Recent Advances in Paleobiological Research of the Late Miocene Maragheh Fauna, Northwest Iran

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I. Historical Background

The fossil localities of Maragheh are located in the eastern Azarbaijan province, northwest Iran at 37° 21’ 08” N latitude and 46° 24’ 40” E longitude. The Maragheh fauna has long been considered one of the three most preeminent western Eurasian late Miocene Pikermian faunas, along with Samos and Pikermi in Greece. As with Pikermi and Samos, Maragheh is a true “Lagerstätte” because of the shear abundance and diversity of its fauna. It is unique amongst the three classical Pikermian faunas in its clear stratigraphic display and layer-cake stratigraphy with several, laterally continuous volcanic ashes that are readily amenable to radioisotopic dating.

A Russian explorer, Khanikoff has been credited with first finding the Maragheh site in 1840 and sending a small collection to Dorpat University (now University of Tartu, Estonia). The Maragheh fauna was initially studied in the latter half of the 19th century (Abich 1858, Brandt 1870, Grewingk 1881). These early works provided data on Maragheh’s similarity to Pikermi. The Austrian paleontologist Pohlig was invited by a merchant from the nearby city of Tabriz to visit the locality in 1884 and it was Pohlig that made the first comprehensive collection and geological study of Maragheh (Pohlig, 1886). Pohlig explored extensively across the Maragheh basin and would appear to have sampled fossils from nearly all, if not all of the Maragheh section. The Pohlig collection in the Naturhistorisches Museum, Wien is extraordinary as an early collection because much of it preserves locality information which facilitates understanding of its stratigraphic provenance. Two other Austrian paleontologists, Rodler and Kittl, visited Maragheh and made an extensive collection of fossils which were later published by Kittl (1887), Rodler (1890), Rodler and...
Weithofer (1890) and Schlesinger (1917). Damon, from the British Museum of Natural History, London made a small collection briefly communicated by Lydekker in 1886. In 1897, the French paleontologist Marcellin Boule secured permission to conduct a paleontological expedition to Maragheh in 1904. The 1904 French expedition to Maragheh was organized at a very grand scale for this time in paleontology. A group of French paleontologists assisted by 12 local laborers excavated a large sample of Maragheh fossils from Kingir, Kopran, Sholleveend and Kermedjawa (Mecquenem 1905, 1906, 1908, 1911, 1924-25).

More than 50 years elapsed before other reported expeditions occurred at Maragheh. Takai of Tokyo University collected Maragheh fossils from Kerjabad (Takai 1958). Robert Savage of Bristol University also visited Maragheh in 1958 and collected fossils. Tobien from the Johannes-Gutenberg University, Mainz made important excavations of the middle portion of the Maragheh sequence in the 1960's (Tobien, 1968). During the 1970’s three scientific groups conducted research at Maragheh: a combined Dutch-German group led by Erdbrink (Erdbrink et al. 1976, Erdbrink 1976 (a,b), 1977, 1978, 1982, 1988), a joint University of Kyoto-Geological Survey of Iran led by Kamei (Kamei et al. 1977, Watabe 1990, Watabe and Nakaya 1991a,b) and the Lake Rezaiyeh Expedition (LRE) led by Campbell (Campbell et al. 1980). Bernor was a student charged with the study of vertebrate fauna for the LRE which resulted in his PhD (1978) and manuscripts on the fauna, biostratigraphy and zoogeographic relationships of the fauna (1986) and the systematic, biostratigraphy and zoogeography of the hipparionine horses (1985). An extensive review of the fauna with systematic, chronologic and biogeographic comparisons to Pikermi and Samos was published by Bernor et al. (1996).

There are three important outcomes from the field work undertaken in the 1970’s including: a) collection of fossils with close regard to stratigraphic provenance which has led to a biostratigraphy of the Maragheh fauna, b) study of all collections to better understand the taxonomy and diversity of the mammalian fauna, and c) application of a variety of geochronologic tools to secure well resolved ages for the Maragheh section and its faunas.

After 30 years cessation of excavation activities in the Maragheh basin, Iran’s Department of Environment (DOE) and National Museum of Natural History (MMTT) started a new initiative and sponsored new excavations in the area which resulted in nomination of 10 km² of Maragheh fossiliferous area as a national protected zone and establishment of a field museum and research station in the Dare Gorg (Gort Daresi) area. The MMTT-University of Helsinki initiative known as the International Sahand Paleobiology Expedition (INSPE) has also been recently started and is currently in progress. This program has undertaken three field seasons between 2007 and 2009, discovering several new localities and numerous fossils. The program has further reinitiated study of the mammalian fauna with the intention of bringing them into a contemporary taxonomic context for comparative paleoecological and paleobiogeographic studies.

**Abbreviations**

INSPE - International Sahand Paleobiology Expedition
MMTT - Muze Meli Tarih Tabiei (National Museum of Natural History), Tehran
MNHN - Muséum National d’Histoire Naturelle, Paris
M2 – Upper second molar
NMW - Naturhistorisches Museum Wien
UCR - University of California, Riverside
II. Geology and Stratigraphy

The Maragheh basin is bounded to the north by the NW-SE trending Anatolian transform fault, also known as the Tabriz fault, on the west by the N-S trending Urmieh fault and on the south by the NW-SE Mendelasar transform fault. Regionally the Maragheh Basin and its associated transform faults are dominated by the Zagros crush zone to the south and west. Also, there are the Urmieh-Bazman (Urmieh-Dokhtar) volcanic belt in the northeast and the Sanandaj-Sirjan metamorphic belt (Mendelassar transform) in the southwest (Fig. 1). The Urmieh-Bazman volcanic belt with its northwest-southeast trend is believed to have resulted from the collision of the Arabian and Iranian plates. The Sanandaj-Sirjan metamorphic belt with a similar trend lies between the main Zagros thrust (crush zone) and the Urmieh-Bazman belt (Davoudzadeh et al. 1997).

