

MAMMALIAN BIOSTRATIGRAPHY, GEOCHRONOLOGY, AND ZOOGEOGRAPHIC RELATIONSHIPS OF THE LATE MIOCENE MARAGHEH FAUNA, IRAN

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ABSTRACT—The classical Late Miocene Maragheh fauna has been collected and studied sporadically for nearly 150 years. This study gives a comprehensive account of the entire mammalian fauna recovered at Maragheh to date and its biostratigraphic, biogeographic and geochronologic contexts. The sequence is divided into Lower, Middle and Upper biostratigraphic intervals, ranging from ca. 9.5 my to 7 my in age, based on the first appearance of a potential evolutionary series of hipparionine horses: "*Hipparion*" *gettyi*, *Hipparion prostylum*, and *Hipparion campbelli*. Stratigraphical ranges of individual mammalian species are given, and biostratigraphic intervals are characterized. A comprehensive zoogeographic analysis of the entire Maragheh mammalian fauna shows its relationships with late Miocene-early Pliocene "savanna-mosaic" assemblages of Eurasia and Africa. It has been found that the Maragheh genera which have the broadest geographic distribution were part of a late early Miocene pan-Eurasian and African dispersal event. Their subsequent diversification may be attributable to biogeographic vicariance with both tectonic and paleoenvironmental factors playing contributing roles.

HISTORICAL BACKGROUND

The fossil vertebrate horizons of Maragheh, in Azerbaijan, Northwest Iran, are among the most renowned of Palaearctica. Maragheh, the name currently used for these deposits (in lieu of Maragha), also has long been used to designate one of the classical "Pontian" savanna-like faunas of Eurasia. Khanikoff, a Russian explorer who visited Iran in 1840, has been credited as being the first to collect fossil vertebrates from the Maragheh district. The Khanikoff collection was sent to Dorpat University (now Tartu University, Estonia) and initially studied by Abich (1858) who reported the occurrence of a fossil proboscidean tusk, remains of fossil "cervids" and horses. Further studies of this collection were made by Brandt (1870) and Grewingk (1881). They presented a more extensive faunal list, reporting the occurrence of *Hipparion*, "*Rhinoceros tichorhinus*", "*Mastodon*", *Helladotherium*, and "*Tragocerus*," and suggested a close faunal correlation with the Pikermi fauna, near Athens, Greece.

In 1884 an Austrian paleontologist, Pohlig, was invited by a merchant from the nearby city of Tabriz to make a geological tour of Persia. He visited Maragheh and made the first comprehensive paleontological and geological studies of the deposits. Pohlig (1886:178) reported: "The fossil bones have been found in the reddish marls at more than six places, at greater or less distances from the city (up to 30 miles) and at different horizons, which, however, do not differ from each other by age and characteristics of the mammalian fauna". Pohlig further noted that there were two stratigraphic

units, the "Pliocene fossil-bearing beds which were fluvio-lacustrine in their origin, and overlying unfossiliferous pebble beds, boulders and blocks of earliest Pleistocene age". He reported an extensive mammalian fauna including: "*Hipparion gracile*", "*Onager*" sp., "*Rhinoceros persiae*", "*Rhinoceros blanfordi*", "*Mastodon*", "*Sus*" sp., *Gazella brevicornis*, *Antelope* sp., "*Bubalus*" sp., "*Cervus*" sp.; *Helladotherium* sp., "*Giraffa attica*"; *Felis brevicornis*, "*Hyaena*" cf. *eximia*; "*Canis*" sp. Pohlig sent most of his collection to the private museum of Professor Von Fritsch at Halle, Germany.

In 1885 two other Austrians, Rodler and Kittl, visited Maragheh and made an extensive collection of fossils under the sponsorship of the Kaiserliche Naturhistorisches Hofmuseum Wien. Kittl (1885) reported a number of vertebrate localities from the Maragheh basin including Kopran, Kopran-Mescha, Zad Baschin, Rasat, and Ketschawa. Their collection was subsequently studied and published by Kittl (1887), Rodler (1890), Rodler and Weithofer (1890) and Schlesinger (1917). These reported fossil occurrences further promoted the faunal resemblance of Maragheh with that of Pikermi.

In 1886, Lydekker wrote a very brief communication on Maragheh fossils collected by Damon of the British Museum (Natural History). Lydekker confirmed the importance of Maragheh for correlation not only with Pikermi and Samos, but also a western extension of the Siwalik faunas. In 1893 Forsyth Major, who had studied the Samos vertebrate fauna, reported a tooth of *Orycteropus* from these same British Museum (Nat. Hist.) collections. In 1889, Gunther collected a small

sample for the British Museum (Nat. Hist.) from one locality, Kirjawa.

In 1897, the French paleontologist Marcellin Boule established a liaison with J. de Morgan (a foreign delegate in Persia) and secured permission to conduct a paleontological expedition to Maragheh. In 1904, a group of French paleontologists assisted by 12 local laborers excavated a large sample of Maragheh fossils from a number of localities including Kirdjawa on the Murditchai River, Kingir, Kopran, Shollovend, Kermedjawa, and a hill just west of the town of Maragheh (Mecquenem, 1924–25:135). R. de Mecquenem, a member of the expedition, undertook the study of this large collection, initially publishing two brief communications (1905, 1906). In 1908 and 1911 he published a preliminary inventory of the collection and finally, having been delayed by World War I, Mecquenem published a monograph (1924–25) on this very fine collection. In his monograph, Mecquenem described 7 families, 26 genera, and 32 species of fossil mammals, and 2 genera of fossil birds. The collection is still preserved in the Museum National d'Histoire Naturelle, Paris.

More than 50 years elapsed before additional reported collections were made at Maragheh. In the autumn of 1956, Takai of Tokyo University, Japan, visited Maragheh and collected fossils from a locality named Kerjabad (Takai, 1958). In 1967, Tobien of the Johannes-Gutenberg University, Mainz, Germany, made some important excavations of the middle portion of the Maragheh sequence (Tobien, 1968). During the 1970's, three scientific groups conducted paleontologic, stratigraphic and geochronologic studies of the fossiliferous sequence. A combined Dutch-German group directed by Erdbrink visited Maragheh from August until November, 1973. They collected a small sample of Maragheh fossils, a number of volcanic tuff samples for radiometric dating, and some paleomagnetic samples for local stratigraphic studies. A joint University of Kyoto-Geological Survey of Iran expedition directed by T. Kamei visited Maragheh from September to November, 1973. They made an extensive collection of vertebrate fossils from one locality and sampled some nearby volcanic tuffs for fission-track dating. The Lake Rezaieyeh Expedition, a joint University of California at Los Angeles, and National History Museum of Iran project directed by Campbell, worked at Maragheh during the spring of 1974 and summers of 1975 and 1976 (Campbell et al., 1980). The program of the Lake Rezaieyeh Expedition included studies of mammalian systematics, physical stratigraphy, sedimentology, biostratigraphy, biochronology, paleoecology, and radiometric dating. Another field season was planned for the summer of 1978 to continue all aspects of the program, but was cancelled because of political unrest in Iran.

The geological and paleontological investigations of Maragheh during the past 25 years have appreciably advanced our knowledge of this very important late Miocene fauna. Precise locality information had not

been documented prior to these studies. However, information provided both in publications, and offered by Tobien and Erdbrink, led to the development of the first biostratigraphy of the Maragheh deposits (Bernor, 1978; Bernor et al., 1979b; Campbell et al., 1980). Nevertheless, the age of the Maragheh fauna has been an issue of some recent debate. Erdbrink et al. (1976) reported at least four distinct faunal horizons ranging from "Vindobonian" to medial Turolian age, and substantiated their claim with a radiometric age bracket of 12.9 to 7.5 my. Kamei et al. (1977) claimed a short chronologic range of 6.9 to 6.6 my for the Maragheh fossil horizons. Campbell et al. (1980) and Bernor et al. (1980) reported the results of 28 fission track and potassium-argon determinations of the Maragheh Formation and underlying basal tuff. These included four of the five horizons dated by Erdbrink et al. (1976), three of the five horizons dated by Kamei et al. (1977), and spanned all but the upper seven meters of fossil localities found by the Lake Rezaieyeh Expedition. The radiometric determinations, coupled with biochronologic correlations, suggest an age range for this fauna of approximately 9.5 to 7 my.

This paper reports the results of systematic, biostratigraphic and zoogeographic studies of the Maragheh mammalian fauna undertaken by the author since 1974. Biostratigraphic information has been assembled from a combination of field and archival research. Solounias (1981) provided systematic studies of the Bovidae and Hyaenidae, and a similar synopsis of the entire vertebrate fauna from Samos and Pikermi, as well as essential background on classical "Pontian" large mammal faunas. Finally, it should soon become apparent to the reader that this paper is not meant to complete research at Maragheh. Maragheh remains one of the richest Miocene vertebrate localities in the world for preservation of diverse and abundant fossil remains, long stratigraphic interval, and potential for close geochronologic control. Completion of research along these lines will require years of study by a diverse group of geologists and paleontologists. The Maragheh basin has the potential for establishing a provincial mammalian systematic and geochronologic standard for southwest Asia.

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 Universität, Mainz.

KNHM—Naturhistorisches Museum, Vienna.

MNHM—Muséum National d'Histoire Naturelle, Paris.

UCR—University of California, Riverside, Department of Earth Sciences.

hipparionine—an informal taxonomic rank referring to equid species belonging to any of the following

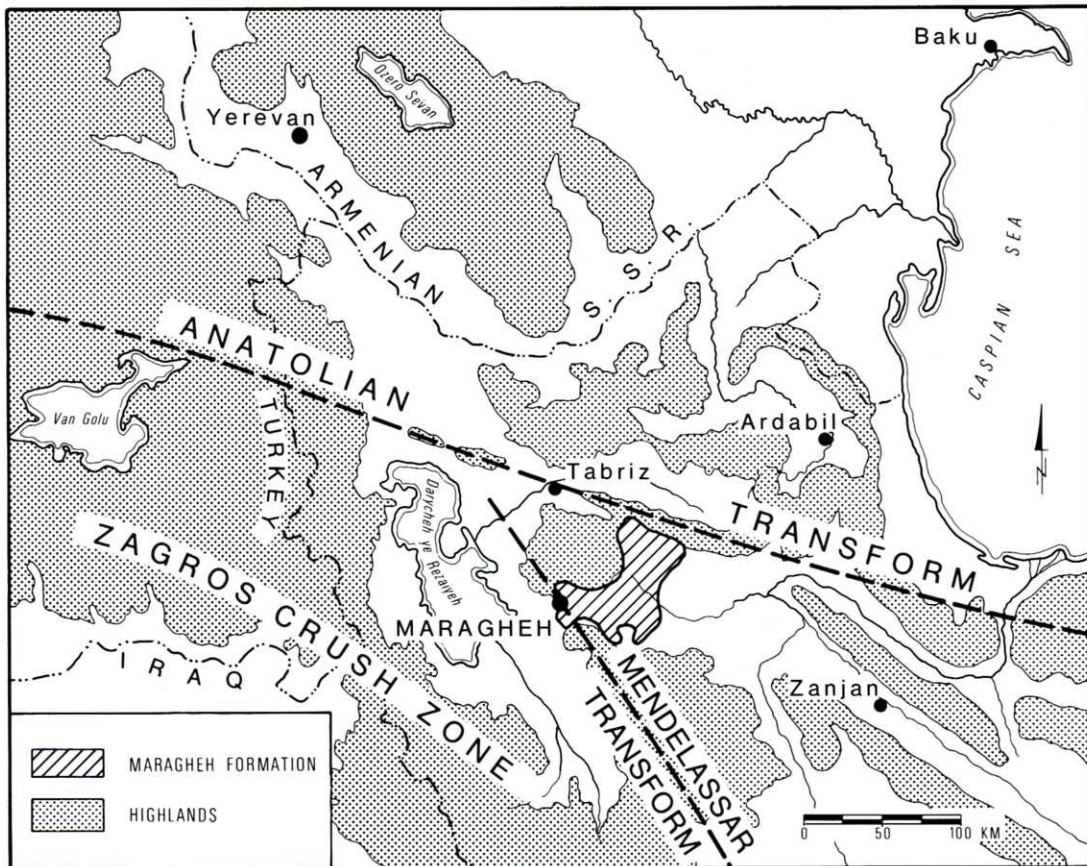


FIGURE 1. Relationship of the Maragheh Formation to the Mendelassar and Anatolian Transform Faults of the Eurasian Plate.

genera: *Hipparion*, *Neohipparion*, *Nannippus*, *Cormohipparion*, *Proboscidipparion*, "*Cormohipparion*" (*Sivalhippus*), *Stylohipparion*.

