to have been collected almost entirely from the middle portion of the section, but precise stratigraphic provenance was never recorded (Bernor, 1986). The AMNH collection has unknown provenance. The nature of this data set, combined with the radiometric data from Maragheh, makes it reasonable in some cases to closely relate the two variables of time and morphology in a biostratigraphic array. Therefore, phylogenetic interpretations can legitimately take into consideration these two variables for hypothesis corroboration. The procedure followed here is to first identify phena using skull and maxillary dentition characters which have proven to be valid for species characterizations. The following section (D) will place species identified on the basis of skulls along with isolated dental and postcranial material of known provenance in a stratigraphic and geochronologic context (after Bernor, 1986). Section E will present a formal systematics of the Maragheh hipparionines.

Table 1 lists the age of individuals and 16 additional variables used for species determination. This character state analysis closely follows Bernor and Hussain (1985), but does include some minor expansions of individual character state categories. These characters were selected because they proved to be useful in discriminating the large suite of Group 1, 2, 3, and Siwalik species, as well as in a recent application to studies of Chinese Neogene hipparionines (Bernor and Qiu, in progress). The data array presented in Table 3 includes five morphological clusters in the Maragheh assemblage.

Cluster 1 includes a single specimen, KNHM-RLB 8401. This specimen has a long facial fossa which is egg-shaped and anteroposteriorly oriented, is moderately long dorsoventrally, has deep posterior pocketing, is moderately deep medially, has a faint anterior rim, its peripheral outline is relatively strongly expressed, ventral border is regular; the preorbital bar is very long; the lacrimal bone is placed approximately one-half the distance from the fossa to the orbit. The nasal notch is above the most anterior edge of P2/. The cheek teeth have complex plications of the pre- and postfossettes when taking into consideration that the wear is past the middle adult stage; pli caballins are persistently double; hypoglyphs are moderately to deeply incised, and could be expected to have been somewhat deeper in middle adult wear; protocones are rounded with slight lingual flattening; P2/ anterostyle is elongate. This specimen is referred here to « *Hipparion* » *gettyi*, an advanced Group 1, or possibly primitive Group 3 horse.

Cluster 2 includes ten individuals: KNHM-RLB 8402, 8403, 8404, A 4848; MNHN-RLB 7914, 7915, 8001, 8002, 8003, and BMNH M3924. This group is characterized as having long facial fossae which are subtriangular shaped and anteroposteriorly oriented, dorsoventral height is great, posterior pocketing is slight, medial depth is great, anterior rim is present in all specimens with the structure preserved, fossa peripheral border outline is strongly to moderately well expressed, all specimens except one (BMNH M 3924) have a regularly contoured fossa ventral border; preorbital bar length is short to very short; the lacrimal bone touches or invades the posterior rim of the fossa in all specimens which have the structure preserved. Nasal notch position is well preserved in only two individuals, and is found above the anterior border of P2/. Adult cheek teeth vary in fossette plication ornamentation from being rather complex and thinly banded in early wear (BMNH M3924) to moderately complex in middle wear (MNHN-RLB 7914 and 7915)

and simple in late wear (the remainder); pli caballin morphology is variably weakly bifid to single; the hypoglyph varies from being deeply to shallowly incised depending on the stage of wear; protocones are generally rounded in middle adult wear except for MNHN-RLB 7914 where they are flattened lingually; P2/ anterostyle is short and rounded on two specimens (BMNH M3924 and MNHN-RLB 7915), while being elongate on another (MNHN/RLB 8003). These specimens are referred here to «*Hipparion*» aff. *moldavicum*.

Cluster 3 includes nine individuals: KNHM A4847, KNHM A4844, JGUM MB 67, MNHN Mar. 18, MNHN Mar. 465, MNHN Mar. 359, MNHN Mar. 71, AMNH 27807 and AMNH 27809. This group is somewhat heterogeneous in some preorbital fossa character states, however distinguishing more than one species here is not possible. The preorbital fossa is shorter in this cluster than Cluster 1, it is generally egg or C — shaped with an anteroposterior orientation; dorsoventral height is uniformly short; posterior pocketing varies from being slight to absent; medial depth is moderate to shallow; anterior rim is faintly expressed to absent; fossa border outline varies from being moderately to weakly expressed; the ventral border is consistently regular shaped; preorbital bar length is between 31 and 40 mm., except in two specimens where it is greater than 41 mm. (MNHN 359 and AMNH 27809). The anteriormost limit of the lacrimal is less than one-half the distance from the fossa to the orbit except in one individual where it is about one-half the distance. The nasal notch is located from just anterior to P2/ to above P2/. In middle adult wear cheek teeth all have moderately complex fossette plications, pli caballins are single in most cases; hypoglyphs vary from being deeply incised to moderately deeply incised; protocone varies from being rounded labially and flattened lingually to having a more rounded/elongate morphology in one specimen (MNHN Mar. 359). This suite of specimens is referred here to *Hipparion prostylum* (*s.l.*).

Cluster 4 includes three individuals: UCR-MMTT 1342, 1343, and 1291. The fossae in these individuals is virtually absent, so that its length, orientation, and dorsoventral height cannot be measured; medial depth is very shallow; there is no posterior pocketing of the fossa, and no anterior rim, nor a ventral border; preorbital bar length consistently is in the 31-40 mm. range; the lacrimal is less than half the distance from the fossa posterior border to the orbit. The nasal notch is slightly retracted, being positioned above P2/. In middle adult wear, the cheek teeth have moderately complex, thinly banded pre- and postfossettes, pli caballin morphology is single, hypoglyphs are deeply to moderately deeply incised; protocones are rounded; P2/ anterostyle is elongate. These specimens are referred to *Hipparion campbelli* sp. nov., an advanced Group 3 horse.

Cluster 5 is represented by one specimen, G.I.U. P100-1958. This individual is characterized as having a moderate length fossa which is anteroventrally oriented, dorsoventral height is moderate (but great when considering the small size of the individual), posterior pocketing is slight, medial depth is moderate, the anterior rim is very faint, the fossa border outline is moderate with a regular ventral border contour; preorbital bar length is short; the lacrimal bone invades the posterior rim of the fossa. The cheek tooth ornamentation of this young adult (M3/'s nearly completerly erupted) is moderately complex, pli caballins are single, hypoglyphs are moderately deeply incised, protocones are somewhat elongate, P2/ anterostyle is short and rounded. This specimen is referred here to «*Hipparion*» *?matthewi*, a dwarf Group 2 horse.

D. CHARACTER STATE AND STRATIGRAPHIC ANALYSIS OF THE UCR-MMTT SAMPLE OF HIPPARIONINE CHEEK TEETH AND POSTCRANIAL REMAINS

Bernor (1986) has recently reported on the mammalian biostratigraphy, geochronology and zoogeographic relationships of the Maragheh fauna. Maragheh is a typical late Miocene «*Hipparion*» chronofauna of the western European, North African, Subparatethyan, Western U.S.S.R. and Chinese bioprovinces (Bernor, 1983, 1984). The fauna ranges from approximately 9.5 to 7 m.y. in age, and shows little change in its species composition, with the exception of the hipparionine horses. Figure 9 gives the stratigraphic ordering of the MMTT localities and hipparionine species vertical ranges. Bernor (1986) has discussed in detail the basis for referral of various museum and university collections, including the hipparionine skull material described here, to the various stratigraphic intervals. For a more complete discussion of the Maragheh fauna and its biostratigraphic, geochronologic and biostratigraphic attributes, the reader is referred to Bernor (1986).

In this section, maxillary cheek teeth, mandibular cheek teeth and postcranial remains not directly associated with UCR-MMTT skulls will be analysed. This analysis will be made in sequential stratigraphic order (from lowest to highest stratigraphic intervals) in an attempt to detect morphologic changes through the sequence, correlate as much of this sample with species recognized by skull morphology as possible, and evaluate the relative value of morphologic characters used by students of hipparionine horses. The Lake Rezaiyeh Expedition collected a number of isolated maxillary and mandibular cheek teeth, as well as postcranial remains of hipparionine horses. Tables 2, 3, and 4 give the metric and character state date on this material. However, a statistical analysis of the material is not attempted here because of the lack of sufficient sample size from any of the stratigraphic intervals sampled. The composite number of adult cheek teeth of any given cheek tooth class is too small (see summaries of Tables 2 and 3) for a valid statistical analysis to be made. This problem is compounded further by the even smaller number of cheek teeth per stratigraphic interval, the fact that the entire sample is derived from a 2.5 m.y. age range (Campbell *et al.*, 1980; Bernor *et al.*, 1980), and that at least five distinct species have been characterized in the sequence from skull and associated maxillary dental morphology.

Maxillary Cheek Teeth

The maxillary cheek teeth and isolated jaw fragments are listed in Table 1 by the following criteria: 1/ first by stratigraphic order (lowest to highest locality); 2/ second by sequential tooth number of deciduous cheek teeth; *i.e.* dP2/ through dP4/ with complete jaw sequences being listed first; 3/ third by sequential tooth number of pemanent cheek teeth; *i.e.* P2/ through P4// again with complete jaw sequences being listed first. Attempts at character state and size trend analyses are confined as much as possible to middle wear adult individuals because of the morphologic variability which occurs during the ontogeny of any given individual (after Bernor and Hussain, 1985).

The lowest stratigraphic interval with maxillary cheek teeth is MMTT 41 (-115 meter interval). This level contains adult middle wear maxillary cheek teeth which have pre- and postfossettes exhibiting moderate, although rather thickly banded plication amplitudes, double pli caballins, deeply incised hypoglyphs and elongate protocones. This constellation of characters is consistent with Group 1 horses generally, and

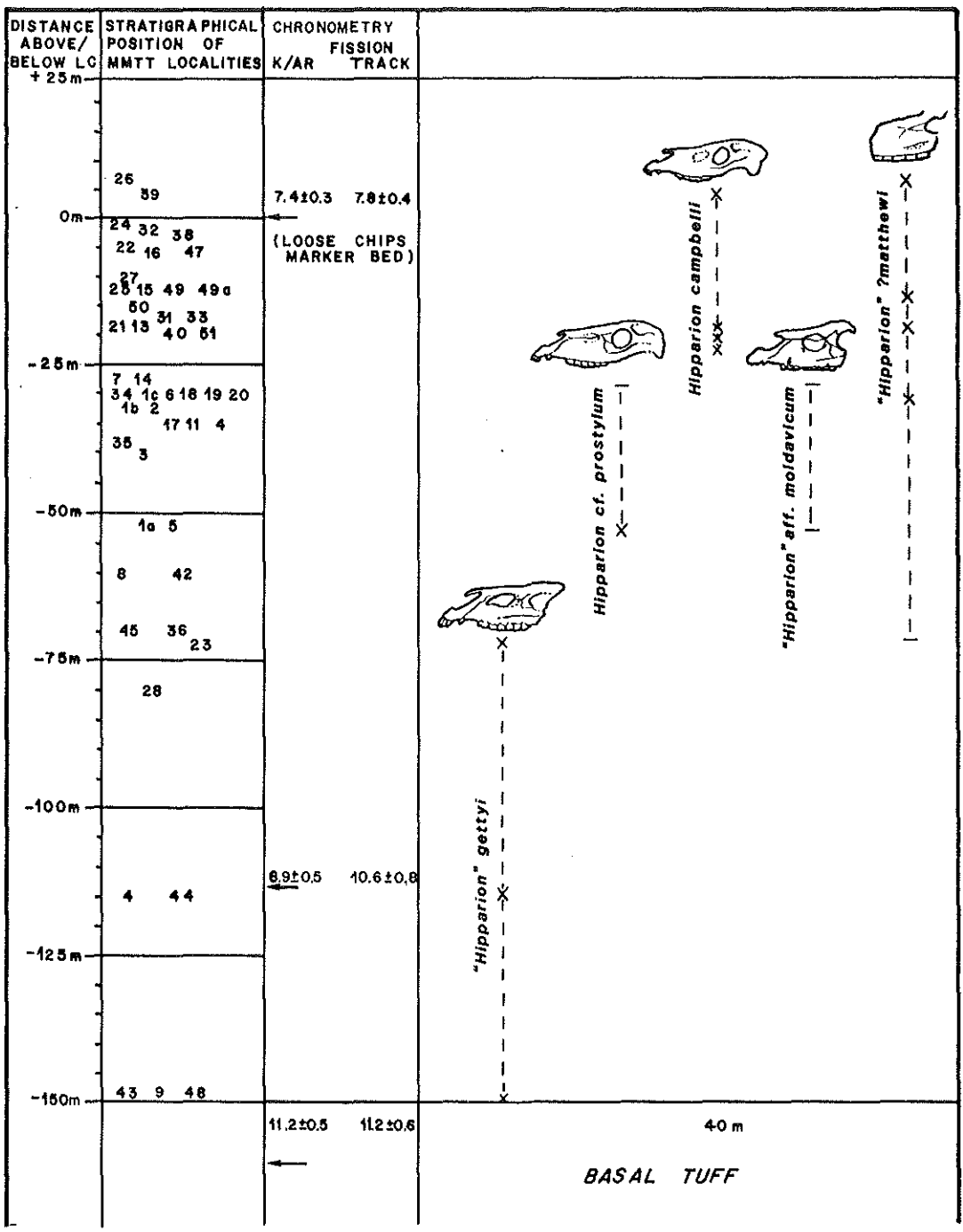


Fig. 9. — Stratigraphic position of Maragheh localities and stratigraphic ranges of the hipparionine species.

«*Hipparion*» *gettyi* specifically, which is known to have been collected within this interval at Maragheh (Bernor *et al.*, 1980; Bernor, 1986). There is no evidence either on the bases of size or morphology for there having been more than one species at this level.

The next highest stratigraphic level with hipparionine maxillary cheek teeth is MMTT 36 (-70 meters), which has a single adult specimen (UCR-MMTT 36/2033) that shows similarities in fossette plication amplitude, banding thickness, and doubling of the pli caballin, but has less deeply incised hypoglyphs and perhaps a less elongate (although not rounded) protocone. Similarly there is no evidence for more than one species from this level, and it is possible that «*Hipparion*» *gettyi* had a chronologic range which extended as high as this level.

MMTT 11, from the -35 meter level, shows the first detectable shift in the Maragheh sequence of upper cheek tooth size and morphology. UCR-MMTT 11/123, an unworn lt. P4/, is similar in size to the MMTT 41 sample, but contains no occlusal morphologic information due to its unworn state. MMTT 11/67 (left M1/) on the other hand is close in size to the MMTT 41 sample and shows similar morphology of pre- and postfossette plication amplitude and protocone elongation, but lacks a bifid pli caballin and has more thinly banded enamel plications of the pre- and postfossettes.

MMTT 18, -30 meter interval, has maxillary cheek teeth which represent the earliest known small hipparionine of the Lake Rezaiyeh Expedition sample. The right M1/ from here, UCR-MMTT 18/1440, appears to be smaller and proportionally narrower buccolingually than older samples in the sequence. This small suite of cheek teeth (UCR-MMTT 18/1598, left dP2/ and 18/1438, right P3/ in addition to 18/1440) shows moderately complex, relatively thinly banded plications of pre- and postfossettes, and single pli caballins (1 specimen only). Hypoglyph and protocone morphology are only preserved in one middle adult wear stage individual, MMTT 18/1438, which shows a deviation from stratigraphically older cheek teeth in its shallowly incised hypoglyph and its more rounded protocone morphologies.

The next highest stratigraphic interval represented by maxillary cheek teeth is the -28 meter interval, MMTT localities 7 and 14. These teeth can not be distinguished on size or visible length/width proportions from individuals found in lower stratigraphic horizons, with the exception of the buccolingually narrow molar cheek tooth from MMTT 18. Morphologically the adult cheek teeth are characterized by having moderately complex, rather thinly banded plications of the pre- and postfossettes, pli caballins are persistently single, hypoglyphs are moderately to shallowly incised from middle to late wear, protocone morphology ranges from being flattened only lingually to being more rounded. However, none of these attributes can in themselves be used to discriminate this suite of specimens as belonging to a particular Maragheh species. «*Hipparion*» aff. *moldavium*, «*Hipparion*» *prostylum*, and *Hipparion campbelli* all have maxillary cheek tooth dimensions and occlusal character states which overlap with this sample.

MMTT 37, the Ilkhchi (=Ildtchi) locality, and 13, the Shollovand quarry, have yielded the next youngest suite of maxillary cheek teeth. MMTT 37 is located in the eastern portion of the basin and has not yet been correlated lithostratigraphically with the rest of the sequence. However, Bernor *et al.* (1979), Bernor *et al.* (1980), and Campbell *et al.* (1980) and Bernor (in press) correlated MMTT 37 most closely to MMTT 13 on biochronologic and radiometric grounds. The MMTT 13 and 37 suite of upper cheek teeth represents the largest single sample in the Lake Rezaiyeh Expedition collection. Of this sample only three specimens appear to have size and length-width proportions similar to «*Hipparion*» *?matthewi* (UCR-MMTT 27/2049, 37/2081, 37/2093); all of the rest fall closely within the range of «*Hipparion*» aff. *moldavicum, Hipparion prostylum* (*s.l.*) and *Hipparion campbelli.* Morphologically the adult cheek teeth of this

suite of specimens can be characterized as having moderate to simple plication amplitude of the pre- and postfossettes (two exceptions: MMTT 37/-- and MMTT 13/118, pli caballins are always single (one exception, MMTT 13/118), hypoglyph incision ranges from moderately deep to shallow from middle to late adult wear; protocone ranges from being slightly elongate to rounded from middle to late adult wear, is never as elongate as seen in the MMTT 41 suite nor is it ever flattened only lingually as seen in the «*Cormohipparion*» (*Sivalhippus) group (Bernor and Hussain,* 1985). This suite of characters does not deviate from those observed in the Maragheh sample of «*Hipparion*» aff. *moldavicum, Hipparion prostylum* (*s.l.*), and *Hipparion campbelli.* However, since MMTT 13 has apparently yielded only one species of horse, this locality's sample, and presumably isochronous MMTT 37 sample, is best referred to *Hipparion campbelli.*

The size and characters exemplified in the MMTT 13 and 37 sample are seen in a small sample from MMTT 21 (-18 meter interval), 31 (-17 meter interval), and 25 (-12 meter interval) with one exception. MMTT 25/1635, a foal right dP2-3/, is quite small and compares in size with «*Hipparion*» *?matthewi.* The referral of all the rest of this small suite of material is best made to *Hipparion campbelli.*

The remainder of the maxillary cheek teeth originate from the localities: one specimen, UCR-MMTT 24/1732, a right M1/, comes from the -1 meter interval; the remainder, originates from MMTT 26 at the +7 meter interval. There would appear to be two size groups represented here: UCR-MMTT 24/1732, 26/1824 and 26/1645 are smaller, more buccolingually narrow teeth; the remainder approximate the size seen in the MMTT 13 and 37 sample. Morphologically the entire sample is nearly uniform in having moderately complex, thinly banded plications of the pre- and postfossettes (one exception, the UCR-MMTT 26/2567 P2/ which is in early wear and shows complex plications), pli caballins are single (two exceptions, MMTT 26/1644's P3/ and M3/ which are faintly bifid); hypoglyphs vary from being deeply incised to shallowly incised depending on wear stage. This sample is referred somewhat equivocally here to «*Hipparion*» *?matthewi* (smaller) and *Hipparion campbelli* (larger).

Mandibular Cheek Teeth

Table 3 lists metric and character state data on UCR-MMTT mandibular cheek teeth which lack, or can not have demonstrated associations with skull material. Recording the measurements and character states given here were recommended during the course of the hipparionine horse methodology conference at the AMNH in 1982. However, the data for this assemblage has proven to be largely useless for stratigraphic and systematic analysis. In the size trend, again some evidence for a smaller hipparionine species with buccolingually rather narrow teeth is seen first in the Lake Rezaiyeh Expedition sample at MMTT 18 (-30 meter level). Evidence for this smaller hipparionine is found in generally increasing abundance at MMTT 37 (-18 meter interpreted level), then MMTT 25 (-12 meter level) and MMTT 24 (-1 meter level), and finally is most abundant at MMTT 26 (+7 meter level). These individuals are referred to «*Hipparion*» cf. *?matthewi* based on their size (see hypodigm for listing of individuals per locality).

The trends in lower molar morphology are equally unrevealing. Ectoflexid morphology shows no clear trends, with premolars and molars showing both character states seemingly randomly through the sequence. Pli caballinids appear to vary from being expressed to rudimentary to absent throughout the sequence until the level of MMTT 37 and 13 where they markedly diminish and then finally disappear from locality 31 (-17 meters) upward. Ectoparastylids show an opposite trend, being absent up to the MMTT

7 and 14 level, then being varyingly expressed from that point upward. Both the linguaflexid and metaconid/metastylid character states are variably expressed through the sequence.

Postcrania

Measurements adhering to the recommendation of the AMNH hipparionine conference were taken on metapodials, astragali, and calcanea. Character states were also recorded for metapodials. Again, sample sizes were too small for all of these elements at each stratigraphic interval to make a statistical analysis meaningful. In the case of metapodials only the -30 (MMTT 20) to +7 (MMTT 26) meter interval is represented. Only two specimens, MMTT 13/1622 (metatarsal) and MMTT 13/--e (metatarsal) that were complete enough for all measurements to be made. The maximum number of astragali per level was 11 (MMTT 37 and 13 combined); these specimens are all similar in size and are referred here to *Hipparion* cf. *campbelli*. The total number of calcanea recovered from the entire sequence was 15; complete specimens where all measurements could be made equal five; MMTT 13 has yielded six, the largest total number of specimens for any given level.

The character state analysis on the metapodials has yielded no consistent differences through the short section sampled. Metatarsals and metacarpals alike are all elongate and gracile. Metatarsal sagittal keels are sharply extended whereas in the metacarpals they vary from being sharply extended to rounded. The ventral surface of both metatarsals and metacarpals vary from having a deep elongate depression to being shallow. The distal dorsal pit is usually deep in metatarsals and shallow in metacarpals. Only three metacarpals preserved the magnum/hamate angle, which varies from 142 to 149 degrees.

Conclusions

The use of standard measurement and character state analyses on maxillary cheek teeth, mandibular cheek teeth, and postcrania has proved less resolute for species identification than the use of the skull character state analysis. The principal problem is the limited usefulness of these more traditional characters alone for accurate species identification and phylogenetic reconstruction. Additionally, sample sizes at Maragheh are too small for any given level to permit a valid statistical analysis. These problems are compounded at virtually all Eurasian Turolian age deposits where as many as 3 or 4 hipparionine species may occur sympatrically (Sen *et al.*, 1978), and extensive interlineage convergence of traditionally used tooth and postcranial characters frequently occur.

In this sequence, the stratigraphic ranges of «*Hipparion*» *gettyi* and «*Hipparion*» *?matthewi*'s were recognized by isolated skeletal parts. However, the other three species recognized on the basis of skull morphology could not be distinguished by isolated specimens. Moreover, «*Hipparion*» *gettyi* was recognized on symplesiomorphic characters and «*Hipparion*» *?matthewi* was recognized primarily on the basis of its size. These are woefully poor criteria for identifying species and making interpretive conclusions. The results of this study will hopefully serve to alert those engaged in studies of hipparionines about the potential pitfalls of assigning species names or even referring isolated cheek teeth and postcranials to specific species. These skeletal elements in themselves simply do not yield the information content for identifying hipparionine species and developing a sound phylogenetic reconstruction.

E. SYSTEMATICS AND EVOLUTIONARY RELATIONSHIPS OF MARAGHEH HIPPARIONINES

Order **PERISSODACTYLA** OWEN, 1848

Suborder **HIPPOMORPHA** WOOD, 1937

Superfamily **EQUOIDEA** HAY, 1902
Family **EQUIDAE** STEINMANN and DODERLEIN, 1890

«*Hipparion*» *gettyi* sp. nov.

Hipparion sp. 2 Bernor, 1978, p. 62, fig. 3b.
Hipparion sp. 3, Bernor *et al.* (1979b), p. 94, fig. 1; Campbell *et al.* (1980), p. 841.
«*Hipparion*» sp. (Kopran horse) Woodburne and Bernor (1980), p. 1343, fig. 5d; Bernor *et al.* (1980), p. 723, fig. 8; Bernor and Hussain (1985), p. 36, fig. 3d.

Etymology: named after Mr. Gordon Getty, sponsor of the Lake Rezaiyeh Expedition.
Holotype: A SKULL/ KNHM-RLB 8401, preserved by the Naturhistorisches Museum, Vienna.
Type locality: Kopran, Maragheh.
Age: ?Late Vallesian - Early Turolian.

Referred specimens: KNHM-RLB 8401 skull of an old adult female with right and left I1/-M3/ (Figure 10 here); KNHM no number, an old adult palate with right P4/-M3/ and left P3/-M3/; KNHM A4866, young adult female mandible with left I/1-M/3; right I/1-P/2 (I/3's just erupting); UCR/MMTT, «*Hipparion*» cf. *gettyi*: 41/2224, left P/2; 41/2464, left M1/; 41/2211, left P4/; 41/2220, left M2/; 41/2248, left M1/; 41/2519, left P/4; 41/2234, left P/4; 36/2022, right dP2/; 41/2213, right dP/x; 41/2216, right dP/x; 36/2027, left P/2; 36/2027, left P/2; 41/2225, right M/2; 43/2489, right M/1; 43/2484, left M/1.