Figure 1 – Geographic position and relationships of the Maragheh area to the major tectonic features (after Dewey et al. 1973 and Huber 1976) in N. W. Iran.

During the Paleogene, northwest Iran experienced a wide range of post collisional arc volcanic activities. After this magmatism event, clastic, evaporate, and carbonate sediments were deposited during the late Paleogene and early Neogene (Lower Red and Qom Formations). By the end of the early Miocene, the last Tethyan seaway incursion regressed from this area ending the local carbonate deposition cycle (Aghanabati 2004). Consequently, at the beginning of the Neogene, this domain emerged above sea level and developed as incipient mountain ranges, basin troughs, and a topography resembling
present conditions (Davoudzadeh et al. 1997). The most significant deposits of this time are terrestrial sediments and evaporites known collectively as the Upper Red Formation. The remains of these deposits are not found in the Maragheh area but mostly occur north of the Tabriz Fault and south of Urmiyeh fault (Fig. 1). It seems that these major faults in the area, which have been active since the Paleozoic (Aghanabati 2004), structurally controlled and prevented deposition of these units in the Maragheh Basin. Volcanic activity was reinitiated in the late Miocene to middle Pliocene interval in the Maragheh Basin and adjacent areas (Moin-Vaziri and Amin-Sobhani 1977).

The Late Miocene Maragheh stratigraphic sequence accumulated on the southern flank of the Mt. Sahand volcanic massif. Mt. Sahand is a large volcanic complex covering an area of about 10,000 km² (Moin-Vaziri and Amin-Sobhani 1977) and regardless of its circular outline, is not a single volcano. A series of distinct volcanic cones are arranged along an east-west trend collectively forming this enormous volcanic massif.

The late Miocene deposits of the Maragheh Basin consist of a thick sequence of volcaniclastic continental strata with a basal pyroclastic unit. Kamel et al. (1977) named the entire 500-600 m thick late Miocene sequence the Maragheh Formation. They differentiated this formation into a lower fossiliferous member (160 m) and an upper non-fossiliferous unit forming the upland hills of Mt. Sahand. Campbell et al. (1980) restricted the Maragheh Fm. to the lower 300 m thick volcaniclastic and fossiliferous series. They also referred to the basal pyroclastic unit as the Basal Tuff Formation. Hence, the fossil-bearing sequence of Maragheh Basin is confined to the lower 150 m of 300 m thick Maragheh Fm. The upper surface of the Maragheh Fm. is erosional with local Pliocene-Quaternary capping of heavily oxidized terrace gravels, pumice breccias, and boulder-ridden soils. These uppermost horizons are more than 350 m thick south of Sahand, but can be as much as 1000 m in thickness in areas near the Anatolian transform (Bernor et al. 1980).

The Maragheh Group
We describe herein the sedimentary horizons of the Maragheh Group as they are expressed in the Maragheh Basin.

The Basal Tuff Fm. represents a single air-fall unit of rhyolite tuff with local thickness of over 80 m. This unit is a uniform, unbedded, structureless deposit of white, devitrified ash with randomly oriented crystals of mica and fresh fragments of feldspar and quartz. The unit represents a tremendous pyroclastic event with substantial outcrops south and northeast of the central fossiliferous area which has also proven to be useful for long-range intra-basin correlations (Campbell et al. 1980, Bernor et al. 1980, Bernor 1986).

The Maragheh Fm. rests unconformably on the Basal Tuff Fm. It is eroded to a thickness of 300 m and consists of strata made up exclusively of detrital fragments of hornblende andesite and dacitic pumice, and is interbedded at widely spaced intervals with layers of pumice-lapilli tuff. In general, the volcaniclastic beds are unlaminated poorly sorted silty grits with lenses of andesite and pumice cobbles, in depositional units ranging in thickness from 1-3 m. The top of each depositional unit is generally marked by a darker, hardly weathered zone with root-casts (Bernor et al. 1980).

Maragheh Fm. deposits are bound to the north by the Anatolian transform (Tabriz fault) (Fig. 1). Between the northwest of Sahand massif and the city of Tabriz possible Miocene-Pliocene deposits are unlike the Maragheh Fm. These beds are composed of diatomites containing fish and mollusks and some lignites with plant remains. Hipparionine teeth and scarce mammalian bones are recorded from these deposits (Rieben 1934), whose nature is quite different from those of
the Maragheh Fm. Recently, abundant mammalian fossils have been discovered in the areas north and northeast of Tabriz (Mirzaei Ataabadi et al. submitted). Although this fossil material resembles that of the Maragheh Fm., their geology, sedimentology, and taphonomy differs. To the west, the Maragheh Fm. is bounded by Lake Urmiyeh (or Urmiah), which is a shallow, hypersaline body of water formed in the Pleistocene by the activities of the Tabriz and Urmiyeh faults (Aghanabati 2004). To the southwest, the limit of Maragheh Fm. is the Mendelassar ridge (Fig.1). This is an uplifted belt of lightly metamorphosed rocks also known as the Sanandaj–Sirjan metamorphic belt.

