

Pliocene vertebrate locality of Çalta, Ankara, Turkey. 4. Rodentia and Lagomorpha

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ABSTRACT

The Çalta vertebrate locality has yielded a rich fauna which contains nine species of rodents and one lagomorph. Eight rodent species had been described in detail in a previous paper (Sen 1977). The present paper describes new material and provides some remarks on the systematic and phylogenetic relationships of these taxa in the light of recent knowledge on the systematics of related groups. Rodents are dominated in number of individuals by a gerbil *Pseudomeriones tchaltaensis* and a spalacid *Pliospalax macoveii*. This paper also describes the Çalta lagomorph which is represented in the material by more than one hundred specimens. The Çalta lagomorph belongs to a new taxon of Ochotonidae, *Ochotonoma anatolica* n.g. n.sp. Its affinities with other taxa, as well as the systematics of some genera and species of Ochotonidae are discussed. In addition, this note presents a historical review of research undertaken at Çalta since its discovery in the 1950s.

KEY WORDS

Rodentia,
Lagomorpha,
Pliocene,
Ruscinian,
Turkey,
biochronology.

RÉSUMÉ

Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie. 4. Rodentia et Lagomorpha. Le gisement de Çalta a livré une riche faune contenant neuf espèces de rongeurs et un lagomorphe. Huit des espèces de rongeurs avaient été décrites en détail dans une précédente note (Sen 1977). Le présent article décrit les nouvelles découvertes et apporte quelques remarques sur la systématique et les rapports phylétiques de ces taxons à la lumière des connaissances récentes. La description d'un nouveau genre et d'une nouvelle espèce de lagomorphe complète l'étude de ces deux ordres. Les rongeurs sont dominés en nombre d'individus par un gerbillidé et un spalacidé. Le lagomorphe de Çalta représente un nouveau taxon d'Ochotonidae, *Ochotonoma anatolica* n.g., n.sp. Ses affinités avec d'autres taxons, ainsi que la systématique de quelques genres et espèces d'Ochotonidae sont discutées. Cet article présente également un historique des recherches effectuées à Çalta depuis la découverte du site.

MOTS CLÉS

rongeurs,
Lagomorphes,
Pliocène,
Ruscinien,
Turquie,
biochronologie.

INTRODUCTION

In a previous paper (Sen 1977), I described the rodents from Çalta collected during the field work of 1972 to 1974. Since 1977, I revisited this locality several times and found additional material, including rodents and lagomorphs. Among the new material, two specimens represent a species of rodents that was not reported in the previous study.

The aim of this paper is to provide some systematic and phylogenetic remarks on the previously described Çalta rodents and to describe the newly found glirid (*Myomimus eliomyoides*). In addition to rodents, the Çalta fauna includes an ochotonid lagomorph which is represented by more than 100 specimens. It belongs to a new taxon that I describe here in detail and compare with other late Neogene and Quaternary ochotonids.

In addition, being the editor of the "Çalta monograph" and also one of the main players in paleontological research at Çalta and its environs, I presume that it would be useful to give a historical analysis of previous studies on the Çalta locality since its discovery.

In this systematic study, measurements are given in millimetres. The length of the tooth is its maximum value along the longitudinal axis, and the width is the maximum value below the occlusal surface, at right angle to the longitudinal axis. When two measurements of the width are given (Ochotonidae), they represent the greatest width of the trigonide and talonide respectively. To describe the dental morphology of the Çalta ochotonid, the nomenclature of Lopez Martinez (1989) is preferred (Fig. 1). All specimens are illustrated as being from the right side, except in figure 5; the left ones are inverted and their labels are underlined.

HISTORICAL ANALYSIS

"Çalta" was first applied as the name of this fossil locality by F. Ozansoy (1955). The site was discovered by this author between 1951-1953, when he was working with a MTA team (Mineral Research and Exploration Institute of

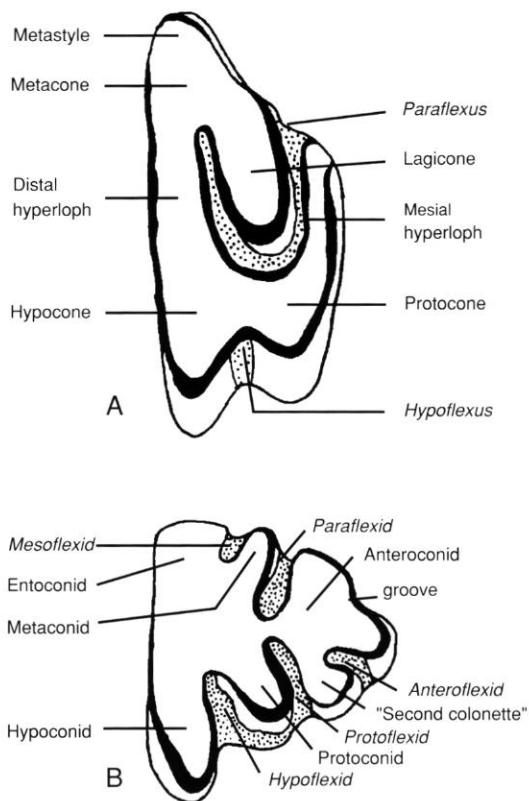


FIG. 1. — Nomenclature of the occlusal pattern in Ochotonidae ; A, right P3; B, right p3.