Diagnosis:

An hipparionine species with preorbital fossa anteroposteriorly long, egg-shaped and anteroposteriorly oriented, dorsoventrally moderately deep, with strong posterior pocketing, medially deep, with a faint anterior rim, and moderately expressed peripheral outline. The preorbital bar is long. The lacrimal bone is placed well posterior to the fossa. The nasal notch is placed above the parastyle of P2/. Adult cheek teeth have complex, moderately thickly banded plications of the pre- and postfossettes, pli caballins are persistently double, hypoglyphs are deeply incised. The protocones are moderately elongate and may have a slight lingual flattening. The P2/ anterostyle is elongate. An uncertainly associated metapodial from Kopran is slender an elongate.

Differential Diagnosis:
«*Hipparion*» *gettyi* differs from other Group 1 horses as follows:

1/ It differs from «*H.*» *primigenium* (Howenegg, Eppelsheim and Inzersdorf) in having a smaller skull, and presumably smaller body size; a facial fossa which is egg-shaped and anteroposteriorly oriented, shorter anteroposteriorly and dorsoventrally, anterior rim and peripheral border are less strongly expressed, preorbital bar is shorter, the nasal notch is slightly more retracted (above P2/ parastyle versus anterior to P2/); cheek teeth are less complexly plicated. Limbs are more elongate and gracile.

2/ It differs from «*Hipparion*» *africanum* (Bou Hanifia) in that the fossa is much shorter anteroposteriorly, facial-maxillary crest dimension is slightly greater (inferring less dorsoventral height), fossa anterior rim and peripheral border are less strongly

expressed. The nasal notch is more retracted. The cheek teeth are less complexly plicated. The limbs are more elongate.

3/ It differs from « *Hipparion* » *catalaunicum* in having a smaller skull and presumably body size; the facial fossa is much shorter anteroposteriorly, shorter dorsoventrally, anterior rim and peripheral border are less strongly expressed. The nasal notch is more strongly retracted (above P2/ parastyle versus anterior to P2/). The cheek teeth have slightly less complex plications of the pre- and postfossettes.

4/ It differs from a large Group 1 hipparionine, « *Hipparion* » sp. (Woodburne and Bernor, 1980; Bernor *et al.*, 1980) from Pikermi and Samos in having a smaller skull, and presumably body size; the snout is relatively shorter and narrower; facial fossa is slightly more anteroventrally oriented, deeper medially, and more deeply pocketed posteriorly.

5/ It differs from « *Hipparion* » *melendezi* (El Lugarejo and Arroyo) in that the fossa has a greater anteroposterior dimension, posterior pocketing is greater, the fossa is not anteroventrally oriented, medial depth is greater, preorbital bar is appreciably longer. The nasal notch is more retracted (above P2/ versus slightly anterior to P2/). The cheek teeth would appear to have slightly greater hypoglyph incisions.

Description:

The holotype of « *Hipparion* » *gettyi* (Figures 10 A,B) is a moderately large sized old female skull (KNHM-RLB 8401) with the entire dentition present, but lacking the posterior portions of the orbits, zygoma, and virtually all of the cranium. The preorbital fossa is relatively large; it is egg-shaped and anteroposteriorly directed, has a moderately well delineated peripheral rim and a weakly expressed anterior rim; it is anteroposteriorly elongate, dorsoventrally and medially deep; it is placed well anterior to the orbit and lacrimal bone and well superior to the facial-maxillary crest; it is deeply pocketed posteriorly and becomes markedly narrow dorsoventrally at its anterior limit. The nasal bones are slightly retracted to a level above the parastyle of P2/. The snout is moderately long and has a very narrow premaxilla and incisive border. The canines are small, rounded, and peg-like in morphology. The maxillary cheek teeth are in a relatively late stage of wear, but still preserve a definitive occlusal morphology. P2/ has a moderately long anterostyle (and somewhat shorter than it would have been in middle adult wear) which is rounded anteriorly, and necked posteriorly. The protocone is generally elongate in all of the cheek teeth, becoming serially more rounded from M3/-M2/-M1/ with P4/-P3/-P2/ having a similar length/width relationship. The snout is moderately long and has a very narrow premaxilla and incisive border. The canines are small, rounded, and peg-like in morphology. The maxillary cheek teeth are in a relatively late stage of wear, but still preserve a definitive occlusal morphology. P2/ has a moderately long anterostyle (and somewhat shorter than it would have been in middle adult wear) which is rounded anteriorly, and necked posteriorly. The protocone is generally elongate in all of the cheek teeth, becoming serially more rounded from M3/-M2/-M1/ with P4/-P3/-P2 having a similar length/width relationship. These differences can be inferred as being largely wear-related. Protocone morphology in middle adult wear can be interpreted to have been closer to the morphology seen in M2/-M3/ and P4/, which is generally elongate with an occasional lingually flattened and labially rounded aspect. The hypoglyph's are deeply incised despite this relatively late wear stage. Similarly, plications of the pre- and postfossettes are thinly banded, but rather complex for this late stage-of-wear. Pli caballins are also thinly banded, and are persistently bifid.

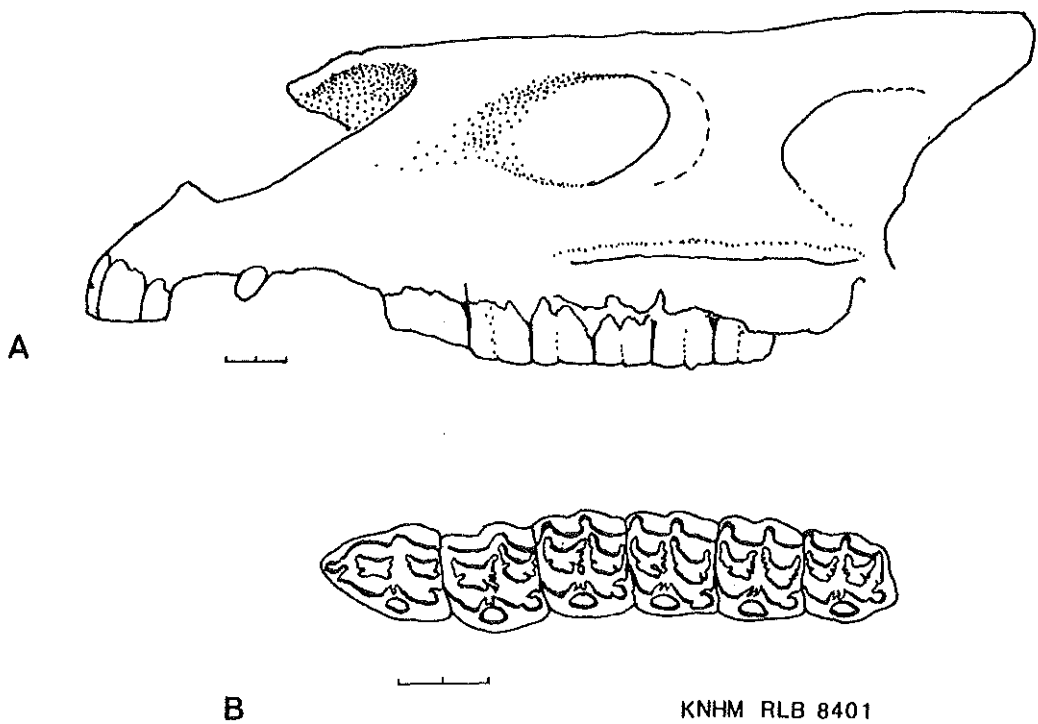


Fig. 10. — «*Hipparion*» *gettyi*, skull; a: RLB 8401, lateral view; b: RLB 8401, occlusal view of maxillary dentition.

A fragmentary maxilla from the Kopran collection in Vienna, KNHM no number, is of a very old adult individual with right P4/-M3/ and left P3/-M3/ (see Table 6 for measurements). The cheek teeth are all very worn, the pre- and postfossettes have lost all plications, the pli caballins are absent and hypoglyphs show no incision (except for the M3/), due to the very advanced stage of wear. Protocones have also become rounded in this advanced stage of wear.

There is also a young adult female mandible in the Vienna collection from Kopran, KNHM A4866. This specimen includes the incisor and symphysial regions with left and right I/1-I/3 (this last erupting), canines (erupting), most of the left mandibular corpus with P/2-M/3 (this last just erupted and unworn), and right corpus with P/2-M/2. The rami are absent on both sides of the mandible. The canines are small and peg-like, being about one-half erupted, and are flush against I/3. The mental foramen is placed directly between posterior I/3 and anterior P/2. P/2 anterostylid is elongate and its metastylid is slightly smaller than metaconid. Ectoflexids separate metastylid and metaconid in P/2, and M/1-M/3, but not P/3 and P/4. Pli caballinids are completely absent. Ectoparastylids are present on P/3, M/1 and M/2, absent on P/2 and P/4. Linguaflexids are shallow on all cheek teeth and metaconid-metastylid have a slight angular shape on P/2, while being rounded on P/3-M/3.

There are a number of maxillary and mandibular cheek teeth not associated with this skull from Kopran which were collected by the Lake Rezaiyeh Expedition. The maxillary cheek teeth are high crowned (maximum of *ca.* 50 mm. unworn). Protocone shape in early to middle adult wear is elongate, labially rounded, lingually flattened with a general elongate oval shape. Plication amplitude of the pre- and postfossettes is relatively complex and moderately thickly banded (see Table 2). The hypocone is very deeply incised. The Kopran sample of mandibular cheek teeth are also relatively high crowned (maximum of *ca.*44 mm. unworn), and have a similar morphology as that described for KNHM A4866 (see Table 3).

Discussion:

Bernor (1978) initially referred the cheek teeth from Kopran to «*Hipparion*» sp. 2. Bernor *et al.* (1979b) and Campbell *et al.* (1980) later referred the holotype and Kopran cheek teeth to «*Hipparion*» sp. 3 in preliminary treatments of Maragheh mammalian systematics and biostratigraphy. Subsequently, Woodburne and Bernor (1980, p. 1343, Figure 5D, p. 1324) and Bernor *et al.* (1980) figured and discussed the holotype referring it to «*Hipparion*» sp. (Kopran). Most recently, Bernor and Hussain (1985) have figured (Figure 3D, p. 37) and briefly discussed the phyletic relationships of the holotype, referring it to «*Hipparion*» sp. (Kopran). In this presentation, all prior referrals cited here are made synonyms of «*Hipparion*» *gettyi*.

The occurrence of «*Hipparion*» *gettyi* at Maragheh has systematic, biostratigraphic and geochronologic significance. The skull (KNHM-RLB 8401) was collected by Pohlig from Kopran, which occurs in the lowest fossil levels of the section (*ca.* 150 to 115 meters below loose chippings). The cheek teeth which are referred here to «*Hipparion*» cf. *gettyi* stratigraphically range from 150 to about 70 meters below loose chippings and have an estimated age range of approximaterly 9.5 about 8.5 million years.

«*Hipparion*» *gettyi* is a derived Group 1 horse with potential Group 3 phyletic relationships. The confusion surrounding Group 1 phyletic relationships arises from the fact that this «group» of hipparionines is united largely by plesiomorphic characters of the facial region and maxillary dentition. They are very heterogeneous in postcranial morphology. «*Hipparion*» *gettyi* is most similar to a specimen from Pikermi (BMNH M42603) currently displayed as part of a prepared exhibit block at the British Museum of Natural History Department of Paleontology. The Pikermi specimen does not differ in any significant details of size, facial fossa morphology, nasal notch retraction, or maxillary molar morphology and it is closely associated with slender, elongate metapodials which are similar to those of a KNHM specimen from Kopran. The Pikermi skull is tentatively referred here to «*Hipparion*» *gettyi*.

As Group 1 horses, these two specimens measure at the lower range of variation in fossa length, dorsoventral height, and preorbital bar dimensions (compare with measurements published by Bernor and Hussain, 1985). Also, the smaller skull size, slight retraction of the nasal notch, less strongly expressed peripheral border outline, reduced expression of the anterior rim, apparent rotation of the fossa orientation from a sharp anteroventral to a distinct anteroposterior orientation, its egg-shape instead of elongate or subtriangular shapes, its reduced banding thickness of maxillary cheek tooth pre- and postfossettes, and elongation of metapodials are polarities divergent from all early Vallesian Group 1 horses, and potentially could directly presage the morphology seen in primitive Group 3 horses. The Group 1 species from Arroyo and El Lugarejo (late Vallesian/early Turolian of Spain), «*Hipparion*» *melendezi*, is even further derived in its reduced fossa anteroposterior dimension, and posterior pocketing, further rotation of the fossa toward an anteroposterior orientation and reduced hypoglyph incision of the

maxillary cheek teeth. The current debate surrounding Group 3 origins and the role that derived, early Turolian Group 1 hipparionines such as « *Hipparion* » *gettyi* and « *Hipparion* » *melendezi* might play will be raised later as a topic of *Hipparion* cf. *prostylum* phylogeny. It is sufficient to cite here that derived Group 1 horses, quite similar in morphology to primitive Group 3 horses, existed in southwestern Europe, the eastern Mediterranean, and southwest Asia by the early Turolian, just before the first known occurrence of Group 3 horses (Bernor *et al.* 1980; Bernor, 1984; Bernor and Hussain, 1985).

Hipparion prostylum (*s.l.*) GERVAIS, 1849

Hipparion sp., de Christol (1832), p. 180.
Hipparion prostylum GERVAIS (1849), p. 284, Pl. 19, figs. 1-7; Sondaar (1974), p. 296, Pl. 46, figs. 1, 2; Skinner & MacFadden (1977), p. 912, fig. 3a; Woodburne & Bernor (1980), p. 1329, figs. 3e, 7f, 7h - m; Bernor & Hussain (1985), p. 40, fig. 3a.
Hipparion diplostylum GERVAIS (1849), p. 284, Pl. 19, fig. 8.
Hipparion mesostylum GERVAIS (1849), p. 284, Pl. 19, fig. 9.
Hipparion gracile GAUDRY (1873), p. 32, Pl. V, figs. 7-10, Pl. VI and Pl. VII, figs. 1-11.
Hipparion mediterraneum ROTH & WAGNER (1855), *sensu* Forsten (1968) (in part), p. 40.

Lectotype: A partial skull, BMNH M33603, preserved by the British Museum of Natural History.
Type locality: Mt. Luberon (= Cucuron or Mt. Luberon).
Age: Early Medial Turolian.
Referred specimens: Maragheh fragmentary skulls of *Hipparion prostylum* (*s.l.*): KNHM A4847, KNHM A4844; JGUM MB 67; MNHN Mar. 71, MNHN Mar. 18, MNHN Mar. 465, MNHN Mar. 359; AMNH 27807; AMNH 27809.
Geographic range: France, Greece, Iran and Afghanistan.

Diagnosis:

An hipparionine species with preorbital fossa anteroposteriorly moderate to short in length; it is faintly egg-to C-shaped and is anteroposteriorly oriented; shallow to very shallow dorsoventrally, slight to no posterior pocketing, moderate to slight medial depth, anterior rim faint to absent, with peripheral rim moderately to weakly expressed. The preorbital bar is moderately long. The lacrimal bone is placed well posterior to the fossa. The nasal notch is placed either just anterior to or above P2/. Middle adult cheek teeth have moderately complex plications of the pre- and postfossetes, pli caballins are usually single but may occasionally be double, hypoglyphs are moderately deeply incised. The protocones vary somewhat in morphology, but are most commonly elongate and compressed labio-lingually in early wear, sometimes showing general rounding or rounding with slight lingual flattening. The P2/ anterostyle is elongate. Metapodials are slender and elongate.

Differential Diagnosis:

Hipparion prostylum differs from other Group 3 horses as follows:

1/ It differs from *Hipparion dietrichi* in having a more distinctly developed fossa, with more prominent peripheral rim; medial depth and posterior pocketing is greater and anterior rim is better expressed in some individuals. Middle wear adult cheek teeth have no consistent differences, but there is a greater incidence of plication complexity of the pre- and postfossettes and bifid pli caballins in the type locality's sample of *Hipparion prostylum* than *Hipparion dietrichi*.

2/ The facial fossa is less reduced and the snout is less elongate and narrow, and nasal notch incision is slightly less than in *Hipparion campbelli*. Also, the cheek teeth have less persistently single pli caballins than *Hipparion campbelli*.

Description:

Nine partial skull specimens of *Hipparion prostylum* (*s.l.*) are present in the hypodigm given here. They include specimens from collections in Vienna (KNHM A4847, KNHM A4844), Mainz (JGUM MB 67), Paris (MNHN Mar. 18, Mar 465, Mar. 359 and Mar. 71) and New York (AMNH 27807 and 27809). These are shown in Figures 6 and 7.

KNHM A4847 (Figure 11 A)is a subadult skull which is nearly complete and includes right C-M3/ (M3/ is only one-half erupted), left C-P4/ and M3/, while lacking the incisors and their alveoli, left M2-3/ and their alveoli and the anterior nasals, posterior one-half of the orbits, zygoma and most of the cranium. The preorbital fossa is moderate sized, extending anteriorly to a level above P4/ mesostyle, is moderately deep dorsoventrally at its posterior end and narrows dorsoventrally towards the anterior end; it is egg-shaped and anteroposteriorly oriented with its anterior limit being up-turned; posterior pocketing is slight, but marked; medial depth is moderate compared to some other individuals of the hypodigm; anterior rim is faintly present; fossa peripheral rim is continuous and somewhat more strongly expressed than other individuals of the hypodigm; it is well posterior to the lacrimal bone. The infraorbital foramen is below the anteriormost portion of the fossa and above P3/. The snout is moderately long, lacking incisors, but with large buccally convex and lingually concave canines. The P1/ is present on the right side, being rounded in its occlusal profile, and quite worn. P2-4/ are in an early stage of wear, and occlusal details are not yet well expressed. However, P2/ and P3/ show moderate complexity of the pre- and postfossettes and the pli caballins are distinctly single. The premolar protocones are rounded generally with P3/ and P4/ showing some lingual flattening due to their early stage of wear; and the hypoglyph is very deeply incised when exposed. The P2/ has an elongate, pointed anterostyle, and is necked posteriorly. The M1/, being the first permanent cheek tooth do erupt and come into full occlusion, has the most well developed occlusal morphology. Its protocone is rounded; its pli caballin is single; the pre- and postfossettes are moderately complex and thinly banded. The M2/ and M3/ are not worn enough to clearly show their adult occlusal morphology.

I refer one palate in the Vienna collection, KNHM A4844, to *Hipparion* cf. *prostylum*. This specimen is a young adult with right and left P2/-M3/ (M3/ erupting), collected from Kara Kend (equals our MMTT 1A - 1B in Middle Maragheh). Just enough of the facial fossa remains on both the right and left sides to reveal that it was well above (*i.e.* 31 mm.) the facial maxillary crest. The infraorbital foramen is not preserved on either side. P2/-P4/ are in early stages of wear and somewhat eroded on the occlusal surfaces. However, the pre- and postfossettes are moderately complex and thinly banded; pli caballins are poorly preserved but appear single on right P3/ and double on right P4/; hypoglyphs are deeply incised on P2/ and P3/ and very deeply incised on P4/; protocones are distinctly rounded labially and flattened lingually. P2/ has an elongate anterostyle. M1/ and M2/ show a similar morphology to the premolars in features of fossettes, hypoglyphs and protocone morphologies, but pli caballins are too poorly preserved to exhibit any morphology. The M3/'s have not yet fully erupted, and are unworn.

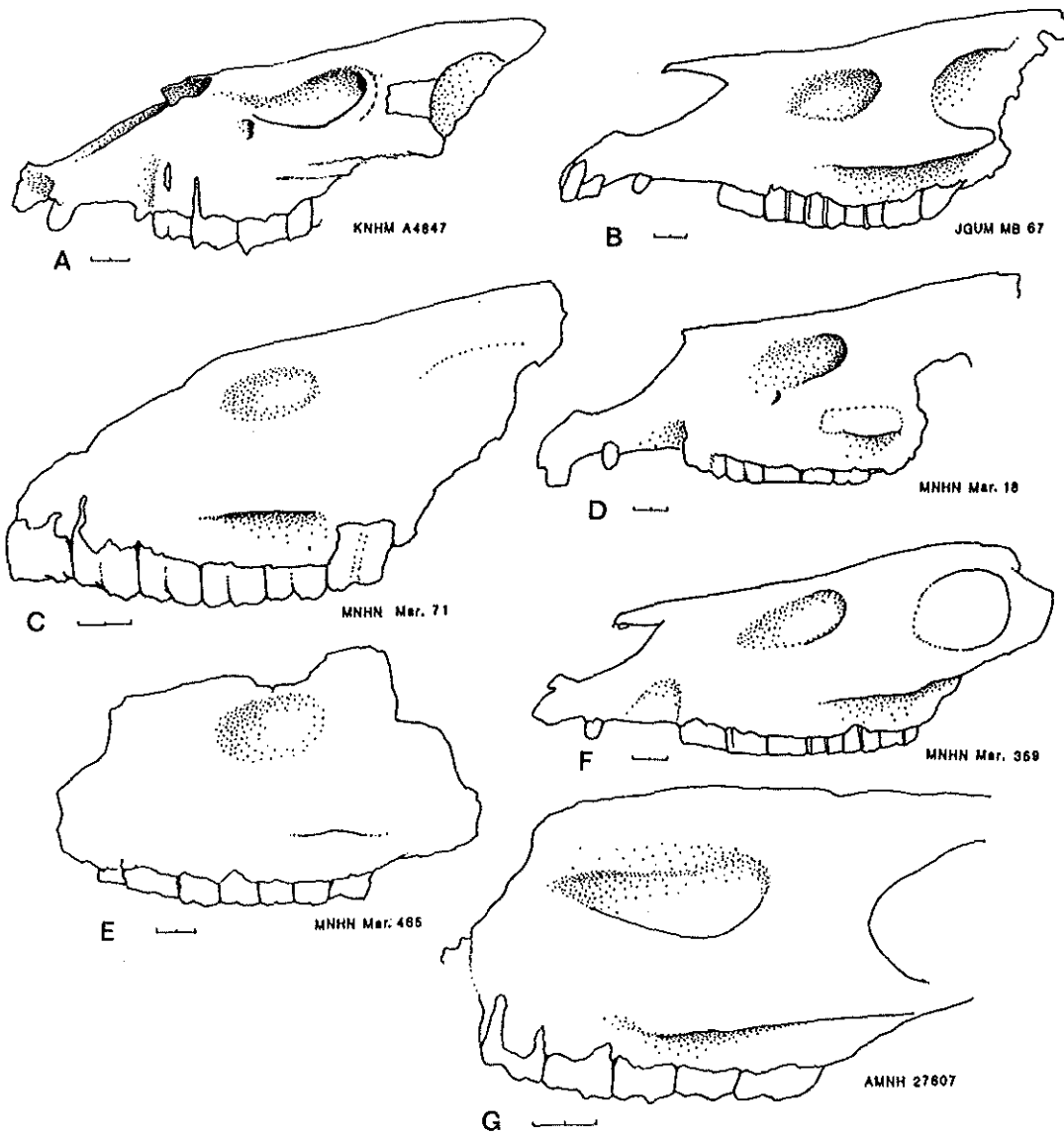


Fig. 11. — *Hipparion* cf. *prostylum*, skulls, lateral view; a: KNHM A4847; b: JGUM MB 67; c: MNHN Mar. 71; d: MNHN Mar. 18; e: MNHN Mar. 465; f: MNHN Mar. 359; g: AMNH 27807; (not available for illustration: AMNH 27809).

JGUM MB 67 (Figure 11b)is a well preserved male subadult skull which is also nearly complete, preserving right and left I1-2/, dI3/, P2/-M2/, with M3/ nearly completely erupted. The snout and nasals are complete, while only half the left orbit and none of the right orbit, the zygoma, nor posterior 4/5ths of the cranium are preserved. The preorbital fossa is only moderately long, extending anteriorly to a level above P3/ mesostyle. The fossa's dorsoventral dimensions, medial depth, peripheral rim morphology, shape and orientation are virtually identical to KNHM A4847. Neither the lacrimal sutures nor the infraorbital foramen are preserved. The snout is rather short and broad in its dimensions. The right and left I1/'s are fully erupted while P2/'s are just beginning to wear and dI3/'s are still present. The canines are partially erupted and distinctly male sized. The P1/'s have disappeared. The premolars are all erupted but are in an early stage of wear so that their fossette and pli caballin morphology are not yet visible. P2/'s protocone is elongate, while that of P3/ and P4/ show a distinct lingual flattening. The hypoglyph is deeply incised on P3/ and P4/. The molars are in a similarly early stage of wear and fossette plications are not yet visible. The pli caballins have also not yet appeared in the molars except in the M1/'s where they are weakly bifid. The hypoglyphs are deeply incised on M1/ and M2/, and have not yet appeared on M3/. The M1/ and M2/ protocones show lingual flattening, while M3/ is not yet worn enough to show any morphological details.

The four MNHN skull fragments show some degree of heterogeneity in their morphology. Two of the skulls are quite similar to one another: MNHN-RLB 18 (Figure 11d), a nearly complete old adult skull, including right and left I3/'s and Cs/ (right broken), right P2/-M2/ and left P2/-M3/, and lacking right and left I1/ and I2/, nasals, orbits and cranium; and MNHN 359 (Figs 11f and 12a), a nearly complete adult skull, including right and left canines and P2/-M3/, lacking only incisors and cranium. In both specimens the preorbital fossa is moderately long, anteroposteriorly oriented, dorsoventrally short, posterior pocketing is absent (although a distinct posterior rim is present), medial depth is slight (although greater in MNHN 359 than MNHN-RLB 18), anterior rim is absent, and ventral border is regular. Both specimens have the lacrimal placed well posterior to the fossa. The nasal notch is preserved in MNHN 359, and is slightly anterior to P2/. On MNHN 359 the cheek teeth have moderately complex plications of the pre- and postfossettes, pli caballin morphology is faintly double on P3/-M2/ (not visible on P2/ and M3/), P2/-P4/, and more deeply incised on M1/-M3/; protocone is elongate on all cheek teeth. P2/ anterostyle is elongate. MNHN 18's cheek teeth are in a very late stage of wear so that comparison with MNHN Mar. 359 is not really valid (see Table 10 for morphological scores).