Campbell et al. (1980) reported that some lithological horizons in the Maragheh Fm. can be traced over wide areas allowing intra-basin correlations. The most distinctive unit for correlation is a diamictitic breccia named “Loose Chippings”. This marker bed best outcrops in the central portion of the study area and has been used for stratigraphic correlation of vertebrate localities in this area (Fig. 2). This bed is recorded as the “scoria bed” by Kamei et al. (1977) and as the “trachytic breccia” by Erdbrink et al. (1976).
Section C (Fig. 2) represents the recent excavations in the Maragheh area by MMTT and INSPE teams. It is correlated to the adjacent sections by a major pumice layer known as the “Pumice Bed 2”. “Pumice Bed 2” is 5-7 m thick and has been widely traced in the study area. This bed was likely accumulated from a single large-scale flow event (Sakai, pers. commun.). The sections in the extreme northeast and southwest (A and H) are correlated based on the Basal Tuff Fm. Maragheh Fm. seems to rest with a low angle regional unconformity on the Basal Tuff Fm. Based on the studies in the central fossiliferous area the regional dip of the Maragheh Fm. is west-southwest with about 5 m/km inclination. Triangulation from the presently known exposures of the Basal Tuff Fm. by the American team in the 1970’s also indicates a consistent dip to the west-southwest with a general inclination of about 15 m/km.

Figure 2 – Lithology and stratigraphy of the Maragheh Formation, N. W. Iran. (See Fig. 3 for location of sections A-H). Sites A and H are correlated based on the Basal Tuff. Sites B and D-G are correlated by the “Loose Chippings” marker bed. Site C is correlated to nearby sections by “pumice bed 2” and corresponds to the recent excavations (MMTT II, DRG1, and AZM1) in the Maragheh area. The position of section C above the basal tuff and below the “Loose Chippings” is certain. However, the details of the base and top of the section are not recorded. The basal tuff is shown at the base of most sections, with topographic elevation. Numbers and letters to the left of each column are fossil localities. R1-R12 and MULB-5 are sites from which radiometric age determinations were obtained (see also Fig. 3 and Table 1). 1A, 1B and 2 in site C indicate pumice beds.

The differences between the dips of these units suggest that the Basal Tuff draped over a west sloping paleoslope/basin that was gradually filled by the Maragheh Fm. These successive beds prograded eastward as the base level rose (Campbell et al. 1980). This interpretation has been generally supported by radiometric (Campbell et al. 1980) and biostratigraphic evidence (Bernor 1978, Bernor et al. 1979, Bernor et al. 1980, Bernor 1986). These data suggest that the beds and associated fossils farthest to the west (Kopran) are the oldest compared to the localities in the easternmost part (Ilkhchi) which are the youngest (Bernor et al. 1980, Bernor 1986).

Major sedimentary facies that have been distinguished in Maragheh are pebble and cobble conglomerate which make less than 5% of the studied sections, grey sandstone and breccia facies which makes up about 25% of the sections, poorly sorted massive siltstones which constitute about 70% of Maragheh strata, and air-fall tuff deposits consisting almost entirely of pumice fragments. It seems that the following sedimentary events are responsible for deposition of the Maragheh Fm.: a) erosion by small streams which made a small disconformity at the base, b) deposition of coarse clastics by lateral accretion in point bar deposits and fine clastics by vertical accretion in overbank deposits, c) soil formation at the top of former units, and d) random airfall deposition. These processes built the extensive Maragheh Fm. as a product of alluviation rather than volcanic activity or lacustrine sedimentation (Campbell et al. 1980, Bernor et al. 1980, Bernor 1986).

Fossil bones in Maragheh Fm. occur as localized concentrations within the un laminated beds, floating in the sediments rather than lying on bedding-planes. A single complete articulated skeleton of the mustelid Promeleus palaeattica has been found from the MMTT 13 quarry (Bernor et al. 1996). Taphonomic studies of these fossil accumulations indicate autochthonous bone assemblages accumulated on overbank or
floodplain deposits of fluvial systems.

A large number of the bones are preserved with articulation of distal limb elements and early weathering stages. Pyroclastic events such as mudflows or ash falls were not directly responsible for mortality. On the other hand, biologic agents were the probable cause of death, as the bones were buried almost immediately or subaerially exposed only long enough to allow removal of some elements by scavengers (Morris 1997).
Bernor (1986) and Bernor et al. (1996) provided an account of the mammalian species reported from Maragheh. Since 1996, there have been a number of taxonomic revisions that affected the documentation of fossils at Maragheh and their comparisons with other penecontemporaneous Eurasian and African mammal faunas. Moreover, there have been a number of studies of Eurasian (Bernor et al. 2003, 2005, Eronen et al. 2009) and Eurasian-African (Bernor and Rook 2008, Bernor et al. 2009) biogeographic relationships for the late Miocene interval that have brought new significance to understanding Old World (Pikermian) chronofaunas in general, and specifically the importance of the Maragheh sequence. Figure 3 is a satellite image indicating the principal vertebrate paleontology collecting areas in the Maragheh Basin. Vertebrate fossil localities crop out across the Maragheh Basin and often are expressed as dense concentrations of fossils up to a Meter in thickness and extending 10s to 100s of Meters laterally. This is particularly true for the Upper Maragheh locality MMTT 13 near the village of Shol’avand. Since the latter part of the 19th century coincident with the Austrian exploration of the Maragheh Basin there has been a growing archive for the stratigraphic provenance of the Maragheh fauna (Bernor 1986).
Figure 4 – Mammalian biostratigraphy of the Maragheh Formation, N. W. Iran. The Stratigraphic provenance of vertebrate localities is given above/below the “Loose Chippings” marker bed. Taxa with * are also recorded from Upper Maragheh Loc. 37

The work by Iranians with Japanese, Dutch, German and American groups in the 1970’s brought marked improvements to this stratigraphic record. Figure 2 provides a summary of 8 stratigraphic sections, arrayed from west to east, of these principal collecting areas with the UCR -MMTT localities (Bernor 1986) and newly discovered INSPE localities indicated.