Turkey) to study the geology of the area between the towns of Kazan and Ayas. Ozansoy did not excavate this locality, but collected a few specimens already appearing on the surface. His main work in this area was the study of mammalian faunas from the Sinap Formation which crops out some 5 to 15 km east of Çalta. Ozansoy excavated several mammal localities, between 1951-1953 and later between 1956-1957, in deposits that he dated as late Miocene and Pliocene around the villages of Yassiören, Sogucak, Sarilar and Evcı, all situated east of Çalta. He prepared his dissertation thesis on the material he collected in this area, and he defended it in the University of Paris in 1958. The main results of this work were published in a monograph (Ozansoy 1965). In this publication

(Ozansoy 1965: 17), he mentioned a short list of species he found at Çalta: "*Equus stenonis* Cochi, Antilope g. et sp. indet., Carnivore g. et sp. indet." He also noted that the continental deposits at Çalta are stratigraphically equivalent to the Upper Sinap Series of the Sinap Tepe area, some 15 km east of Çalta. In the Upper Sinap Series, he collected in the 1950s a fauna with *Equus*. Based on these assumptions, he dated the Çalta locality as Villafranchian. The material determined as *Equus stenonis* from Çalta is at present exhibited in the Natural History Museum of Ankara. It consists of a metatarsal and a first phalanx which belong in fact to a robust *Hipparion*. In 1967, from May to September, MTA organized a campaign of excavations in the Sinap Tepe area, under the leadership of Ozansoy, to collect mammalian fossils for a future Natural History Museum at Ankara. As MTA staff, I. Tekkaya and I participated in this field work. During the summer of 1967, we excavated four rich mammal localities along the slopes of Sinap Tepe, and a few others in the ravines and small hills in its vicinity. More than twenty local workers were employed to dig. In June 1967, I visited, together with Ozansoy, the locality of Çalta, and we observed bones on the surface. In July 1967, a student of Ozansoy, Gerçek Saraç excavated this locality alone during about two weeks in order to prepare his master thesis (Saraç 1968). The material he collected is housed in the MTA collections at Ankara.

During the summer of 1969, MTA organized a new campaign of excavation in the localities of İnönü and Kavakdere which are situated some 5 km east of Çalta. F. Ozansoy, I. Tekkaya, E. Kaptan and I conducted this work, which lasted two months. We visited Çalta once more but did not collect fossils.

In 1972, É. Heintz and L. Ginsburg obtained an authorization from the MTA to undertake paleontologic excavations in "Villafranchian" localities of the Ankara region. M. Gürbüz and I were asked by the director of the MTA to accompany them. During all the month of July 1972, this team worked in the sector of Sinap Tepe and at Çalta. We began excavations in the locality of Gavur Tepe (= Upper Sinap Series), previously found by Ozansoy (1965) and known by a small

fauna with *Equus stenonis*. After one week of excavation, É. Heintz decided to abandon this locality because of the scarcity and fragmentary state of fossils. He asked me if I knew another Villafranchian locality in the region, and I indicated the locality of Çalta. With the help of three local workers, we excavated this locality during two weeks, and extracted an important quantity of fossils. The essential part of the large mammalian remains described in various papers that figure in this monograph comes from these excavations.

In August 1973, É. Heintz and I went to Çalta for a half-day visit and collected some fragmentary specimens in the scree of previous excavations and filled a sack of sediment to wash.

In August 1974, the MTA allowed me to work at Çalta, together with F. Arslan from that institution. During fifteen days, we collected about 500 kg of sediment, and screen-washed it for small mammals.

Between 1973 and 1976, I prepared my "thèse de 3^e cycle" on the rodent fauna from Çalta, and defended it June 14, 1976, at the University Paris VI. This study was published in 1977.

In mid-seventies, Çalta was visited by Prof. G. Demarcq from the University Claude-Bernard at Lyon. A few specimens he collected are in the collections of that university.

In 1975 and 1976, a team from MTA under the leadership of I. Tekkaya studied stratigraphic relationships of Neogene continental deposits between Kazan and Ayas. Paleontologists from MTA excavated several localities in the area, including Çalta where during fifteen days they collected small and large mammals (Tekkaya *et al.* 1977; Saraç 1994). Their specimens are stored in the MTA collections. Of this material, a fragmentary skull of *Hipparion*, some cranial remains of Carnivora and Bovidae and a molar of glirid are included in the related papers of the present volume.

Between 1989 and 1995, an international team carried out integrated geological and paleontological research on Neogene deposits in the area northwest of Ankara, in the frame of the "International Sinap Project" organized by M. Fortelius (Helsinki), J. Kappelman (Austin, Texas) and B. Alpogut (Ankara). Marginal to this

project, in June 1994 and June 1995, J. Kappelman, J. P. Lunkka, D. Ekart and I worked in the Çalta region to study the stratigraphy and sedimentology of Neogene deposits. During this period, we also sampled a section of 195 m across the fossil locality for magnetostratigraphy and took samples for palynology. The results of stratigraphic observations and sedimentologic analyses are presented in this volume by Lunkka *et al.* Samples taken for magnetostratigraphy have been analyzed by J. Kappelman at the University of Texas. It appeared that most samples are remagnetized probably because of the tectonic deformation of related deposits. Thus it was not possible to obtain a reliable polarity succession for the Çalta section. The eight palynological samples I collected in and around the Çalta mammal locality were analysed by N. Combourieu-Nebout (CNRS) at the University Paris VI, but they unfortunately turn out to be sterile.

Since the 1972 excavation, several papers have been published on preliminary results, for amphibians and reptiles, one species of *Hipparion* and rodents (Ginsburg *et al.* 1974; Sen *et al.* 1974; Heintz *et al.* 1975; Rage & Sen 1976a, b; Sen & de Bruijn 1977; Sen & Heintz 1977; Sen & Rage, 1979; Sen 1975, 1977, 1978). The material collected between 1972 and 1974 and studied by the contributors of the present volume is stored in the collections of the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris.

SYSTEMATIC STUDY

Order RODENTIA Bowdich, 1821

Family MURIDAE Gray, 1821

Genus *Centralomys* de Giuli, 1989

***Centralomys magnus* (Sen, 1977)**

Castillomys magnus Sen, 1977.