"*Hipparion*"—following MacFadden and Woodburne (1982), Bernor and Hussain (1984) and Bernor (1984): Old World hipparionine horses with facial morphologies that differ from either *Hipparion* or *Cormohipparion* (includes groups 1, 2, and 3 of Bernor and Hussain, 1984 and Bernor, in press).

GEOLOGY

The geological context of the classical Maragheh fossil district has only recently been described adequately (Erdbrink et al., 1976; Campbell et al., 1980; Bernor et al., 1980). The Maragheh stratigraphic sequence accumulated on the southern flank of the Mt. Sahand volcanic massif, which is a large complex structure approximately 100 km in circumference. Despite its nearly circular outline, Mt. Sahand is not a single volcano, but rather a series of distinct cones arranged along an east-west system of fissures and vents, including several parasitic cones. Erdbrink et al. (1976) observed that eight high points can be seen looking

southeast from the city of Tabriz, the highest being Quch Goli Dagh (3703 m). They further noted that the eastern sector of the massif seems to have been subjected to erosion for a longer time than the western sector. Campbell et al. (1980) and Bernor et al. (1980) described the lithology, stratigraphy and sedimentology of the Maragheh Basin, which is summarized as an introduction to the biostratigraphy. For more detailed presentations of the geology, the reader is referred to these studies.

The late Miocene deposits of the Maragheh Basin consist of a thick sequence of volcanoclastic continental strata with a basal pyroclastic unit on the southern and eastern sides of the Sahand volcanic massif. On the southern side, these strata show a virtually undeformed, very gentle inclination to the west-southwest. To the northeast, where these strata are bound by the Anatolian Transform Fault (Bernor et al., 1980; Fig. 1, this paper), they are thrown into a steep monoclinical fold that dips away from the fault. While Kamei et al. (1977) termed the entire late Miocene section of the Maragheh Formation, Campbell et al. (1980) restricted this name to the volcanoclastic series, and distinguished

a basal pyroclastic unit, the Basal Tuff Formation, on lithological grounds (Fig. 2).

The fossil-bearing sequence of Maragheh is confined to the lower 150 m of the approximately 300 m thick Maragheh Formation, which is overlaid by thick Quaternary terrace sediments informally named the Kerajek Formation (Campbell et al., 1980). The Maragheh Formation has been lithologically characterized by J. A. Van Couvering as containing strata consisting exclusively of detrital fragments of hornblende, andesite lava and pumice, interbedded at widely spaced intervals with layers of pumice-lapilli tuff (Van Couvering in Campbell et al., 1980). The Basal Tuff Formation apparently represents a single airfall unit of rhyolite tuff with a local thickness of over 80 m. The unit is a uniform, unbedded, structureless deposit of white, devitrified ash with many randomly oriented crystals of mica and fresh fragments of feldspar and quartz (Campbell et al., 1980).

Between the northwest sector of the Sahand Massif and the city of Tabriz, sedimentary strata are exposed that are unlike the Maragheh Formation (Fig. 2). These beds consist of diatomaceous silts containing fish and mollusk remains, with minor volcanic sands and gravels. The Sahand Massif is bounded to the west by a large, very shallow lake, Lake Rezaiyeh, which has a surface area of some 5000 km and an average depth of 7 m (Erdbrink et al., 1976). The western Sahand Massif extends to Lake Rezaiyeh and consists of andesitic and trachytic volcanics and extensive deposits of layered travertine. The limits of the Maragheh Formation appear to be: 1) the base of the Sahand Massif, on the northwest; 2) the Mendelassar Ridge, an uplifted fault-block consisting of lightly metamorphosed Mesozoic carbonates and phyllites, on the southwest; 3) an erosional feather-edge, beyond which there are exposures of underlying sparsely exposed altered Eocene volcanics, on the south and east; and 4) a probable continuation of an exposure area of unknown extent that may be bounded in part by uplift of the Anatolian Transform Fault, to the north and east (Fig. 1). Contrary to Erdbrink et al. (1976), Campbell et al. (1980) reported that lithologic horizons can be traced over wide areas allowing intrabasin lithologic correlations (see also Kamei et al., 1977). The most distinctive unit in correlation is a diamictic breccia named "Loose Chips" found in the central portion of the study area (Fig. 2). Stratigraphic correlation of vertebrate localities in the central area is considered very reliable by Campbell et al. (1980).

The Basal Tuff Formation represents a tremendous pyroclastic event which has also proven to be useful for long-range intrabasin correlations. In addition to its substantial outcrops northeast and southeast of the town of Maragheh, additional outcrops of this tuff were observed at Eshrat Abad, Tozejan, Davazim, Suma Pa'in, and Rodler's old locality of Ilkhchi. While the late Miocene Maragheh deposits are generally flat-lying, Campbell et al. (1980) reported that the Maragheh Formation seems to rest on the Basal Tuff with a low-

angle regional unconformity. Triangulation from the presently known exposures of Basal Tuff indicates a consistent dip to the west-southwest with a general inclination of about 15 m/km, steepening slightly near the town of Maragheh.

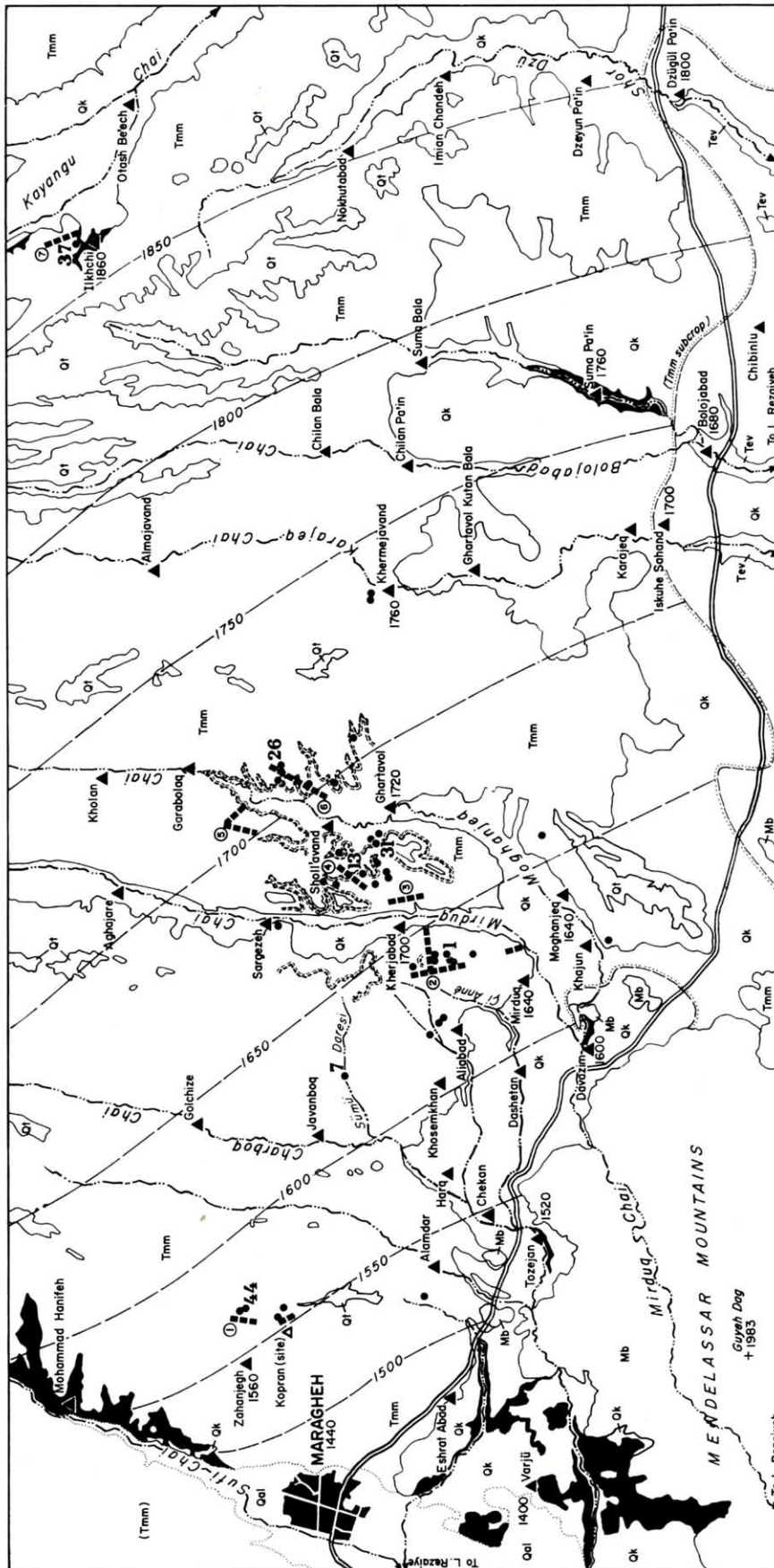
Detailed stratigraphy in the central fossiliferous area, in the lower drainage of Mordaq Chai and Morganjeg Chai, suggest that the regional dip of the Maragheh Formation is also to the west-southwest, but is virtually horizontal, about 5 m/km. The differences in dip between the two units suggested to J. A. Van Couvering (in Campbell et al., 1980; Bernor et al., 1980) that the Basal Tuff draped over a west sloping paleoslope/basin that was gradually filled by the Maragheh Formation, the successive beds prograding eastward as base level rose. This interpretation generally has been supported by radiometric (Campbell et al., 1980) and biostratigraphic (Bernor, 1978; Bernor et al., 1979b; Bernor et al., 1980) evidence. These data further strongly suggest that the beds farthest to the west, and fossils which they contain (near Kopran), were the earliest to have been deposited, whereas Ilkhchi, the easternmost locality, correlates to the younger localities in the central area, although it lies directly on the Basal Tuff. Figure 3 presents our current understanding of the physical stratigraphy of the Maragheh Basin.

J. A. Van Couvering, Dickenson and Morris (in Campbell et al., 1980) have studied the sedimentologic aspects of the Maragheh Formation and distinguished four major sedimentary facies: 1) a pebble and cobble conglomerate constituting less than 5% of any stratigraphic section in the study area, 2) a gray sandstone and breccia facies which makes up about 25% of most measured sections, 3) poorly sorted massive siltstones which constitute about 70% of the Maragheh strata, and 4) airfall tuff deposits that are almost entirely composed of pumice fragments located in various levels of the section. They interpreted the four facies to represent five geologic events, from base upwards: 1) erosion by small streams to produce a small disconformity; 2) deposition of coarse clastic sediments (cobble to medium sand) by lateral accretion in point bar deposits; 3) deposition of fine clastic material (silts and muds) by vertical accretion in overbank deposits; 4) alteration of the upper part of the fine-grained clastic sequence by soil-forming processes; 5) random airfall deposition of pumice blanketing the entire alluvial basin, which affected the local depositional processes to some extent by temporarily killing vegetation, choking streams, and absorbing rainfall rather than shedding it. The authors believe that these processes built the extensive Maragheh Formation as a product of alluviation, rather than volcanic activity or lacustrine sedimentation.