Bernor (1978, 1986) integrated all known stratigraphic records of fossil mammals to develop the first Maragheh mammalian biostratigraphy. He originally subdivided the Maragheh Fm. into three units based on the stage-of-evolution of the Hipparion s.s. lineage: Lower Maragheh whose base was defined by the first occurrence of Hipparion gettyi at Kopran; Middle Maragheh whose base was defined by the first occurrence of Hipparion prostylum; and Upper Maragheh whose base was defined by the first occurrence of Hipparion campbelli. Recent studies of the Maragheh hipparion samples housed by the MNHN and Howard University Laboratory of Evolutionary Biology suggest that Hipparion prostylum, originally defined based on skull morphology alone, does not occur at Maragheh. The Paris sample (MNHN) originally believed to be referable to Hipparion prostylum (Woodburne and Bernor 1980, Bernor et al. 1980, Bernor 1985) yields no postcrania characteristic of Hipparion prostylum s.s (Mt. Luberon sample) or Hipparion campbelli (Howard University Maragheh sample). However, there are postcrania in the Paris collection and Tobien’s collection that are referable to Hippotherium brachypus, and we believe that this is a more likely referral for the Paris and Tobien collections of hipparions with a reduced fossa placed high on the skull. We find therefore that the MNHN Maragheh Hipparion assemblage includes two distinct skull morphologies and two distinct postcranial morphologies. The skulls with a large, single, preorbital fossa (POF) placed close to the orbit are believed to be associated with elongate slender metapodials and likely referable to Cremohipparion aff. moldavicum, whereas the skull with a single, highly reduced POF is likely associated with short, stout metapodials referable to Hippotherium brachypus. In that the MNHN assemblage is believed to be stratigraphically derived mostly from the middle portion of the section we now need to recognize that the biostratigraphic subdivisions are not based on the evolution of a continuous lineage, but simply as biozones.

Current evidence suggests the following horse sequence: Hipparion gettyi occurs at Kopran, the oldest set of localities in the Maragheh Basin with its stratigraphic range being from the -150 to -75 Meter interval of the section; Hippotherium brachypus and Cremohipparion moldavicum occur in the -52 to -25 Meter interval of the section; Hipparion campbelli is first known to occur at the -20 Meter interval and is believed to be present at the + 7 Meter interval of the section. Small horses which we believe to be best referred to Cremohipparion?matthewi occur from about -115 to + 7 Meter interval of the section. There are likely multiple species of small Cremohipparion known from Western Eurasia (i.e. Cremohipparion matthewi, Cremohipparion nikosi and Cremohipparion minus and potentially others) and there is simply too little cranial and complete metapodial data to determine which of these occur at Maragheh. The Maragheh hipparion assemblage is numerically abundant and species diverse and is undergoing extensive new systematic analysis by Mirzaie Ataabadi, Bernor, and Wolf (in progress). Figure 4 updates Bernor’s
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Swisher (1996) provided new single crystal Argon ages for the Maragheh fauna. Swisher (1996) significantly revised Campbell et al.'s (1980) biostratigraphy of the Maragheh mammal fauna. Swisher (1996) and Bernor et al. (1996) initial report on zircon fission track ages and K-Ar ages. These are summarized by stratigraphic interval, in Table 1 here which shows that the ages are internally coherent and the oldest ages being stratigraphically succeeded by progressively younger ages.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Weighted Mean (100)</th>
<th>Isochron Age (96)</th>
<th>Sample</th>
<th>K-Ar Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>R 10</td>
<td>7.420 ± 0.107</td>
<td>7.536 ± 0.111 (11 pt.)</td>
<td>R 10</td>
<td>7.5 ± 0.4</td>
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<td>R 5</td>
<td>7.3 ± 0.5</td>
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<td>R 5</td>
<td>7.7 ± 0.5</td>
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<tr>
<td>R 6</td>
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<td>R 6</td>
<td>7.0 ± 0.5</td>
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<td>R 7</td>
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<td></td>
<td>R 7</td>
<td>5.5 ± 1.0</td>
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<td>R 9</td>
<td>7.642 ± 0.033 (8 pt.)</td>
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<td>R 12</td>
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</tr>
<tr>
<td>R 11</td>
<td>7.7 ± 0.5</td>
<td></td>
<td>R 11</td>
<td>7.4 ± 0.3</td>
</tr>
<tr>
<td>R 3</td>
<td>8.667 ± 0.040</td>
<td>8.635 ± 0.029 (9 pt.)</td>
<td>R 3</td>
<td>6.4 ± 0.5</td>
</tr>
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<td>R 4</td>
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<td>R 4</td>
<td>8.9 ± 0.5</td>
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<tr>
<td>R 4</td>
<td>10.1 ± 0.5</td>
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<td>R 4</td>
<td>9.3 ± 0.1</td>
</tr>
<tr>
<td>R 7</td>
<td>11.2 ± 6.0</td>
<td></td>
<td>R 7</td>
<td>11.3 ± 1.0</td>
</tr>
<tr>
<td>R 7au</td>
<td>9.3 ± 0.1</td>
<td></td>
<td>R 7au</td>
<td>9.3 ± 0.1</td>
</tr>
</tbody>
</table>