The main characters of this species are: on M1, the cusps t1 and t3 have strong posterior spurs connected to t5, t1 situated notably backward from t2, t1 bis and t2 bis well-developed, the

cusps of second and third lophs all connected to form a perfect garland; M2 with a rounded t1, not bilobed as in *Occitanomys* and with four roots; M3 with t8 connected to t6; m1 without anteromedian cuspule, and m1 and m2 with medial spur issuing from the entoconid and directed anteriorly (see Sen 1977 for detailed description).

I initially included this species in the genus *Castillomys* Michaux, 1969 because of its similarities with *C. crusafonti* Michaux, 1969. *C. crusafonti* was at that time the unique species of *Castillomys*, well-known in Ruscinian localities of southern France and Spain, and also from Maritsa in Greece (de Bruijn *et al.* 1970). Later on, several new taxa were described as new subspecies (*C. crusafonti gracilis* van de Weerd, 1976) or new species (*C. margaritae* Antunes *et* Mein, 1989; *C. rivas* Martin Suarez *et* Mein, 1991). De Giuli (1989) attributed to a new subgenus and new species the rich material from Brisighella-1 in northern Italy: *C. (Centralomys) benericettii*.

The increase of fossil documentation on *Castillomys* and on supposedly related taxa provided the opportunity to review the systematics of this group, and thus Martin Suarez & Mein (1991) proposed a new classification. Following these authors, all the western European populations are included in four species of *Castillomys*: *C. gracilis*, *C. crusafonti*, *C. rivas* and *C. margaritae*. These authors also demonstrated that the first three species probably form an anagenetic lineage in southern France and Spain, ranging in time from the latest Miocene to early Pleistocene. *C. margaritae* from the latest Miocene of Portugal is considered as belonging to a lineage apart.

Martin Suarez & Mein (1991) stated that *Centralomys* should be considered as a distinct genus with two species: *C. benericettii* (type species) and *C. magnus*. *Centralomys* is characterized, according to these authors (Martin Suarez & Mein 1991: 68) by "Teeth with voluminous cusps. Anteroconid of m1 symmetrical. Lower molars with broad labial cingulums and reduced longitudinal spurs. Upper molars with weak longitudinal connections. M2 with four roots". In my opinion, the clear distinctive characters of

Centralomys are the larger size of molars in comparison to the equivalent age *Castillomys* species, the presence of four roots on M2 and the weak longitudinal spurs on lower molars. The other distinctive features that Martin Suarez & Mein (1991) used are at least partly shared with *Castillomys* species. Thus, the cusps are not much less voluminous in *Castillomys crusafonti*, the anteroconid has symmetrical cuspids in *C. gracilis* and its shape is variable in other species, a broad labial cingulum of m1 and m2 is often present in *C. crusafonti* and even much more in *C. rivas*, and the longitudinal connections on M1 are not stronger in *C. gracilis* and *C. crusafonti* than in *Centralomys magnus*.

The material from Maritsa (Isle of Rhodes) and from Develi (western Turkey) that I attributed (Sen *et al.* 1989) to a new species of *Castillomys* should belong, according to Martin Suarez & Mein (1991) to *Occitanomys*. They justified this attribution noting "the t1 placed very far backwards, often isolated from t5, and sometimes connected to t5 by a longitudinal crest". In fact the position of t1 is very variable in the Maritsa population, and the general pattern and the size of teeth from Maritsa are very similar in the Brisighella-1 population that de Giuli (1989) has abundantly illustrated. Whatever the systematic assignment of the Maritsa and Develi materials, they are obviously closer to *Castillomys* and *Centralomys* than to any other murid.

All these resemblances are probably indicative of some phylogenetic relationships between the western European *Castillomys* and its eastern European and Anatolian relatives. In western Europe, the populations attributed to *Castillomys* have been recorded in more than twenty localities. On the other hand, "*Castillomys*-like" murids are known in one locality in Italy (Brisighella-1), one locality in Greece (Maritsa) and two localities in Turkey (Develi and Çalta). This partly explains the reason why difficulties arise in the identification of diagnostic characters that allow unambiguous specific and generic distinctions. For a better statement of the systematics of *Castillomys* and *Castillomys*-like populations, and of the phylogenetic relationships between different taxa, more material and more detailed analyses are needed.

Genus *Occitanomys* Michaux, 1969

Occitanomys sp.

Six isolated teeth from Çalta are referred to this species. In size, they are similar to *Centralomys magnus* from Çalta, but they differ in their morphology: M1 is widened and has a clear antero-lingual notch between t1 and t2, and t1 is situated backwards, close to t5, and connected to its flank by a spur; t1bis very small; t4-t8 connection strong; on M2 t1 is bilobed. Lower molars of this species are unknown at Çalta.

At the time I described *Occitanomys* sp., the genus was restricted to western Europe with *O. brailloni* Michaux, 1969 (type species, Ruscinian) and *O. adroveri* (Thaler, 1966) from the middle-late Turolian. Van de Weerd (1976) pulled down this genus with his new species *O. sondaari* from the early Turolian of Spain. In the meantime, de Bruijn (1976) referred with some doubt to *Occitanomys* two new species from the middle-late Turolian localities in Greece. This genus was also mentioned at Samos S3 and Maramena in Greece, and Kavurca in Turkey (Black *et al.* 1980; van der Meulen & Kolfshoten 1986). Van de Weerd (1979) attributed to *Occitanomys brailloni* some remains from Ptolemais-3 (MN15, Greece). More recently Storch (1987) referred to *Occitanomys* a late Miocene species *Stephanomys? pusillus* Schaub, 1938 from Inner Mongolia.