FAUNA

Biostratigraphy

Although many paleontological expeditions have taken place, the Maragheh mammalian biostratigraphy has only recently been adequately developed. Pohlig



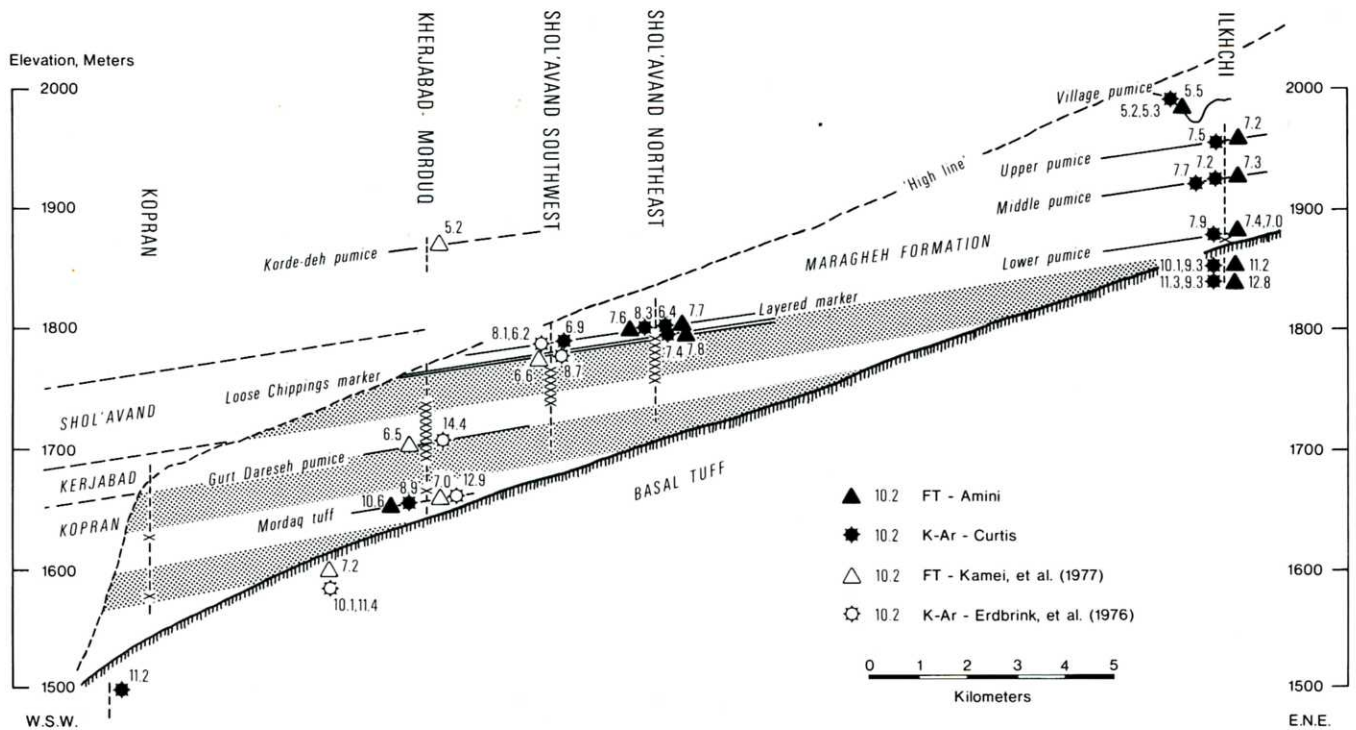


FIGURE 3. Stratigraphic array of isotopic age determinations from the Maragheh Formation and Basal Tuff. Refer to Table 3 for sample documentations.

(1886) was the first to recognize that fossil bones in the Maragheh region can be collected from several horizons. Rodler (1887), who collected at least 50 localities throughout the Maragheh Basin, did not believe that recording their stratigraphic occurrence was important. Mecquenem (1908) claimed that there were two distinct fossil-bearing horizons with no differences in the faunas. Tobien (1968), and later Erdbrink et al. (1976) have argued for three or four distinct fossil-bearing horizons, with several meters of barren strata separating them. Use of the "Loose Chips" and Basal Tuff marker beds (Campbell et al., 1980) has afforded an accurate correlation of several fossil vertebrate localities in the Maragheh Basin ("Loose Chips" was also used by Kamei et al., 1977, but was not related to so many localities as by Campbell et al., 1980). However, the "Loose Chips" marker bed is limited in its lateral extent and the Basal Tuff is exposed only in a few places

across the basin. Furthermore, as noted above, biostratigraphic information suggests that the northeastern-most vertebrate locality of Ilkhchi, in beds that unconformably rest upon the Basal Tuff, is substantially younger than those localities found on the presumed same tuff in the southwestern portion of the basin.

The mammalian faunal composition compiled here (Table 1) is based on a number of sources including:

- X: taxa collected by the Lake Rezaiyeh Expedition
- 1: taxa collected by the KNHM
- 2: taxa collected by Erdbrink et al., Laboratory for Zoological Ecology and Taxonomy, Utrecht University
- 3: taxa collected by Kamei et al., Department of Geology, University of Kyoto
- 4: taxa collected by Mecquenem, MNHN

FIGURE 2. Geographic Sites and Fossil Localities of the Maragheh Basin, N.W. Iran. Contours on the upper surface of the Basal Tuff strike N-NW. Data points for elevations are Ilkhchi, Suma Pa'in, Davazim, Eshrat Abad, and Maragheh. Three point solutions of attitude from these points indicate a moderate flexure near Maragheh, in the vicinity of the Mendelassar trend, and small faults (not shown) displace the lower Maragheh beds near Koprán. Heavy dashed lines represent the sections shown in figure 6 of Bernor et al. (1980). Dots are fossil localities (some represent more than one). The 7 major localities (1, 31, 37, etc.) are shown by heavy numbers. Circled numbers (1-7) correspond to the stratigraphic columns of figure 6 of Bernor et al. (1980). Mb: Pre-Tertiary basement. Tev: Eocene volcanic rock. Tmm: Maragheh Formation (Basal Tuff shown in black). Qk: Kerajek Beds (alluvial). Qt: Uppermost terrace gravel.

TABLE 1. Maragheh mammalian species.

Mammalian species	Collection
Order Primates Linnaeus, 1758	
Family Cercopithecidae Gray, 1821	
<i>Mesopithecus pentelici</i> Wagner, 1839	(4)
Order Carnivora Bowdich, 1821	
Family Ursidae Gray, 1825	
<i>Indarctos maraghanus</i> Mecquenem, 1924	(4)
Family Mustelidae Swainson, 1835	
<i>Martes</i> sp. indet.	(X)
<i>Promeles palaeattica</i> Zittel	(X)
<i>Melodon maraghanus</i> Kittl, 1887	(1)
<i>Parataxidea polaki</i> Kittl, 1887	(1)
Family Hyaenidae Gray, 1869	
Ictitheriinae gen. and sp. indet.	(X)
<i>Ictitherium viverrinum</i> Roth and Wagner, 1854	(X, 1, 4)
<i>Thalassictis wongii</i> (Zdansky, 1924)	(X, 1)
<i>Percrocuta eximia</i> (Kaup, 1828)	(X, 1, 4)
Family Felidae Gray, 1821	
<i>Metailurus orientalis</i> Zdansky, 1924	(1)
<i>Felis attica</i> Wagner, 1857	(1, 4)
<i>Machairodus aphanistus</i> Kaup, 1833	(X, 1)
Order Tubulidentata Huxley, 1872	
Family Orycteropodidae Bonaparte, 1850	
<i>Orycteropus</i> sp.	(X, 6)
Order Proboscidea Illiger, 1811	
Family Gomphotheriidae Cabrera, 1929	
<i>Choerolophodon pentelici</i> Gaudry, 1862	(X, 1, 3)
Family Deinotheriidae Bonaparte, 1845	
<i>Deinotherium</i> sp. indet.	(2)
Order Perissodactyla Owen, 1848	
Family Equidae Gray, 1821	
" <i>Hipparion</i> " <i>gettyi</i> Bernor, in press	(X, 1)
<i>Hipparion prostylum</i> Christol, 1832	(X, 1, 7, 4, 5, 8)
<i>Hipparion campbelli</i> Bernor, in press	(X)
" <i>Hipparion</i> " aff. <i>moldavicum</i> Gromova, 1952	(X, 1, 4, 6)
" <i>Hipparion</i> " ? <i>matthewi</i> Kormos, 1911	(X, 1, 7)
Family Chalicotheriidae Gill, 1872	
Chalicotheriidae gen. and sp. indet.	(X)
<i>Ancylotherium pentelici</i> (Gaudry, 1862)	(X)
Family Rhinocerotidae Owen, 1845	
<i>Diceros neumayri</i> Mecquenem, 1905	(1, 4)
<i>Chilotherium persiae</i> Pohlig, 1887	(X, 1, 4)
Order Artiodactyla Owen, 1848	
Family Suidae Gray, 1821	
<i>Microstonyx erymanthius</i> Roth and Wagner, 1855	(X, 1, 4)
Family Cervidae Gray, 1821	
Cervidae gen. and sp. indet.	(5)
Family Giraffidae Gray, 1821	
Giraffinae gen. and sp. indet.	(X)
<i>Palaeotragus coelophrys</i> (Rodler and Weithofer, 1890)	(X, 4)
<i>Samotherium neumayri</i> (Rodler and Weithofer, 1890)	(1)

TABLE 1. Continued.

Mammalian species	Collection
<i>Samotherium</i> sp. indet.	(X)
<i>Helladotherium</i> cf. <i>duvernoyi</i> Gaudry, 1890	(X, 1, 4)
Family Bovidae Gray, 1821	
Bovidae n. gen. and n. sp.?	(X)
<i>Miotragocerus</i> sp. indet.	(X)
<i>Miotragocerus amalthea</i> (Roth and Wagner, 1847)	(X, 1, 6)
<i>Miotragocerus</i> sp.	(X, 4)
<i>Gazella deperdita</i> (Gervais, 1847)	(X, 4)
<i>Gazella rodleri</i> Pilgrim and Hopwood, 1928	(X, 1)
" <i>Prostrepsiceros</i> " <i>rotundicornis</i> (Weithofer, 1888)	(4)
<i>Prostrepsiceros houtumschindleri</i> (Rodler and Weithofer, 1890)	(X, 1, 4)
<i>Protragelaphus skouzesi</i> Dames, 1883	(X, 1, 4)
<i>Urmiatherium polaki</i> Rodler, 1889	(?X, 1)
<i>Oioceros atropatenes</i> (Rodler and Weithofer, 1890)	(X, 1, 4)
<i>Oioceros rothii</i> (Wagner, 1857)	(X, 4)
<i>Protoryx crassicornis</i> (Schlosser, 1904)	(X)
<i>Protoryx laticeps</i> Andree, 1926	(1, 4)

5: taxa collected by Tobien, JGUM

6: taxa acquired by Damon for the BMNH

7: cast of specimen presented by P. Y. Sondaar to UCR

8: taxa collected by the AMNH

This list includes 6 orders, 15 families, 37 genera, and 37 species (10 species indet.) of fossil mammals. Of this assemblage, the Lake Rezaiyeh Expedition has collected specimens belonging to 5 orders, 11 families, 21 genera, and 25 species (6 species indet.) of the entire known fauna. The mammalian taxa collected by the Lake Rezaiyeh Expedition and shipped to the United States by the National Natural History Museum of Iran, Tehran, are the primary basis for the biostratigraphy presented in Figure 4. However, some precise locality information has been provided by Kamei et al. (1977), Tobien (Bernor et al., 1979b) and Erdbrink (pers. comm.) and gleaned from Museum research.