Table 1 – Summary of the isotopic age determinations from the Maragheh Formation and Basal Tuff (after Bernor 1986 and Swisher III 1996).
Table 2- Locality ages of UCR-MMTT fossil localities of Maragheh Formation, N. W. Iran, inferred from the estimated sedimentation rates. Ages with * are isotopic age determinations of zero level which corresponds to “Loose Chippings” and -110 level which corresponds to Mordaq (Murdag) tuff (see also Fig. 5 and Table 1). Localities with * have an estimated level with respect to “Loose Chippings”.

Bernor et al. (1996) suggested that based on estimated sedimentation rates the Maragheh fauna ranges from about 9 m. y. to 7.4 m. y. Table 2 represents a calculation of ages for localities in the western and central portion of the sequence based on the estimated sedimentation rates (0.008 m. y. per Meter).

Thus, the oldest locality is Kopran I (8.96 m. y. estimated age) and the youngest is MMTT 26 (7.68 m. y. estimated age), located 7 Meters above the “Loose Chips” marker bed. Figure 5 summarizes the geochronology of the Maragheh Basin and shows that the Ilkhchi fauna is located in an eastern section calibrated as being between 7.58 +/- .11 m. y. (R8) and 7.42 +/- 0.11 m. y. (R10).

Table 3 provides a summary of Maragheh mammalian taxa by biostratigraphic interval as originally defined by Bernor (1986). Here we update a number of the mammalian groups. Taxonomic changes over Bernor (1986) include: within the Hyaenidae we recognize Adcrocuta (not Percrocuta) eximia; the large machairodont cat is now recognized as being Amphimachairodus (not Machairodus) aphanistus (Lars Werdelin, pers. commun.); within the Proboscidea we now recognize the deinother as being Deinotherium gigantissimum following the specimens discovered at MMTT31 (Erdbrink et al. locality K1) by Schmidt-Kittler; the equids are as described above; amongst the Rhinocerotidae we recognize Iranotherium morgani and a Rhinocerotidae new gen. and sp. for Maragheh (Giaourtsakis, pers. commun.); the single suid occurring at
Maragheh corresponds to a population of small-medium sized Microstonyx major (=erymanthius) (Kostopoulos pers. data); for the giraffids, we currently recognize Helladotherium duvernoyi, Samotherium neumayri, Palaeotragus coelophrys and Bohlinia attica (not the specimen mentioned by de Mequenem 1925: Pl. II, Fig. 3), but a revision of the material is certainly needed in order to clarify chronogeographic relationships (Kostopoulos, pers. data); the Bovidae are undergoing extensive revision (Kostopoulos and Bernor, in progress) and we recognize the following taxa for Maragheh: Gazella capricornis (not cf. deperdita), Gazella cf. ancyrensis, “Gazella” (not Gazella) rodleri, Oioceros atropatenes, Oioceros rothii, Nisidorcas sp., Prostrepsiceros houtumschindleri, Prostrepsiceros cf. vinayaki, Prostrepsiceros fraasi, Prostrepsiceros cf. rotundicornis, Protragelaphus skouzesi, ?Palaeoeras sp., Skoufotragus laticeps, Palaeoryx sp., Urmiatherium polaki, ?Criotherium sp., Mirabilocerus cf. maurus, Miotragocerus cf. valenciennesi, Tragoportax cf. amalthea (not Miotragocerus rugosifrons), and Samokeros minotaurus. The additional presence of Skoufotragus schlosseri (=Pachytragus crassicornis) is possible but not substantiated by the current revision. We also recognize the presence of Hystrix in Maragheh based on material in MNHN.

In summary, the Maragheh fauna has a chronologic range of nearly 9 m.y. to less than 7.6 m.y. but the bulk of fossil material is from the middle and upper parts of the section. The Lower Maragheh fauna is mostly comprised of taxa with very long time distributions that cannot be used in fine time-resolution interregional comparisons. For the best-known Middle Maragheh localites (1A, 1B, and 1C), where several groups have collected fossils, the current oldest age is for locality 1A, 8.16 m. y. (Table 2, estimated), and the youngest localities in the Shol’avand area (MMTT 26) date 7.68 m. y. (Table 2, estimated). To the east, the youngest localities of Ilkhchi (MMTT 37) would appear to be ca 7.4 m. y.
Table 3- Mammalian species, biostratigraphic intervals with their estimated ages, and UCR-MMTT fossil localities of Maragheh Formation, N. W. Iran (modified after Bernor 1986).