MNHN Mar. 465 (Figures 11e and 12c)and Mar. 71 (Figures 11c and 12b) are adult skull fragments, the former a very old individual, the latter an adult. Both have right and left P2/-M3/, lacking snout, orbits and cranium. These individuals are morphologically the most extreme variants of *Hipparion* cf. *prostylum* in their reduction of the facial fossa. Like other individuals, they have egg-shaped anteroposteriorly directed preorbital fossae and exhibit no essential differences other than the reduced length, dorsoventral height, medial depth, expression of peripheral rim, and complete lack of fossa posterior pocketing. I choose to refer these to *Hipparion* cf. *prostylum*. In many regards, MNHN Mar. 465's facial fossa is similar to MMTT 13 specimens of *Hipparion campbelli* except for slightly greater development. Only MNHN 71 has cheek teeth well enough preserved to comment on the morphology. The pre- and postfossettes are moderately complex on all of the cheek teeth, pli caballins are faintly bifid on P3/, P4/, M1/, M3/, and single on P2/ and M2/; hypoglyphs are shallowly incised on P2-3/, moderately

deeply incised on P4/-M2/, and very deeply incised on M3/; protocone is elongate on all of the cheek teeth. These characteristics are atypical for *H. campbelli*.

The American Museum retains two skull fragments from Maragheh referrable to *Hipparion* cf. *prostylum*. AMNH 27807 (Figure 11g) is a skull fragment of an old adult individual with right P3/-M3/, left P4/-M3/, lacking snout, cranium, and orbit. AMNH 27809 is a subadult skull fragment with right P2/-M3/ and left P3/-M3/ (P4/ and M3/ emerging from crypts), lacking snout, anterior 1/2 of maxilla, right orbit and cranium. AMNH 27807 has a facial fossa morphology similar to KNHM A4847 including length, dorsoventral height, very slight degree of pocketing, moderate medial depth, faint anterior rim, and moderately expressed peripheral rim, and a nearly identically shaped and oriented fossa. The posteriormost portion's dorsoventral height is great compared to the anteriormost portion which tapers sharply anteriorly and is up-turned. The anteriormost portion appears to have undergone a superiorly directed rotation from a former, more primitive, anteroventral orientation. The facial morphology of AMNH 27809 differs from 27807 in that the fossa of the former is shorter anteroposteriorly, shallower medially, and has a less pronounced peripheral border outline. The cheek teeth of these individuals are either too unworn (AMNH 27809) or too worn (AMNH 27807) to preserve a definitive occlusal morphology.

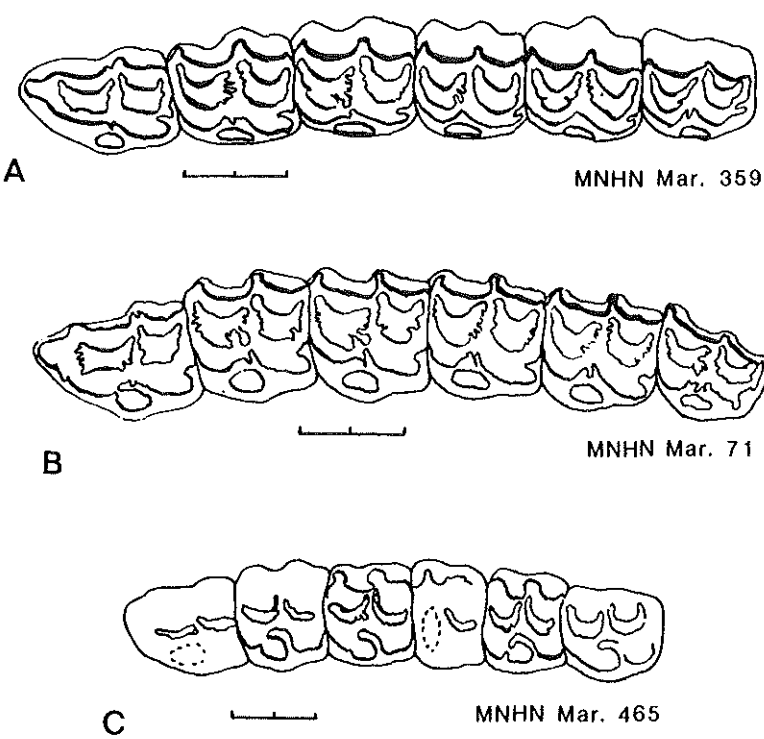


Fig. 12. — *Hipparion* cf. *prostylum*, maxillary cheek teeth occlusal view; a: MNHN 359; b: MNHN Mar. 71; c: MNHN 465.

Discussion:

The systematics of *Hipparion prostylum* is particularly complicated. M.O.Woodburne's (ms) recent review of this problem is excerpted below. The genotype *Hipparion* was named by Christol (1832) for material collected from Mt. Luberon. Christol noted that this horse was characterized (in part) by three toes on each foot and an isolated protocone. In 1849, Gervais reiterated these two characteristics and further mentioned the occurrence of additional stylids on lower deciduous molars. Gervais (1849) followed by designating three Mt. Luberon species, *H. prostylum, H. diplostylum,* and *H. mesostylum,* based on the position and frequency of accessory mandibular cheek tooth stylids. Later, Gervais (1859) reunited all of these species into *Hipparion prostylum,* recognizing the usual variability in these characters. Gaudry (1873), Osborn (1918), and Skinner and MacFadden (1977) have followed Gervais (1859) in referring all of the Mt. Luberon material to *Hipparion prostylum.* Woodburne (personal communication) has noted that Gaudry (1873, Pl. 6, Fig. 1) illustrated the first material from Mt. Luberon which shows the morphology of the face anterior to the orbit. This specimen has been re-illustrated by Skinner and MacFadden (1977, Fig. 3A). A formal type has not been designated by any of these authors. Sondaar (1974) stated that the specimen figured by Gervais (1859, Pl. 19, Fig. 2; a maxilla fragment with P3/-M2/) is the holotype of *Hipparion prostylum* (*sic*, a lectotype informally designated by Sondaar, 1974).

Sondaar (1974) noted that some postcranial elements indicate a rare second species of *Hipparion* at Mt. Luberon. Woodburne (ms.) also suggested the possibility of a rare second species of hipparionine horse at Mt. Luberon, which he characterized as having more robust metapodials and a slightly more complex plication of the upper and lower molars. Bernor and Hussain (1985) expanded the suite of measurements on the facial fossa complex originally used by Woodburne and Bernor (1980). Bernor and Hussain, 1985 have argued for the discrimination of BMNH M22617 from other Mt. Luberon and Group 3 horses of Woodburne and Bernor (1980) in the dorsoventral height and facial-maxillary crest dimensions. Additionally, this specimen is more primitive than other *Hipparion prostylum* specimens in its slightly greater complexity of the cheek tooth plications and persistently bifid pli caballins. These two character states seem to segregate BMNH M22617 from the remainder of the *Hipparion prostylum* sample.

BMNH M33603 (Figure 7J; Woodburne and Bernor, 1980) is the most complete, well preserved adult individual of the *Hipparion prostylum* sample known. It is a virtually complete skull with P2/-M3/, lacking the premaxilla and posteriormost cranium, and conformable in all essential details with the diagnosis given here. I hesitate to remove BMNH M26617 from the hypodigm of *Hipparion prostylum*, and elect instead to refer it to *Hipparion* aff. *prostylum.* I do this because it is derived in its facial morphology compared to the «stage-of-evolution» in derived Group 1 horses as exemplified by *Hipparion gettyi* (*i.e.* reduced posterior pocketing and less strongly outlined border all around the facial fossa). Also, I believe that BMNH M26617 represents a viable morphological predecessor of *Hipparion prostylum* (*sensu stricto*).

At Maragheh, *Hipparion prostylum* (*sensu lato*) is known from Tobien's collection and the Vienna specimen to occur at Kara Kend, our localities 1A, 1B, and 1C, or about -52 to -28 meters below loose chippings. This was perhaps the best collected of all the Maragheh vertebrate localities, and it is not unreasonable to presume that other paleontological expeditions collected fossils specimens there. Although Mecquenem did not report, and presumably did not record, precise locality information, he has stated (1908) that he collected fossils from two closely related levels all across the basin. The Group 3 horses in the MNHN collection include a range of facial morphology that overlaps samples of known Middle and Upper Maragheh specimens. Bernor *et al.*

(1979b), Campbell *et al.*, (1980), and Bernor *et al.* (1980) reported a potential three-part stage-of-evolution of hipparionine species at Maragheh: « *Hipparion* » *gettyi* - *Hipparion* sp. 4 (=*Hipparion prostylum* (*s.l.*) here) - *Hipparion dietrichi* (=*Hipparion campbelli* here). This viewpoint is changed here as a result of further systematic and phyletic studies of Eurasian hipparionines. The problems with the « stage-of-evolution » interpretations of this series include the uncertainly about Group 3 origins, the morphological limits of *Hipparion prostylum*, and the recognition that the Upper Maragheh hipparionine is a different species than *Hipparion dietrichi.*

Recently, MacFadden (1980) has reviewed *Hipparion prostylum* from the type locality at Mt. Luberon, and suggested a number of referrals of North American species to this genus and Group 3 hipparionines of Woodburne and Bernor (1980). In his hypodigm of *Hipparion s.s.*, MacFadden has included *Hipparion prostylum*, *Hipparion dietrichi*, and *Hipparion antelopinum* from the Old World, and « *Hipparion* » *tehonense* and « *Hipparion* » *forcei* of the New World to a single generic group which he has termed *Hipparion s.s.* MacFadden (1980) has argued that because the North American members of the hypodigm came from demonstrably older horizons than the Old World species, they represent the earliest members of *Hipparion s.s.*, and consequently that the Old World forms appear as the result of a second, early Turolian, emigration event from North America to Eurasia. Bernor and Hussain (1985) have argued that the reduction of the facial fossa in Old World and New World species of MacFadden's « *Hipparion s.s.* » potentially represents a phylogenetic convergence, and cite a substantial suite of differences in facial and maxillary dental features between the Old World and New World species.

The origin of Group 3 hipparionines remains equivocal. As cited above, « *Hipparion* » *gettyi* has some morphologic features which presage Group 3 hipparionines. These include its reduced size, preorbital bar length, dorsoventral height and facial maxillary crest measurements. The morphology and measurements of these features are within the range of variation seen in the type series of *Hipparion prostylum* from Mt. Luberon, and just slightly larger in the mean dimensions of those characters (Bernor and Hussain, 1985) than the Maragheh hypodigm of *Hipparion prostylum* (*s.l.*) cited here. « *Hipparion* » *gettyi* is clearly more primitive and Group 1-like in the greater posterior pocketing, length and medial depth of the fossa. The cheek teeth of *Hipparion gettyi* have greater pre- and postfossette complexity and more consistently bifid pli caballins than *Hipparion prostylum s.l.* However, the hypoglyphs of *Hipparion prostylum* s.l. from Mt. Luberon and Maragheh retain almost the same degree of incision in middle to later adult wear. Additionally, the orientation of the preorbital fossa in *Hipparion gettyi* would appear to presage to some degree the superior rotation seen in KNHM A4847 and AMNH 27807. Therefore, in its total morphologic pattern of size, the preorbital fossa, and dental morphology, *Hipparion gettyi* is the closest Group 1 species to *Hipparion prostylum* studied by this investigator to date.

I currently recognize four species of Group 3 hipparionines: *Hipparion prostylum s.l.*, with a geographic range including France, Greece, Iran and Afghanistan; *Hipparion antelopinum* from the Siwaliks, *Hipparion dietrichi* from Samos, Greece, and *Hipparion campbelli* from Iran. *Hipparion prostylum* (*s.l.*) has the greatest geographic distribution, and would appear to be the oldest species of bonafide Group 3 hipparionines. *Hipparion prostylum* has been used by Bernor *et al.* (1980) to correlate western European and eastern European Turolian age localities with Maragheh. The Middle Maragheh specimens (specifically KNHM A4847 and AMNH 27807) are the most primitive members of the Maragheh *Hipparion prostylum* (*s.l.*) hypodigm in facial and dental morphology, and compare closely with the Mt. Luberon, Saloniki, and Pikermi speci-

mens of *Hipparion prostylum* (Woodburne and Bernor, 1980; Bernor *et al.* 1980; Bernor and Hussain, 1985). The Kara Kend localities (UCR-MMTT 1A, 1B, and 1C),and hence Pikermi, Saloniki, and Mt. Luberon are calibrated by potassium-argon as being ca. 8.5-8 m.y. old (Campbell *et al.*, 1980).

Other specimens referrable to *Hipparion prostylum*, as well as all other Group 3 species show various degrees of facial fossa reduction, nasal retraction, cheek tooth plication, pli caballin simplification, and reduction of hypoglyph incision. *Hipparion antelopinum* (*sensu* MacFadden and Woodburne, 1980 and Bernor and Hussain, 1985) first appeared ca. 9-8 ma. (Barry *et al.*, 1982; MacFadden and Woodburne, 1982; Bernor and Hussain, 1985; Hussain and Bernor, 1983). The type series has a smaller body size, and a facial fossa reduced in its length, dorsoventral height, and posterior pocketing. The type series of *Hipparion antelopinum* has further derived cheek tooth morphology with simplified plications of the pre- and postfossettes, single pli caballins, rounded protocones, and less deeply incised hypoglyphs. An 8 million year first occurrence of this species in the Siwaliks (Bernor and Hussain, 1985) appears to be biochronologically congruous with its stage-of-evolution relative to the oldest known individuals of *Hipparion prostylum*.

Hipparion dietrichi and *Hipparion campbelli* similarly are progressively derived in facial and cheek tooth morphology. *Hipparion dietrichi*'s facial fossa is reduced to a distinct depression with no posterior or peripheral rim, and *Hipparion campbelli* has no depression, but a small, distinct posterior fossa rim. The nasal notches are slightly retracted to a level above P2/. The cheek teeth of both species are simplified compared to *Hipparion prostylum* in their reduced plication frequency of the pre- and postfossettes, single pli caballins, rounded protocones, and reduced hypoglyph incision. *Hipparion campbelli* is yet more derived than *Hipparion dietrichi* in its lengthened and narrowed snout. A 7 m.y. age for *Hipparion dietrichi* and *Hipparion campbelli* (Bernor *et al.*, 1980) is also congruous with the evolutionary interpretations cited here.

While the origin of Group 3 hipparionines is uncertain, the pattern and chronology of their distribution allow for some interesting evolutionary and zoogeographic interpretations. One could reasonably predict that a Group 3 hipparionine species first appeared in the northern Mediterranean and southwest Asian area *circa* 9 million years ago. This hypothetical species, and subsequent derivative of the Group 3 lineage, apparently evolved to a medium sized species with reduced to absent facial fossae, simplified cheek teeth, and elongate metapodials. The interval between 9 and 6 million years ago (or less?) time in these sectors of Eurasia has been characterized by Bernor (1983 and 1984) as a time of maximum transgression of so-called « Pontian » large mammal faunas. The distribution and biochronology of Group 3 hipparionines suggest that western Europe, the eastern Mediterranean, southwest Asia and the Siwaliks were not in continuous contact, but that episodic immigrations between these sectors occurred. If Group 3 hipparionines are monophyletic, as it currently appears, then one can perhaps deduce that a primitive Group 3 hipparionine species intermediate in morphology to « *Hipparion* » *gettyi*, and *Hipparion prostylum* appeared in the Mediterranean -southwest Asian area, transgressed the entire known range of Group 3 hipparionines in a relatively short interval of time, and subsequently evolved vicariantly, as distinct species. The facial fossa and cheek tooth structures of Group 3 species appear to have been destabalized from more primitive Group 1 patterns, and were progressively lost and/or simplified. The virtually continuous morphoclinal change in these features of the facial fossa make drawing species limits difficult, and in the case of Maragheh *Hipparion prostylum* (*s.l.*), the morphological limits used here are admittedly somewhat extended.

Hipparion campbelli sp. nov.

Hipparion dietrichi WEHRLI (1941), *sensu* Bernor (1978), p. 50, fig. 2; Bernor *et al.* (1979b), p. 94; Woodburne & Bernor (1980), p. 1344, figs. 7a, 7b; Campbell *et al.* (1980), p. 841; Bernor *et al.* (1980) (in part), p. 724, fig. 8; Bernor & Hussain (1985), p. 40, fig. 5c.

Etymology: named after Professor Bernard G. Campbell, Director of the Lake Rezaiyeh Expedition.
Holotype: A skull, MMTT 13/1342 (Figure 13a), an with associated lower jaw, UCR-MMTT 13/1341 (Figure 15a), preserved at the Department of Earth Sciences, University of California, Riverside.
Type Locality: Shollovend, Upper Maragheh, Iran.
Age: Late Turolian, ca. 7 m.y.

Referred Specimens: UCR-MMTT skull material referred to *Hipparion campbelli*: 13/1342 adult female skull with left and right P2/-M3/; 13/1343, juvenile skull with right and left I1-2/, dP1-4/, M1/; 13/1291, juvenile skull fragment with right and left dP2-4/, M1-2/ and left P1/; 13/1333, juvenile palate fragment with left dP3-4/, M1-2/ and right dP4/, M1-2/. UCR-MMTT mandible material associated with the above skulls referred to *Hipparion campbelli*: MMTT 13/1341, adult mandible with right and left I/1 - M/3; 13/1736, old adult mandible with right and left I/1 - M/3; 13/2353, juvenile mandible with right and left dP/2-4; 13/1289, juvenile mandible with right and left dP/2-4 and M/1. UCR-MMTT material referred to *Hipparion* cf. *campbelli*: 13/84, right M1/; 13/86, right P3 or 4/; 13/85, left M1/; 13/1224, right mandibular fragment with P/2-3; 13/1270, left M1/; 13/1347, juvenile palate with right and left dP2-3/; 13/1349, left M2/; 13/1392, right P2/; 13/1404, left maxillary cheek tooth; 13/1414, right mandibular cheek tooth; 13/1452, left dP4/ with erupting P4/; 13/1497, right M/1; 13/1500, dP3-4/; 13/1502, mandibular cheek tooth fragment; 13/1503, left P3/; 13/1516, right dP/4; 26/1572, right M2/; 13/1719, left dP3 or 4/; 13/1727, left M/2; 13/2353, right mandible with dP/2-4 and left mandible with dP/2-3; 13/2475, left maxillary fragment with P2-4/; 31/1900, left P2/ - M3/; 37/2427, left mandible with dP2-4/; 37/2096, left P2/; 37/2421, right P2/ unerupted; 13/1993, right P3/; 37/2088, right P2/; 13/2233, right M2/; 37/2068, right M1/; 31/1856, left M2/; 13/2264, right dP3/; 37/2392, left P/2-M/1; 37/2391, left P2/-M1/; 37/2756, right P2/; 37/2264, right dP3/; 37/2391, left P2/-M1/; 37/2556, right P2/; 37/2397, right P3/; 31/1894, right P3/.

Geographic Range: Iran.

Diagnosis:
An hipparionine species with a long slender snout; preorbital fossa markedly reduced, egg-shaped and anteroposteriorly directed, with a small vestigial posterior rim and slight medial depression; preorbital bar moderately long; lacrimal bone placed well posterior to the fossa; nasal notch placed above mesostyle of P2/; middle wear adult maxillary cheek teeth have moderately complex and very thinly banded plications of the pre- and postfossettes, pli caballins are single, hypoglyphs are moderately deeply incised; protocones are oval shaped; P2/ anterostyle is elongate; mandibles are elongate with a slender symphysial region; canines are placed immediately distal to I/3, mental foramen is placed approximately 1/2 the distance between I/3 and P/2; in middle adult wear P/2 anterostylid is elongate, ectoflexids do not separate metastylids and metaconids in the premolars, but do in the molars; pli caballinids and ectoparastylids are absent; linguaflexids are shallow; metaconids and metastylids are rounded; metapodials are slender and elongate.

Differential diagnosis: Refer to *H. prostylum* differential diagnosis.

Description:

Hipparion campbelli is the most abundantly represented hipparionine species in the Lake Rezaiyeh Expedition sample. The most complete specimen is the holotype, a female skull UCR-MMTT 13/1342. MMTT 13 has also yielded juvenile skulls of varying completeness (UCR-MMTT 13/1343, 13/1291, and 13/1333). A number of jaw fragments including UCR-MMTT 13/1341, 13/1289, 13/2352, and 13/1726 as well as isolated teeth of *Hipparion campbelli* are included within the UCR-MMTT sample. Postcranial material associated with *Hipparion campbelli* in bonafide quarry samples is not abundant, but substantial enough to show that this species had elongate and gracile metapodials.

The adult female skull, UCR-MMTT 13/1342 (Figures 13A, 14a), is moderate size and nearly complete except for the occipital portion of the cranium, the anteriormost nasal bones, left I3/ and C. The snout is long and has a narrow incisive border. The preorbital fossa is moderately distant from the orbit, occupies a position high on the maxilla, has a faint egg-shape and anteroposterior orientation, but is clearly vestigial; it is short anteroposteriorly and dorsoventrally, shallow medially, and has a very small vestigial posterior rim, and no posterior pocketing. There is no anterior rim, but rather the fossa is completely confluent anteriorly with the maxilla. The infraorbital foramen is large and located anteroventrally to the fossa and above the interstitial contact of P3/-P4/. The incisor region is very narrow and I3/ is not completely erupted. The right canine is small, and has a rounded peg-like morphology. The cheek teeth are elongate with the premolars somewhat larger than the molars. The P2/ has a well developed, long, and rounded anterostyle; the enamel plications are only faintly expressed but show mode-

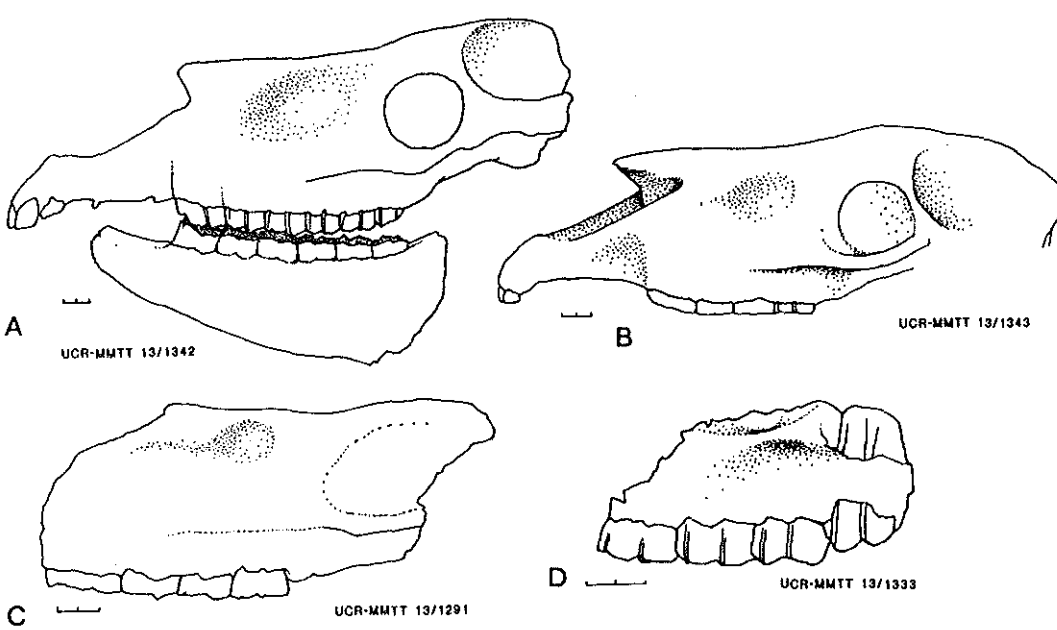


Fig. 13. — *Hipparion campbelli*, skulls, lateral view; a: UCR-MMTT 13/1342; b: UCR-MMTT 13/1343 (slightly obliquely oriented); c: UCR-MMTT 13/1291; d: UCR-MMTT 13/1333.

rate complexity; the hypoglyph is moderately incised; the protocone is oval shaped. P3/ and P4/ also have faintly delimited, thinly banded enamel plications; the posterior borders of the prefossettes are just touching the anterior borders of the postfossettes; the hypoglyphs are moderately deeply incised; the protocones are slightly oval, with each having a «vestigial» anterolabial enamel pli. The M1/ and M2/ are substantially smaller and more square-shaped; the fossette enamel plications are faintly expressed, but have a moderate amplitude; the hypoglyphs are moderately deeply incised; the protocones are round. M3/ is not completely erupted, with only its anterior one-half having begun to wear, and therefore the occlusal topography is not yet well expressed. Pli caballins are single on all of the cheek teeth.