The Maragheh biostratigraphic framework is represented in Table 2 and Figure 4. The stratigraphic position of vertebrate localities was determined by J. A. Van Couvering, who measured their distance above and below the "Loose Chips" marker bed (Campbell et al., 1980; Bernor et al., 1980). In Table 2, species are grouped by biostratigraphic unit as defined by the first known occurrence of successive stages of a single potential mammalian lineage (procedure after Woodburne, 1977). Figure 4 gives vertical ranges of the species in the UCR-MMTT vertebrate sample.

Primates

Only one species of primate is known from Maragheh, *Mesopithecus pentelici*, collected by Mecquenem

(1924–25). The provenance of this specimen is not precisely known. Mecquenem (1908:43) reported that he collected fossils from two levels of 1 m and 0.6 m thickness each, and only a few meters apart vertically. He reportedly collected these horizons along a course that was 5 to 6 km wide, 30 km long, and supposedly between 1620 and 1650 m elevation. His principal collections came from Kirdjawa (–52 to –28 m interval of this paper), but also from areas near Sholovend, Kingir and Kopran, which probably did not include any higher levels, but could have mistakenly included levels as low as the –115 m level of this paper (i.e. upper Kopran). If Mecquenem's observations of the stratigraphic provenance of his own collections are correct, the best estimate of *Mesopithecus pentelici*'s occurrence would fall within the –52 to –28 m interval.

Carnivora

Twelve carnivore taxa are known from Maragheh: *Martes* sp. indet., *Promeles palaeattica*, *Melodon maraghanus*, *Parataxidea polaki*, *Indarctos maraghanus*, *Metailurus orientalis*, *Felis attica*, *Machairodus aphanistus*, *Ictitherium viverrinum*, *Thalassictis wongii*, and *Percrocuta eximia*. Of these, Rodler's (1887) collection included a *Metailurus* (= *Paramachairodus*) *orientalis*, *Felis attica*, *Thalassictis wongii*, *Percrocuta eximia* from Ildtschi (= our Ilkhchi); and *Melodon maraghanus*, *Machairodus aphanistus*, and *Parataxidea polaki* from Ketschawa. *Indarctos maraghanus* was collected by Mecquenem presumably from somewhere within the middle interval of the Maragheh sequence. The Lake Rezaieyeh Expedition has collected a number of carnivore species from the Maragheh Basin. These include a left mandible of *Martes* sp. indet. from MMTT 7 (–28 m interval), a nearly complete skeleton of *Promeles palaeattica* from MMTT 13 (–18 m interval); a mandible fragment of *Ictitherium viverrinum* from Ilkhchi (correlates with –18 m interval); a partial skull and isolated teeth of *Thalassictis wongii* from MMTT 13 (–18 m interval) an isolated tooth from MMTT 25 (–12 m interval) and skull material from Ilkhchi; a skull of *Machairodus aphanistus* from MMTT 13 (–18 m interval), as well as postcrania and isolated teeth from MMTT 7 and 14 (–28 m interval) and postcrania from MMTT 3 (–40 m interval).

The Ilkhchi specimens are biostratigraphically best correlated with the –28 to +7 m interval based upon the co-occurrence of *Hipparion* cf. *campbelli* and "*Hipparion*" ?*matthewi* as well as a 7.4 my date based upon K-Ar and fission track determinations (Campbell et al., 1980). These correlations would place the Ilkhchi locality closely equivalent in age to the Lake Rezaieyeh Quarry at MMTT 13 (–18 m level). The Ketschawa locality is believed to be the same as the MMTT 1A, 1B, and 1C localities of this paper (–52 to –30 m interval) reported by Campbell et al. (1980) as well as Tobien (1968), Erdbrink et al. (1976), and Kamei et al. (1977).

TABLE 2. Biostratigraphic intervals of Maragheh mammalian species.

Upper Maragheh –20 to +7 meters above/below Loose Chips:

Vertebrate localities (in descending stratigraphic order): UCR-MMTT 26, 39, 24, 32, 38, 22, 16, 47, 27, 25, 15, 49, 49a, 50, 31, 33, 21, 13, 37, 40, 51

Mammalian fauna: *Promeles palaeattica*, *Metailurus orientalis*, *Felis attica*, *Machairodus aphanistus*, *Ictitherium viverrinum*, *Thalassictis wongii*, *Percrocuta eximia*, *Orycteropus* sp. indet., *Choerolophodon pentelici*, *Deinotherium* sp. indet., *Hipparion campbelli*, "*Hipparion*" ?*matthewi*, *Ancylotherium pentelici*, *Microstonyx erymanthus*, *Palaeotragus coelophrys*, *Samotherium* sp. indet., *Miotragocerus* undescr. sp., *Gazella* cf. *deperdita*, *Oioceros atropatenes*, *Protoryx crassicornis*, *Urmia-therium polaki*

Middle Maragheh –52 to –20 meters below Loose Chips:

Vertebrate localities: UCR-MMTT 7, 14, 34, 1c, 6, 18, 19, 20, 1b, 2, 17, 11, 4, 35, 3, 1A, 5

Mammalian fauna: *Mesopithecus pentelici*, *Indarctos maraghanus*, *Martes* sp. indet., *Melodon maraghanus*, *Parataxidea polaki*, *Felis attica*, *Machairodus aphanistus*, *Thalassictis wongii*, *Percrocuta eximia*, *Choerolophodon pentelici*, *Hipparion prostylum*, "*Hipparion*" aff. *moldavicum*, "*Hipparion*" ?*matthewi*, *Chilotherium persiae*, *Diceros neumayri*, *Microstonyx erymanthus*, Cervidae gen. and sp. indet., Giraffinae gen. and sp. indet., *Palaeotragus coelophrys*, *Samotherium neumayri*, *Helladotherium duvernoyi*, *Miotragocerus* sp., *Gazella* cf. *deperdita*, *Prostrepsiceros houtumschindleri*, *Protragelaphus skouzesi*, *Oioceros rothii*, *Oioceros atropatenes*, *Protoryx laticeps*

Lower Maragheh –150 meters to –52 meters below Loose Chips:

Vertebrate localities: 8, 42, 45, 36, 23, 28, 41, 44, 43, 9, 48

Mammalian fauna: *Choerolophodon pentelici*, "*Hipparion*" *gettyi*, "*Hipparion*" ?*matthewi*, *Chilotherium persiae*, *Microstonyx erymanthus*, *Samotherium neumayri*, *Miotragocerus amalthea*, *Gazella deperdita*, *Prostrepsiceros houtumschindleri*, *Oioceros atropatenes*

Tubulidentata

The only known occurrence of a tubulidentate with stratigraphic provenance is an *Orycteropus* sp. indet. tibia-fibula from MMTT 13 (–18 m level).

Proboscidea

A species of Proboscidea retrieved by the Lake Rezaieyeh Expedition is *Choerolophodon pentelici* from localities 1-A (–52 m level), MMTT 13 (–18 m level), and MMTT 37 (= Ilkhchi). Erdbrink et al. (1976) reported the occurrence of "*Synconolophus*" (a synonym of *Choerolophodon*; Tassy and Madden, pers. comm.) from the Kerjabad and Ci Anne (–52 to –28 m interval), and Kamei et al. (1977) reported a complete skull of *Choerolophodon pentelici* from locality 1-B (–32 m interval). The KNHM collection also contains *Choerolophodon pentelici* from Kopran Mescha (–150

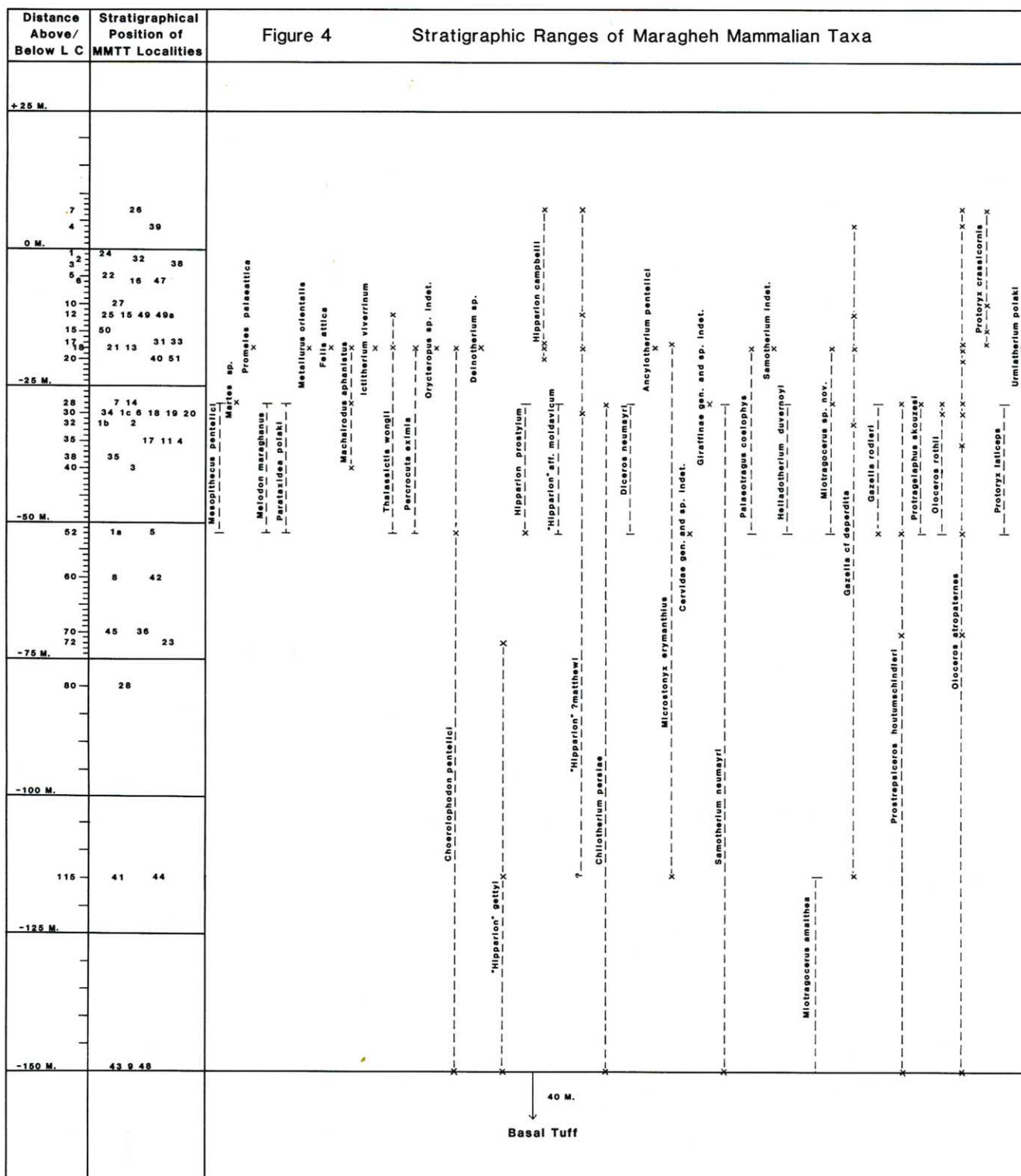


FIGURE 4. Mammalian biostratigraphy of the Maragheh Formation. The stratigraphic provenance of vertebrate localities is given above/below the Loose Chips marker bed.

m interval) and Ilkhchi (= Upper Maragheh). Erdbrink et al. (1976) reported remains of another proboscidean, *Deinotherium*, from their K1 locality, which is identical to the MMTT 31 locality of this paper (-17 m level).