Such a wide geographic distribution, from Spain to China, is quite exceptional for a murid genus. One can reasonably wonder if the grouping of these species in the same genus may in fact be due to a parallel evolution of some morphological features. In southwestern European populations, which are considered as derived from *Progonomys hispanicus* Michaux, 1971 (Mein *et al.* 1993; Michaux *et al.* 1997), the evolutionary trends are the increase of stephanodonty and the reduction of the posterior cingulum on M1 and M2, the t1bis more frequent in these molars, the widening of M1, the strengthening of the t3-t5 connection on M1 and in some extent on M2, and the reduction of the posterior heel on m1. The age of the specimens from Çalta fits well with such a scenery since their morphology cor-

responds to that of late Turolian and Ruscinian populations from Spain and southern France. However, the other species described from the Turolian localities of Greece and Inner Mongolia have a mixture of suggestedly primitive and derived characters. Consequently, it is not easy to identify lineages including different species. This study is not aimed to analyze their phylogenetic relationships. It is now obvious that *Occitanomys* is not endemic to western Europe, but was represented in a wide area across Eurasia, and has a long history than previously supposed.

Genus *Orientalomys*
de Bruijn *et* van der Meulen, 1975

Orientalomys galaticus (Sen, 1975)

Euxinomys galaticus Sen, 1975: 318.

This species was described in detail in Sen 1977. Çalta is the unique locality in Anatolia with *Orientalomys*. Another species, *O. similis*, was found in the Odessa catacombs in Ukraine and Tourkobounia-1 in Greece (Bruijn & van der Meulen 1975).

The representatives of this genus in East Asia are apparently more abundant than their relatives in eastern Europe. Storch (1987) recorded *O. similis* at Ertemte (Inner Mongolia) which is also the oldest locality with *Orientalomys*. The other species referred to this genus, *O. sibiricus*, *O. adirganus* and *O. schaubi*, are only known in eastern Asia (Erbaeva 1976; Tjutkova & Kaipova 1996; Storch 1987). According to Storch (1987), *Chardinomys* Jacobs *et* Li, 1982 is a junior synonym of *Orientalomys*. This hypothesis is rejected by Flynn (1997). *Chardinomys* is represented in North Chinese localities with three species spanning in age from the latest Miocene to early Pleistocene. In my opinion, although *Orientalomys* and *Chardinomys* represent different genera, their molar pattern presents many common characters leading to suggest that they are probably derived from a common ancestral stock. The available data show that *Orientalomys* is mainly an Asiatic taxon known since the latest Miocene in Inner Mongolia, and emigrated to western Asia and eastern Europe during the Pliocene.

Genus *Apodemus* Kaup, 1829

Apodemus dominans Kretzoi, 1959

Although very common in almost all Pliocene small mammal localities all over Europe, and exceptionally in North Africa and Asia, this species is poorly represented at Çalta (four molars; Sen 1977). Its type locality is a fissure filling in Hungary, Csarnota-2 (MN15). This species is characterized as a middle-sized *Apodemus*, with M1 and M2 having a constant $\tau 7$ and cusps of second and third lophs forming a complete garland, M1 with its typical amygdaloid outline, m1 with anteromedian cuspule, and lower molars with very weak or absent longitudinal crest. The dimensions of the Çalta specimens are within the range of variation of *A. dominans* that Pasquier (1974) reviewed from several European Pliocene localities. In the Aegean area, the occurrence of this species was mentioned in a dozen localities (van der Meulen & Kolfshoten 1986).

Family CRICETIDAE Murray, 1866
Genus *Mesocricetus* Nehring, 1898

Mesocricetus sp. cf. *M. primitivus*
de Bruijn, Dawson *et* Mein, 1970

Since I described this species in 1977, no other Pliocene *Mesocricetus* has been recorded. In the Çalta population, M1 has anterocone with two distinct cusps; the connections between the four main cusps of upper molars, particularly on M2 and M3, are strong; mesolophs and mesolophids are of medium size or even absent on m1; m3 is as long as m2.

The type locality of *M. primitivus* is Maritsa on Rhodes Island, Greece. It is similar in size and in general pattern of teeth to the Çalta population; the main difference between these two samples is that the ridges connecting the cusps of upper molars are stronger at Maritsa.

All fossil and living representatives of *Mesocricetus* are restricted to the area between the Balkans and Middle East. The extant Anatolian species *M. brandti* (Nehring, 1898) is known since the middle Miocene.

Family GERBILLIDAE Alston, 1876
Genus *Pseudomeriones* Schaub, 1934

***Pseudomeriones tchaltaensis* Sen, 1977**

57% of the rodent remains from Çalta belong to this species. It is characterized by its small size, narrow first upper and lower molars, alternation of cusps and cuspids on M1, m1 and m2, straight mesosinus on M2, and shallow protosinusid on m2, very reduced third molars which totally lack the anteroloph(id).

All these derived characters imply that the Çalta population represents the more evolved, and also stratigraphically the youngest species of *Pseudomeriones*. I have to note that the oldest representatives of this genus have been mentioned from the late Vallesian localities of Kaleköy and Karaözü in Central Anatolia (Sümenen *et al.* 1990) and the youngest one has been mentioned by Tong (1989: 105) from the locality of Shuimogou in Gansu, China, dated as "*Pliocène supérieur ou début du Pléistocène inférieur*".

The Çalta species was first described as a new subspecies of *P. abbreviatus* (Teilhard, 1926), and later on, it was raised to the species level (Sen 1983). In the meantime, several localities in Greece, Turkey and Afghanistan yielded more remains of *Pseudomeriones* (Sen 1977, 1982, 1983; Armour-Brown *et al.* 1979; Black *et al.* 1980; van der Meulen & Kolfscoten 1986; Sen *et al.* 1989). Consequently, the evolutionary trends of the dentition in this genus became better known.

At present, five species are referred to *Pseudomeriones* in the time range of late Vallesian to late Ruscinian. The late Vallesian material, from the localities of Kaleköy and Karaözü in Central Anatolia is still undescribed (Sümenen *et al.* 1990). Three species are known in Turolian localities: *P. abbreviatus*, *P. pythagorasi* and *P. latidens* (see Sen in press). *P. abbreviatus* was also found in the early Pliocene of Pul-e Charki in Afghanistan (Sen 1983). The two exclusively Pliocene species are *P. rhodius* and *P. tchaltaensis* from Greece and Turkey.