UCR-MMTT 13/1343 (Figures 13b, 14b), is a juvenile female skull with right and left I1-2/, canine alveoli, dP2-4/, M1/; 13/ and M2/ are slightly exposed in their crypts. Both zygomatic arches are missing, but otherwise the skull is virtually complete. This specimen is very similar to the adult female skull, UCR-MMTT 13/1342, and was very closely associated with it in the Shollovend Quarry. The preorbital fossa is identical in morphology to UCR-MMTT 13/1342. The lacrimal is well delimited and clearly lies posterior to the preorbital fossa. The infraorbital foramen is large, located anteroventral to the preorbital fossa and above dP3/, whose lingual border is partially exposed in

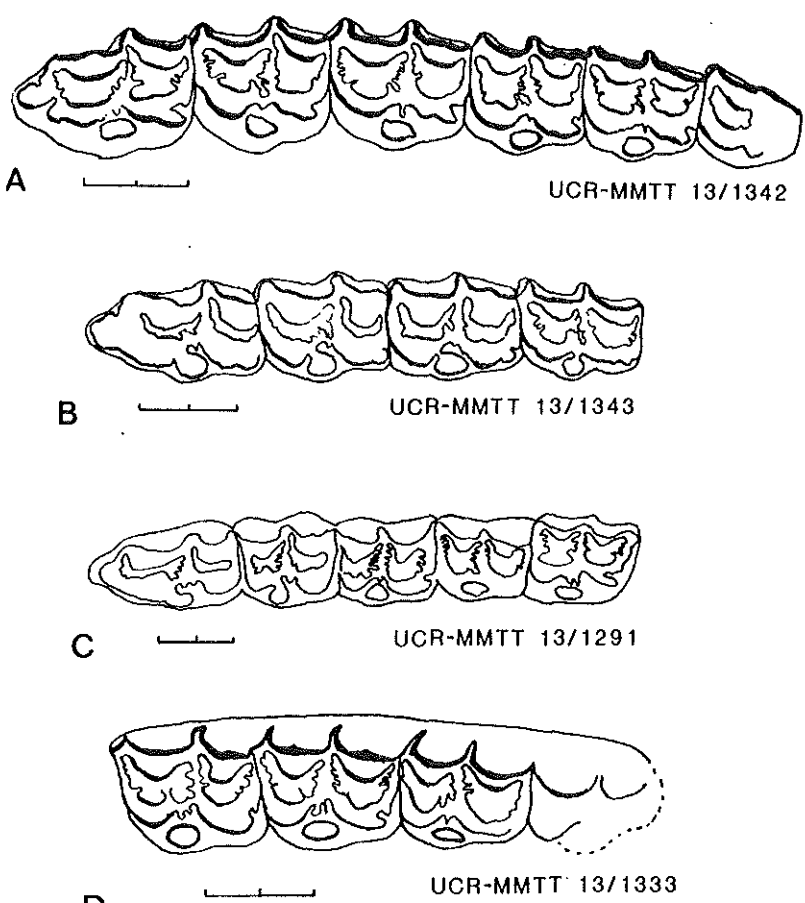


Fig. 14. — *Hipparion campbelli*, skulls, occlusal view; a: UCR-MMTT 13/1342; b: UCR-MMTT 13/1341; c: UCR-MMTT 13/1291; d: UCR-MMTT 13/1333.

the maxillary wall. The incisor region is very narrow and 13/ is still unerupted. The canines are missing, but their alveoli are perfectly preserved and suggest that these teeth were small and rounded. dP2-4/ are very worn and show no complexity of the pre- and postfossettes; the protocone is round on all of these and connected with the protoloph on dP2-3/; the hypocones are very shallowly incised. The anterostyle of dP2/ is as in the adult female, UCR-MMTT 13/1342. M1/ is too unworn to illustrate clear occlusal morphology.

A third specimen, UCR-MMTT 13/1291 (Figures 13c, 14c), from the Shollovend quarry, is a juvenile skull fragment with right and left dP2-4/ and M1/ present. The posterior border of the orbits, the cranium, nasals and premaxillary regions are absent. Details of the preorbital fossa are identical to other aformentioned crania of this species. DP2/'s pre- and postfossettes plications are simple due to their advanced stage of wear, whereas dP3-4/ and M1/ are moderately complex; all cheek teeth have single pli caballins; hypoglyph incisions are shallow on dP2-4/ and deep on M1/ (wear related differences); protocone is rounded on dP2-4/ while not yet worn on M1/.

UCR-MMTT 13/1333 (Figures 13d, 14d), also found in the Shollovend Quarry, is a palate fragment with left dP3-4/, M1-2/ and right dP4/, M1-2. This specimen is referred to *Hipparion campbelli* based principally on the size and length/width proportions of the teeth. DP3/ has a rounded protocone while dP4/'s protocone is more elongate and M1/ is elongate and flattened; these intra-individual differences can be largely attributed to their various stages of tooth wear. Pre- and postfossette plications of dP3-4/ are moderate and their pli caballins are complex; M1/'s pli caballin is clearly single; hypoglyph incisure is slight on dP3/ and moderate on dP4/. Occlusal topography is not well enough expressed yet on M1/ or M2/ (erupting) to illustrate details of the hypoglyph and fossette morphology.

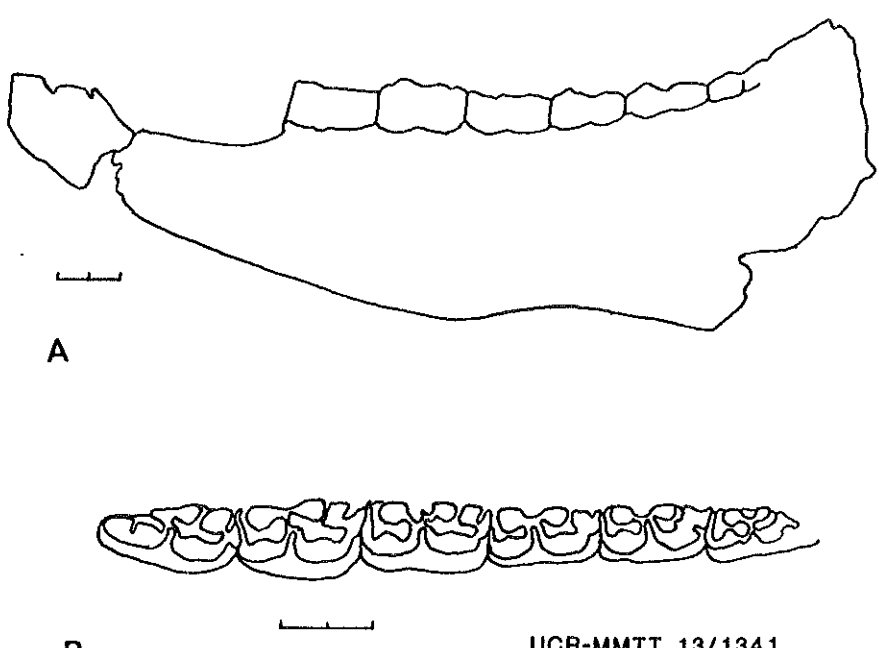


Fig. 15. — *Hipparion campbelli*, mandibular cheek teeth UCR-MMTT 13/1341; a: lateral view; b: occlusal view.

A number of mandibles were closely associated with the skulls and skull fragments in the Shollovend quarry. Associations cited here have been determined by proximity in the quarry, comparable eruption and closeness of occlusion between maxillary and mandibular dentitions. UCR-MMTT associations are interpreted to be as follows: mandible 13/1341 (Figures 15a,b) with skull 13/1342; mandible 13/1289 with skull 13/1333; mandible 13/2353 with palate 13/1291. A fourth mandible, 13/1736, belongs to an old individual.

UCR-MMTT 13/1341 is a nearly complete mandible missing the superior 2/3rds of the ascending ramus; also, the mandible is broken just posterior to the canines. As with the maxillary dentition, 13/ and M3/ are still not completely erupted. The diastema is elongate, the canines are small, rounded, and peglike, and placed immediately distal to I/3. The premolars are quite elongate and substantially larger than the molars. P/2 mirrors P2/ in its strongly extended and anteriorly rounded anterostylid. The mental foramen is slightly closer to P/2 than I/3; P/2's anterostylid is elongate and its metastylid is larger than the metaconid; ectoflexid does not separate metastylid and metaconid; pli caballinid is absent; ectoparastylid is absent; linguaflexid is shallow and broadly opened buccally; metaconid and metastylid have a slightly angular contour. P/3 and P/4 are identical in occlusal morphology to P/2 except that the metastylid and metaconid are rounded. M/1-3 show serial size reduction in both length and width measurements, and they differ from P/2-4 in that the metastylid and metaconid are separated by the ectoflexid. In details of pli caballinid, ectoparastylid, linguaflexid and metaconid/metastylid morphology, M/1-3 are identical to P/3-4.

UCR-MMTT 13/2353 is a juvenile anterior mandible with left dP/2-3 and right dP/2-4. Although not entirely preserved, snout length would appear to be elongate; the teeth are highly worn, but preserve some morphological features. DP/2's anterostylid is elongate; metastylid is approximately equal in size to the metaconid; ectoflexid does not separate metastylid and metaconid; pli caballinid is rudimentary to absent; ectoparastylids are round shaped; dP/3 and dP/4 have an occlusal morphology identical to dP/2; ectometastylids occur on all of the premolars.

UCR-MMTT 13/1289 is a juvenile mandible fragment with left dP/2-4, M/1 and M/2 (erupting) and right dP/2-4, M/1. DP/2 has an elongate anterostylid; metastylid is slightly smaller than metaconid; ectoflexid does not separate the metastylid and metaconid; pli caballinid is absent, ectoparastylid is absent; linguaflexid is shallow; metaconid and metastylid are rounded. DP/3 is similar in occlusal morphology to dP/2 except that it has a large ectoparastylid. DP/4 differs from dP/2 and 3 in that the ectoflexid separates metastylid and metaconid and the linguaflexid is U-shaped; as seen in dP/3, the ectoparastylid is present. All of the dP/'s have prominent ectometastylids buccally. M/1 is just beginning to wear and its morphology includes an ectoflexid which does not yet separate the metaconid and metastylid; it has a simple pli caballinid; ectoparastylid is absent; linguaflexid is U-shaped; metaconid and metastylid are angular-shaped.

UCR-MMTT 13/1736 is a mandible of a very old adult which includes right and left I/1 - I/3, canine roots and P/2 - M/3. The cheek teeth are very worn, but some morphological features are preserved. The canine is placed just posterior to I/3, the snout is elongate and slender, the mental foramen is intermediate in position between I/3 and P/2. P/2 anterostylid is shortened due to wear; the metastylid is larger than the metaconid; ectoflexid does not separate metastylid and metaconid; pli caballinid is absent; ectoparastylid is absent; linguaflexid is shallow; metaconid and metastylid are angular shaped. P/3 and P/4 are identical in morphology to P/2 except for the linguaflexids which are V-shaped. M/1 resembles P/3 and P/4 in morphology, differing only in

that the ectoflexid separates the metastylid and metaconid, and the linguaflexid is V-shaped. M/2 differs from M/1 only in that the linguaflexid is U-shaped; M/3 does not preserve the linguaflexid on either side of the mandible.

Discussion:

Hipparion campbelli has previously been referred to *Hipparion dietrichi* by Bernor (1978), Bernor *et al.* (1979), Woodburne and Bernor (1980), Campbell *et al.* (1980); and *Hipparion* cf. *dietrichi* by Bernor *et al.* (1980) and Bernor and Hussain (1985). The known stratigraphic range of this species is restricted to the uppermost Maragheh horizons, although it is possible it could occur somewhat lower in the section. The Shollovend quarry specimens are recognized as a species distinct from *Hipparion dietrichi* principally because of the more slender elongate snout, and a preorbital fossa which is more restricted, egg-shaped, and consistently shallower in its medial dimension. *Hipparion campbelli* also differs consistently from *Hipparion dietrichi* in having a shallower, more restricted facial fossa depression.. Definitive data on cheek tooth morphology is not currently available for *Hipparion dietrichi*, making comparisons with *Hipparion campbelli* impossible. As cited earlier, *Hipparion campbelli* most probably evolved from a local population of *Hipparion prostylum* (*s.l.*). Bernor *et al.* (1980) once suggested that *Hipparion dietrichi* (=*Hipparion dietrichi* from Samos + *Hipparion campbelli* from Upper Maragheh) might have been ancestral to the East African late Miocene hipparionine, « *Hipparion* » *turkanense*, because of their mutual loss of the facial fossa. Bernor and Hussain (1985) have since presented evidence for facial fossa loss in multiple lineages of Old World and New World hipparionines and consequently rejected the purported phylogenetic relationship between advanced Group 3 horses and « *Hipparion* » *turkanense*. Rather, the authors have suggested that « *Hipparion* » *turkanense* may be an advanced species of their « *Cormohipparion* » (*Sivalhippus*) group.

« *Hipparion* » aff. *moldavicum*

Hipparion mediterraneum ROTH & WAGNER (1855); *sensu* Forsten (1968) (in part), p. 40.
Hipparion species 1, Bernor (1978), fig. 3a; Bernor *et al.* (1979b), p. 94.
Hipparion species 2, Bernor (1978), fig. 3b.
Hipparion mediterraneum, Campbell *et al.* (1980), p. 841; Bernor *et al.* (1980), p. 728, fig. 8; Bernor & Hussain (1985), p. 39, fig. 4b.
« *Hipparion* » sp. Gp. 2, Woodburne & Bernor (1980), p. 1329, figs. 6a-d.

Holotype: P.I.N. n° 1256-3639, Academy of Sciences Paleontological Institute of the U.S.S.R., figured by Gromova, 1952, Figures 1-3.
Type Locality: Tarkalia, Republic of Moldavia, District of Benderi, U.S.S.R.
Age: Meotian (= Medial Turolian, MN 12, of Mein, 1975, 1979).

Referred Specimens (Maragheh only): BMNH M3924, skull fragment, BMNH M3925, skull fragment; KNHM A4848, left maxillary fragment with P2/ - M3/; KNHM-RLB 8403, right maxillary fragment with P2/ - M3/; KNHM 8404, left maxillary fragment with dP2-4/, M1/; MNHN-RLB 7914, skull fragment; MNHN-RLB 7915, skull fragment; MNHN-RLB 8001, skull fragment; MNHN-RLB 8002, skull fragment; MNHN-RLB 8003, skull fragment; MNHN-RLB 8004, skull fragment.

Geographic range: western U.S.S.R. and southwest Asia.

Diagnosis (Translated from Gromova, 1952: 154-155):

Medium size, basal length of cranium = 271-273 mm.; length of cheek teeth = 121-141 mm.; muzzle elongate; index of orbital-facial length = 67; index of anatomical axes = 214.6. Frontals narrow, width index = about 38.2; fronto-basal index = 261.4 mm. Dental series short; index of length to basal width = 33.5; to the premolars, 41.2 - 46.8; diastemato-dentary index = 66.1 - 28.9. Upper molars large relative to premolars; molar-premolar index = 82.4-91. A single preorbital fossa, very long and elevated, index of position relative to orbit =26.6 - 37.8; relative to the facial crest, 16.7 - 64.3. Nasal notch moderately deep, its posterior border is at the level of, or slightly anterior to, the anterior border of P2/. The diastema is well developed, its index is 60.4 - 77. Protocone is short and wide, length index of P3/ - M2/ in little or moderately worn individuals is 20.7 - 37.5, in very worn teeth, 25 - 43.3; index of form in the same conditions 42.8 - 78.3 and 57.1 - 92.3. Enamel plication is moderate in upper cheek teeth, on the posterior wall of the prefossette and anterior wall of the postfossette; when P3,4/ and M1,2/ are very worn or moderately worn they have 3.5 - 6.5 to 9.5 plis. Cheek teeth have a height-length index on P3,4/ of 156 - 195.5; on M1-3, 204.3 - 232.5; on P/3-4 and M/1-2 159 - 200. A double knot of the *Hipparion* type. External depression in lower cheek teeth deep, complementary elements little developed. The islette occupies the anterior portion of the 13/ crown. The postcranials are gracile and elongate; index of width in the lower articulation relative to the width of MC III, 14.5 - 16.3; to the length of MT III, 12.4 - 14.2. Metapodial length relative to width: MT/T = 74.4. Lateral digits are moderately developed; moderate indicies of lower extremities diameters MC II and IV to MC III, 75.8 - MT II and IV to MT III, 66.8; moderate indicies of length of the first phalanges of the lateral digits to those of the anterior median digits, 58.2; posterior 53.8. Extremities recurved to the level of articulations; moderate index of the pisiform bone 114.3 mm.; anterior 3rd phalanx narrow; length-width index of posterior 3rd phalanx 71.4 - 86.6.

Emended diagnosis: A medium sized hipparionine with an elongate snout. Preorbital fossa single, subtriangular shaped, anteroposteriorly oriented and elongate, dorsoventrally and medially deep, with slight posterior pocketing and a distinct anterior rim, and strongly expressed peripheral outline. The preorbital bar is short. The lacrimal bone invades the posterior edge of the preorbital fossa. The nasal notch is incised at a level either just above the anterior edge of P2/, or slightly anterior to it. Middle wear adult cheek teeth have moderately complex plications of the pre- and postfossettes, protocones are generally rounded, but show lingual flattening in some individuals. P2/ anterostyle is usually elongate, but can be short and rounded in some individuals.

Differential diagnosis: The « *Hipparion* » *moldavicum* type series described and figured by Gromova (1952, not seen by Bernor) differs from other Group 2 horses (*sensu* Bernor and Hussain, 1985) as follows:

1/ It differs slightly from « *Hipparion* » aff. *moldavicum* from Maragheh (described below) in apparently having a more elongate snout (only one Maragheh specimen, BMNH M3924, has the snout preserved), a slightly greater range of variation for fossa length (68-85 mm. *versus* 63.5-79.9 mm.), dorsoventral height (41-60 mm. *versus* 42.0 - 54.9 mm.), preorbital bar length (20.5-28 mm. *versus* 23.6-29.8 mm.) and facial maxillary crest (10-28.5 mm. *versus* 12.2-21.5 mm.). However, the Maragheh specimens are closest to the type series of « *Hipparion* » *moldavicum* in these measurements, the presence of a single large anteroventrally oriented fossa, absence of an intermediate fossa between the preorbital and buccinator fossae, degree of nasal notch retraction, cheek tooth plication amplitude (as described by Gromova, 1952), and likely postcranial morphology.

2/ It differs from the Pikermi species « *Hipparion* » *mediterraneum* (Bernor and Hussain, 1985) in greater dorsoventral height of the preorbital fossa; the preorbital bar and facial maxillary crest measurements overlap the Pikermi horse's range, but include individuals who have longer dimensions; there is no intermediate fossa.

3/ It differs from « *Hipparion* » *proboscideum* from Samos in being consistently smaller; metrically, the preorbital bar overlaps, but has individuals which usually have longer absolute size dimensions of P.O.B.; the nasal notch is significantly less retracted (above P2/ *versus* above P3/); it lacks a distinctive intermediate fossa between the preorbital and buccinator fossae. However, the type series of « *Hipparion* » *moldavicum* and « *Hipparion* » *proboscideum* share close similarities in their lengthened snout, extreme fossa length and dorsoventral height, and low range of facial-maxillary crest measurements.

Description:

There are a number of moderately well preserved partial skulls of « *Hipparion* » *moldavicum* from Maragheh preserved in the British Museum (Nat. Hist.), London, the Kaiserlisches Naturhistorisches Museum, Vienna, and the Museum National d'Histoire Naturelle, Paris. BMNH M3924 (Figure 16a, 17a), the most completely preserved individual of this suite, is a moderate sized sub-adult male skull with C's (erupting), and P2/ - M2/ (right M3/ erupting). Other than the incisor crowns, a portion of the nasals, posterior orbits, zygomatic arches, and a majority of the cranium, this specimen is complete. The preorbital fossa is long, subtriangular shaped, anteroposteriorly oriented, dorsoventrally deep, slightly pocketed posteriorly, medially very deep with distinct, concentrically shaped pits, has an anterior rim and moderately strongly expressed peripheral rim. The preorbital bar is short and the lacrimal bone clearly invades the posterior rim of the fossa. The nasal notch is retracted to a level above P2/ parastyle. The infraorbital foramen is placed above the posterior portion of P3/ and just inferior to the anteroventral rim of the fossa. The cheek teeth are only moderately high crowned, and the left cheek tooth series has been sectioned to show occlusal morphology in a later, more mature stage of wear. All of the cheek teeth have rather complex, thinly banded plications of the pre- and postfossettes, irregularly shaped bifid pli caballins (P2/ - M1/), hypoglyphs are deeply (P2/ - P4/) to moderately deeply (M1/) incised, protocones are rounded to elongate shaped (P2/ - M2/); P2/ anterostyle is short and rounded. The muzzle is moderate length and slender in proportion. Another BMNH specimen, M3925 is a very poorly preserved adult skull fragment with left M3/ that preserves a similar facial fossa morphology, but is otherwise too poorly preserved to be characterized.

Four skull fragments of « *Hipparion* » *moldavicum* are preserved by the Kaiserlisches Naturhistorisches Museum, Vienna, including: KNHM-RLB 8402, KNHM A4848, KNHM-RLB 8403, KNHM-RLB 8404. KNHM-RLB 8402 was collected from Ketschawa (=our localities 1A, 1B, 1 from Middle Maragheh) and is a palate fragment of a very old adult containing only right P2/ - M3/, right preorbital bar and the ventral 2/3rds of the facial fossa. The fossa is large, subtriangular shaped and anteroposteriorly oriented, anteroposteriorly elongate, dorsoventrally deep, slightly pocketed posteriorly, medially deep, anterior rim has been lost as has the majority of the peripheral rim. The preorbital bar is distinctly short and the lacrimal bone can be seen invading the posterior rim of the fossa. The cheek teeth are very worn simplifying fossette and pli caballin morphology. Therefore, fossettes have become simple in their plication amplitude on P2/ - M1/, while remaining moderate on M2/ - M3/. Pli caballin morphology is single on P2/ - P4/, and M2/, double on M3/, and not preserved on M1/. Hypoglyphs are

obliterated on P2/ - P4/, shallowly incised on M1/ - M2/, and moderately deeply incised on M3/. P2/ anterostyle is elongate.

KNHM A4848 (Figure 16b) was collected from Zad Baschi and is a maxillary fragment of a very old adult with left P2/ - M3/, right P3/, P4/ - M3/ and the ventral border of the left facial fossa. Enough of the ventral portion of the facial fossa is present to reveal that it was dorsoventrally deep (closely approaches the facial maxillary crest),

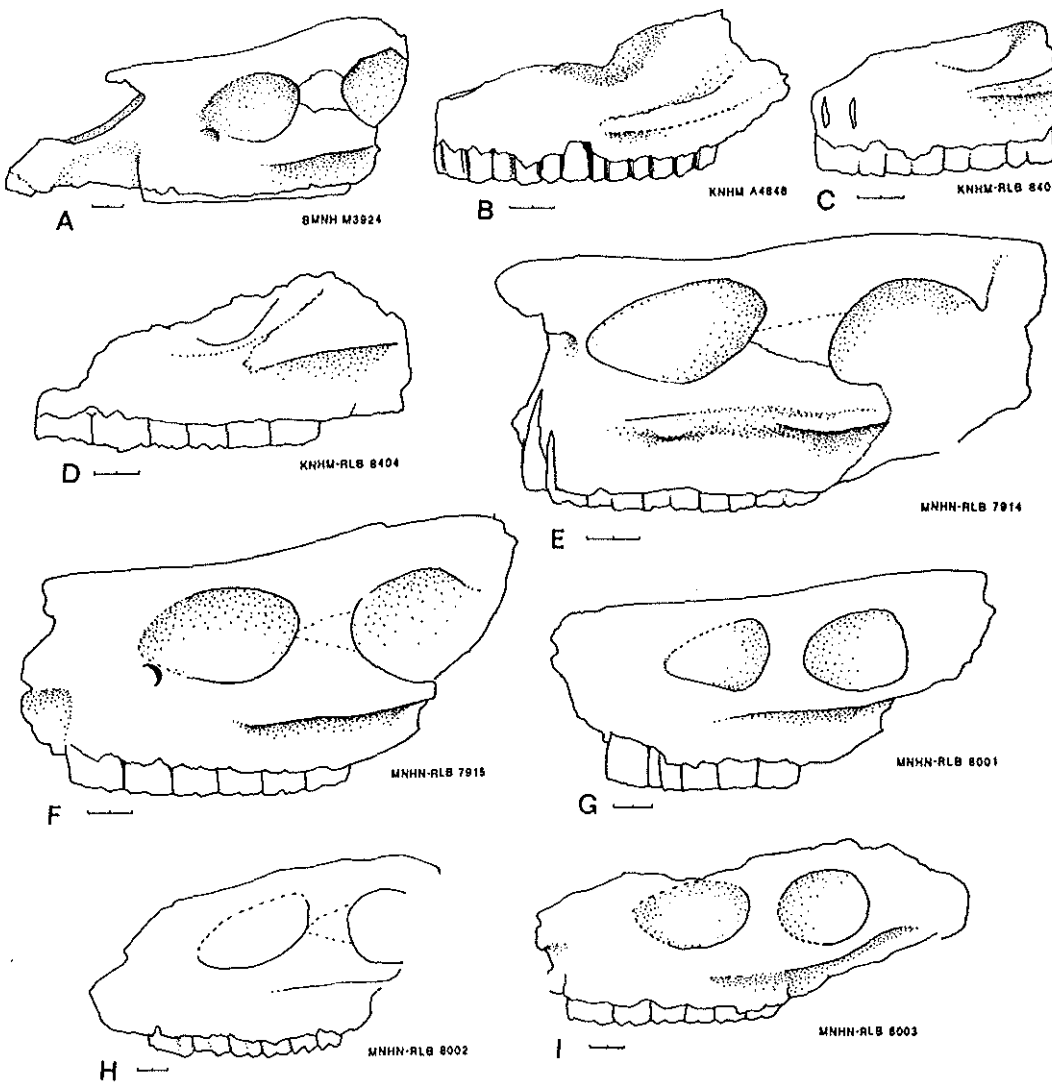


Fig. 16. — «*Hipparion*» aff. *moldavicum*, skulls, lateral view; a: BMNH M3924; b: KNHM A4848; c: KNHM-RLB 8403; d: KNHM-RLB 8404; e: MNHM-RLB 7914; f: MNHN-RLB 7915; g: MNHN-RLB 8001; h: MNHN-RLB 8002; i: MNHN-RLB 8003; (unfigured specimens: BMNH M3925, MNHN-RLB 8004).

it was slightly pocketed posteriorly, and was medially deep. The cheek teeth are as worn as in KNHM-RLB 8402, and have similarly obliterated details of the fossettes and pli caballins. The pre- and post fossettes of P2/ - M1/ retain no topographic details while M2-3/ show moderate complexity. The pli caballin is completely worn on P2/, while being single on P3/ - M3/. The hypoglyph is absent on P2/ - P4/, shallowly incised on M1/ and M2/, and moderately deeply incised on M3/. The protocone is round on all of the cheek teeth. The P2/ anterostyle is elongate.