Perissodactyla

At least four genera of Perissodactyla have been collected at Maragheh: "*Hipparion*" (s.l.), *Ancylotherium*, *Chilotherium*, and *Dicerus*. *Ancylotherium pentelici* is represented by a complete palate of a juvenile indi-

vidual collected from Ilkhchi, and some postcranial elements referable to Chalicotheriidae incertae sedis have been recovered from MMTT 13 (-18 m level). A nearly complete skull and lower jaw of *Chilotherium persiae* was recovered from MMTT 7 (-28 m level), but other than this specimen there are only a few postcranial remains of Rhinocerotidae collected by the Lake Rezaiyeh Expedition. The KNHM collection records *Chilotherium persiae* from Kopran Mescha (-150 m interval) and Kara Kend (= 1A, 1B, 1C localities, -52 to -30 m interval). The MNHN collection includes both *Chilotherium persiae* and *Diceros neumayri*, which were presumably derived from the -52 to -28 m interval.

Five species of hipparionine horses have been recognized from Maragheh: "*Hipparion*" *gettyi*, *Hipparion prostylum*, *Hipparion campbelli*, "*Hipparion*" aff. *moldavicum*, and "*Hipparion*" ?*matthewi*. "*Hipparion*" *gettyi* is represented by a skull and mandible housed by the KNHM from Kopran Mescha (-150 to -115 m interval), as well as several cheek teeth from MMTT 43 (-150 m level), MMTT 41 (-115 m level) and MMTT 36 (-70 m level). *Hipparion prostylum* is represented by skulls, dentitions, and postcrania from MMTT 1A (-52 m level; JGUM collection), by skulls from unknown provenance in the MNHN and AMNH collections. *Hipparion campbelli* is represented by skulls and lower jaws from the -18 m interval, and teeth and postcranial remains from the -20, -18, -17, and +7 m intervals. "*Hipparion*" aff. *moldavicum* is represented by several skulls in the MNHN collection (-52 to -28 m interval), a single skull in the BMNH collection, and some skull fragments in the KNHM collection derived from Ketschawa (-52 to -28 m interval) and Zad Baschi (unknown provenance). "*Hipparion*" ?*matthewi* is represented in the Lake Rezaiyeh collection by teeth from the -28, -18, -10 and +7 m intervals, from Kopran II (?-115 m level) in the KNHM collection, and a skull fragment of unknown provenance in the GIU collection.

Artiodactyla

Seventeen species of Artiodactyla are known from Maragheh including the families Suidae (*Microstonyx erymanthius*), Cervidae (gen. and sp. indet.), Giraffidae (Giraffinae gen. and sp. indet., *Palaeotragus coelophrys*, *Samotherium neumayri*, *Samotherium* sp. indet., and *Helladotherium* cf. *duvernoyi*) and Bovidae (*Miotragocerus* sp. nov., *Miotragocerus* sp. indet., *Gazella* cf. *rodleri*, *Gazella* cf. *deperdita*, *Prostrepsiceros houtumschindleri*, *Protragelaphus skouzesi*, *Oioceros rothii*, *Oioceros atropatenes*, *Protoryx crassicornis*, *Protoryx laticeps*, and *Urmitherium polaki*).

The Suidae and Cervidae are the least evolutionarily diverse and least abundant families of all the Artiodactyla. The suid *Microstonyx erymanthius* is represented in the Lake Rezaiyeh Expedition collection by a few teeth and postcranial fragments from MMTT 41 (-115 m level) and MMTT 13 (-18 m level). There are more abundant remains of this species in the Mecquenem collection including skulls, teeth and postcrania

remains, which most likely were collected within the -52 to -28 m interval. The KNHM collection contains *Microstonyx erymanthius* from Ketschawa (-52 to -28 m interval). The Cervidae are represented by one antler fragment with pedicle collected by Tobien from MMTT 1-A (-52 m level).

The Giraffidae are relatively diverse but the number of specimens is low in the various Maragheh collections. A Giraffinae gen. and sp. indet. palate was retrieved by the Lake Rezaiyeh Expedition from MMTT 7 (-28 m level) and is the only specimen of this species known. Postcrania and teeth of *Palaeotragus coelophrys* were collected from MMTT 13 (-18 m level) and are also present in Mecquenem's collection (-52 to -28 m interval). *Samotherium neumayri* is found in the Vienna collection originating from Kopran Mescha (-150 m interval), Kara Kend, and Ketschawa (-52 to -30 m interval). *Samotherium* sp. indet. is represented by teeth and postcrania from MMTT 13 and 37 (-18 m level and ca. -18 m level respectively). Finally, the large sivatherine *Helladotherium* cf. *duvernoyi* is represented by teeth and postcrania in the Mecquenem collection (-52 m to -28 m interval).

Remains of Bovidae are relatively abundant and evolutionarily diverse in the various Maragheh assemblages. There are two *Miotragocerus* species known from Maragheh, a smaller more primitive form, *Miotragocerus amalthea* collected by Rodler (skull, teeth, postcrania) from Kopran (-150 to -115 m interval) and a larger, more advanced form *Miotragocerus* undescr. sp. collected by the Lake Rezaiyeh Expedition from MMTT 7 (-28 m level) and MMTT 13 (-18 m level) as well as Mecquenem (-52 to -28 m interval). The gazelles are also represented by two species, *Gazella rodleri* and *Gazella* cf. *deperdita*. *Gazella rodleri* was collected by the Lake Rezaiyeh Expedition from MMTT 1-A (-52 m level) and was reported by Pohlig (1886) from Ketschawa (-52 to -28 m interval). *Gazella deperdita* has been collected by the Lake Rezaiyeh Expedition from MMTT 44 (-115 m interval), MMTT 1b (32 m interval), MMTT 13 (-18 m interval, MMTT 25 (-12 m interval), MMTT 26 and 39 (+7 m interval). It is also known in the MNHN collection (-52 to -28 m interval). *Prostrepsiceros houtumschindleri* is a relatively well known species, having been collected by the Lake Rezaiyeh Expedition from MMTT localities 43 (-150 m level), 36 (-70 m level), 1-A (-52 m level), the -30 m level, and MMTT 7 (-28 m level). Mecquenem's collection includes a good sample of skull, tooth, and postcranial remains presumably from the -52 m to -28 m interval. *Protragelaphus skouzesi* is represented in the Lake Rezaiyeh collection by horn and dental material from MMTT 7 (-28 m level), while being more completely represented by skull and tooth material in the Mecquenem collection. *Oioceros rothii* is represented in the Lake Rezaiyeh Expedition sample by horn material from MMTT 1C and 7 (-30 m and -28 m levels respectively), as well as Mecquenem's collection (-52 to -28 m interval). *Oioceros atropatenes* is the most abundant single species in the Lake Rezaiyeh Expedition sample, being rep-

resented by numerous skull fragments, teeth and postcrania from throughout the section including the -150, -70, -52, -40, -32, -28, -20, -18, -17, +4 and +7 m levels. This taxon is also well represented in the Mecquenem collection (-52 to -28 m interval). *Protoryx crassicornis* is represented in the Lake Rezaieyeh Expedition sample by a partial skull, horns, jaw fragments and postcrania from MMTT localities 13 (-18 m), 31 (-17 m) 27 (-10 m), 26 (+7 m) and 37 (Upper Maragheh). *Protoryx laticeps* includes skull and dental material collected by Mecquenem (-52 to -28 m interval). The holotype of *Urmiatherium polaki* was collected by Rodler from Ilkhchi, which is biostratigraphically and geochronologically correlated most closely with MMTT 13 (-18 m level).

The evolutionary relationships of the hipparionine horse series is the best understood of all Maragheh mammalian species (Bernor, in press). This series has led Bernor et al. (1979b), Campbell et al. (1980), and Bernor et al. (1980) to suggest the subdivision of the Maragheh Formation into three biostratigraphic intervals. These intervals are referred to here as: Lower Maragheh, characterized by the occurrence of "*Hipparion*" *gettyi* from as low as -150 m to as high as -52 m; Middle Maragheh, characterized by the occurrence of *Hipparion prostylum* from -52 to -28 m; Upper Maragheh, characterized by the occurrence of *Hipparion campbelli* from -18 to +7 m. I refrain from defining biozone boundaries and erecting formal biostratigraphic or geochronologic zones using this morphocline series because of the uncertainty surrounding the phylogenetic relationships of these species, the uncertain provenance of the "*Hipparion*" *gettyi* skull, the significant stratigraphic hiatuses between each biostratigraphic interval, and the need for more stratigraphic and geochronologic work in the Maragheh Basin. The other characterizing mammalian species for these three intervals are included in Table 2. Their geochronologic and zoogeographic significance will be discussed in the following sections.

GEOCHRONOLOGY AND ZOOGEOGRAPHIC RELATIONSHIPS OF THE MARAGHEH FAUNA

Late Miocene "Pontian" savanna-like faunas have for years particularly interested vertebrate paleontologists. Osborn (1910:264) considered these faunas to be highly distinctive and sharply demarcated in Palearctica from older Miocene faunas by the great abundance of "grazing and cursorial types". Osborn (1910), and later Matthew (1915, 1939) considered the "Pontian Mammal Age" as a dispersal period of savanna forms which they believed had originated in Asia, and eventually became restricted to East Africa. They marked the appearance of these faunas by the first immigration of "*Hipparion*" (s.l.) into the Old World.

During the last two decades, research on Eurasian and African large mammal faunas has yielded data that

suggest that these savanna-like faunas did not appear instantaneously, but rather had a long period of evolution. Bernor et al. (1979a) and Bernor (1983; in press) discussed this issue in detail and concluded that the evolution of Old World "Pontian" faunas can be traced into the early Miocene, and that these faunas show varying degrees of provinciality throughout their temporal and geographic ranges. The early Miocene of North Africa, North China and western Asia contained faunas that reflect a more open country character. By the Middle Miocene, an open country chronofauna diversified in advanced large carnivores (Felidae, Hyaenidae) and ruminants (Giraffidae and Bovidae) expanded its geographic range to include a broad zoogeographic corridor including North Africa, Saudi Arabia, southwest Asia and North China.

Western Europe underwent a series of late Miocene dispersals of open country large mammals, and their communities more closely approximated the ones in the eastern Mediterranean during the Turolian. Central and eastern Europe however underwent a retarded and less extensive transgression of this open country fauna. Steininger and Papp (1979) and Bernor (1983, 1984) have argued that this savanna-like mammalian biofacies transgressed the Pannonian and Vienna Basins in the latest Turolian and is directly related to the striking regression of the Paratethys to small lakes, and resulting greater seasonality of the adjacent countryside (Leuger, 1978). There is no evidence that this fauna ever transgressed the tropical areas of central Africa and southeast Asia (Bernor, 1983; in press).