The genus *Pseudomeriones* has a very wide geographic distribution since it is found in China, Turkmenistan, Afghanistan, Turkey, Greece,

Czech Republic and Spain. Most localities are in China, Afghanistan, Turkey and Greece. Strange is its occurrence in the Czech Republic and Spain, one tooth in each country in faunas considered close to the Turolian/Ruscinian boundary (Fejfar & Heinrich 1990; Agusti 1989, 1990, 1991). Even more strange is the fact that these two teeth compare better in size and in pattern with *P. abbreviatus* from King-yan-fou in China than with any other population.

From the late Vallesian to the late Ruscinian, the dentition of *Pseudomeriones* undergoes changes that can be interpreted as evolutionary trends: the first and second upper and lower molars become narrower, and the third molars are reduced; cusps and cuspids become alternate on M1, m1 and m2; the shape of the m1 anteroconid becomes symmetrical and triangular; the mesosinus of M2 becomes shorter and transverse; the anterosinusid of m2 becomes reduced; third molars lose the anteroloph(id).

In spite of increasing data on this genus, its origin and phylogenetic relationships with other gerbillids remain obscure, and this led Tong (1989) to classify *Pseudomeriones* as Gerbillidae *incertae cedis*.

Because of its wide geographic distribution, *Pseudomeriones* is a useful tool for biochronologic correlations between the localities of East Asia, Afghanistan and the Aegean area.

Family ARVICOLIDAE Gray, 1821
Genus *Mimomys* Major, 1902

***Mimomys davakosi* van de Weerd, 1979**

In 1977, I described the Çalta *Mimomys* as *M. gracilis* (type locality at Csarnóta-2 in Hungary). *M. gracilis* is a common species of "Csarnotian" (late MN15 and early MN16) localities in Central Europe (Fejfar & Heinrich 1990). Van de Weerd (1979) erected the new species *M. davakosi* from the early MN15 locality of Ptolemais 3 in northwestern Greece; this locality also includes *Occitanomys brailloni*, *Apodemus dominans*, *Rhagapodemus frequens*, *Micromys kozaniensis* and *Castor fiber*, showing clearly central and western European affinities.

Van de Weerd *et al.* (1982: 110) suggested that the Çalta *Mimomys* fits better with *M. davakosi* than *M. gracilis* “judging by the size and the height of the enamel free area of the M_1 ”. It is true that the size of the Çalta specimens is globally larger than in *M. gracilis* from Csarnóta-2, and the Çalta specimens have stronger roots. From the lateral view, m_1 from Çalta has very low enamel free area, as is in *M. davakosi* from Ptolemais 3 and *M. occitanus* from Apolakkia (Rhodes Island, Greece). The line of the enamel free area is much more sinuous (advanced) in Csarnóta-2 m_1 . The flatness of this line is indicative of a primitive stage of evolution in arvicolid phylogeny. *M. occitanus* is ruled out because it differs from *M. davakosi* (Ptolemais 3 and Çalta) in having anteriorly curved lingual reentrant folds on m_1 , *vs* transverse lingual folds in *M. davakosi*. Apart from its type locality, *M. davakosi* is known at Çalta, Serrat-d'en-Vacquer in France (Mein & Aymar 1984; Bachelet 1990) and Villalba-Alta 1, Arquillo 3 and Sarrion-2 in Spain (Fejfar *et al.* 1990).

Radulescu & Samson (1989) have a different opinion. They referred to *Mimomys moldavicus* Kormos, 1932 the specimens from Çalta and Ptolemais 3, thus considering *M. davakosi* as a junior synonym of *M. moldavicus*. The latter species was first described from Malusteni (Romania) based on a lower jaw belonging to a very old individual with worn m_1 - m_3 . Radulescu & Samson (1989) reported to this species another lower jaw with damaged m_1 - m_2 and a M_1 from its type locality. Moreover, from the localities of Musaid and Etulia in Moldavia, some other remains have been described as *M. moldavicus* respectively by Aleksandrova (1986) and Shushpanov (1985). I did not see these last two papers. According to Radulescu & Samson (1989: 47), *Mimomys* from Çalta “possessing somewhat higher dentine tracts and a better developed m_1 relative to m_2 , represents a more advanced form in the frame of *M. moldavicus*. The teeth from Çalta seem to be close (although probably more primitive judging by the upper molars which are three-rooted) to the corresponding middle-sized *Mimomys* specimens at Etulia (dominance of the two-rooted condition in M_3)”.

The opinion of Fejfar *et al.* (1990) is radically

different: they consider that the Malusteni species should be included in the genus *Promimomys* because it is very similar, if not totally identical, to *Promimomys cor* Kretzoi, 1955 which is known by a surface finding m_1 near the Csarnóta-2 fissure filling in Hungary. For them, the presence of *Mimomys*-like arvicolid at Malusteni is not proved, and consequently the specimens from Ptolemais 3 and Çalta, characterized by their mimomyian dental features, belong to a different taxon, *M. davakosi*.

My opinion is that the scanty state of the type material referred to *M. moldavicus* and *P. cor* is at the origin of this debate. As long as a new material with well-preserved fresh teeth is not collected from Malusteni and Csarnóta-2, the systematic position of these species will remain unsolved. For the time being, I prefer the attribution of the Çalta *Mimomys* to *M. davakosi* because of the great resemblances of the samples from Çalta and Ptolemais 3.

Family SPALACIDAE Gray, 1821
Genus *Pliospalax* Kormos, 1932

Pliospalax macoveii (Simionescu, 1930)

Prospalax macoveii Simionescu, 1930: 21, 22.