KNHM-RLB 8403 (Figure 16c) was collected from Ketschawa and is an older adult right maxilla fragment with P2/ - M3/ and the ventral border of the facial fossa. Once again enough of the ventral portion of the facial fossa is present to reveal that it was dorsoventrally deep (closely approaches the facial maxillary crest), it was slightly pocketed posteriorly, and was medially deep. Details of the cheek teeth are better preserved than the previous two KNHM specimens. Pre- and postfossettes are thinly banded and moderately complex on all cheek teeth. Pli caballins are double on P3/ - M2/, single on M3/, and not preserved on P2/. Hypoglyphs are moderately deeply incised on P2/ and M3/ and shallowly incised on P3/ - M2/. The protocone is rounded on P2/ - M3/. The P2/ anterostyle is elongate.

KNHM-RLB 8404 (Figure 16d) was also collected from Ketschawa and is a juvenile left maxilla fragment with dP2-4/, M1/ (just erupted and unworn). The facial fossa is preserved just as in KNHM-RLB 8403 and has the same morphological attributes. Pre- and postfossette plications are preserved well enough on dP2-4/ to reveal a thinly banded and moderately complex morphology. Only dP3/'s pli caballin is preserved, and it is double. The hypoglyph is shallowly incised on dP2-4/ and not yet present on M1/ (due to early stage of wear). The protocone is rounded on dP2-3/ and elongate on dP4/ - M1/. The P2/ anterostyle is elongate.

An old adult mandible from Zad Baschi in the Vienna collection, KNHM A4845, compares closely in size, occlusion and preservation mottling to the left maxillary fragment KNHM A4848. KNHM A4845 consists of a right fragmentary mandible with P/2 - M/3, and a left mandible fragment with P/2 - M/1. This specimen is important because it is the only known Maragheh mandible which can be referred with reasonable certainly to « *Hipparion* » aff. *moldavicum*. In this specimen the cheek teeth are generally large and rather square in occlusal outline. The premolar ectoflexids do not separate metastylid/metaconid, pli caballinids are not present, ectoparastylids are absent on P/2-3 and present on P/4, linguaflexid is shallow on P/2 and V-shaped on P/3-4, metaconids/metastylids are round on all of the premolars, all molar ectoflexids separate metaconids and metastylids, pli caballinids are absent on all molars, ectoparastylids are absent on M/1 and present on M/3, linguaflexids are U-shaped on all molars, and metaconids/metastylids are angular on all molars. P/2 anterostylid is elongate. The cheek teeth of the smaller Group 2 species « *Hipparion* » *matthewi* contrast strongly with these in their smaller size, more labio-lingually compressed cheek tooth morphology, which consistently lack ectoparastylids and have more consistently rounded metaconids/metastylids (see description below of « *Hipparion* » *matthewi*).

There are five relatively well preserved skulls of « *Hipparion* » aff. *moldavicum* in the Museum National d'Histoire Naturelle, Paris, all unnumbered. Bernor and Hussain (1985) have referred these to the following numbers: MNHN-RLB 7914, 7915, 8101, 8102, and 8103. MNHN-RLB 7914 (Figures 16e and 17b) is a large adult individual skull lacking snout and cranium, and with a right and left P3/ - M3/ preserved. The fossa is large, subtriangular shaped, anteroposteriorly long, dorsoventrally deep, slightly pocketed posteriorly, medially deep, has a distinct anterior rim, and a strongly expressed peripheral border. The preorbital bar is short and the lacrimal bone invades the posterior rim of

the fossa. The cheek teeth have relatively complex, thinly banded plications of the pre- and postfossettes, the pli caballins are single on P3/ - M1/ and faintly double on M2-3/, hypoglyphs are shallowly incised on P3-4/ and moderately deeply incised on M1-3/; P3/ protocone is rounded while P4/ - M3/ protocone is lingually flattened.

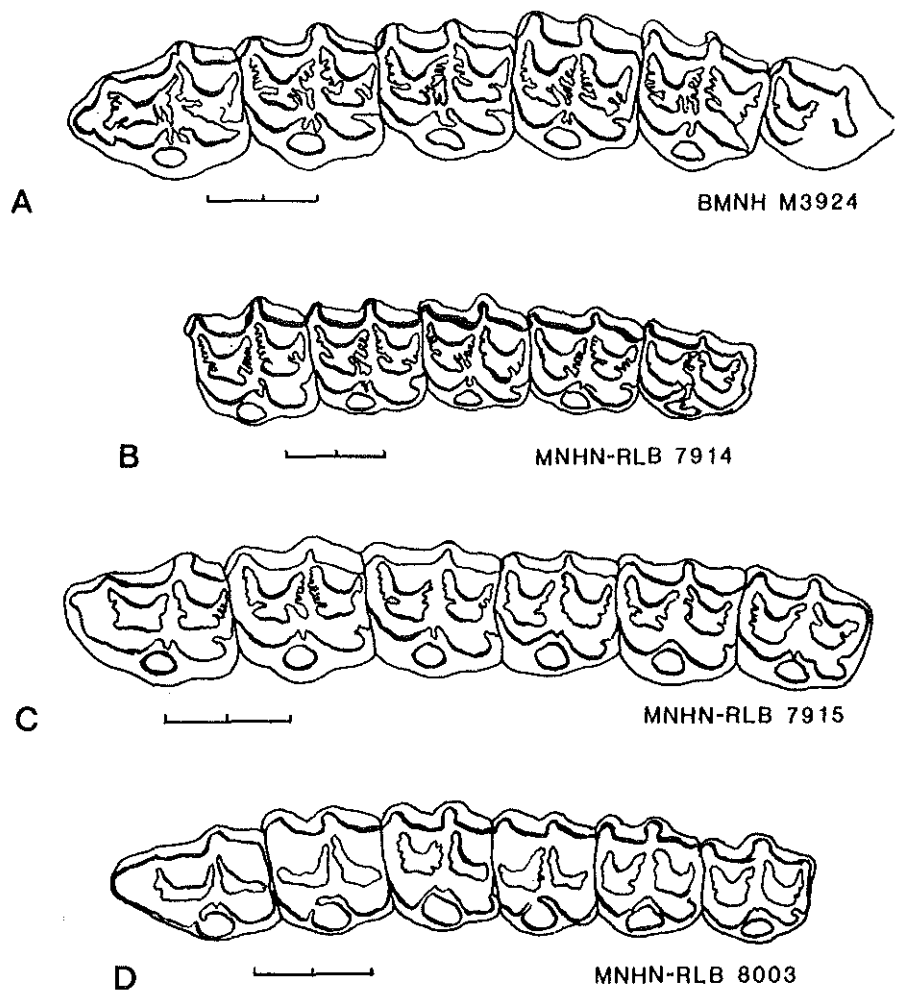


Fig. 17. — « *Hipparion* » aff. *moldavicum*, maxillary cheek teeth occlusal view; a: BMNH M3924 (sectioned cheek teeth); b: MNHN-RLB 7914; c: MNHN-RLB 7915; d: MNHN-RLB 8003.

MNHN-RLB 7915 (Figures 16f and 17c) is a smaller adult fragment, lacking snout, cranium and the right one-half of the maxilla and orbit, but preserving the entire left cheek tooth dentition, nasal bone, and all but the most posterior aspect of the orbit. The preorbital fossa is virtually identical in its morphology and dimensions to MNHN-RLB

7914; the preorbital bar is slightly shorter; the nasal notch is less retracted, to a level just anterior to P2/. The cheek teeth are less worn than MNHN-RLB 7914, but show approximately the same degree of plication complexity and pli caballin morphology. The protocones are distinctly more rounded than MNHN-RLB 7914, and hypoglyph incision is uniformly moderate. MNHN-RLB 8001, 8002, 8003 are preserved similarly to MNHN-RLB 7914; 8001 has right and left P3/ - M3/; 8002 (MNHN 466) has right and left P2/ - M3/; 8003 has right and left P2/ - M3/. Their facial fossae are all quite similar to MNHN-RLB 7914 and 7915 in morphology, and size. The nasal notches are not preserved; the preorbital bars all have the same dimensions as the other Maragheh specimens referred to this taxon; the lacrimal bone of 8001 is as seen in MNHN-RLB 7914 and 7915. MNHN-RLB 8001(Figure 16g), 8002(Figure 16h), and 8003 (Figures 16i and 17d) are all old adult individuals with details of the cheek teeth too worn for valid morphological comparison.

This suite of fossils exhibits a moderate range of variation in cheek tooth size. The relevant measurements in Tables 15 and 16 may underemphasize this observation because the specimens with larger, more squarely shaped teeth (MNHN-RLB 7914, 8001, 8002, 8003, 8004, KNHM-RLB 8402, 8403, 8404 and KNHM A4848 and A4845) are all in relatively late stages of wear while the smaller specimens (BMNH M3924 and MNHN 7915) are young adults in an early stage of wear. It is possible that these two size groupings, which are admittedly not well differentiated, presage a local evolutionary divergence in the Maragheh Group 2 hipparionines.

Discussion:

Woodburne and Bernor (1980) first recognized that Group 2 hipparionines constituted a superspecific group. Later, Woodburne *et al.* (1981) suggested that Group 1 and Group 2 hipparionines may have been derived as distinct lineages from a North American late Barstovian-early Clarendonian age species close to *Cormohipparion sphenodus*. They cited the shared-derived characteristic of a subtriangular shaped, anteroventrally oriented preorbital fossa found in all of these hipparionines. The authors further posited that these two groups became increasingly distinct from one another by Group 1 becoming larger, increasing its cheek tooth fossette complexity, attaining a wider preorbital bar, and diminishing the strength of the anterior rim. Group 2, they believed, retained a relatively smaller size and lesser dental complexity. The length of the preorbital bar was reduced, and the preorbital fossa migrated more posteriorly.

Bernor and Hussain (1985) disagreed with this interpretation and argued for a direct derivation of Group 2 horses from a Group 1 species morphologically very close to «*Hipparion*» *primigenium*. They reported the presence of complex plications and multiple pli caballins in middle adult wear cheek teeth of *Hipparion proboscideum* and *Hipparion mediterraneum*. Furthermore, they reported that Group 2 hipparionines show close similarities to *Hipparion primigenium* in preorbital fossa size, shape, all metric dimensions, orientation, strong development of its anterior rim, and large dorsoventral height relative to the facial maxillary crest dimensions. Bernor and Hussain (1985) considered these to be synapomorphies between Groups 1 and 2 Old World hipparionines, and not necessarily related (in toto) to *Cormohipparion sphenodus*.

Group 2 hipparionines are united, and are morphologically derived relative to Group 1 horses, in the markedly reduced posterior pocketing of the facial fossa, shortened preorbital bar with lacrimal invading the posterior border of the fossa, somewhat reduced cheek tooth ornamentation (but still substantially more complex

than seen in *Cormohipparion sphenodus*), less deeply incised hypoglyphs, and rounding of protocones. *Hipparion moldavicum* from Tarkalia, *Hipparion* aff. *moldavicum* from Maragheh, and *Hipparion mediterraneum* from Pikermi, are close to one another morphologically, but differ in some distinct morphological details. *Hipparion proboscideum* is quite derived in its morphology compared to these other taxa.

In many regards, the MNHN-RLB specimens are the least evolutionarily derived Group 2 hipparionines. In these specimens, the skull size is reduced relative to «*Hipparion*» *primigenium*, the preorbital bar shows a relatively high range of variability in its length (30-24 mm.), compared to other Group 2 species. However, preorbital bar length is markedly reduced compared to all Group 1 species. The fossa is subtriangular shaped as in «*Hipparion*» *primigenium*, but its anterior aspect has undergone a slight upward rotation compared to the more primitive dorsoventral one. The nasal notch is either anterior to, or above the anterior one-half of P2/. The cheek teeth are less complex, have rounded protocones and less incised hypoglyphs than Group 1 species, but retain bifid pli caballins in some individuals, and have moderately complex plications of the pre- and postfossettes. Postcrania of the Maragheh sample can not be assigned with any reasonable degree of certainty because of the lack of reported quarry associations.

«*Hipparion*» aff. *moldavicum* is closely allied with the type series of *Hipparion moldavicum* in the similarly slight degree of nasal notch retraction, dimensions of the preorbital fossa, apparent lack of an intermediate fossa, cheek tooth morphology and dimensions. The type series of *Hipparion moldavicum* have very long snouts, which may foreshadow «*Hipparion*» *proboscideum*. None of the MNHN-RLB specimens have a preserved snout, making comparisons impossible. However, BMNH M3924 has the snout preserved, and it is substantially shorter and narrower than *Hipparion moldavicum*, and clearly can not be included in that species. The type series of *Hipparion moldavicum* shows a similar range of variability in preorbital bar length to the Maragheh sample.

The Pikermi Group 2 hipparionine species has been referred to *Hipparion mediterraneum* by Woodburne and Bernor (1980), Bernor *et al.* (1980), and Bernor and Hussain (1985). Wagner (1850: Figure IX) originally figured a specimen from Pikermi with this morphology, and referred it to *Equus primigenium*. Roth and Wagner (1855:438) later described this specimen and referred it to *Hipparion gracile* var. *mediterraneum*. Later, Hensel (1860) recognized this Pikermi hipparionine as a distinct species, *Hipparion mediterraneum*. Unfortunately the holotype of *Hipparion mediterraneum* can not be located, and is believed to have been destroyed by allied bombing of the Munich Museum during World War II. A very fine skull with articulated mandible from Pikermi, seemingly identical in morphology to the figured holotype, currently exists in the Museum National d'Histoire Naturelle, MNHN Pik. 259. This specimen was figured by Gaudry (1867: Pl. 35, Figure 1) and referred to *Hipparion gracile*. I believe that it is the most suitable candidate for a neotype of «*Hipparion*» *mediterraneum*.

The Pikermi type series of *Hipparion mediterraneum* differs from *Hipparion moldavicum* and *Hipparion* aff. *moldavicum* in its slightly greater retraction of the nasal notch, and presence of a distinct intermediate fossa. Gromova (1952) also reports that the Pikermi species has more robust metapodials. I have personally seen no metapodials from Pikermi such as the one that Gromova (1952) has described and figured for *Hipparion moldavicum*. «*Hipparion*» *mediterraneum* also differs from the Maragheh hypodigm of «*Hipparion*» aff. *moldavicum* in the consistently shorter dimensions of the preorbital bar. In this dimension, and in the morphological details of the preorbital fossa including size, shape, presence of strong anterior rim, presence of a distinct

intermediate fossa, and retraction of nasal notch, *Hipparion moldavicum* potentially foreshadows «*Hipparion*» *mediterraneum* in morphology.

«*Hipparion*» *proboscideum* is the most derived Group 2 hipparionine presently reported in its strongly developed preorbital, intermediate, and buccinator fossae, very elongate snout, and strong retraction of the nasal notch. This species retains relatively complexly plicated pre- and postfossettes and bifid pli caballins in middle adult wear. Protocones tend to be rounded and hypoglyphs are usually not deeply incised in middle adult wear. Morphologies cited in both the type series of «*Hipparion*» *moldavicum* and «*Hipparion*» *mediterraneum* foreshadow features seen in «*Hipparion*» *proboscideum.*

The stratigraphic range of «*Hipparion*» aff. *moldavicum* at Maragheh is not well documented. The MNHN sample is believed to be derived largely from the middle portion of the section (Mecquenem, 1908) and the maxillary fragments housed by the Naturhistorisches Museum, Vienna, have provenance data indicating their collection from Ketschawa (=Kara Kend, Kerjawa, and our localities 1A, 1B, and 1C), also indicative of a Middle Maragheh age range. Therefore, the known stratigraphic range of this taxon is approximately -52 meters to - 28 meters below the loose chippings marker bed. The calibrated radiometric range would be 8.5 to around 8 million years.

Group 2 hipparionines apparently first occur in the medial Turolian (=MN 12 of Mein, 1975, 1979; MN 12a of Bernor, 1983, and Bernor, 1985), ca. 9-8 ma., and are known to occur in the eastern Mediterranean and southwest Asia as late as 7 or less million years ago (uppermost Maragheh and Samos). They range from the eastern Mediterranean as far eastward as Iran, and northward to the western U.S.S.R. Recent investigations of the American Museum and Uppsala Chinese Neogene collections by Bernor has revealed that a diverse assemblage of Turolian-Ruscinian (and potentially younger) Group 2-like species occurred in China. This assemblage is currently under study by Bernor and Qiu. The mode of their zoogeographic differentiation is not ascertainable at this time because of the need for a thorough systematic and phyletic study.

«*Hipparion*» *?matthewi* KORMOS, 1911

Referred specimens: «*Hipparion*» *?matthewi*: KNHM-RLB 8405, left mandible fragment with P/2 - M/2; KNHM-RLB 8407, right mandible with M/1-2; KNHM-RLB 8408, left mandible with M/1-2; KNHM-RLB 8408, left mandible with M/1-2; KNHM A4837, metacarpal. G.I.U. P100-1958 (cast), skull fragment with right and left P2/ - M3/; UCR-MMTT numbers referred to «*Hipparion*» cf. *?matthewi*: 18/1438, right P2/; 18/1447, left dP3/; *18/1443, left dP3/; 18/1440, right M1/; 37/2089, left dP3/; 37/2093, left P4/; 37/2049, right M1/; 25/1635, unerupted dP2-3/; 24/1732, right M1/; 24/1682, right calcaneum; 26/1828, right dPx/; 26/2563, left dP/2; 26/2562, left dP/3; 26/1874, left P4/; 261827, right P/3; 26/1645, left M1-2/, right M2/; 26/1591, right M/2; 26/1640, left M/2; 26/1677, left astragalus; 26/1682, right calcaneum; *26/1684, articulated distal left metapodial, astragalus, navicular.

*Specimens currently held in Tehran, Iran.

Geographic Range: Greece, Iran, ?Turkey, ?Southwest U.S.S.R.
Diagnosis: not given due to the uncertainty of the Holotype's morphology.

Description:

Paul Sondaar presented the University of California, Riverside, with a cast of a skull fragment of a small sub-adult hipparionine horse, G.I.U. P100-1958 (figs. 18a,b) collected from an unknown locality at Maragheh. This specimen lacks the nasals, snout and cranium, but

the cheek teeth and preorbital fossa regions are intact. The fossa is anteroposteriorly moderately long, subtriangular shaped and anteroposteriorly oriented, dorsoventrally moderately deep, only very slightly pocketed posteriorly, medially shallow, the anterior rim very faintly expressed, fossa peripheral border outline is moderately strong. The preorbital bar is short and the anterior portion of the lacrimal invades the posterior rim of the fossa. The cheek teeth are all small, elongate, and buccolingually narrow; pre- and postfossette plications are preserved on P2/ - M2/ and are relatively simple in amplitude; pli caballins are preserved on P3/, M1/ and M2/ and are single; hypoglyphs are preserved on P2/ - P4/ and are deeply incised as well as M1/ which is shallowly incised; protocone is preserved on P2/, P3/ and M1/ and has a rounded morphology while being flattened lingually on M2/.

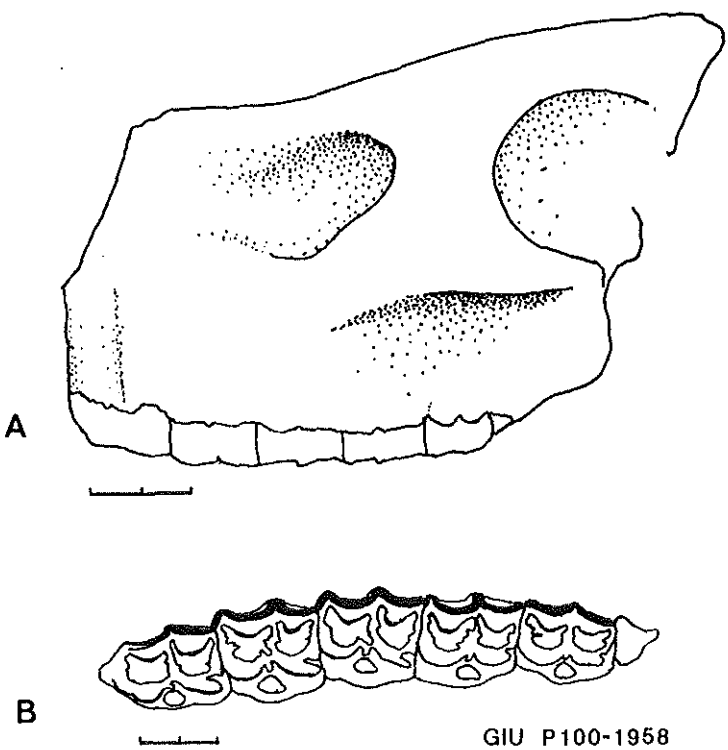
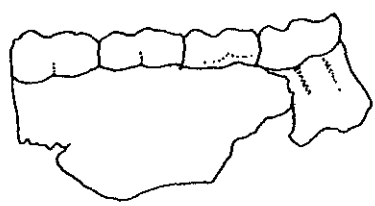


Fig. 18. — « *Hipparion* » cf. *?matthewi*, skull GIU P100-1958; a: lateral view; b: maxillary cheek teeth occlusal view.

Several isolated maxillary cheek teeth are referred here to « *Hipparion* » cf. *?matthewi*. They share a number of morphological features including: relatively buccolingually narrow and anteroposteriorly elongate; posterior border of the prefossette and anterior border of the postfossette are the heaviest plicated, protocone is rounded or flattened lingually until late wear, hypoglyph is moderately deep, and boucle prefossette is prominent and rounded. This suite of characters compare closely with the G.I.U. P100-1958 skull fragment described here. Measurements of individual cheek teeth are included in Table 18.

Mandibular cheek teeth (Figure 19a,b) are less certainly characterized since many of their character states are common to hipparionine species found throughout the stratigraphic sequence. Individual mandibular cheek teeth of the Lake Rezaiyeh Expedition sample referred to «*Hipparion*» cf. *?matthewi* are consistently small, buccolingually narrow and anteroposteriorly elongate; they tend not to have pli caballinids; ectoflexids tend not to separate metastylid and metaconid in the premolars, while doing so in the molars; ectoparastylids are rare; linguaflexids and metaconid/metastylid shapes are variable. These features are best preserved in a fragmentary mandible with P/4 - M/3, MMTT 26/1573.



A

UCR-MMTT 26/1573

B

Fig. 19. — «*Hipparion*» cf. *?matthewi*, mandible fragment UCR-MMTT 26/1573; a: lateral view; b: occlusal view.

A recent review of the Vienna collection has revealed a suite of small lower cheek teeth and a small metacarpal referrable to «*Hipparion*» cf. *?matthewi*. The mandibular remains include KNHM-RLB 8405, 8406, 8407 and 8408 (assigned by Bernor) from Kopran II (uppermost Kopran?). KNHM-RLB 8405 is an adult left mandible fragment with P/2 - M/2. The cheek teeth are small and have an elongate, somewhat buccolingually compressed occlusal profile. Ectoflexids do not separate metastylids/metaconids on the premolars while they do so on the molars. Pli caballinids are absent on all of the cheek teeth; linguaflexids are shallow on P/2, U-shaped on P/3 - M/1 and V-shaped on M/2; metaconids and metastylids are rounded on all of the cheek teeth. KNHM-RLB 8406 is an adult left mandible with P/4 - M/2. The cheek teeth have a somewhat more squared occlusal outline than KNHM-RLB 8405 because of their more advanced stage of wear. Ectoflexids separate metaconid and metastylid in all of the cheek teeth; pli caballinids and ectoparastylids are as in 8405; linguaflexids are all U-shaped; metaconids/metastylids are rounded. KNHM-RLB 8407, a right mandible with M/1-2, and KNHM-RLB 8408, a left mandible with M/1-2 are both old adults and have square-shaped occlusal outlines. Their morphological attributes for M/1 and M/2 are identical to those of KNHM-RLB 8406.