These lines of evidence have made it increasingly apparent that the evolution of Old World late Miocene open country faunas is far more complex than envisioned by earlier workers. These faunas are not homogeneous, but rather show distinct provinciality in their distribution and community evolution (Bernor, 1983, 1984). Changes in regional geography influenced climatic and environmental shifts that played an integral part in spawning interprovincial to intercontinental scale faunal exchanges and biotic successions. Synchronization of these events has been the purpose of a large group of paleontologists, geologists and geophysicists who have used a growing array of geochronologic tools to adjust and "fine-tune" the geological time scale. The Maragheh fauna represents an important one for these same purposes because of its key geographical position, species abundance, species diversity, its long stratigraphic range, and extensive chronologic documentation.

Campbell et al. (1980) and Bernor et al. (1980) recently reported on an extensive suite of 28 age determinations of the Basal Tuff and Maragheh Formations. These included both fission track and K/Ar dates from 10 stratigraphic levels in the sequence, including four of five horizons dated by Erdbrink et al. (1976) and three of five horizons dated by Kamei et al. (1977). This information is given in Table 3 and displayed in Figure 3. While Campbell et al. (1980) and Bernor et al. (1980) report general concordance between the fis-

TABLE 3. Isotopic age determinations from the Maragheh Formation and Basal Tuff.

		Zircon FT Bernor et al., 1980	K-Ar	Zircon FT Kamei et al., 1977	K-AR Erdbrink et al., 1976
+100	Korde-deh Pumice (Murdag Chai)			5.2 730-04	
+90 est.	Upper Pumice (Ilkchi)	7.2 ± 0.4 R10	7.5 ± 0.4 R10pl		
+60 est.	Middle Pumice (Ilkchi)	7.3 ± 0.5 R 5	7.7 ± 0.5 R 5pl 7.2 ± 0.5 R 6pl		
+15 est.	Lower Pumice (Ilkchi)	7.4 ± 0.4 R 8 7.0 ± 0.4 R 8	7.9 ± 0.7 R 8pl		
+15 est.	Village Pumice (Ilkchi)	5.2 ± 0.3 R 9 5.3 ± 0.3 R 9	5.5 ± 1.0 R 9pl		
+7	Layered Marker Pumice (Shollovend)	7.6 ± 0.5 R 2	8.3 ± 0.9 R 2pl		8.1 ± 0.4 VIIwr 6.2 ± 0.6 VIIhb
0	Loose Chippings Pumice (Shollovend)	7.8 ± 0.4 R11	7.4 ± 0.3 R11pl 6.4 ± 0.6 R12pl 6.9 ± 0.3 M 5hb	6.6 730-19	8.7 ± 0.4 IIIwr
-50	Gürt Daresch Pumice (Murdag)			6.5 730-17	14.4 ± 0.7 Vwr
-110	Ignimbritic Tuff (Murdag)	10.6 ± 0.8 R 3	6.4 ± 0.5 R 3pl 8.8 ± 0.5 R 3pl 8.9 ± 0.5 R 3pl	7.0 730-10	12.9 ± 0.7 Iwr
	Basal Tuff (western area)		11.2 ± 0.5 M 1bi	7.2 730-20	10.1 ± 0.5 IXwr 11.4 ± 0.5 IXbi
	Basal Tuff (Ilkchi)	11.2 ± 0.6 R 4	10.1 ± 0.5 R 4bi 9.3 ± 0.1 R 4an		
		12.8 ± 0.5 R 7	11.3 ± 1.0 R 7bi 9.3 ± 0.1 R 7an		

Measured stratigraphic relationships of dated levels in the Mirdug-Shollovend area and in the Ilkchi area are correlated by projecting the regional dip of the Maragheh Formation in the central area to Ilkchi. Sample numbers are given to the right of each determination. All fission-track (FT) ages were obtained on zircon crystals; the analytical uncertainty of the FT ages published by Kamei et al. (1977:158-159) is stated to be approximately 20% of each measurement. The K-Ar ages were obtained from materials indicated by the suffixes to the sample numbers, as follows: wr (whole rock), pl (plagioclase), hb (hornblende), bi (biotite) and an (anorthoclase) (from Bernor et al., 1980).

sion track and K/Ar determinations, Table 3 and Figure 3 show considerable contradictions at each stratigraphic level. However, the implementation of hipparionine biochronology by Bernor et al. (1980) was found to be generally in agreement with the higher quality potassium-argon and fission track determinations from the sequence.

The frequent relatively large error ranges within and between K/Ar and fission track determinations is in part thought to be the result of inclusions of accidental pebbles and grains of detrital andesite. Whole rock determinations reported by Erdbrink et al. (1976) are thought to be particularly suspect because of this supposed contamination problem. However, Drake (pers. comm.) reports further problems with the consistent discrepancy between anorthoclase K/Ar ages on the one hand, and biotite K/Ar and zircon fission track ages on the other, especially in the Basal Tuff Formation. Nevertheless, Campbell et al. (1980) and Bernor et al. (1980) believed that a 9.5-7 my interval

represents the best estimate for the age range of the Maragheh fauna. This assessment was based on the stage-of-evolution of "*Hipparion*" *gettyi*, *Hipparion* cf. *prostylum*, and *Hipparion campbelli* compared to other closely related Eurasian horse species as well as an assessment of the radiometric determinations. Bernor et al. (1980) estimated that Lower Maragheh ranged from 9.5 to 8.5 my, Middle Maragheh ranged from 8.5 to 8 my, and Upper Maragheh ranged from 8 to 7 (or fewer) my in age. A synopsis of the zoogeographic relationships and geochronologic significance of the Maragheh fauna comprises the remainder of this section.

The primate *Mesopithecus pentelici* has been revised by Delson (1973) from the Turolian of Greece (Pikermi, Vathylakos), Yugoslavia (Titov Veles), Bulgaria (Kalimanci, Gorna Susica, Kromidovo), the Ukraine (Grebentiki, Taraklia?, Grossulovo?), Germany (Wissberg), Italy (Baccinello V3), Hungary (Hatvan; ?Polgardi). Of this suite of localities, Pikermi is demon-

strably the oldest (ca. 9 my after hipparionine biochronologic correlations by Bernor et al., 1980). The occurrences of *Mesopithecus pentelici* in Middle Maragheh and Vathylakkos are very close in age, but perhaps slightly younger than Pikermi. The age of Titov Veles, the Bulgarian, Ukrainian, and German localities is not certain, but may generally be considered as being medial-late Turolian. The Baccinello fauna is substantially younger (MN 13; Mein, 1975, 1979), as are the Hungarian faunas of Hatvan and Polgardi (MN 12/13, ca. 7 my, Steininger and Papp, 1979). The conspicuous absence of *M. pentelici* from the upper biostratigraphic interval at Maragheh and the extensive Samos assemblage, contrasted with its comparatively late occurrence in the Hungarian localities, suggests that its range extended northwestward into eastern and Central Europe along with the late dispersal of the more wooded part of the Turolian savanna-biotope.

The Maragheh carnivore assemblage is extensive and includes species of the families Ursidae, Mustelidae, Hyaenidae, and Felidae. Generally speaking, all of these have a broad Eurasian, and in some cases African and North American geographic range at the generic level. The one ursid species, *Indarctos maraghanus* is unique to Maragheh. However, closely related late Miocene age species are known from China (*I. sinensis*; Zdansky, 1924); Hasnot, the Siwaliks (*I. punjabiensis*; Lydekker, 1886; Erdbrink, 1953); Greece (*I. atticus*, Samos and Pikermi; Solounias, 1981); Spain (*Indarctos vireti*—Can Llobateres, Can Ponsich, Villadecavalls; *I. atticus adroveri*—Concud; *I. atticus*—Los Mansuetos; *I. sp.*—La Fontana; Alberdi, 1974); North Africa (*I. atticus*—Sahabi; Howell, 1982).

Martes is a chronologically long ranging and geographically widely distributed genus and is of little biochronological significance here. Of the three species of Melinae from Maragheh, *Promeles palaeattica* is the most primitive morphologically, but is found in the upper Maragheh interval. This species is also known from Samos and Pikermi, the western U.S.S.R. (Borissiak, 1962), and together with the Maragheh skeleton suggests a provincial age range of ca. 9–7 my. *Melodon maraghanus* has been collected from Ketschawa, Middle Maragheh, with an estimated age of 8.5 my. This species is morphologically very close to *Melodon* ("Parataxidea") *sinensis* (Zdansky, 1924; pl. X, figs. 5–10), and may eventually prove to be the same. *Parataxidea polaki* is also from Ketschawa, Middle Maragheh, and similarly shows close morphological identity to Chinese species of *Parataxidea* (Zdansky, 1924).

Hyaenidae are relatively diverse at Maragheh, and broadly characteristic of late Miocene Old World large mammal faunas. *Ictitherium viverrinum* is only recorded from the Upper Maragheh interval (locality of Ilkhchi) and its morphology is virtually identical to specimens from Samos and Pikermi (Solounias, 1981). Solounias also reports that this species is similar to a Chinese species *Ictitherium sp.* *Thalassictis wongii* is a larger ictitheriine hyaenid which has a distribution in late Miocene horizons of Greece (Samos), Turkey

(?Garkin, ?Kinik), the western U.S.S.R. (Borissiak, 1962) and China (Solounias, 1981). Solounias separates *T. wongii* from *T. hipparionum* on several morphological grounds. The latter has a reported geographic occurrence in southwest Europe (Guérin and Mein, 1971; Alberdi, 1974) during the late Miocene. Within Solounias' (1981) synonymy there are contained species of the genus *Palhyaena*. Pilbeam et al. (1979) have reported two species of *Palhyaena*, from the Nagri and Dhok Pathan Formations: *P. sivalense* (Chronozones 7–9) and *P. indicum* (Chronozone 10). *Percrocuta eximia* is the largest Maragheh hyaenid, and has a geographic range including Europe, the western U.S.S.R., southwest Asia, and North Africa.

The felids are a diverse group of carnivores at Maragheh. *Metailurus* (= *Paramachairodus*) *orientalis* is reported from the western U.S.S.R. (Tchobrouchi, Novolissavetovka, Tarkalia; Pilgrim, 1931); Hungary (Polgardi; Kormos, 1911), Greece (Veles, Schlosser, 1921; Pikermi, Solounias, 1981), and China (Zdansky, 1924). *Felis attica* has been reported from Pikermi and Samos by Solounias (1981), and from Vathylakkos by Arambourg and Piveteau (1929). Closely related species occur in China (*Felis paleosinensis*; Zdansky, 1924, pl. 32, fig. 1), the western U.S.S.R. (*Felis sp.*; Borissiak, 1962), the Siwaliks (*Felis sp.*, Chronozone 10; Pilbeam et al., 1979; Barry et al., 1982), Spain (*Felis vireti*, Alberdi, 1974). *Machairodus aphanistus* has a late Miocene pan-European and west Asian distribution (Pilgrim, 1931), and has closely related species reported from China (*Machairodus planderi* and *Machairodus tingii*, Zdansky, 1924), and North Africa (Sahabi; Howell, 1982).

The genus *Orycteropus* was broadly distributed throughout Eurasia and seasonal parts of Africa during this time. Its earliest record extends to the beginning of the Astaracian (MN 6) of Turkey (locality of Pasalar; Sickenberg et al., 1975).

The proboscideans *Choerolophodon pentelici* and *Deinotherium* were also broadly distributed throughout much of Eurasia during the middle and late Miocene. *Choerolophodon* is an advanced member of the Gomphotheriidae that is first reported from the East African early middle Miocene locality of Maboko (ca. 15 my; Tassy, 1977), subsequently dispersed and diversified in western Asia (Sickenberg et al., 1975), and demonstrably later in the Siwalik Province (Pilbeam et al., 1979). Its occurrence is currently unrecorded from Europe and China. Identification of *Deinotherium* (Erdbrink, pers. comm.) is not significant here because of its long chronologic (MN 4–MN 13 of Europe) and geographic (Eurasian–African) ranges.