<table>
<thead>
<tr>
<th>Biostratigraphic Interval</th>
<th>Lower Maragheh (-150m to -52m)</th>
<th>Middle Maragheh (-52m to -20m)</th>
<th>Upper Maragheh (-25m to +7m)</th>
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</thead>
<tbody>
<tr>
<td>Distance from zero level (i.e. Loose Chips)</td>
<td>8.96-8.16 m. y.</td>
<td>8.16-7.9 m. y.</td>
<td>7.9-7.68 m. y.</td>
</tr>
<tr>
<td>Estimated Age</td>
<td>10/11</td>
<td>11</td>
<td>11/12</td>
</tr>
<tr>
<td>MN-equivalent zone</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>UCR-MMTT fossil localities</td>
<td>8, 28, 41, 44, 43, 9, 48</td>
<td>7, 14, 34, 1c, 6, 18, 19, 20, 1b, 2, 17, 11, 4, 35, 3, 1A, 5, 33, 21, 13, 37, 40, 51</td>
<td>26, 39, 24, 32, 38, 22, 16, 47, 27, 25, 15, 49, 49a, 50, 31,</td>
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Order Primates Linnaeus, 1758
Family Cercopithecidae Gray, 1821
Mesopithecus pentelicu Wagner, 1839 X
Order Carnivora Bowdich, 1821
Family Ursidae Gray, 1825
Indarctos maraghanus Mecquenem, 1924 X
Family Mustelidae Swainson, 1835
Promeles palaeattica Weithofer, 1888 X
Melodon maraghanus Kittl, 1887 X
Parataxidea polaki Kittl, 1887 X
Martes sp. X
Family Hyaenidae Gray, 1869
Ictitherium viverrinum Roth and Wagner, 1854 X
Thalassocitcs wongii (Zdansky, 1924) X X
Aderocutus eximia (Kaup, 1828) X X
Family Felidae Gray, 1821
Metailurus orientalis Zdansky, 1924 X
Felix attlo Wagner, 1857 X X
Amphilachairidus aphaniustus (Kaup, 1832) X X
Order Tubulidentata Huxley, 1872
Family Orycteropodidae Bonaparte, 1850
Orycteropus sp. X
Order Probosciidea Illiger, 1811
Family Gomphotheriidae Cabrera, 1929
Choerolophodon pentelici Gaudry, 1862 X X X
Family Deinotheriidae Bonaparte, 1845
Deinotherium gigantissimum Stefanesca, 1892 X
Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
“Hipparion” gettyi Bernor, 1985 X
Hippotherium brachypus Hensel, 1862 X
Hipparion campbelli Bernor, 1985 X
Cremohipparion aff. moldavicum Gromova, 1952 X
### Table 3- cont.

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<td>Rhinocerotidae gen. and sp. nov.</td>
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<td>Order Artiodactyla Owen, 1848</td>
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<td>Family Suidae Gray, 1821</td>
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<td><em>Microstonyx major</em> (Gervais, 1848)</td>
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<td><em>Samokeros minotaurus</em> Solounias, 1981</td>
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<td><em>Palaeoryx</em> sp.</td>
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<td><em>Nisidoceras</em> sp.</td>
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<td><em>?Palaeoteras</em> sp.</td>
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<td><em>?Crotherium</em> sp.</td>
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<td>Order Rodentia Bowdich, 1821</td>
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<td>Family Hystricidae Burnett, 1830</td>
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<td>Hystrix sp.</td>
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The correlation of Maragheh with Samos and Pikermi, the classical mammal fossil localities of the Eurasian late Miocene, is still open to discussion. Although this problem has been previously addressed (Bernor et al. 1996) and local
biostratigraphy and geochronology of Maragheh and Samos has been greatly improved in the past years (Bernor et al. 1996, Swisher III 1996, Kostopoulos et al. 2003). Pikermi remains badly resolved, being dated only indirectly.

According to the latest magnetostratigraphic correlation the Samos fauna ranges from ca 7.8 to 6.7 m.y., but the core of the Samos fauna referred to as the Samos Dominant Faunal Assemblage (DMAS) is dated between 7.2 and 6.9 m.y. (Kostopoulos et al. 2003, Koufos et al. 2009a). This chronology (Fig. 6) would make Middle-Upper Maragheh generally correlative with the lower fossil horizons (PMAS) at Samos (7.8-7.4 m.y.), but the Maragheh localities, as currently understood, appear somewhat older than those producing the Samos Intermediary (IMAS) and Dominant Mammal Assemblages (7.4-6.9 m.y., Koufos et al. 2009a).

**Figure 6** – Chronostratigraphic position of Maragheh, Samos and Pikermi fossiliferous sites and faunal assemblages according to data presented in this paper and Koufos et al. (2009a).
However, this conclusion is not always consistent with the evolutionary stage of several mammalian taxa and their combined presence in both Samos and Maragheh (i.e. *Melodon* (=Parataxidea) *maraghanus*, *Hyacinctictherium* (=Thalassictis) *wongii*, *Adrocuta eximia*, *Hippoptherium brachypus*, "Cremohipparion" cf. *matthewi*, *Diceros neumayri*, *Skoufotragus laticeps*, *Miotragocerus valenciennesi*, *Gazella capricornis*, *Prostrepsiceros fraasi*, *Tragoportax*, *Palaeoryx*, *Protragelaphus*, *Palaeotragus*, *Samotherium*; Kostopoulos, pers. data), which dates to the 7.4-6.9 m.y. interval of Samos but appears to be older in Maragheh.

The Maragheh mammal association as it is shown in Fig. 4 is in part constructed from the old provenance data of the Vienna (NMW) and the Paris (MNHN) collections developed in Bernor (1986). However, the Tobien collection does have stratigraphic provenance and was collected from the same part of the stratigraphic sequence where MMTT localities 1A-1C were collected (Tobien, pers. commun.)