The Ilkhchi metacarpal, KNHM A4837, is complete. It is the smallest complete metacarpal that I have seen from Maragheh. It is relatively elongate and very gracile in shape, the sagittal keel is relatively sharply extended for a metacarpal, the ventral surface is deeply set between two ridges; the distal dorsal pit is very deep, accentuated by a raised proximal rim which would have given a sharper contact with the proximal first phalanx during dorsiflexion of the manus; magnum/hamate angle is 143 degrees.

Discussion:

The nomen *Hipparion matthewi* has traditionally been used for dwarf species from later Turolian levels of the eastern Mediterranean, southwest Asia, and the western U.S.S.R. Bernor's (1978) original assignment of the small hipparionine material from Maragheh to *Hipparion matthewi* was based primarily on a size comparison of the Lake Rezaiyeh collection's fragmentary jaws, teeth, and postcrania to a very well preserved skull from Samos housed in the Naturhistoriches Museum, Vienna (KNHM A4742; Bernor and Hussain, 1985, Figure 6A). Bernor *et al.* (1980) cited this example as having a facial morphology similar to Group 3 hipparionines. Woodburne and Bernor (1980) also noted that some small hipparionines commonly referred to *Hipparion matthewi* show facial morphologies similar to Group 2 hipparionines. Bernor and Hussain (1985) discussed this problem further and concluded that the Maragheh skull fragment (G.I.U. P100-1958) and several skull fragments from Samos show a Group 2-like facial morphology. Characters they cited as showing Group 2 affinities include: short preorbital bar, relatively large dimensions of fossa length and dorsoventral height, slight posterior pocketing, lacrimal invading the posterior edge of the facial fossa.

«*Hipparion*» cf. *?matthewi* is derived compared to other Group 2 species in its greatly reduced size, lesser facial fossa medial depth, reduced cheek tooth complexity, pli caballin single, hypoglyph more shallowly incised. The metapodials from Samos and Maragheh reveal that the small horses from these localities had elongate and very slender metapodials. A number of small horses with different facial morphologies is most probably indicative of extensive convergence amongst late Miocene dwarf hipparionines. Bernor (1984) and Bernor and Hussain (1985) have cited the occurrence of potentially distinct lineages of small late Miocene hipparionines from Spain, North Africa, East Africa and the eastern Mediterranean - southwest Asia.

Recently, Koufos (1984) has described a new Vallesian age species of hipparionine, *Hipparion macedoniensis*, from Ravin de la Pluie of the Lower Axios Valley, Greece. This is a remarkable report, since dwarf hipparionines are generally accepted as first occurring in the medial Turolian (Sen *et al.*; 1978; Bernor *et al.*, 1980). Morphologically, Koufos (1984) cites *H. macedoniensis* small size, short mandibular symphysis, elongate snout, high enamel plication frequency, confluent fossettes in the P2/, elliptical and free protocone, well developed deciduous premolar ectostylids, a well developed protostylid and longer molar than premolar series. The size characteristics of this purported taxon are indeed on the small size, but it should be noted that the holotype's (RPL-21) P/2 - M/3 length dimension would fall within the lower range of variability of medium sized hipparion species (such as «*Hipparion*» *moldavicum*, here). Koufos (1984) does not cite the holotype's stage of wear, but it would appear to be somewhat advanced, which may account in part for the small size.

More disturbing is the choice of characters used to distinguish *Hipparion macedoniensis*. Characters such as: short mandibular symphysis and elongate snout are not compared with a series of species which have controlled stratigraphic or a quarry population context, making these characters of dubious value. The citation of high enamel plication of the maxillary cheek teeth are not supported by Koufos (1984) Figure 4a, rather this figure reveals commonly derived cheek tooth conditions of moderately

complex enamel plications, moderate to shallowly incised hypoglyphs, ostensibly single pli caballins and rounded protocones. The occurrence of confluent fossettes in the P2/ and well developed deciduous premolar ectostylids are distributed throughout so many different hipparionine species as to make these useless characters. The longer molar than premolar series length dimension is difficult to evaluate because of its possible wear-relatedness.

The age of this species is based on a biochronologic, not a radiometric or magnetostratigraphic calibration. Koufos (1984:309) cites the cooccurrence of *Progonomys cathalai*, *Adcrocuta eximia leporyncha, Hipparion primigenium* and *Decennatherium pachecoi* as indicating a Vallesian age for the fauna. The *Adcrocuta* would appear to be a new subspecies, but its relationships to the typical Turolian species have not been detailed so that this age can be properly evaluated. The nomen *Hipparion primigenium* has been inappropriately extended to taxa ranging throughout the Vallesian and Turolian. Koufos (1984) has not sufficiently characterized his concept of this species for one to pursue a pertinent commentary. *Progonomys cathalai* is usually found in Vallesian levels, but has also been found to occur in horizons as late as early Ruscinian age of North Africa (Bernor and Pavlakis, in press). A later, Turolian occurrence of this taxon can not be ruled out. This leaves the giraffid *Decennatherium pachecoi*, a taxon common to the Spanish Vallesian, but also known from Maragheh levels dating 8.5 - 8 m.y. (Erdbrink, 1976; Bernor, 1986). There would appear to be questionable evidence of both a morphologic and stratigraphic nature to support Koufos (1984) claim of a Vallesian age dwarf hipparionine species from Ravin de la Pluie.

In contrast, small hipparionine species are first certainly known to occur at Maragheh in the Lake Rezaiyeh Expedition sample about 35 meters below loose chippings, and become more abundant towards the top of the section. They are not well represented by fossil material, but an inferred chronologic range of 7.5 to under 7 m.y. has been made (Campbell *et al.*, 1980; Bernor *et al.*, 1980). Their age corresponds closely with Samos, Greece, and a number of Turkish localities which also have small hipparionines (Sen *et al.* 1978). A recent review of Maragheh hipparionine materials in the KNHM has revealed the occurrence of « *Hipparion* » *matthewi* sized individuals from Kopran II. The stratigraphic provenance of Kopran II is not certain, but may potentially be as low as -70 meters, which would make the KNHM sample the oldest presently known (8.5 m.y.) of any locality of the Subparatethyan Province (*sensu* Bernor, 1983, 1985).

Koufos (1984) report of a smaller hipparionine from Greece is an important contribution to our understanding of trhe evolutionary radiation of small hipparionine horses. His study, and this report of a potentially earlier first occurrence of small hipparionines at Maragheh than previously thought, suggests the possibility of an early Turolian, if not latest Vallesian first appearance of dwarf hipparionines in the Subparatethyan Province. It appears that Group 2 (*sensu* Bernor and Hussain 1985 and Bernor, here) included a dwarf species that ranged from Greece eastwards as far as Iran, and northward into the western U.S.S.R. However, it is not certain that the Ravin de la Pluie species and « *Hipparion* » *?matthewi* from Maragheh are identical species, or even members of the same clade.

SUMMARY

The Maragheh hipparionines are a diverse assemblage representing at least three superspecific taxonomic groups. A character state analysis of twentyfive Maragheh skulls and skull fragments with a detailed systematic comparison to twenty other Eurasian and African hipparionine species was made in the identification and characterization of five species: « *Hipparion* » *gettyi* sp. nov. *Hipparion prostylum* (*s.l.*), *Hipparion campbelli* sp. nov. « *Hipparion* » aff. *moldavicum* and « *Hipparion* » *?matthewi*. Postcranial morphology is known from direct quarry associations in only two species (*Hipparion prostylum* - Mainz collection, and *Hipparion campbelli*, Lake Rezaiyeh Expedition sample), inferred from museum and field studies in two others (« *Hipparion* » *gettyi* and « *Hipparion* » *?matthewi*); and inferred by previous studies of one species (« *Hipparion* » aff. *moldavicum*; Gromova, 1952). An analysis of individual cheek teeth with close stratigraphic control has allowed the recognition of « *Hipparion* » *gettyi*, « *Hipparion* » *?matthewi*, but not the clear differentiation of *Hipparion prostylum* from *Hipparion campbelli* nor the distinction of « *Hipparion* » *moldavicum*. The characterization of each hipparionine species is as follows:

1/ « *Hipparion* » *gettyi* is a medium sized advanced Group 1 horse with a well developed facial fossa placed well anterior to the orbit and lacrimal bone, complex enamel ornamentation of the cheek tooth pre- and postfossettes, double pli caballin, and elongate slender metapodials. Stratigraphically, this species is known to occur in the lowest Maragheh levels (within the -150 m. to -70 m. interval). « *Hipparion* » *gettyi* has uncertain evolutionary relationships with later Turolian species, but is believed to closely approximate the ancestral condition for Group 3 species.

2/ *Hipparion prostylum* (*s.l.*) is a medium sized Group 3 horse with a small facial fossa set well anterior to the orbit and lacrimal bone. It has moderately complex ornamentation of the pre- and postfossettes, variable pli caballin morphology, and elongate-slender metapodials. Stratigraphically this species is known to occur in the Middle Maragheh levels (within the -52 m. to -28 m. interval). *Hipparion prostylum* is believed to be a good potential ancestor for the younger species *Hipparion dietrichi* and *Hipparion campbelli*.

3/ *Hipparion campbelli* is a medium sized advanced Group 3 horse with an elongate and slender snout, no facial fossa (except for a slight medial depression and vestigial posterior rim), thinly banded but moderately complex ornamentation of the cheek teeth pre- and postfossettes, single pli caballin, and elongate-slender metapodials. Stratigraphically this species is known to occur in the Shollovend quarry (-18 meter level) and has an interpreted stratigraphic range of -28 m. to +7 m. Evolutionarily it is the most derived Group 3 horse currently recognized.

4/ « *Hipparion* » aff. *moldavicum* is a medium sized, primitive Group 2 hipparionine which has a large well developed preorbital fossa set close to the orbit and with the lacrimal bone invading its posterior border; cheek teeth pre- and postfossettes are moderately complex, and the pli caballins are usually bifid in middle adult wear. Stratigraphically, this species is known to occur in the Middle Maragheh levels (within the -52 to -28 meter interval). « *Hipparion* » aff. *moldavicum* morphologically represents a good potential ancestor to all other Group 2 hipparionines including « *Hipparion* » *?matthewi*, « *Hipparion* » *mediterraneum*, and « *Hipparion* » *proboscideum* and perhaps multiple species of Chinese Group 2 hipparionines.

5/ « *Hipparion* » *?matthewi* is a small sized Group 2 hipparionine which has a weakly developed preorbital fossa set close to the orbit and with the lacrimal bone invading its posterior border; cheek tooth pre- and postfossettes are moderately complex and pli caballins are single in middle adult wear. Stratigraphically, this species is known to occur within the -35 m. to +7 m. interval.

ACKNOWLEDGEMENTS

This work is a direct outgrowth of the Lake Rezaiyeh Expedition which engaged in active field work in northwest Iran between 1972 and 1974. Funds supporting field and associated museum work were provided by the generosity of Mr. Gordon Getty and the L.S.B. Leakey Foundation. I would like to speak for the members of the expedition in thanking these individuals for making this, and other work on Maragheh by our research group possible. I would also like to thank the project director, Dr. Bernard G. Campbell for his encouragement and help throughout the course of my studies. I would like to thank the many project members and support staff from the Iranian National Museum (MMTT) for their efforts in collecting fossils and making my work so enjoyable. I would also like to thank the dozens of curators and staff at the natural history museums and universities throughout Europe for providing me with all possible courtesies during my many visits to their institutions. I would like to thank Drs. William Akersten, Daryl Domning, Richard Estes, Taseer Hussain, Bruce MacFadden, Nikos Solounias, Richard Tedford, John Van Couvering, Mr. George T. Jefferson, and one anonymous reviewer for reading various stages of this manuscript. Mrs. Jennifer Emry provided hours of considerable labor in preparing the illustrations for the manuscript. Finally, I would like to thank Dr. Michael O. Woodburne for several years of guidance during the earlier phases of this work and the countless drafts of manuscript revised and miles of Eurail travelled in support of these efforts.

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TABLE 1a

CHARACTER STAGE ANALYSIS OF HIPPARIONINE HORSE SKULLS - SUMMARY: GROUPS 1, 2, 3 AND "*CORMOHIPPARION*" (*SIVALHIPPUS*)

Definition of symbols used in the characterstate analysis:

1/ Age: 1 = foal; 2 = juvenile; 3 = adult; 4 = old.
2/ Length of fossa: 70+ = o; 60-69 = +; 50-59 = *; 40 - 49 = -; 40 = --
3/ Fossa orientation: Subtriangular anteroventral = +; subtriangular anteroposterior = *; egg-shaped anteroposterior = -; C-shaped anteroposterior = o; vestigial to absent = x.
4/ Fossa dorsoventral height: 50+ = +; 40-49 = *; 39-30 = -; less than 30 = o.
5/ Fossa posterior pocketing: pocketed = +; slightly pocketed = *; unpocketed = -.
6/ Fossa medial depth: deep = +; moderate = *; shallow = -.
7/ Anterior rim: present = +; faint = *; not present = -.
8/ Fossa border outline: strong = +; moderate = *; weak = -.
9/ Fossa's ventral border irregular: yes = +; no = -.
10/ Preorbital bar length: 41+ = o; 31-40 = +; 25-30 = *; less than 25 = -.
11/ Anteriormost limit of lacrimal: touching or invading posterior rim of fossa = +; less than 1/2 the distance from fossa to orbit = *; 1/2 the distance of more from fossa to orbit = -.
12/ Nasal notch position: anterior to P2/ = +; above P2/ = *; above P3/ = -; posterior to P3/ = o.
13/ Cheek tooth fossette ornamentation: complex = +; moderate = *; simple = -.
14/ Pli caballin morphology: double = +; single = -.
15/ Hypoglyph: deeply incised = +; moderately incised = *; shallowly incised = -.
16/ Protocone: rounded = +; flattened only lingually = *; elongate = -.
17/ P2/ anterostyle: elongate = +; short and rounded = -.

NA = not applicable.
RM = rock matrix obscuring structure's morphology.

Use of character states:

Table 1, and subsequent tables that record character states may include multiple symbols separated by /. This indicates that not a single, but multiple states are observed for that particular character. Also, some characters may be recorded by double symbols, such as character state 2 for "*H*". *catalaunicum*, which indicates that the length of the preorbital fossa is much longer than 70 mm. The symbol ? before a character state reveals uncertainty about the state's morphology. The symbol ? is used to indicate approximate morphology of a state. Wherever possible, cheek tooth character states are recorded only for middle stage-of-wear adults, to avoid ontogenetic biasing of the data. Likewise, facial fossa morphology is determined for adult individuals only, wherever possible. In column 1, the symbol —'s means multiple individuals of the species under consideration were known of the particular age class. In column 15, the symbol & means that more than one character state was known for the species under consideration.

SPECIMEN Nb	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
GROUP 1																	
1. *"H." primigenium* Hovenegg	3	0	–	+	+	+	+	+	–	0	–	*	+	+	+&/*	–	+/–
2. *"H." africanum* Bou Hanifia	3	0	+	a–	+	+	+	+	–	0	?–	?	+	?+	?+/*	?–	+
3. *"H." catalaunicum* Hostalets Superior	3	00	+	*	+	+	+	+	–	0	–	+	+	+	?+/*	–	+
4. *"H." melendezi* Spain	4	+	–	*	+	?*	–	*	–	+	?*	?	+	+	*	+	+
5. *"H."* sp. Pikermi	3'5	0/a+		–						+/0							
6. *"H."* sp. Samos	3'5	+/0	–	–	*	+	+	*	–	0/+	?*	?+/*–	+	+	+	+/–	+
GROUP 2																	
7. *"H." cf. moldavicum* ? Middle Maragheh	3'5	0/+	–	+/*	*	+	+	+/*	–/+	*/–	+	+/*	–/*	–/+	–/*	+	–/+
8. *"H." mediterraneum* Pikermi	3'5	0/a–	–	*	*	+?*	+	+	–	–/– –	+	+/*/*	–	–	–	+	?
9. *"H." proboscideum* Samos	3'5	0/00	–	+/a–	*/–	+	+	+	–	–	++/+	–	*	–	–	+	+
10. *"H." ?matthewi* Samos	3'5	–	?–/+	0	*	+	–	*	–	–	+	?	–	–	*&*/–	+	–

TABLE 1 a

SPECIMEN Nb	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
GROUP 3																	
11. *H. prostylum* Mt Lubéron	3'5	-/∂*	+	0	*	*	-	*	-	+	*	+	*	+/-	+&+/*	+	+
12. *H.* cf. *prostylum* Pikermi	2	*	+	0	*/-	+/-	-	*/-	-	+	-	NA	NA	NA	NA	NA	NA
13. *H.* cf. *prostylum* Middle Maragheh	3'5	--/-	+	0/00	*/+/-	-/+/-	-/?+/-	*/-	+/-	++/+/0	*	+/+/*	-	-	*/+/+	+/*/-	+
14. *H.* cf. *prostylum* Middle Maragheh	3'5	-	+ +/-	0	*/-&-	*/-&-	+/-&-	*&*/-	-	+	*/-	*&+/*	*/?	?	+&+/*	+/*	+
15. *H. campbelli* Upper Maragheh	3'5	NA	NA	NA	-	—	-	—	NA	+	*	*	*	-	*/+	+	+
16. *H. dietrichi* Samos	3'5		-	-&-/*	-	-	-	*/-	-	0	?/*	NA	?*	-	*/+	+&+/*	+
17. *H. antelopinum* Middle Siwaliks	2/3	?	?-	?	?*	-	?	-	-	?	?	?	*	-	*	+/-	?
SIWALIK "C." (S.) GROUP																	
18. *"C." (S.) theobaldi* Middle Siwaliks	3	00	-	+	+	++	+	++	-	?	?-	?	+	+	+	*	+
19. *"C." (S.)* sp. Middle Siwaliks	3	∂-	-	*	?	*	*	*	-	?	?	?	+	+	+	*	+
20. *"C." (S.) perimense* Middle Siwaliks	3'5	*/-	+/-	-/0	*/-	*/-	*/-	*	+/-	++	-	+/*	+	+	+	*	+

TABLE I a (cont.)

TABLE 1b
CHARACTER STATE ANALYSIS OF HIPPARIONINE HORSE SKULLS FROM MARAGHEH, IRAN.

SPECIMEN Nb	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
13. KNHM A4847 Middle Maragheh	2+	**	X	0	*	*/-	*	*	–	+	*	*	NA	?	+(i)	+/*	+
14. KNHM A4844 Middle Maragheh	3–	NA	NA	NA	NA	?*/-	NA	NA	–	NA	NA	NA	*	+/-	+	*	+
15. JGUM MB 67 Middle Maragheh	3–	*	–	–	*	*	–	*	–	+	NA	+/*	NA	NA/+	+/++	*/-	+
16. MNHN Mar. 18 Middle Maragheh	4	–	–	0	–	–	–	–	–	a++	–	NA	*	–	*/+	+/*	+
17. MNHN Mar. 465 Middle Maragheh	4	a*	–	a0	–	–	–	–	–	a+	a–	NA	NA	NA	NA	NA	+
18. MNHN Mar. 359 Middle Maragheh	3	+	–	–	–	–	–	*/-	–	0	*	+	*	+/-	*/+	+/-	+
19. MNHN Mar. 71 Middle Maragheh	3	NA	NA	0	–	–	–	—	–	a0	*	NA	*	+/-	*/+	+/-	+
20. AMNH 27807	4	+	–	–	*/-	*	*	*	–	+	?	NA					
21. AMNH 27809	2+	NA	–	–	*/-	*	*	*	–	0	*	NA					
22. UCR-MMTT 1342 Upper Maragheh	3	–	X	NA	–	—	–	—	NA	+	*	*	*	–	*/+	+	+
23. UCR-MMTT 1343 Upper Maragheh	2	–	X	NA	–	—	–	–	NA	+	*	*	NA	NA	NA	NA	+
24. UCR-MMTT 1291 Upper Maragheh	2	–	X	NA	–	—	–	–	NA	+	?	NA	NA	NA	NA	NA	+

SPECIMEN Nb	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. KNHM un-numb. Lower Maragheh	4	+	X	–	+	+/*	*	*	–	0	–/*	*	+/*	+	+	+	+
2. MNHN/RLB 7914 ?Middle Maragheh	3	0	*	+	*	+	+	+	–	*	?+	NA	*/+	–/+	+/*/–	*	NA
3. MNHN/RLB 7915 ?Middle Maragheh	3	0	*	**	*	+	+	+	–	–	+	+	*	–	*	+	–
4. MNHN/RLB 8001 ?Middle Maragheh	4	0	*	**	*	+	+	+	–	*	+	NA	–	+/–	–	+	NA
5. MNHN 466/RLB 8002 Middle Maragheh	4	0	*	*	*	+	+	+	–	*	+	NA	–	+/–	–	+/*	NA
6. MNHN/RLB 8003 ?Middle Maragheh	4	+	*	@**	*	+	+	*	–	@*	?+	?+/*	–	–	–/*	+	+
7. KNHM/RLB 8402 Middle Maragheh	4	@++	*	NA	*	+	NA	NA	–	–/*	+	NA	NA	NA	NA	+	+
8. KNHM A4848 Zad Baschi	4	NA	NA	NA	*	NA	NA	NA	–	NA	NA	NA	NA	NA	NA	+	+
9. KNHM/RLB 8403 Middle Maragheh	3+	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	*	+/–	–	+	+
10. KNHM/RLB 8404 Middle Maragheh	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	*	NA	NA	+	+
11. BMNH M3924	3–	+	*	*	*	+	+	*	+	*	+	*	*/+	+	*/+	+/–	–
12. GIU P100-1958	2+	*	–	–	*/–	*/–	*/–	*/–	–	*/–	+	?	*	–	*	+/–	–

TABLE 1 b (cont.)

TABLE 2
MEASUREMENTS AND OBSERVATIONS ON ISOLATED MAXILLARY CHEEK TEETH.