The hipparionine species have proven to be the most sensitive biochronologic indicators of the Maragheh fauna. The oldest Maragheh hipparionine, "*Hipparion*" *gettyi*, is an advanced Group 1 species that most closely compares with *Hipparion melendesi* of the Spanish late Vallesian and with a specimen from Pikermi (BMNH M42603; Bernor and Hussain, 1984). Furthermore, I have argued (Bernor, in press) that de-

tails of the facial fossa, dentition and postcrania of *Hipparion gettyi* are not so morphologically distant from *Hipparion prostylum* as to preclude their close evolutionary relationship. A 9.5 to 8.5 my age range appears to be compatible with "*Hipparion*" *gettyi* stage-of-evolution.

Hipparion prostylum has been found in medial Turolian horizons in France (Mt. Luberon), Greece (Vathyakkos, Pikermi) and Afghanistan (pers. observ.). *Hipparion antelopinum* from the Middle Siwaliks of the Indian Subcontinent appears to be a closely related species. An 8 my (or slightly older) age estimate for the Maragheh assemblage of *Hipparion prostylum* presented by Bernor (in press) corresponds to age estimates for *Hipparion prostylum* and the closely related form *Hipparion antelopinum* from Europe/western Asia and the Indian Subcontinent. *Hipparion campbelli* is the most advanced Group 3 horse currently known. It is closest morphologically in details of the skull, dentition and postcrania to the Samos species *Hipparion dietrichi* and an undescribed skull fragment of a *Hipparion* sp. from Shansi, China (Bernor and Qiu, ms.).

The Group 2 horses "*Hipparion*" aff. *moldavicum* and "*Hipparion*" aff. *matthewi* are similarly significant from geochronologic and zoogeographic standpoints. Group 2 horses occur only in western Asia, western U.S.S.R., and China during the late Miocene. "*Hipparion*" aff. *moldavicum* most closely resembles the type "*Hipparion*" *moldavicum* series from Tarkalia, Moldavia (U.S.S.R.), which Mein (1975, 1979) correlates with MN 12 of Europe. The closely related species "*Hipparion*" *mediterraneum* from Pikermi is also believed to be of MN 12 age (= MN12a of Bernor, 1983, 1984). The potential occurrence of "*Hipparion*" aff. *moldavicum* from Middle and Upper Maragheh levels (ca. 8.5–7 my) falls within the known temporal range of this species in the western U.S.S.R. (i.e. MN 12a and 12b, ca. 9–7 my; Bernor, 1983; in press). Biochronologic and zoogeographic relationships of "*Hipparion*" *matthewi* are difficult to assess because of the current confusion surrounding the morphology of the holotype and probable parallel evolution of a number of separate lineages of dwarf-sized species (Bernor, in press). However, the geographic and chronologic ranges of this species may well be limited to eastern Europe, western U.S.S.R. and western Asia during MN 12 and possibly MN 13. The occurrence of "*Hipparion*" *matthewi* from Middle and Upper Maragheh appears concordant with its other presumed occurrences in Eurasia.

The Maragheh rhinoceroses, *Chilotherium persiae* and *Diceros neumayri* have been recovered only from the Lower and Middle Maragheh horizons. *Chilotherium persiae* has only been reported from Iran, although the genus was broadly distributed during the late Miocene in southwest Europe (Spain; Alberdi, 1974), the eastern Mediterranean (several species in Turkey, Sickenberg et al., 1975; and Greece, Solounias, 1981), the western U.S.S.R. (Borissiak, 1962), the Si-

waliks (Pilbeam et al., 1979) and China (Chiu et al., 1979). *Diceros neumayri* has a reported distribution from the late Miocene of Greece (Samos and Pikermi; Solounias, 1981), Turkey (Kayadibi; Heissig, 1982), possibly the western U.S.S.R. (Borissiak, 1962), and the Basal Pliocene of North Africa (Sahabi; Heissig, 1982). The genus has also been reported by Sickenberg et al. (1975) from the Vallesian and Turolian age localities of Esme Akcakoy and Kayadibi. The chalicothere *Ancylotherium pentelici* is an exotic element in late Miocene faunas and has been reported from Spain (Alberdi, 1974), the Greek localities of Samos and Pikermi (Solounias, 1981), Veles (Coombs, 1973), Vathyakkos (pers. observ.), Kalimanci, Bulgaria, and Novo Ukrainka, U.S.S.R. (Coombs, 1973).

The only suid known from Maragheh, *Microstonyx erymanthius*, has a geographic range including southwest Asia and the western U.S.S.R. and is known from early Vallesian through Turolian age horizons. It may share some close phylogenetic relationships with *Dicoryphochoerus* reported from Turkey (Sickenberg et al., 1975) and the Siwaliks (Pilbeam et al., 1979).

The ruminants are an especially diversified group at Maragheh. The Giraffinae gen. and sp. indet. is an exotic element in the Maragheh fauna, as it is in late Miocene faunas of the eastern Mediterranean (Samos, Pikermi; Solounias, 1981), China (Bohlin, 1926) and North Africa (Upper Beglia; Solounias, 1981). It is possible that giraffines were exotic elements of pan-Eurasian and African middle-late Miocene open country faunas of Eurasia and Africa.

Palaeotragus coelophrys is a large paleotragine species that has been reported from medial Turolian age localities of Garkin and Kinik Turkey (Sickenberg et al., 1975), Samos (Solounias, 1981), the late Vallesian age locality of Agha Jari (Thomas et al., 1980) and the late Miocene of China (Bohlin, 1926). The genus *Palaeotragus* has a chronologic range from the middle to late Miocene. Geographically, the genus is recorded early from East Africa (*P. primaevus*, Fort Ternan, ca. 14 my; Churcher, 1970), North Africa (*P. lavocati*, Beni Mellal, MN 7; Heintz, 1976), Turkey (*P. sp.*, Sofca, MN 7; Sickenberg et al., 1975). Late Miocene species of *Palaeotragus* were broadly distributed in Spain (*Palaeotragus sp.*, Can Ponsich, MN 9; Alberdi, 1974), France (*Palaeotragus sp.*, Soblay, MN 10; Guérin and Mein, 1971); Greece (*P. roueni*, Samos, Pikermi; *P. coelophrys*, Samos; Solounias, 1981); Turkey (*P. decipiens*, Esme Akcakoy; *P. germani*, Kayadibi; *P. quadricornis*, Kayadibi; *P. coelophrys*, Garkin, Kinik; Sickenberg et al., 1975); the western U.S.S.R. (*P. roueni*; Borissiak, 1962); China (*P. microdon*, *P. coelophrys*; Bohlin, 1926). *Palaeotragus* has never been reported from the Central European or Siwalik Provinces.

The genus *Samotherium* similarly has a long chronologic and broad geographic range. Churcher (1970) reported an early *Samotherium*, *S. africanum*, from Fort Ternan while Sickenberg et al. (1975) recovered another primitive form *Samotherium sp.* from the middle Miocene Turkish locality of Candir. Its pres-

ence in Turkey is not again found until the late (?medial) Turolian locality of Kinik, which contains *Samotherium "neumayri"* (Sickenberg et al., 1975). From Spain, Alberdi (1974) reported the possible occurrence of a *Samotherium* sp. indet. from Vallesian levels of Hostalets de Pierola. Solounias (1981) recorded two varieties of *Samotherium boisseri* from Samos, one of which (var. A) he also identified at Maragheh. Borissiak (1962) reported *Samotherium expectens* from the Sarmatian and *Samotherium boisseri* from the Meotian of the western U.S.S.R. The record in China has an uncertain age range, including *Samotherium sinense*, *S. neumayri*, *S. sp. 1* and *S. sp. 2* (Bohlin, 1926). Finally, Harris (1982) noted the occurrence of a probable *Samotherium* species from the early Pliocene locality of Sahabi, Libya. The genus *Helladotherium* appears to have a more restricted chronologic and geographic range, being limited to late Miocene horizons of the Western U.S.S.R. (Borissiak, 1962) and Subparatethyan Provinces (Solounias, 1981).

Among the bovids, the genus *Miotragoceros* has one of the broadest geographic and longest chronologic ranges known within the Miocene. This genus has been reported from a number of middle and/or late Miocene localities of southwest Europe (Alberdi, 1974; Guérin and Mein, 1971), Central Europe (Thenius, 1959), western U.S.S.R. (Gabunia, 1979); the eastern Mediterranean (de Bonis et al., 1979; Solounias, 1981), southwest Asia (Sickenberg et al., 1975); North China (Bohlin, 1935); the Siwaliks (Thomas, manuscript); North Africa (Thomas, 1979; Lehman, 1982); and East Africa (Smart, 1976). The great number of species and lack of rigorous revision of the entire group currently prohibits any meaningful attempt to discuss its evolutionary and zoogeographic history despite the great quantity of material.

Gazella is another chronologically long ranging and geographically broadly distributed genus. The earliest reported occurrence of *Gazella* is from the early Miocene locality of Gebel Zelten (Hamilton, 1973). Its middle Miocene distribution includes Turkey (Candir; Sickenberg et al., 1975) and East Africa (Fort Ternan; Gentry, 1966). By the late Miocene the genus undoubtedly was distributed in savanna-like biotopes throughout Eurasia and Africa. The gazelle *G. rodleri* is known only from Middle Maragheh. However, *G. desperdita* has a relatively broad geographic and long chronologic range including the Vallesian of Spain (Alberdi, 1974) and Iraq (Thomas et al., 1980), and several Turolian localities of France (Guérin and Mein, 1971) and Spain (Alberdi, 1974).

The species of *Prostrepsiceros* and *Protragelaphus* appear to have limited chronologic and geographic ranges. The Agha Jari form "*Prostrepsiceros* aff. *houtumschindleri*" (Thomas et al., 1980) is the smallest and most primitive species of this group. It appears that by the early Turolian this group diversified into at least three species as represented at Pikermi (ca. 9 my, Bernor et al., 1980): *Prostrepsiceros houtumschindleri*, "*Prostrepsiceros*" *rotundicornis*, and *Pro-*

tragelaphus skouzesi. These same three species seem to have ranged through the medial Turolian, during which time they are recorded from Samos and Maragheh (Solounias, 1981). Sickenberg et al. (1975) also report *Prostrepsiceros* sp. from Garkin (MN 12?), and cf. *Protragelaphus* sp. from Kayadibi (MN 13). A late occurrence of *Prostrepsiceros* has been reported from the early Pliocene Libyan locality of Sahabi by Lehman (1982). It should also be mentioned that Pilbeam et al. (1979) recorded a possible occurrence of cf. *Prostrepsiceros houtumschindleri* from the Siwaliks. *Protragelaphus* is a monospecific genus found at Pikermi (Solounias, 1981), Maragheh, and during the Meotian of the western U.S.S.R. (Borissiak, 1962).

The earliest occurrence of the genus *Oioceros* is from the late early Miocene locality of Xieja, China (Chiu et al., 1979). Subsequently, *Oioceros* appears to have had a broader geographic range during the middle Miocene that included China (*O. noverca* and *O. grangeri* from Tung Gur; Pilgrim, 1934; Chiu et al., 1979), East Africa (*O. tanyceras* from Fort Ternan; Gentry, 1971), and Turkey (*Oioceros* sp. from Candir and Kinik; Sickenberg et al., 1975). The first known late Miocene distribution is limited to Greece, Turkey, and Iran. According to Solounias (1981), the late Miocene species *Oioceros rothii* and *Oioceros atropatenes* are more primitive than the very large species *O. wegneri*. *Oioceros rothii* is known to occur at Pikermi and in Middle Maragheh, while *Oioceros atropatenes* is known from Pikermi and Maragheh. *Oioceros wegneri* has only been reported from Samos (Solounias, 1981).