This is the second most abundant rodent species of Çalta with 16% of remains. In 1977, I reported from this locality two species: *Pliospalax macoveii* and *P. compositodontus*. Later examination of specimens and their comparison with other living and fossil spalacids provide evidence that the three teeth determined as *P. compositodontus* are in fact fresh m_2 of *P. macoveii*. In *Pliospalax* and *Spalax*, the attrition notably modifies the occlusal pattern of teeth, because shallow synclines, such as the anterior and posterior reentrant folds, become enamel islands or even disappear when teeth are worn even only a little.

Since I described this species in 1977, no new record of Pliocene spalacid has been reported, nor any other study on their systematics and phylogeny has been published. It is morphologically supported that the genus *Pliospalax* is the

probable ancestral stock for the extant *Spalax*. All fossil and living spalacids are known in territories from Ukraine to Egypt, including the Balkans, Greece, Turkey and the Middle East. Consequently, they are considered as typical local forms of this area, as to some extent is the genus *Mesocricetus*.

Family GLIRIDAE Thomas, 1897
Genus *Dryomimus* Kretzoi, 1959

***Dryomimus eliomyoides* Kretzoi, 1959**
(Fig. 2)

MATERIAL. — Two M2 (ACA-1158 and 1159): 1.10 × 1.19 and 1.15 × 1.22.



FIG. 2. — *Dryomimus eliomyoides* Kretzoi, 1959 : A, M2 (ACA-1158); B, M2 (ACA-1159). Scale bar: 1 mm.

During the excavations made at Çalta in 1976, Tekkaya *et al.* (1977) collected one M2 of a gliroid (ACA-1159; MTA collections). In 1995, I found another M2 (ACA-1158) screen-washing one sac of sediment. These two isolated M2 clearly belong to Myomiminae Daams, 1981 because of their concave occlusal surface, reduced number of riges, absence of endoloph, etc. These molars have four main lophs and a posterior centroloph. The anteroloph is not connected to the endoloph, nor to the paracone. The posterior centroloph reaches almost half of the tooth width. The occlusal pattern fits with morphotype B of Daams (1981), which is recorded in Myomiminae since the early Vallesian (Pedraueras Ilc in Spain), and becomes more frequent in Ruscinian and later age localities (Daams 1981). Several genera are included in this subfamily among which the characters of the Çalta specimens fit with that of *Dryomimus*. It is hitherto represented by one species, *D. elio-*

myoides from Csarnóta-2 (type locality, Kretzoi 1962) and Tourkobounia-1 (Daams & de Bruijn 1995). The general features of its dental pattern led these authors to consider it as a descendent of *Myomimus*. Çalta is therefore the third locality where this species is recorded.

Order LAGOMORPHA Brandt, 1885
Family OCHOTONIDAE Thomas, 1897
Genus *Ochotonoma* n.g.

TYPE SPECIES. — *Ochotonoma anatolica* n.sp.

ETYMOLOGY. — A combined name from *Ochotona* (pika) and *nomae* (nomadic) because this taxon is found beyond the extant distribution of ochotonids.

SPECIES INCLUDED. — *Ochotonoides csarnotanus* Kretzoi, 1962 (Csarnóta-2 and Ciuperceni-2), *Ochotonoides* sp. (Apolakkia) and *Ochotonoides primitivus* Zheng et Li, 1982 (Songshan).

DIAGNOSIS. — Small to middle-sized ochotonid. On p3 anteroconid is large, with one or two anterior flexids filled with cement, or at least with depressions; protoflexid and paraflexid with smooth enamel borders. P2 with one anterior flexus. M2 with a strong posterolingual process.

DIFFERENTIAL DIAGNOSIS. — This new genus differs from *Ochotona* Link, 1795 by the presence of flexids filled with cement on the anteroconid of p3, deeper protoflexid and paraflexid, and widened anteroconid, but resembles this genus in having triangular shaped p3. *Ochotonoma* differs from *Pliolagomys* Erbajeva, 1983 by the anteroconid-protoconid connection which is much more labial in this last genus, and consequently the paraflexid is deeper and protoflexid shorter. Moreover, *Pliolagomys* p3 generally lacks cemented flexids on the anteroconid. The species attributed to *Pliolagomys* are larger than *Ochotonoma*. *Proochotona* Khomenko, 1914 has simple anteroconid on p3, and in this it resembles *Ochotona* more than any other genus. *Ochotonoides* Teilhard et Young, 1931 includes large-sized species with p3 in which enamel is plicated along the protoflexid and paraflexid, and its anteroconid is wide with a labial angle forming a strong "colonette" which extends in width beyond the protoconid.

***Ochotonoma anatolica* n.sp.**
(Figs 3-7)

Ochotona antiqua Pidoplitshko, 1938 – Sen 1977: 92. – Sen & Rage 1979: 157.

TABLE 1. — Measurements of upper and lower teeth of *Ochotonoma anatolica* n.g. n.sp. from Çalta. Asterisk indicates that for incisors, "length" is antero-posterior diameter, "width" is transverse.

Teeth	Length		N		Width	
	Range	X			Range	X
I1*	1.02-1.40	1.20	11		1.63-2.03	1.82
I2*	—	0.54	1		—	1.09
P2	0.64-0.74	0.69	3		1.13-1.66	1.42
P3	0.96-1.25	1.08	10/8	trig.	1.23-1.78	1.45
			8	tal.	2.00-2.73	2.30
P4, M1	1.11-1.33	1.24	10/9	trig.	1.83-2.61	2.18
		1.40	10	tal.	2.05-2.37	2.29
M2	1.20-1.57	1.39	11/10	trig.	1.64-2.29	1.99
			8	tal.	1.72-2.05	1.90
i1*	1.03-1.29	1.17	3		1.56-1.72	1.68
p3	1.12-1.63	1.41	15/14		1.06-1.78	1.48
p4, m1, m2	1.29-1.75	1.57	32/39	trig.	1.38-1.84	1.65
				tal.	1.37-1.87	1.65
m3	0.60-0.75	0.69	8		0.95-1.30	1.14

Ochotonoides csarnotanus Kretzoi, 1959 – Terzea & Boroneant 1979: 179, fig. 4. – Terzea 1997: 655, fig. 3.