Legend:
element - tooth.
length - a = length at occlusal surface.
- b = length 10 mm above base of tooth.
width - a = width at occlusal surface.
- b = width 10 mm above base of tooth.
height MES/MCD - MST: height at mesostyle (in maxillary dentition) / metaconid - metastylid (in mandibular dentition).
height protocone - height at lingual surface of protocone.
Pli - pli caballin morphology: double or multiple = +; single = -.
Foss - fossette plication frequency: complex = +; moderate = *; simple = -.
Hyp - hypoglyph morphology: deeply incised = +; moderately incised = *; shallowly incised = -.
Pr - protocone morphology: rounded = +; flattened only lingually = *; elongate = -.
P2/ - P/2 anterostyle: elongate = +; short and rounded = -.
MEC/MES - metaconid/metastylid shape: rounded = +; angular = -.
ECT - premolar and molar ectoflexids: separates metaconid/metastylid = +; does not separate metaconid/metastylid = -.
LING - linguaflexid (enamel projection between metaconid and metastylid): U-shaped = +; V-shaped = -.
NA - not applicable.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
41/2519 (2) (unerupted)	lt. P^2	34.9	24.9 22.3	45.8					+
41/2477 (3)	rt. P^4	20.7 27.1	23.4 22.3	49.8	*	+	++	--	
41/2211 (3)	lt. P^4	21.2 25.9	21.2 26.4	59.6	+/*	+	++	--	
41/2487 (2)	lt. P^4	25.3 27.4	24.0 24.3	47.1					
41/2464 (2)	rt. M^1	22.3 24.4	23.3 19.7	51.6			++	--	
41/2248 (2)	lt. M^1	26.8	19.7						
41/2244 (2)	rt. M^2	20.6 24.2	21.1 19.2	58.7					
41/2220 (2)	lt. M^2	20.1 23.7	21.8 22.0	53.7			++	--	
41/2221 (4)	rt. M^2	20.2 22.0	21.2 23.2	19.7	*	-	*	-/+	
41/2227 (4)	rt. M^3	23.8 24.4	21.8 21.3	21.8	*/-	-		-	
41/2516 (4)	rt. M^3	22.6 23.0	20.7 20.2	17.1	*	+	+	-	

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
36/2022 (2)	rt. dP^2	40.3							
36/2033 (3)	rt. M^2	24.0 23.7	18.6 23.0	35.7	?*	+	*	-	
3/712	rt. M^2	20.4 24.1	21.2 19.4	49.7					
11/123	lt. P^4	23.9 27.4	21.8 21.6	51.1					
11/67 (3)	lt. M^1	19.7	21.5	51.8	**	-		--	
18/1598 (2)	lt. dP^2	 38.5	 21.8	16.1	*/-		+	+	
18/1438 (4)	rt. P^2	30.1 31.6	22.1 24.0	25.8	+/*		-	+/-	
18/1440 (3)	rt. M^1	20.5 21.7		44.4	*				
1/12 (4)	lt. P^2	24.9 25.6	13.0 13.7	23.6					
7/2145 (3+)	lt. P^3	23.5 25.4	25.2 27.4	26.6	*/-		-	*	
7/2144 (4)	lt. P^3	20.2 21.7	23.9 24.6	22.7	*	-	*	-	
7/70 (3)	lt. P^4	23.4 24.9	23.8 23.3	29.2	*	-	**	+/-	
7/1992 (2) (unerupted)	rt. M^1	22.7 22.8	19.9 17.5	44.6					
14/1527 (2)	lt. dP^x	25.2	20.9	14.6	*			+	
14/1561 (2)	lt. dP^3	26.9	18.5	18.2		?-	++	-	
14/1537 (4)	lt. P^3	22.6 22.3	24.1 25.3	25.2		?-	-	+	
40/2214 (2+)	rt. M^2	19.0 23.0	21.2 20.7	55.3		-	+	--	
37/2059 (1)	rt. dP^x	25.8 27.8	21.5 17.8	20.5					
37/2056 (2)	lt. dP^x	27.1	20.1	21.3					
37/2421 (2)	rt. dP^2	35.5	20.8	20.0					
37/2079 (2)	rt. dP^3 or dP^4	24.5 28.2	21.4 19.7	21.1	-		+	*	
37/2043 (2)	rt. dP^3 or dP^4	26.2 28.6	22.2 17.8	21.2					

TABLE 2 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
37/2391 (3)	lt. P^2M^1								
	P^2-P^4	82.5							
	P^2	33.0	21.6	41.7	-	-	-	-	+
	P^3	25.8	24.2	38.8	*	-	*	+	
	P^4	24.6	25.1	35.6	*	-	*	+	
	M^1	25.5	23.2	41.8	*	-	*	+	
37/2556	rt. P^2	30.6 33.1	22.7	36.3	*/-	-	*	+/-	+
37/2246 (2)	lt. P^2	22.6 22.3	24.1 25.3	25.2		?-	-	+	
37/2089 (4)	lt. P^3	17.8	21.2	18.4					
37/2571 (3)	rt. P^3	20.2 20.5	20.6 21.5	31.3	*	-	*	-	
37/2398 (3)	rt. P^3	22.2	23.4	39.4					
37/2397 (3)	rt. P^3	21.0 26.2	23.4 24.4	39.9	-	-	*	-	
37/-- (4)	lt. P^4	21.0 22.2	21.7 22.6	21.5	+/*		*	+/-	
37/2093	lt. P^4	20.5	22.6	18.5	*	-	*	+/-	
37/2572 (2)	lt. P^4	22.1	22.8	20.6					
37/2049 (3)	rt. M^1	20.1 21.2	20.9 22.2	28.6	*	-	*	+	
37/2210 (3)	lt. M^2	19.6 26.3	22.3 21.9	56.9	-	-	+	--	
37/2105 (4)	lt. M^3	21.6	20.3	12.6	-		*	+	
37/2072 (4)	lt. M^3	21.9 21.2	19.9 18.6	21.2	*	-	*	-	
37/2180 (2)	rt. M^3	20.2 18.8	18.9 16.2	43.3					
37/2069 (3)	rt. M^3	19.8 22.0	20.0	18.5	-	-	*	+	
37/2051 (2+)	lt. M^3	24.0 21.5	18.0 15.1	44.6					
13/1347 (2)	palate w/dP^{2-3}								
	dP^2	35.7	19.6	20.7					
	dP^3	30.7	18.8						

TABLE 2 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
13/1728 (1)	lt. dP^2	35.6 34.7	22.3 19.3	19.5					
13/1503	lt. dP^4	29.2	21.8	14.7	*		-	*	
13/1719 (2)	lt. dP^3 or dP^4	30.4	23.1	20.8	*	-	+	-	
25/1631 (1)	lt. dP^x	29.4 34.7	22.5 18.7	27.4					
25/1635 (1) (unerupted, small hipparion)	rt. dP^2-dP^3								
	dP^2	28.5	14.5	17.9					
	dP^3	21.9	13.4						
24/1723 (3) (typical *"H." matthewi*)	rt. H^1	18.0 22.0	20.3 19.2	44.4	*	-	+	-	
26/2562 (1)	lt. dP^4	24.1 26.3	19.4 15.4	21.6					
26/1644 (3) (unarticulated)	rt., P^2-H^3								
	P^2	23.5	18.5 21.0	25.7	*	-	*	+	
	P^3	20.3 23.2	19.5 21.7	26.9	*	+	*	+	
	P^4	21.9 24.3	23.7 25.4	34.8	*	-	*/-	+	
	M^1	18.2 21.3	22.7 23.8	31.8	*	-	*	+	
	M^2	18.6	21.5	31.6	*	-	*	+	
	M^3	20.2 22.0	20.1 19.3	34.0	*	+	+	-	
26/2567 (2+) (unarticulated)	lt., P^2-H^3								
	P^2	28.1 31.3	19.6 23.5	38.9	+		+	*/-	
	P^3	23.4 26.1	21.6 25.5	46.6			+	*/-	
	P^4	25.6	24.5	52.3			+	*/-	
	M^1	21.0 23.6	24.1	47.0	*		+	-	
	M^2	20.5 24.4	21.2 21.2	52.3			+	*	
	M^3	20.6 22.0	18.7 16.6	49.5					
26/2570	rt. P^2	26.8	21.3	7.0					
26/2532 (3)	lt. P^3	18.7	18.7	44.1					
26/1823 (3)	lt. P^4	18.3 20.7	21.3 21.3	35.6	*	-	-	+	

TABLE 2 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
13/2475 (4)	lt. max. frag. with P^2-P^4								
	P^2-P^4	80.9							
	P^2	34.2	22.4	17.5		-		-	+
	P^3	24.7	25.4	20.3		-		-	
	P^4	21.9	24.8	21.7		-		-	
13/1993 (4+)	rt. P^3	24.1	23.6	17.4	-		-	+	
13/1374 (4+)	rt. P^3	19.9		15.1	-		-	+	
13/1993 (4)	rt. P^3	24.4	26.1	14.5					
13/1503a (2)	lt. P^3	30.4	28.4	@55.8					
13/1503b (2)	lt. P^3	30.4	27.9						
13/86 (4)	rt. P^3 or P^4	20.8 24.2	15.2 25.9	24.7		-		-	
13/118 (3+)	rt. P^4	@20.0		32.7	++	+	*	+	
13/1270 (2)	lt. M^1	22.1	22.6	58.9					
13/84 (3)	lt. M^1	22.6 25.2	22.2 23.2	43.5	**		**	+	
13/85 (2)	lt. M^1	22.6	22.1	47.5	*	-	+	*	
13/1623 (3)	rt. M^1	22.5 24.8	23.0 24.0	48.7	*		*	-	
13/118	rt. M^2	19.8 21.2	20.9	41.5	*	-	*	+	
13/1715 (4)	rt. M^3	21.9 24.3	20.8	25.4	*	-	+	-	
13/1498 (2+)	rt. M^3	22.0 22.7	18.5 17.1	51.0					
13/2233 (2+)	rt. M^3	22.2	19.2	60.8					
21/1651 (3)	lt. P^4	21.6 22.7	22.6 21.8	44.7	*	-	*	+/-	
31/1984 (3)	rt. P^3	21.2 24.7	22.2 24.4	31.8	*	-	*	+	
26/1824 (3)	lt. P^4	17.6 19.0	19.7 19.9	30.5	*	-	*	+	
26/1646 (2)	lt. P^4	22.3	19.1						

TABLE 2 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
26/1822 (3)	lt. M^1	19.4 21.7	21.4 22.6	34.6	*	-	*	+	
26/1826 (4)	lt. M^1	16.1	20.6	16.2	*		*	+	
26/1645 (2+)	lt. M^1	18.3 22.2	20.4 19.0	42.5	*	-	+	-	
	lt. M^2	19.5 22.1	19.4 16.2	49.5	*			-	
	lt. M^3	19.2	18.9						
26/1618 (4+)	lt. M^3	22.1	19.9	10.0					
26/2561 (3)	rt. M^3	20.9 19.7	18.3 18.0	36.8	*	-	+	-	

TABLE 2 (cont.)

TABLE 2 (Annex)
NUMBER OF PERMANENT MAXILLARY CHEEK TEETH PER STRATIGRAPHIC INTERVAL.

LOCALITIES BY STRATIGRAPHIC LEVEL	P^2	P^3	P^4	M^1	M^2	M^3
24, 26	3	3	5	5	3	5
21, 31, 25	0	1	1	0	0	0
37, 13	4	10 or 11	6 or 7	5	2	8
7, 14, 40	0	2	1	0	0	1
1, 18	2	0	0	1	1	0
3, 11	0	0	1	1	1	0
36	0	0	0	0	1	0
41	1	0	3	2	3	2
TOTALS	10	16 or 17	17 or 18	14	10	16

TABLE 3

MEASUREMENTS AND OBSERVATIONS ON MANDIBLES AND INDIVIDUAL MANDIBULAR CHEEK TEETH IN THE LAKE REZAIYEH EXPEDITION SAMPLE.

Legend:
Element = element.
Length = 1st measurement: length 10 mm. above base; 2nd measurement: at occlusal level.
Width = 1st measurement: length 10 mm. above base; 2nd measurement: at occlusal level.
Height = height taken at metaconid/metastylid to base of roots.
CAN. POS. = canine position: closer to I/3 than P/2 = +; closer to P/2 than I/3: -.
SNT. LNGT = relative snout length: P/2 - I/1 dimension greater than P/2 - M/3 dimension: +; P/2 - I/1 dimension less than P/2 - M/3 dimension: -.
MENT. FORM. = mental foramen position: closer to I/c than P/2: +; closer to P/2 than I/3: -.
P/2 ANT. = P/2 anterostylid: rounded: +; elongate: -.
ECT. FLX. = premolar and molar ectoflexids: separates metaconid/metastylid : +; does not separate metaconid/metastylid: -.
PLI = pli caballinid: complex: +; rudimentary to single: *; absent: -.
ECT.PAR. = ectoparastylids: present: +; absent: -.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
43/2496 (3)	rt. P_2	24.3 27.0	12.9 13.0	38.1				-					-	-
43/2484 (2+)	lt. M_1	21.4 25.4	12.8 13.4	41.2						+	-	-	*	+
43/2489 (4)	rt. M_1	24.8	14.2	40.2						+	-	-	+	+/-
41/2216 (2)	rt. dP_x	31.4	12.7	16.3										
41/2216 (2)	rt. dP_x	31.4	12.7	16.3										
41/2213 (2)	dP_x	27.5	14.4	13.2										
41/2224 (4)	lt. P_2	26.0 27.2	15.2	16.8				-	-	-	-	-	+	+
41/2218	lt. P_2	31.8	16.0					-	+	-	-	-	+	+
41/2234 (3)	lt. P_4	27.1	18.2	40.6						-	*	-	-	+
41/2245 (3)	lt. P_4	24.2 24.9	15.4	42.4						+	**	-	-	-
41/2478	lt. M_1	21.4 25.1	12.2	47.9						+	*	-	-	-
41/2509	lt. M_1	21.1 22.0	13.3 15.5	14.0						-	-	-	*	+

TABLE 3

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
41/2225 (2+)	rt. M_2	19.5 26.3	12.3 13.9	43.7						-	-	-	-	+
44/2494 (3)	lt. P_2	23.5 28.1	13.3 11.9	37.8				-	+	-		-	com- plex	-
44/2481 (3)	lt. P_4	22.9 26.3	13.1 12.6	57.5										
23/1647	lt. P_4	24.8 26.3	15.5 17.8	39.2						-	*	-	*	+
23/1647 (3)	lt. P_4	25.4 26.8	15.9 19.1	39.9										
36/2027 (4)	lt. P_4	27.1 28.0	13.6 15.0	19.5										
1-B/39 (2)	rt. mandible with dP_2-M_1, M_2 in crypt							-	+					
	dP_{2-4}	95.3												
	dP_2	34.9	12.6								-	-	+	-
	dP_3	28.1	14.4							+	-	+	-	-
	dP_4	31.5	13.0							+	-	+	*	-
	M_1	28.6	19.5							+	-	-	-	-
1/12	lt. P_2	24.2 25.8	12.6 11.0	26.2						-	-	-	+	+
1/13	lt. P_4	22.4 24.4	14.2 14.2	45.3						-	*	-	*	-
1/548 (2+)	lt. M_3	25.2 21.3	10.9 10.4	40.8								-	+	-

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
2/___ (3)	lt. M_2	23.5	12.8							+	?*	-	*	+/-
4/108 (3)	rt. M_1	22.3 24.7	12.8 11.5	36.2						+	-	-	+	+
18/1447 (2)	lt. dP_3	27.0	11.2	10.0						+	+	+	+	+
18/1443 (2)	lt. dP_3	25.6	13.2	7.8						+	+	-	+	+
18/1441 (3)	lt. M_1	23.4	14.5	@35						-	*	-	+	-
18/1437 (3)	lt. M_1	23.0	25.4											
20/1706 (2)	rt. dP_4	32.8	13.8	14.6						+	*	-	*	+
20/1696 (3)	lt. M_2	19.4 23.0	11.4 9.9	36.2						+	+	-	-	+
7/1991 (3)	lt. P_2-M_2													
	P_{2-4}	79.9												
	P_2	28.6	17.6						-	*	+	*	-	+
7/2242 (3)	rt. P_{2-4}	82.6												
	P_2	26.4 29.3	14.7 18.5	29.2				-	+	-	*	-	+	+
	P_3	24.9 26.3	15.0 20.6	37.5						-	*	-	+	-
	P_4	23.2								-	*	-	+	-

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
7/2241 (3)	rt. M_{1-2}													
	M_1	24.1	16.3	35.7						+	-	-	+	-
	M_2	24.5	14.2	42.1						+	-	-	+	-
7/2318 (4)	lt. M_3	29.9	13.6	11.3						+	+	+	+	-
7/1957 (3)	rt. M_3	21.0 27.0	12.7 12.2	56.3						-	-	-	+	-
14/1562 (4)	lt. P_2	24.0	13.4	9.5				+	+	+	-	-	+	+
14/1557 (4)	lt. P_2	23.8	13.2	10.0				+	+	+	-	-	+	+
14s/1542 (3)	lt. M_1	20.4 23.4	12.7 13.8	42.2						+	-	-	+	+
14w/1546 (3)	rt. M_3	22.7 29.1	13.9 13.2	52.8						+		+	-	-
14/1547 (4)	rt. M_3	25.1	17.5	14.7										
40/2228 (3)	lt. P_2	25.1 28.6	13.0 13.2	33.6				-	+	-		-	+	+
40/2215 (3)	rt. P_4	21.9 25.3	13.2 14.7	45.0						-	**	-	+	+

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
40/2226 (3)	rt. M_1	20.6 24.3	11.6 13.0	43.8								-	+	+
40/2240 (3)	rt. M_2	19.9 23.9	13.2 13.8	39.3						+	-	-	+	+
37/2427 (1)	lt. mandible with dP_{2-4}													
	dP_2	31.2	12.7					-	+			-		
	dP_3	28.8	12.9									-	*	+
	dP_4	33.6	12.0							-	-	-	*	+
37/2084 (1)	rt. dP_3	29.4	23.4	10.5						+	-	-	*	+
37/2065 (2)	rt. dP_3	28.5	13.4	7.2						+	-	-	+	+
37/2416 (1)	rt. dP_3	28.4	12.0							-	-	-	+	-
37/2071 (3+)	rt. P_2	23.7	13.6 12.4	26.9					*	-	-	-	+	+
37/2076 (3)	lt. P_2	25.0 27.5	13.0 15.2	30.1				-	*	-	*	-	+	+
37/2083 (3)	lt. P_2	24.3 27.1	13.1 13.7	29.4				-	+	+	*	-	*	-
37/2088 (3)	rt. P_2	26.4 27.8	12.5 14.2	29.2				-	*	-	*	-	+	+
37/2066 (3)	rt. P_4	23.0 24.5	14.9 16.8	36.8						-	-	-	+	+

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
37/2398 (3)	lt. P_4	23.9 24.9	14.2 16.5	29.9						+	–	–	*	+
37/2179 (3)	lt. P_4	22.0	14.3	33.5						–	*	–	*	–
37/2068 (3)	rt. P_4	20.6 24.5	14.3 15.5	47.1						–	–	–	–	+
37/2043 (3)	lt. M_1	21.8 23.8	14.0 14.9	50.0						+	?*	–	*	+
13/2353 (2)	anterior mandible with rt. dP_{2-4} and lt. dP_{2-3}													
	rt. dP_{2-4}	86.5												
	dP_2	33.1	14.4	6.8										
	dP_3	26.1	14.5	5.2										
	dP_4	24.5	19.1	5.8										
13/1224 (3)	rt. P_{2-3}													
	P_2	27.3	14.7	9.2				–	*	–		+	+	+
	P_3	24.8	17.2	9.6						–	–	+	+	–
13/2265 (1)	lt. dP_2	33.7	10.8											
13/1516 (2)	rt. dP_4	29.5	14.3	16.5										
13/1728 (2)	lt. dP_2	36.4	20.5	19.7										
13/118 (4)	rt. P_2	24.4	14.5	13.4				+	+	–	–	–	–	+/–

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
13/1497 (3)	rt. M_1	20.5 24.1	14.1 17.6	39.6						-	-	-	+	-
13/1349 (3)	lt. M_2	19.7 22.0	13.0 14.8	38.1										
13/1439 (3)	lt. M_2	19.0 22.3	13.0 15.0	36.4						-	-	-	-	-
13/1727 (3)	lt. M_2	21.2 23.2	 12.7	36.8						+	-	-	*	-
31/1854 (2)	lt. dP_2	34.1	14.5	10.8						-	-	+	+	+
31/1900 (3)	lt. P_2-M_3													
	P_{2-4}	75.5												
	M_{1-3}	76.8												
	P_2	26.0	14.8					-	+	-	-	-	+	+/-
	P_3	25.2	16.5	34.5						-	-	-	+	+/-
	P_4	23.4	13.7	34.1						+	-	-	-	+
	M_1	24.5	17.5							-	-	-	+	+
	M_2	23.3	13.7	38.0						+	-	-	*	+
	M_3	26.1	11.1							+	-	-	*	+
31/1916 (4+)	lt. mandible fragment with P_2-M_2													
	P_2-P_4	65.3												
	P_2	26.4	11.7	9.2					-	+	+	+	-	+
	P_3	18.8	13.6	6.7							+		-	+
	P_4	21.1	14.2	9.5							+	+	-	-

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
31/1916 (cont.)	M_1	17.7	12.4	5.2							-	+	-	*
	M_2	19.7	11.9	5.9							-	+	-	*
31/2165 (3)	rt. mandible with P_3-M_3													
	M_1-M_3	70.3												
	P_3	25.8	19.2							-	-	-	+	+
	P_4	25.7	18.5							-	-	-	+	+
	M_1	21.6	15.2							+	-		*	+
	M_2	23.6	14.1							+	-		*	+
	M_3	24.6	13.0							+	-	-	+	+
31/1806 (3)	lt. M_2	@27	10.6							-	-	-	+	+
31/1892 (4+)	rt. M_3	25.3	12.4	13.6						-	-	+	+	+
25/1674 (1)	lt. dP_{2-4}	83.9												
	dP_2	31.1	10.2											
	dP_3	26.5	11.1											
	dP_4	26.7	9.9											
25/1610 (1)	lt. dP_2	32	13.7	16.6										
25/1612 (4)	lt. P_2	27.2	14.7	22.0				-	*	-		-	-	+/-
25/1612 (4)	lt. P_2	25.8	13.4	22.6										

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
25/1637 (4)	rt. M_3	26.6	12.2	16.7						+	-	-	*	+
25/1636 (4)	rt. M_3	25.8 25.0	10.6 12.5							+	-	-	-	+
25/1613 (3)	rt. M_3	23.6 21.7	10.0 10.8	32.9						+	-	-	-	+
25/1607 (4)	rt. M_3	26.6	11.1	19.7										
22/1636 (4)	lower lt. cheek tooth	24.6	17.9											
24/1640 (3)	lt. M_2	19.8 22.7	16.5 9.4	39.7										
38/2175 (2+)	rt. P_2	25.8 27.8	12.1 13.6											
38/2173 (3)	rt. M_2	20.3 25.4	12.0 13.0	38.7						+		-	*	+
26/1580 (2)	rt. dP_2	28.5	7.8	10.7										
26/1530	rt. dP_2	28.5	10.0											
26/2563 (2)	lt. dP_2	29.1	10.6	10.1				-	+	-	*	-	-	+/-
26/1828 (2)	rt. dP_4	24.9	13.1	7.0						+	-	-	+	+

TABLE 3 (cont.)

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
26/1568 (4+)	lt. P_2-P_4													
	P_2	25.1	13.5							-	-	-	-	+
	P_3	19.6	15.0							-	-	-	-	+/-
	P_4	18.4	15.5	10.0						-	-	-	-	-
26/1573 (3)	rt. mandible with P_4-M_3													
	M_1-M_3													
	P_4	22.3	12.8											
	M_1	20.9	12.9											
	M_2	18.6	11.0											
	M_3	22.3	9.6							+	-	-	*	+
26/2557 (4+)	lt. P_4-M_2													
	P_4	18.5	13.6	5.8						-	-	-	+	+
	M_1	16.1	12.8							-	-	-	+	+
	M_2	16.9	11.7							-	-	-	+	+
26/1640 (3)	rt. M_1	20.6	10.3	21.6						+	-	-	*	+/-
26/1591 (3)	rt. M_2	18.6	12.1	35.8										
		22.2	12.3											
26/1591 (3)	rt. M_2	21.4	12.0	31.4						+	-	-	+	+
26/1590 (3)	rt. M_2	17.0	12.4	49.4						-	-	+	*	-
		25.8	11.5											
26/1576 (3)	lt. M_3	24.5	10.8	33.3						+	-	-	*	+
26/1586 (4+)	lt. M_3			8.7						+	-	-	-	+
		25.0	11.8											

TABLE 3 (end)

TABLE 3 (Annex 1)
SUMMARY OF THE NUMBER OF PERMANENT MANDIBULAR CHEEK TEETH PER STRATIGRAPHIC INTERVAL.

STRATIGRAPHIC INTERVAL	P_2	P_3	P_4	M_1	M_2	M_3
24, 38, 26	2	2	3	3	7	3
21, 31, 25	4	3	3	3	3	7
37, 13	5	0	4	2	3	0
7, 14, 14w, 40	7	1	1	3	2	4
4, 1B, 1, 2, 18, 20	1	0	1	3	2	1
23, 36	0	0	3	0	0	0
41, 44	3	0	3	2	1	0
43	1	0	0	2	0	0
TOTALS	23	6	18	18	18	15

TABLE 3 (Annex 2)
VARIABILITY IN PERMANENT MANDIBULAR CHEEK TOOTH CHARACTER STATES PER STRATIGRAPHIC INTERVAL.

STRATIGRAPHIC INTERVAL	ECT. FLX.	PLI.	ECT. PAR.	LING. FLX.	MEC. MSTD.
24, 38, 26	P_s: - M_s: -,+	- -	- +(one)	-,+ -,*,+	+,+/, -,+
31, 25, 22	P_s: -,+ M_s: -,+	- -	-,+ -,+	0,*,+ -,*,+	-/+,+ -,*,+
37, 13	P_s: -,+ M_s: -,+	-,* -,*	-,+ -,-	-,*,+ -,*,+	-,+ -,+
7, 14, 14w, 40	P_s: -,+ M_s: +	-,*,**,+ -,+	-,* -,+	-,+ -,+	-,+ -,+
4, 1B, 1, 2, 18, 20	P_s: - M_s: +	-,* -,*	- -	*,+ -,*,+	-,+ -,+/-,-
23, 36	P_s: M_s:	-	-	*	+
41, 44	P_s: -,+ M_s: -,+	-,** -,*	- -	-,+ -,*	-,+ +
43	P_s: M_s: +	-	-	+,*	- +,+/-

TABLE 4
MEASUREMENTS AND CHARACTER STATE ANALYSIS OF METAPODIALS AND MEASUREMENTS OF ASTRAGALI AND CALCANEA IN THE LAKE REZAIYEH EXPEDITION SAMPLE.

Legend:
1 - 14 = measurements of AMNH Hipparionine Conference.
LGT. = Length: elongate: +; short = -.
SDIAM. = shaft diameter: gracile: +; robust = -.
SAG. KEEL = metatarsal distal sagittal keel: sharp extended crest: +; flat and rounded: -.
VENT. SURF. = ventral surface: deep: +; shallow: -.
DIST. PIT = deep: +; shallow: -.
MAG/HAM = magnum/hamate angle (metacarpals): slight: +; great: -.
LING. FLEX. = linguaflexid (enamel projection between metaconid and metastylid): shallow: +; U-shaped: *; V-shaped: -.
MCD/MSTD = metaconid/metastylid shape: rounded: +; angular: -.