Protoryx laticeps and *Protoryx crassicornis* have both been collected at Maragheh. *Protoryx laticeps* was recovered by Mecquenem's expedition, and as argued earlier here would probably have been collected within the Middle Maragheh biostratigraphic interval. The smaller and more advanced species, *Protoryx crassicornis* (Gentry, 1971 = his *Pachytragus crassicornis*), has been collected by the Lake Rezaiyeh Expedition only in the upper biostratigraphic interval. The apparent stratigraphic relationships of these species suggest that Gentry's (1971) hypothesis that *Protoryx crassicornis* was evolutionarily more advanced than *Protoryx laticeps* is supported to some degree by biochronologic and geochronologic information given here. If the provenance of the Maragheh specimens and radiometric-biochronologic assessments at that locality are proven accurate by future investigations, then the age range of the two species at Maragheh could be as much as 1.5 my or more, with *Protoryx crassicornis* apparently replacing *Protoryx laticeps* in the 8 to 7 my interval. The possibility nevertheless remains that the two species coexisted provincially for a significant interval and that they are not useful for detailed biochronologic interpretation. In addition to these localities, *Protoryx* has also been reported from the late Miocene of China (Bohlin, 1935), the middle Miocene of Turkey (Sickenberg et al., 1975) and possibly from Sahabi (Lehman, 1982).

The type locality of *Urmitherium polaki* is Ilkhchi,

TABLE 4. Provincial zoogeographic and chronologic ranges of Maragheh mammalian species.

Species	Provinces								Age range estimates
	1	2	3	4	5	6	7	8	
<i>Mesopithecus pentelici</i>	X	X	X	X					9-6 ma.
<i>Promeles palaeattica</i>			X	X					9-7 ma.
<i>Ictitherium viverrinum</i>				X				cf.	9-7 ma.
<i>Thalassictis wongii</i>			?	X				X	8-? ma.
<i>Percrocuta eximia</i>	X	X	X	X					?-5 ma.
<i>Felis attica</i>				X					?-7 ma.
<i>Machairodus aphanistus</i>	X	X	X	X				cf.	12-5 ma.
<i>Choerolophodon pentelici</i>			?	X					9-7 ma.
" <i>Hipparion</i> " <i>gettyi</i>				X					9.5-8.5 ma.
<i>Hipparion prostylum</i>	X			X		aff.			9-7.5 ma.
<i>Hipparion campbelli</i>				X				aff.	ca. 7 ma.
" <i>Hipparion</i> " <i>aff. moldavicum</i>			X	X					8.5-7 ma.
" <i>Hipparion</i> " <i>?matthewi</i>			?	X	?				8.5-7 ma.
<i>Diceros neumayri</i>			?	X	X				?9-7 ma.
<i>Ancylotherium pentelici</i>	X	X	X	X					9-7 ma.
<i>Microstonyx erymanthius</i>			X	X					9-7 ma.
<i>Palaeotragus coelophrys</i>			?	X					10-7 ma.
<i>Helladotherium duvernoyi</i>			X	X					9-7 ma.
<i>Prostrepsiceros rotundicornis</i>				X					9-8 ma.
<i>Gazella cf. deperdita</i>	X		?	X					9-7 ma.
<i>Prostrepsiceros houtumschindleri</i>				X					9-7 ma.
<i>Oioceros rothii</i>				X					9-8 ma.
<i>Protoryx laticeps</i>				X					9-8 ma.
<i>Protoryx crassicornis</i>				X					8-7 ma.

Legend—Provinces 1-8 are of Bernor (1984) and include: 1) Western and Southern European Province; 2) Eastern and Central European Province; 3) Roumania and Western U.S.S.R. Province; 4) Sub-paratethyan Province; 5) North African Province; 6) Siwalik Province; 7) East African Province; 8) China Province.

Maragheh. This species appears to have had a restricted geographic distribution that includes the middle and late Miocene of Turkey (Candir, MN 7; Kayadibi, MN 9; Garkin, MN 12; Kinik, MN 13; Sickenberg et al., 1975; Erdbrink, 1978), Iran (Maragheh) and China (Bohlin, 1935).

Tables 4 and 5 summarize information on the zoogeography and geochronology of Maragheh mammals reported here. Table 4 indicates that no Maragheh species occur throughout Eurasia and Africa. However, several species including *Mesopithecus pentelici*, *Percrocuta eximia*, *Machairodus aphanistus* and *Ancylotherium pentelici* are reported as occurring throughout Europe, the western U.S.S.R. and the Subparatethyan Province (sensu Bernor, 1983, 1984). Several other species including *Promeles palaeattica*, *Thalassictis wongii*, *Choerolophodon pentelici*, *Diceros neumayri*, *Microstonyx erymanthius*, *Palaeotragus coelophrys*, *Helladotherium duvernoyi*, and *Gazella deperdita* may also occur in the western U.S.S.R. (Borissiak, 1962). Species common to southern and western Europe and the Subparatethyan Province not cited above include *Hipparion prostylum* and *Gazella deperdita*. Species in common between Maragheh and the basal Pliocene of Libya (Sahabi fauna; Bernor, 1982) include *Percrocuta eximia*, *Machairodus aphanistus*, *Diceros neumayri*, and a form very close to *Miotragocerus* sp. indet., *Miotragocerus cyrenaicus* (Thomas,

1979). Only two species, *Hipparion prostylum* and (potentially) *Microstonyx erymanthius* share close phylogenetic relationships with a Siwalik species (*Hipparion antelopinum* and *Microstonyx* aff. *erymanthius*), while three carnivore species share close relationships with Chinese late Miocene species (*Ictitherium viverrinum*, *Thalassictis wongii*, and *Machairodus aphanistus*). The remainder of the Maragheh mammalian species listed here are reported from other localities in the Subparatethyan Province. Chronologically, most of the Maragheh species range in age between 9 and 7 my with the notable exception of *Machairodus aphanistus* (ca. 12-5 my).

Table 5 gives the provincial zoogeographic and geochronologic ranges of genus and superspecific group taxa that are not monospecific and whose geographic ranges are known to extend beyond the Subparatethyan Province. In this category there are several cosmopolitan taxa that have long chronologic ranges including *Martes* sp. (?-Recent), *Orycteropus* sp. (15 my-Recent), *Deinotherium* (18-2 my), *Miotragocerus* (14-5 my), and *Gazella* (?18 my-Recent). One carnivore genus, *Indarctos* (12-5 my) ranges from western Europe and North Africa eastward through the Subparatethyan, Siwalik and Chinese Provinces. Three other taxa, *Metailurus* (= *Paramachairodus*; ca. 9-6 my), *Felis* (?-Recent) and *Chilotherium* (9-7 my) show European, Subparatethyan, Siwalik and Chinese provincial re-

TABLE 5. Provincial zoogeographic ranges of Maragheh mammalian taxa of genus or superspecific taxonomic rank.

Taxon	Province								Age range estimates
	1	2	3	4	5	6	7	8	
<i>Indarctos</i>	X			X	X	X		X	12–5 ma.
<i>Martes</i> sp.	X	X	X	X	X	X	X	X	?–Recent
<i>Melodon</i>				X				X	8.5–? ma.
<i>Parataxidea</i>				X				X	8.5 ma.
<i>Thalassictis</i>			?	X		X		X	9–? ma.
<i>Metailurus</i> (= <i>Paramachairodus</i>)		X	X	X		X			?9–6 ma.
<i>Felis</i>	X		X	X		X		X	?–Recent
<i>Orycteropus</i>	X	X	X	X	X	X	X	X	15 ma.–Recent
<i>Deinotherium</i>	X	X	X	X	X	X	X	X	18 ma.–?
<i>Choerolophodon</i>			X	X		X	X		15–?7 ma.
“ <i>Hipparion</i> ” Gp. 1	X	X	X	X	X			?	12–7 ma.
“ <i>Hipparion</i> ” Gp. 2			X	X				X	9–7 ma.
<i>Hipparion</i> Gp. 3	X			X		X			9–7 ma.
<i>Chilotherium</i>	X		X	X		X		X	9–7 ma.
<i>Palaeotragus</i>	X	X	X	X	X		X		14–7 ma.
<i>Samotherium</i>	X		X	X	X		X	X	14–5 ma.
<i>Miotragocerus</i>	X	X	X	X	X	X	X	X	14–5 ma.
<i>Gazella</i>	X		X	X	X	X	X	X	18 ma.–Recent
<i>Prostrepsiceros</i>				X	X	?			9–5 ma.
<i>Protragelaphus</i>			X	X					9–8 ma.
<i>Oioceros</i>				X			X	X	16–7 ma.
<i>Protoryx</i>				X	aff.		aff.	X	9–7 ma.
<i>Urmiatherium</i>				X				X	ca. 7 ma.

Legend—see Legend for Table 4.

relationships. A number of taxa show African–Asian relationships including *Choerolophodon* (15–7 my), *Palaeotragus* (14–7 my), *Samotherium* (14–5 my), *Prostrepsiceros* (9–5 my), *Oioceros* (16–7 my) and *Protoryx* (9–7 my). The three supraspecific groups of hipparionine horses show distinctly different zoogeographic relationships from one another: Group 1 is found in Europe, the Subparatethyan Province, probably North China, but not in the Siwaliks or East Africa. Group 2 hipparionines are restricted to the Subparatethyan, Western U.S.S.R., and Chinese Provinces. Group 3 hipparionines are found in a relatively narrow west–east latitudinal belt from southern and western Europe to Indopakistan.

Some interesting generalized patterns emerge from this analysis. First, cosmopolitan taxa usually have the longest chronologic ranges, and include genera that were involved in the initial late Orleanian/Astaracian deployment of African or trans-African/Subparatethyan mammals throughout many sectors of Eurasia. Species of these groups may have evolved by vicariance subsequent to their early migration into non-seasonal subtropical regions. The mechanism isolating their populations could have been the diachronous transgression of progressively more seasonal environments (Bernor, 1983, 1984). Second, the Maragheh mammals that show close evolutionary relationships with North and East African mammals are first known to occur in the late Miocene. Thomas et al. (1982) argued for the origin of many of these species in Eurasia

and Bernor (1982, 1983, 1984) has cited this as a basal Pliocene “regression” of the “Pontian” chronofauna. Third, the zoogeographic relationships of Maragheh taxa with those of the Siwalik Province appear to be phylogenetically and chronologically more distant from the ones with western Europe, Central Europe, the western U.S.S.R., China, and North Africa. Fourth, the Maragheh mammal fauna shows striking species and genus/superspecific group zoogeographic relationships within the Subparatethyan and Western U.S.S.R. Provinces. This zoogeographic analysis largely verifies Bernor’s (1978, 1983, 1984) and Bernor et al.’s (1979a) earlier reconstruction of the general evolution and zoogeographic relationships of the classic “Pontian” large mammal faunas.

SUMMARY

The Maragheh mammalian assemblage represents a savanna-mosaic chronofauna (sensu J. A. H. Van Couvering, 1980) that shows a long and complicated evolutionary history. The geochronologic evidence cited here suggests that during the interval of time represented by the Maragheh fauna, little change took place in its community structure; there were no major faunal turnovers. The characterization and rough definition of biostratigraphic intervals using a potential lineage of hipparionines, combined with radiometric dating, has allowed broad provincial and interprovincial zoogeographic comparisons with late Miocene mammal-bearing deposits throughout Eurasia and Africa.

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