HOLOTYPE. — Right lower jaw with p3-m3, ACA-1001, Figs 4A, 6A.

PARATYPES. — One premaxilla with I1 and I2, 12 isolated I1, 3 P2, 10 P3, 113 P4 or M1, 11 M2, 12 other lower jaws with various or without cheek teeth, 6 i1, 13 p3, 22 p4 or m1 or m2, 3 m3. All these specimens are numbered from ACA-1002 to ACA-1105. They are preserved in the collections of the Muséum national d'Histoire naturelle, Paris.

TYPE LOCALITY. — Çalta, Department of Ankara, Turkey.

ETYMOLOGY. — From Anatolia, the home country of the species.

MEASUREMENTS. — See table 1.

DIAGNOSIS. — Small-sized ochotonid. p3 with, in addition to three main flexids, additional flexids on its anteroconid. Anteroconid triangular shaped and widened; it is connected centrally to the trigonid complex by a narrow enamel bridge. The pattern of the anteroconid variable in having deep labial and lingual grooves (without cement) or flexids (with cement). Mesoflexid occasionally present. p4, m1 and m2 similar in size and shape.

DIFFERENTIAL DIAGNOSIS. — *O. csarnotanus* p3 differs from *O. anatolica* n.sp. by its deeper and wider paraflexid, its transverse protoflexid; the hypoflexid of this species penetrates lingually more than half of the talonid width. *O. primitivus* differs by its larger size and p3 elongated.

DESCRIPTION

The only fragment of upper jaw is a left premaxilla on which I1 and I2 are preserved. The curve of the upper diastema and of I1 is as in living *Ochotona*. On cheek teeth, the cement fills only reentrant folds, and is absent elsewhere on tooth faces.

The first upper incisor is strongly curved. Its anterior groove is rather deep; it divides the shaft into two unequal parts, two third lateral and one third medial. The medial wall of this groove is steep and high while the lateral one is gently rounded and low.

The second upper incisor is placed ventrally to the first one. Its section is elliptical.

P2 has one anterior flexus which is directed toward the posterolabial angle. The lingual face is marked by a more or less strong ridge. The shaft of this tooth is curved backward and labially.

On P3, the mesial hyperloph covers two third of the mesial face. The paraflexus is U-shaped. The metastyle and metacone form the highest parts of the occlusal surface. The hypoflexus is moderately wide and variably deep. In one P3, it is double folded in its inner part, while in seven others it is simple. The shaft is curved labially.

P4 and M1 are formed of two lophs separated by a deep hypoflexus which almost reaches the labial margin. On P4, the anterior and posterior lophs are of almost equal width, while on M1 the posterior loph is narrower. The shaft

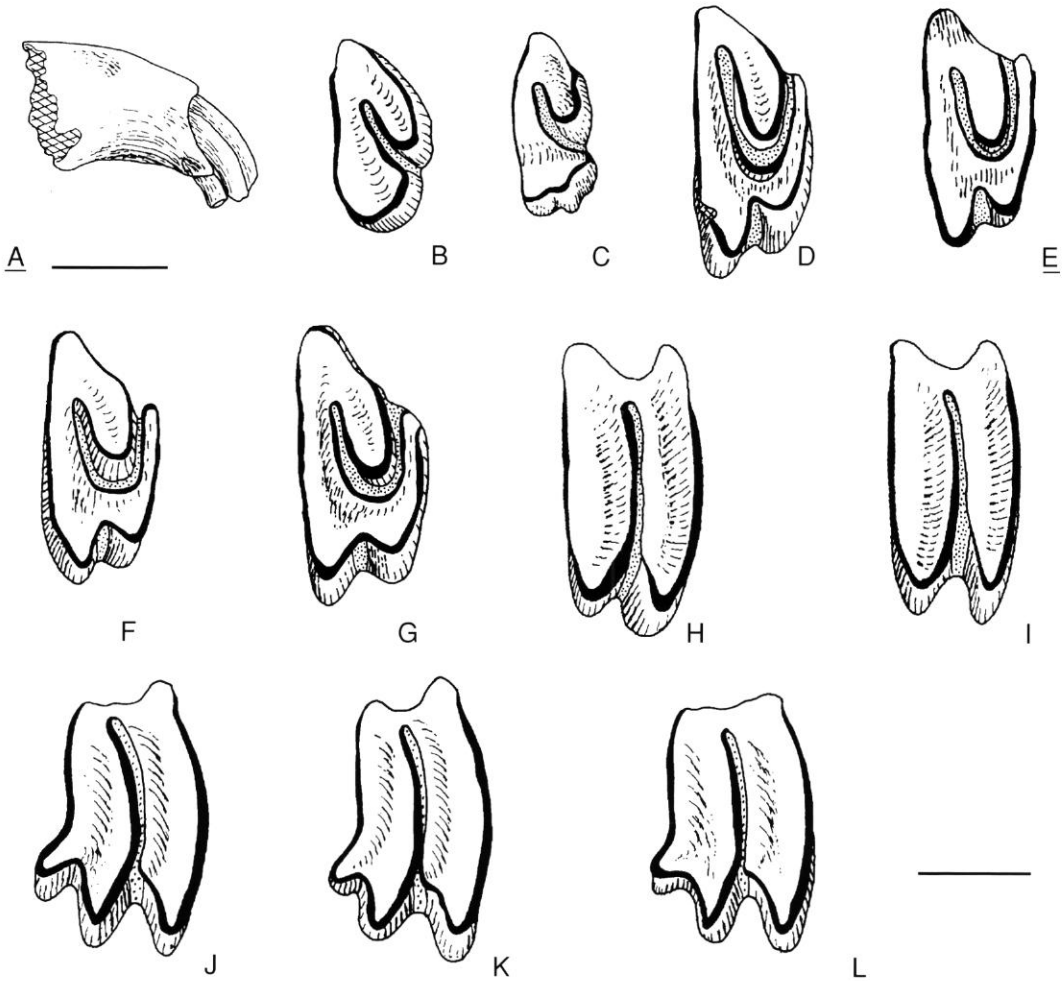


FIG. 3. — *Ochotonoma anatolica* n.g. n.sp. from Çalta; A, fragment of premaxilla with I1 and I2; B, C, P2; D-G, P3; H, I, P4; J-L, M2. Scale bars: A, 0.5 mm; B-L, 1 mm.