One of the present authors (RLB) correlates Middle Maragheh, 8.1-7.9 m.y. (estimated) with Pikermi based principally on the occurrence of *Hippoptherium brachypus* which is very similar to the Pikermi form and *Cremohipparion moldavicum* which is the sister taxon to *Cremohipparion mediterraneum*, also known from Pikermi (Koufos, 1987). Another (DSK) holds that the apparent faunal relationships between Pikermi and Maragheh, also evidenced by several artiodactyl taxa do not conform such ages, as the mammal association of Pikermi appears to be more advanced than those from Vathyllakkos-2, Prochoma and Perivolaki (Greece), magnetostratigraphically dated between 7.4-7.2 m. y. (Koufos et al. 2006). In addition, *Hippoptherium brachypus* and *Cremohipparion moldavicum* are also present in Akkaşdağ (Turkey, dated 7.1 m. y.) while the type locality of *Cr. moldavicum* is Taraklija of the late Tuulorian.

Clearly a conclusive correlation between Maragheh, Samos, and Pikermi will have to await resolution of the apparent mismatch between the available geochronological and biochronological evidence. Without anticipating we note that the main explanations available at this time are: a) mistakes in the radiometric or magnetostratigraphic dating, b) mismatches in the correlation of old localities with new stratigraphic evidence, c) major diachrony in the occurrence of species between these localities, and d) a mistaken attribution of ecomorphs to chronospecies.

IV. Paleobiogeography and Paleoecology

We follow recent investigations on paleobiogeographic analysis by Bernor et al. (2001) and Fortelius et al. (1996) by undertaking genus-level faunal resemblance index (FRI) studies using both the Simpson’s (1943) and the Dice (Sokal and Sneath 1963) indices. Dice FRI is highly recommended by Archer and Maples (1987) and Maples and Archer (1988) and is calculated as 2C/2(A+B), where C is the number of shared taxa between two faunas, and A and B are the total number of taxa present in fauna 1 and fauna 2. Simpson’s FRI also has a long tradition of use (Bernor 1978, Flynn 1986, Bernor and Pavlakis 1987) and is calculated as C/smaller of (A and B).

We also used the ungulate tooth crown height (Bernor et al. 2001) to show the contrast between the localities under consideration. The three part subdivision of crown height includes: brachydont whereby M2 crown length is greater than its crown height; mesodont whereby M2 crown length is roughly the same as crown height; hypsodont whereby M2 crown height is more than 2 times that of crown length.
All data have been downloaded from the NOW (Neogene of Old World) database on September 30, 2009 (http://www.helsinki.fi/science/now/). Our analyses here consider only large mammals because small mammal records vary greatly across the faunas as a result of taphonomic and sampling bias.

Figure 7 illustrates the plot of genus level (G) FRI in pair-wise comparisons between Maragheh and 10 other localities under consideration. Among the early Vallesian (MN 09) localities compared to Maragheh, the Western and Central European localities, all plot with an index value of less than 20% for both Dice and Simpson’s FRI. However, Sinap loc.12 (hominid zone), Turkey, has 9 genera in common with Maragheh and a Dice FRI of 30% and Simpson’s FRI of 47% which is the highest among these early Vallesian localities. The shared genera between Sinap loc. 12 and Maragheh are: *Chilotherium, Choerolophodon, Criotherium, Gazella, Hipparion, Orycteropus, Palaeoreas, Palaeotragus* and *Tragoportax*.

![Figure 7](image)

**Figure 7** – Genus level Faunal Resemblance Index (GFRI); pair wise comparison of localities under consideration with Maragheh: Can Llobateres, Spain; Eppelsheim, Germany; Rudabanya, Hungary; Sinap loc.12 , Turkey (MN09); Samos and Pikermi, Greece; Baode loc. 49, China (MN12); Baode loc.30, China; Sahabi, Libya and Middle Awash, Ethiopia (MN13 equivalent).

Analysis of crown height (Fig.8) also demonstrate that Western and Central European (MN09) localities of Rudabanya, Eppelsheim and Can Llobateres have low incidence of mesodont and hypsodont forms (5-10% of mesodont and 5-10% hypsodont taxa) compared to more than 85% of brachydonts. This suggests that Central and Western Europe during Vallesian was forested with warm climates and low seasonality. The hypodonty in these faunas is only due to occurrence of the invasive species of hipparionine horses (*Hippotherium*) which show adaptation to closed environments with a significant amount of browse in their diets (Bernor et al. 2003). In remarkable contrast is the Sinap loc. 12, showing stronger mesodonty and hypsodonty signals. Sinap loc. 12 exhibits 35% brachydonts, 28% mesodonts and 35% hypsodont forms. As demonstrated before...
Figure 8 – Crown height diagrams for Vallesian and Turolian localities under consideration: Can Llobateres, Spain; Eppelsheim, Germany; Rudabanya, Hungary; Sinap loc.12, Turkey (MN09); Samos and Pikermi, Greece; Maragheh, Iran; Baode loc. 49, China (MN12); Baode loc.30, China; Sahabi, Libya and Middle Awash, Ethiopia (MN13 equivalent).

(Fortelius et al. 2003), later Vallesian Western Eurasian faunas are very similar in their community structure to regional Turolian faunas. They might be called “proto-Pikermian” showing the origin of “Pikermian Chronofauna” which is characterized best by the Maragheh-Pikermi-Samos triad (Eronen et al. 2009).

Maragheh’s closest resemblance is to the Greek locality of Samos. Maragheh has 28 genera (22 species) in common with Samos and its GFRI is 68% for Dice and 74% for Simpson’s. The next closest relationship of Maragheh is clearly to Pikermi, Greece. Maragheh shares 28 genera (20 species) with this locality and its GFRI is 61% for Dice and 63% for Simpson’s. These classical “Pikermian Chronofaunas” show more stable community structures. Maragheh and Samos have about 45-35% of brachydont taxa, 30% of mesodonts and 25-35% of hypsodonts (Fig. 8). However, Pikermi has a lower percentage of hypsodont forms which reflects the warm temperate (more) wooded settings at this locality (Solounias 1999).