Specimen \ Measurement	1	2	3	4	5	6	7
41/2492	52.5	52.5	48.8	25.4	37.9	30.9	44.0
44/2566				26.3	42.0	30.5	
3/48	53.6	55.4		25.0	42.3	33.0	44.8
4/107	48.0	49.3	47.4	24.6			
7/1913	58.5	59.0	50.3	30.6	45.2	36.4	50.3
14/1522	55.0	53.2	55.5			33.5	46.6
37/2415	46.4	45.6	42.8	20.1	36.0	36.0	39.2
13/____a	48.7	48.3	44.4	19.6	33.3	27.1	48.3
13/____b	47.5	45.6	43.3	21.3	35.0	27.0	38.6
13/1731	47.8	45.0	41.8	20.9	35.1	27.7	36.1
13/1366	48.7	48.8	46.9	21.2	37.0	28.8	40.6
13/1189	54.6	54.3	52.4	24.0	43.7	30.0	54.5
13/1228			51.2	26.2	40.8	30.6	
13/2321	49.2	49.0	43.2	18.7	34.0	29.1	48.0
13/1274	49.5	49.4	46.1	21.1	36.8	27.8	39.8
13/2548	46.9	45.9	44.6	22.8	34.6	28.6	36.6
13/____	50.9	50.8	48.6	20.9	37.3	31.2	50.8
25/1687	49.5	49.5	50.0	20.9	37.7	29.5	42.3
39/2375	52.7	47.8	50.3	23.0		28.6	40.5
26/2565	40.0	41.6	40.8	19.3	31.5	23.1	32.7
26/1677	40.0	40.7	39.2	18.5	32.8	29.5	33.7
26/1581	50.8	50.7	48.6	21.0	39.0	29.5	42.6

TABLE 4 (ASTRAGALI)

Specimen \ Measurement	1	2	3	4	5	6	7
41/2002				19.0	30.0	41.1	
1-A/1840			35.6	17.4			45.6
3/49	102	65.0	g44.7	20.5	27.0	42.9	42.3
4/107			@37.1	@15.5			39.1
4/1524				20.0			47.9
14/1553			42.7				42.9
13/___f	102.3		45.2	17.4	30.3	42.8	42.2
13/1194					31.0	40.3	
13/1385	97.9	67.5	37.3	15.5	25.3	41.1	41.0
13/___d	96.5	66.0	38.7	15.3	28.3	38.0	40.3
13/964					32.1	39.0	
13/___c							
31/1919			37.9				42.0
47/___	81.9	54.1	37.3	17.4	25.7	35.5	38.0
26/1882	81.3	54.2	29.4	15.7	23.7	32.0	33.8

TABLE 4 (CALCANEA)

SPECIMEN	1	2	3	4	5	6	7	8	9	10	11
20/1692 (MP)											28.3
14/1525 (MP)											31.5
37/2428 (MP)										35.5	34.8
13/120 (MP)										33.6	32.6
31/1899 (MP)										28.2	28.0
39/2373 (MP)										25.4	25.7
39/2382 (MP)											27.9
39/2371 (MP)										32.7	32.9
26/1821 (MP)										28.1	25.9
20/1698 (MT)										31.8	30.6
7/2302 (MT)					39.4	33.1	35.7	10.1	5.5		
7/2314 (MT)					38.3	34.0	33.4	11.1	6.7		
7/2147 (MY)					41.8	31.3	35.8	10.1	5.0		
13/1380 (MT)			20.4	21.0							
13/1384 (MT)			22.2	25.4							
13/1378 (MC)			24.6	22.5						32.7	33.4
13/1622 (MT)	254.1	253.4	23.2	25.0	37.3	31.0	33.7	12.3	4.9	33.5	31.6
13/1156 (MT)										30.7	31.8
13/RLB 26										30.9	33.5
13/___e (MT)	252.7	248.2	23.6	24.2	34.3	28.4	31.1	10.1	4.9	30.7	31.7
39/2374 (MT)					33.9	24.5	30.3	7.7	5.1		
39/2372 (MT)					36.6	33.0	34.9	7.3	6.7		
26/1681 (MT)					35.1	29.8	32.5	7.6	5.3		
20/1657 (MC)										30.8	31.0
20/1655 (MC)										32.0	31.0
7/1997 (MC)					43.0	34.9					
7/1995 (MC)										38.4	36.6
14/1529 (MC)										39.4	37.1
37/2194 (MC)			25.7	21.9	38.7	23.0	29.5	10.8 8.9	5.7		
37/2040 (MC)					37.8	26.3	33.0	10.0	6.1		
13/1154 (MC)					37.6	23.6	30.7	8.9 7.6	5.1		

TABLE 4 (METAPODIALS)

12	13	14	LGT.	SDIAM	SAG KEEL	VENT SURF	DIST PIT	MAG/ HAM
20.5	23.7				+			
28.9	23.7	25.2			+			
31.4	24.1	26.8			+	-	++	
@24	21.3	25.0			+		?	
26.1	21.0	22.7			+	-	+	
23.0	28.2	20.6			+	-	+	
26.6	20.5	20.2			+	-	+	
27.2	22.3	22.2			+	+	-	
24.4	21.6	23.5			+		+	
30.0	24.1	25.9			+		-	
						-/+		
						-		
			+	+		-/+		
			+	+		-		
27.4	23.7	25.3	+	+	+	+	-	
28.9	23.7	26.0	+	+	+	-	+	
	23.3	26.8			+	-	+	
30.0	23.4	26.7			+	-	+	
28.4	22.3	26.6	+	+	+	-	+	
						+		
						+		
						+		
26.3	22.0	22.1			-			
27.9	23.5	24.5			-/+		-	
						+		
29.6	23.4	27.3			+			
30.4	25.9	26.7			-	-	-	
			+	+		+		149°
								148°
								142°

TABLE 4 (end)

TABLE 5
SKULL MEASUREMENTS OF "*HIPPARION*" *GETTYI*, KOPRAN, LOWER MARAGHEH, SPECIMEN KNHM-RLB 8401 (ADULT).

Measurement		Measurement	
1	101.9	20	NA
2	@105.0	21	NA
3	NA	22	NA
4	NA	23	NA
5	NA	24	NA
6	NA	25	88.2
7	76.0	26	NA
8	62.1	27	NA
9	137.8	28	@45
10	NA	29	NA
11	NA	30	127.4
12	NA	31	133.7
13	NA	32	44.0
14	33.6	33	67.8
15	40.0	34	69.8
16	NA	35	39.3
17	NA	36	29.9
18	NA	37	32.0
19	NA	38	56.0

TABLE 6
MEASUREMENTS AND OBSERVATIONS ON MAXILLAE AND MAXILLARY CHEEK TEETH OF "*HIPPARION*" *GETTYI*.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
KNHM-RLB 8401 (4)	rt. P^2	31.1	23.6	23.2	+/*	+	+	-	+
	P^3	24.2	26.8	22.1	+/*	+	+	-	
	P^4	22.0	26.2	23.7	+/*	+	+	-	
	M^1	21.3	26.0	20.7	+/*	+	+	-	
	M^2	20.3	24.7	21.6	+/*	+	+	-	
	M^3	18.9	21.2		+/*	+	+	-	
KNHM - RLB 84 -	rt. P^4	24.3	27.1	13.0	NA	NA	NA	-	
	M^1	19.9	24.6	7.3	NA	NA	NA	-	
	M^2	20.5	24.4	10.0	NA	NA	NA	-	
	M^3	25.6	21.8	9.5	NA	NA	NA	-	
	M^1-M^3	66.8							
KNHM-RLB	lt. M^1-M^3	58.3							
	P^3	24.4	24.9	10.5	NA	NA	NA	-/+	
	P^4	22.1	25.0	10.5	NA	NA	NA	-/+	
	M^1	17.4	24.9	12.2	NA	NA	NA	-/+	
	M^2	19.5	23.4	10.0	NA	NA	NA	-/+	
	M^3	22.1	21.9	8.2	NA	NA	NA	-/+	

TABLE 7
MEASUREMENTS ON MANDIBLE OF "*HIPPARION*" *GETTYI*, SPECIMEN KNMH A4846.

Measurement		Measurement	
1	NA	8	NA
2	104.9	9	NA
3	@86.5	10	NA
4	76.7	11	69.6
5	164.5	12	NA
6	NA	13	72.5
7	44.6	14	30.5

TABLE 8
MEASUREMENTS AND OBSERVATIONS ON MANDIBLE AND INDIVIDUAL MANDIBULAR CHEEK TEETH OF "*HIPPARION*" *GETTYI*, SPECIMEN KNMH 4866, MANDIBLE WITH rt. I/1-I/3, C, P/2, l. I/1-I/3, C, P/2-M/3.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
KNHM A4866	lt. P_2-M_3	164.5												
MANDIBLE WITH RIGHT	P_2-P_4	@86.5												
$I_{\overline{1}}$ - $I_{\overline{3}}$, C, $P_{\overline{2}}$;	M_1-M_3	76.7												
LEFT $I_{\overline{1}}$-$I_{\overline{3}}$, C, $P_{\overline{2}}$-$M_{\overline{3}}$	P_2	29.4	13.5	NA						+	-	-	+	-
	P_3	28.3	16.6	NA						-	-	+	+	+
	P_4	27.5	16.4	NA						-	-	-	+	+
	M_1	25.2	14.5	NA						+	-	+	+	+
	M_2	25.9	12.8	NA						+	-	+	+	+
	M_3	24.7	10.4	56.5						NA	NA	NA	NA	NA

TABLE 9
SKULL MEASUREMENTS OF *HIPPARION PROSTYLUM.*

Measurement	KNHM A4847 3-	KNHM A4844 3-	JGUM MB 67 3	MNHM Mar. 18 3	MNHM Mar. 465 4	MNHM Mar. 359 3	AMNH 27807 3	AMNH 27809
1	44.0		104.2	90.6				
2		107.9	102.5	@103.5		114.5		
3								
4								
5								
6								
7	83.5	88.0	83.7	71.5	66.4	78.6	64.8	
8	70.4	68.4	66.2	64.8	55.8	65.5		
9	148.2	152.6	147.3	134.3	122.4	143.7		
10			47.1					
11	32.8	36.5						
12	39.1	40.7	@31.2					
13	@60	70.0	63.7	42.9		66.9		
14	30.8		36.9	36.0		59.7		
15			56.2	52.5				
16								
17								
18								
19								
20								
21								
22								
23			290.8					
24								
25			86.2			76.4		
26			99.8					
27								
28	@52.0					58.3		
29	@47.0		53.0			49.6		
30			123.9					
31	130		137.8			157.2		
32	36.5		36.1	g39		46.4	38	
33	62.0		57.0	46.8		62.7	46.4	
34	61.4							
35	37.4		35.1	27.9		36.0	28.0	
36	28.4	31.5	31.3	37.0	40.3	43.5	38.7	
37	39.5							
38	51.5		49.7	41.4		64.3	46.8	

TABLE 10
MEASUREMENTS AND OBSERVATIONS ON MAXILLAE AND INDIVIDUAL MAXILLARY CHEEK TEETH OF *HIPPARION PROSTYLUM.*

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
KNHM A4847 (3-)	P^2	33.5	25.1	@37	*	-	+	-	+
	P^3	26.4	27.0		*	-	+		
	P^4	23.4	24.8		*	NA	NA	*	
	M^1	23.3	23.3		*	-	+	-	
	M^2	@23.8	22.4		*	-	+	-	
	M^3	25.0	NA		*				
KNHM A4844 (3-)	P^2	35.4	25.9	@38	*	NA	+	*	
	P^3	28.1	27.6		*	+	+	*	
	P^4	24.9	27.0		*	+	+	*	
	M^1	23.2	23.4		*	NA	+	NA	
	M^2	24.0	22.5		*	NA	+	*	
	M^3	21.5	NA		NA	NA	NA	NA	
MB 67 (3-)	P^2	33.0	24.1	41.6	NA	NA	+	-	+
	P^3	27.5	26.4		NA	NA	++	*	
	P^4	25.5	25.1		NA	NA	++	*	
	M^1	23.7	24.2		NA	+	+	-	
	M^2	24.1	22.1		NA	NA	++	-	
	M^3	19.8	15.8		NA	NA	NA	NA	
MNHN Mar. 18 (3)	P^2	26.7	22.0	13.5	NA	NA	NA	NA	+
	P^3	22.8	24.2		NA	NA	*	-	
	P^4	21.0	24.5		*/-	-	*	-	
	M^1	19.7	25.0		NA	-	*	-	
	M^2	20.1	24.1		NA	-	*	+	
	M^3	24.3	22.0		*/-	?	+	-	
MNHN Mar. 465 (4)	P^2	27.2	20.0	8.3	NA	NA	NA	NA	
	P^3	19.9	24.4	6.1	NA	NA	NA	NA	
	P^4	17.9	23.1	10.1	NA	NA	NA	NA	
	M^1	16.5	23.8	6.8	NA	NA	NA	NA	
	M^2	16.7	22.9	7.6	NA	NA	NA	NA	
	M^3	19.9	22.0		NA	NA	NA	NA	
MNHN Mar. 359	P^2	31.2	21.8		*	NA	*	-	+
	P^3	25.7	25.2		*	+	*	-	
	P^4	23.1	24.9		*	+	*	-	
	M^1	21.0	23.9		*	?+	+	-	
	M^2	21.6	23.3		*	+	+	-	
	M^3	21.5	19.8		*	NA	+	-	

TABLE 11
SKULL MEASUREMENTS OF *HIPPARION CAMPBELLI.*

Measurement	UCR-MMTT 13/1342 3	UCR-MMTT 13/1343 2	UCR-MMTT 13/1291 2	Measurement	UCR-MMTT 13/1342 3	UCR-MMTT 13/1343 2	UCR-MMTT 13/1291 2
1	107.2	105.5		20			
2	111.6	95.7	104	21			
3	91.2	92.2		22		85.6	
4		84.0		23	295.0	289.0	
5		174.6		24		@150	
6		371.8		25	@89	83.8	
7	87.1	91.1	92.0	26	94.9	87.3	
8	68.3			27		7.0	
9	154.3			28	50.5	55.5	
10		60.0		29	49.8	40.0	
11	25.0	28.7		30	145.6	@151.7	
12	26.6	32.5	33.7	31	120.2	116.8	
13	44.3	48.6	53.5	32	34.0	35.6	A33
14	29.8	28.6		33	59.4	47.2	
15	39.8	@40.5		34	53.4		
16	70.9			35	40.0	30.9	@31.2
17		96.2		36	36.8	30.0	@32
18	123.8	114.2		37	55.7	@28.3	
19	138.4			38	61.2	49.0	48.2

TABLE 12
MEASUREMENTS AND OBSERVATIONS ON MAXILLAE AND INDIVIDUAL MAXILLARY CHEEK TEETH OF *HIPPARION CAMPBELLI.*

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
13/1342 (3)	P^2	34.8	23.1	34.1	*	-	**	-	+
	P^3	26.8	26.0		*	-	*	-	
	P^4	26.9	25.1		*	-	*	-	
	M^1	22.3	22.3		*	-	*	-	
	M^2	24.4	21.6		*	-	*	-	
	M^3	21.2	16.9						
13/1343 (2)	dP^2	36.2	22.3		-		-	+	+
	dP^3	27.3	23.9		-		-	+	
	dP^4	28.0	22.8		-		-	+	
	M^1	27.5	21.0						
13/1291	dP^2	39.0	21.4		-	-	-	+	+
	dP^3	26.9	24.8		*	-	-	+	
	dP^4	27.2	24.0		*	-	-	+	
	M^1	26.8	23.3		*	-	+		
13/1333 (2)	dP^3	27.3	25.2		*	+	-	+	
	dP^4	26.9	23.9		*	+	*	-	
	M^1	24.4	22.3			-		-	
	M^2			48.8					

TABLE 13
MEASUREMENTS AND OBSERVATIONS ON MANDIBLES AND INDIVIDUAL MANDIBULAR CHEEK TEETH OF *HIPPARION CAMPBELLI.*

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
MMTT 13//1341 (3)	I_1-M_3				+	+	-							
	P_2	29.6	15.7					-	-	-	-	-	+	-
	P_3	27.1	15.4							-	-	-	+	+
	P_4	26.6	15.6							-	-	-	+	+
	M_1	23.6	11.7							+	-	-	+	+
	M_2	23.5	11.4							+	-	-	+	+
	M_3	23.7	8.9							+	-	-	+	+
MMTT 13/1376 (4+)	I_1-M_3				+	+	*							
	P_2	26.8	14.3					+	-	-	-	-	+	-
	P_3	20.9	17.8							-	-	-	-	-
	P_4	21.0	18.2							-	-	-	-	-
	M_1	17.2	15.2							+	-	-	*	-
	M_2	17.3	14.6							+	-	-	*	-
	M_3	26.2	11.7							+	-	-		-
MMTT 13/2353 (2)	dP_{2-4}				?+	?+	?*							
	dP_2	33.3	13.2					-	*	-	-	-	+	+
	dP_3	25.0	14.3							-	-	-	+	+
	dP_4	25.2	15.4							-	-	-	+	
MMTT 13/1289 (2)	dP_{2-4}, M_1													
	dP_2	30.7	15.0					-	+	-	-	-	+	+
	dP_3	24.8	15.6							-	-	+	+	+
	dP_4	27.3	14.2							+	-	+	*	+
	M_1	26.9	11.6							-	-	-	-	-

TABLE 14
MEASUREMENTS ON SKULLS OF "*HIPPARION*" AFF. *MOLDAVICUM*.

Measurement	KNHM -RLB 8402 (4)	KNHM A4848 (4)	KNHM -RLB 8403 (3+)	KNHM -RLB 8404 (2)	KNHM -RLB 7914 (3+)	KNHM -RLB 7915 (3)	KNHM -RLB 8001 (4)	KNHM -RLB 8402 (4)	KNHM -RLB 8403 (4+)	KNHM -RLB 8404 (3)	KNHM 3924 (3-)
1											@91
2											@96.5
3											
4											
5											
6											
7	69.1	75.1	69.9	81.7		69.8		@74	70.5	87.7	80.3
8	58.0	64.6	59.6		69.8	58.1	60.5	61.3	57.0		66.3
9	126.3	138.8	120.0			127.3		134	126.6		141.3
10											
11											
12											@22
13	@52.7				56.4			@56.7	57.5		51.2
14											29.4
15											41.3
16											
17											
18											
19											
20											
21											
22											
23											271.8
24											
25						85.9					77.5
26											
27											
28					@57	@53	49.3		@57		g48
29					51.5	50.5	g44.4	51.8	g46.5		@50
30											111.5
31						139.5					132.2
32	24.5				29.2	23.6	25.1	29.8	@24		25.8
33	@68				77.9	79.9	71.6	74.0	?63.5		64.4
34						69.6	61.1				
35					54.2	51.9	46.7	@46.5	@42		48.5
36	12.2	16.3	16.8	11.1	21.1	19.0	16.5	@21.5	@18.5		@21.2
37						38.4	43.1				39.3
38	35.5				50.0	48.5	43.3	46.4	g33		46.0

TABLE 15
MEASUREMENTS AND OBSERVATIONS ON MAXILLAE AND INDIVIDUAL MAXILLARY CHEEK TEETH OF "*HIPPARION*" AFF. *MOLDAVICUM*.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
BMNH 3924 (3-)	rt. P^2	32.1	24.4	37.7	*	+	NA	+	-
	P^3	25.0	26.6	@43.3	+/*	+	+	-	
	P^4	23.7	25.1		+/*	+	+	-	
	M^1	22.7	23.6		+/*	+	*	-	
	M^2	23.1	23.5	@44	+/*	-	NA	*	
	lt. M^3	@23.0	14.9		NA	NA	NA	NA	
KNHM-RLB 8402 (4)	rt. P^2	28.1	21.9		-	-	NA	+	+
	P^3	20.9	23.4		-	-	NA	-	
	P^4	20.2	24.1		-	-	NA	-	
	M^1	16.8	21.9		-	NA	NA	-	
	M^2	18.3	21.1		*	-	-	-	
	M^3	21.4	19.8		*	+	-	-	
KNHM A4848 (4+)	lt. P^2	30.6	24.0		NA	NA	NA	-	+
	P^3	22.8	27.5	25.2	NA	-	NA	-	
	P^4	23.0	29.0	14.6	NA	-	NA	-	
	M^1	20.1	25.9		NA	-	-	-	
	M^2	20.4	23.8		*	-	-	-	
	M^3	26.0	22.4		*	-	*	-	
KNHM-RLB 8403 (4)	rt. P^2	27.9	22.1		*	NA	*	+	+
	P^3	21.7	24.0		*	+	-	+	
	P^4	20.1	23.5		*	+	-	+	
	M^1	19.4	21.1		*	+	-	+	
	M^2	19.1	20.8		*	+	-	+	
	M^3	20.1	18.5		*	-	*	+	
KNHM-RLB 8404 (2)	lt. dP^2	32.1	22.5		*		-	+	+
	dP^3	29.5	23.0		*	+	-	+	
	dP^4	25.5	21.6		*	NA	-	-	
	M^1	24.5	20.7		NA	NA	NA	-	
MNHN-RLB 7914 (3+)	rt. P^3	26.3	26.9		*	-	-	+	
	P^4	23.9	25.7		*	-	-	*	
	M^1	23.1	24.9		*	-	*	*	
	M^2	22.7	23.7		*	+	*	*	
	M^3	24.8	20.8		*	+	+	*/-	

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
MNHN-RLB 7915 (3)	lt. P^2	26.4	21.0	25.3	*	-	*	+	
	P^3	22.1	23.0		+	-	*	+	
	P^4	21.2	22.4		*	-	*	+	
	M^1	16.3	21.2		*	-	*	+	
	M^2	19.4	20.6		*	NA	*	+	
	M^3	20.1	18.3		*	-	*	+	
MNHN-RLB 8001 (4)	lt. P^3	22.1	24.2	19.7	NA	+	-	+	
	P^4	19.9	24.5	21.0	NA	+	-	-	
	M^1	19.1	23.5		NA	-	-	+	
	M^2	20.0	21.9		NA	NA	*	-	
	M^3	21.0	19.8		NA	NA	*	-	
MNHN-RLB 8002 (4)	rt. P^2	NA	23.3		*	-	-	+	NA
	P^3	23.0	25.0		*	+	-	+	
	P^4	21.6	25.4		*	+	-	+	
	M^1	20.6	21.8		*	-	-	+	
	M^2	20.8	22.1		*	-	*	+	
	M^3	21.5	20.0		*	-	*	+	
MNHN-RLB 8003 (4)	lt. P^2	28.5	22.5		-	-	NA	+	+
	P^3	21.2	24.7		-	-/+	NA	+	
	P^4	19.7	24.0		-	-/+	-	+	
	M^1	18.2	23.3		-	-	NA	+	
	M^2	18.4	22.4		-	-	-	+	
	M^3	20.0	19.9		-	-	*	+	

TABLE 15 (cont. & end)

TABLE 16
MEASUREMENTS AND OBSERVATIONS ON MANDIBLES AND INDIVIDUAL MANDIBULAR CHEEK TEETH OF "*HIPPARION*" AFF. *MOLDAVICUM*.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
KNHM A4845 (3+)	rt. P_2-M_3	165.8			NA	NA	NA							
	P_2-P_4	85.6												
	M_1-M_3	81.7								-	-	-	+	+
	P_2	32.0	17.7							-	-	-	-	+
	P_3	27.3	19.8							-	-	+	-	+
	P_4	26.4	21.1							+	-	-	*	-
	M_1	26.4	17.9							+	-	-	*	-
	M_2	26.5	17.5							+	-	-	*	-
	M_3	31.2	15.5							+	-	+	*	-

TABLE 17
SKULL MEASUREMENTS OF "*HIPPARION*" *?MATTHEWI*, SPECIMEN G.I.U. P-100/1958 (2 +).

Measurement		Measurement	
1		20	
2	@92	21	
3		22	
4		23	
5		24	
6		25	
7	66.9	26	
8	@55.5	27	
9	@121.9	28	
10		29	
11		30	
12		31	
13	41.9	32	26.9
14		33	58.1
15		34	?48.4
16		35	35.6
17		36	22.5
18		37	?30.5
19		38	44.6

TABLE 18
MEASUREMENTS AND OBSERVATIONS ON MAXILLARY AND INDIVIDUAL MAXILLARY CHEEK TEETH OF "*HIPPARION*" *?MATTHEWI*, SPECIMEN G.I.U. P-100/1958.

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	FOSS	PLI	HYP	PR	P2
	P^2	25.9	18.5		-		+	+	
	P^3	21.8	20.3		-	-	+	+	
	P^4	19.8	19.7		-		+		
	M^1	21.1	19.3		-	-	-	+	
	M^2	19.6	17.1		-	-		*	
	M^3								

TABLE 19
MEASUREMENTS AND OBSERVATIONS ON MANDIBLES AND INDIVIDUAL MANDIBULAR CHEEK TEETH OF "*HIPPARION*" *?MATTHEWI.*

SPECIMEN AND AGE	ELEMENT	LENGTH	WIDTH	HEIGHT	CAN. POS.	SNT. LNGT.	MENT. FORM.	P_2 ANT.	P_2 MET.	ECT. FLX.	PLI	ECT. PAR.	LING. FLEX.	MEC. MSTD
KNHM-RLB 8405 (3)	lt. P_2-P_4	68.4			NA	NA	NA	–	*					
	P_2	24.7	13.6							–	–	–	+	*
	P_3	21.4	14.7							–	–	–	*	+
	P_4	21.2	14.6							–	–	–	*	+
	M_1	20.5	13.7							+	–	–	*	+
	M_2	20.5	12.5							+	–	–	–	+
KNHM-RLB 8406 (3)	lt. P_4-M_2				NA	NA	NA	NA	NA					
	P_4	19.4	14.4	@30						+	–	–	*	+
	M_1	16.7	12.7							+	–	–	*	+
	M_2	17.4	11.5							+	–	–	*	+
KNHM-RLB 8407	rt. M_{1-2}				NA	NA	NA	NA	NA					
	M_1	18.2	13.5	@21.5						+	–	–	*	+
	M_2	18.4	12.7							+	–	–	*	+
KNHM-RLB 8408	lt. M_{1-2}				NA	NA	NA	NA	NA					
	M_1	17.6	14.5	@14.0						+	–	–	NA	+
	M_2	18.1	13.1	@15.1						+	–	–	NA	+

TABLE 20
MEASUREMENTS AND CHARACTER STATE ANALYSIS ON THE METAPODIALS OF "*HIPPARION*" *?MATTHEWI.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	LGT	SDIAM	SAG KEEL	VENT SURF	DIST PIT	MAG/HAM
KNHM A4837 (MC)	205.1	198.4	22.5	20.0	33.5	24.0	28.5	9.3	3.3	31.2	29.6	24.9	20.6	22.9	+	++	+/-	+	++	143