Recently, Kostopoulos (2009) showed that the paleoecological profile in Pikermi includes the tree-dwelling semi-terrestrial primate Mesopithecus, diversified felids and mustelids, and browse-dependent proboscideans, rhinos, giraffes and bovids. In contrast, Samos has no primate and browse-dependent taxa and has diversified hipparionine horses and gazelles with grazing rhinos, giraffes, and bovids. Maragheh paleoecological profile is remarkable in this context by having a mixture of Samos and Pikermi characters (see Koufos et al. 2009b: Fig.7). Not only primates are present in Maragheh, diversified felids, mustelids and hipparionine horses also exist. Browsing and grazing proboscideans, rhinos, giraffes and bovids also occur in Maragheh. Therefore, although Maragheh is more similar to Samos than it is to Pikermi (Fig. 7), environmentally it has more wooded settings in its dominant grass/bushy vegetation. For this...
reason, as mentioned by Strömberg et al. (2007), presence of a climatic and vegetational gradient across the Greco-Iranian province (east-to-west pattern) is not clearly evident.

In the Middle Turolian (Kostopoulos 2009) evidently great intercontinental dispersion of large carnivores and ungulates of “Pikermian chronofauna” occurred and some of the core Pikermian genera extended their geographic range so that a sizable number of genera are shared among Western Eurasian “Pikermian chronofaunas” (Eronen et al. 2009), Chinese MN 13-equivalent faunas (Mirzaie Ataabadi et al. submitted), and the terminal Miocene north and east African faunas (Bernor and Rook 2008, 2009).

Baode loc. 30 (MN13 equivalent) has 13 genera in common with Maragheh and a Dice FRI of 40% and Simpson’s FRI of 56%. Baode loc. 49 (MN12 equivalent) has 11 genera in common with Maragheh and its Dice FRI is 32% and Simpson’s FRI 41%. North African (Libyan) locality of Sahabi shows a similar level of similarity. Sahabi has 9 genera in common with Maragheh and its Dice FRI is 27% and Simpson’s FRI 37%.

The Chinese localities of Baode 49 and 30, being the eastern extensions of the “Pikermian Chronofauna” (Mirzaie Ataabadi et al. submitted) exhibited Pikermian-type community structures. The MN 12-equivalent locality of Baode 49 is similar to Pikermi with about 12% hypsodont taxa, 30% mesodonts and 59% brachydonts. On the other hand, the MN13-equivalent locality of Baode 30 is very similar to Maragheh and Samos with about 33% hypsodont taxa (Fig.8). This locality is also more similar to Maragheh than locality 49 in terms of GFRI (Fig. 7). Taxa shared between Baode localities and Maragheh are: Adcrocuta, Amphimachairodus, Felis, Deinotherium, Hipparion, Hyaenictitherium, Hysterix, Ictitherium, Indarctos, Metalurus, Palaeotragus, Samotherium, Thalassictis and Urmiatherium. The large elasmothere rhinoceros, Iranotherium

morgani, also occurs in early Late Miocene of Linxia basin, northwestern China (Deng 2005). This taxon has apparently first appeared in northwestern China during Vallesian and immigrated to Maragheh later in the Turolian. The terminal Miocene Libyan locality of Sahabi is also similar in community structure to Maragheh. High percentage of hypsodont taxa (32%) occurs with 23% mesodont and 45% brachydont forms in this locality which is as similar to Maragheh as are the Chinese Baode localities (Fig. 7). Taxa shared between this locality and Maragheh are: Adcrocuta, Amphimachairodus, Ceratherium (Diceros), Cremohipparion, Gazella, Indarctos, Prostrepsiceros, Samotherium, and Tragoportax.

The late Miocene Middle Awash fauna, Ethiopia is less than 20% similar to Maragheh in terms of GFRI. However, it has almost similar community structure but with less hypsodont and more brachydont taxa. These African faunas clearly had “Pikermian” elements that were vicariant and evolved independently subsequent to an early-middle Turolian extension (Bernor and Rook 2008, 2009).

Conclusions

Apart from widely distributed Pikermian taxa (e.g. Adcrocuta, Amphimachairodus, Felis, Deinotherium, Hipparion, Hyaenictitherium, Hysterix, Ictitherium, Indarctos, Metalurus, Palaeotragus, Samotherium), the giraffid Bohlinia and bovids such as “Gazella” rodleri, the large Palaeoryx, and Mirabiloceros cf. maurus and hipparionine horses like Cremohipparion moldavicum indicate affinities of the Maragheh fauna to the Northern Black Sea region. Some taxa like Prostrepsiceros aff. vinayaki show relationships with the western Asian (Arabia, Afghanistan and Indian sub-continent) region, while Gazella cf. ancyrensis, Prostrepsiceros fraasilhoutumschindleri, Samokeros and
Skoufotragus suggest affiliations with the Anatolia and Samos. Urmiatherium and Iranotherium are certainly common elements with China. Regardless of the absence of real time resolution and mismatch between some geochronological and biochronological data, it is evident that the Maragheh area was affected by biogeographically distinct late Miocene areas, representing the crossroads of several provinces.

Acknowledgements

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