is curved labially, but not as much as P3. M2 resembles M1 in its general outline, but it differs in having a posterolingual process. This process first occurs in a tiny form in the middle Miocene genus *Bellatona*, and in later times it characterizes the genera *Proochotona*, *Pliolagomys*, *Ochotonoides* and *Ochotona*. Other ochotonids lack this process. The hypoflexus does not reach the labial margin, but it ends very near to it. The posterior loph is narrower than the anterior one. The shaft is curved labially, and slightly distorted posteriorly.

Thirteen fragmentary lower jaws are preserved.

The angle between horizontal and ascending ramus is measured on one specimen as 125° . The horizontal ramus reaches its maximum depth below m1 (range, 5.09-5.92; mean, 5.59; N, 12). The diastema is short (4.16 mm in ACA-1001 and 5.25 mm in ACA-1003). On the lateral face of the mandible, there are two mental foramina, one below p3 and the other below m2, both near the ventral border. Moreover, several smaller foramina occur below p3 and some below m1. The lower incisor ends below m1 where it forms a strong ventral bulge.

Another foramen is situated just behind m3 at

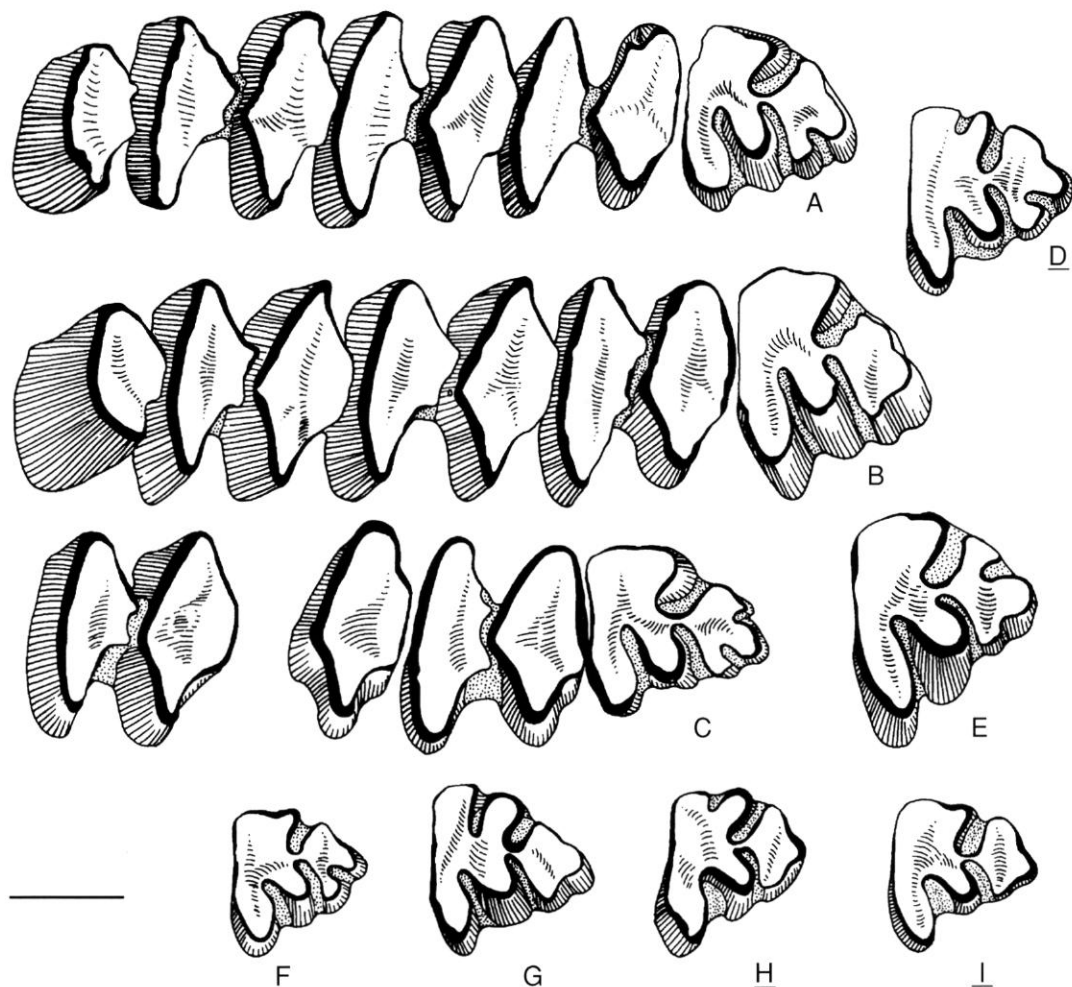


FIG. 4. — *Ochotonoma anatolica* n.g. n.sp. from Çalta, lower teeth; A, p3-m3 (holotype), B, p3-m3, C, p3-m2, D-I, p3. Scale bar: 1 mm.

the base of the ascending ramus. On the medial face, the end of the incisor forms a protuberance. The mandibular foramen is wide and dorso-ventrally elongated; it is situated at the anterior end of the medial masseteric fossa. The coronoid process is very reduced; it is a trace on some specimens, and a tiny process on others.

The lower incisor is slightly curved. Its cross section is almost triangular. Only the anterior face is covered by enamel.

p3 is the most characteristic tooth of the ochotonid dentition. The shaft is curved posteriorly and

lingually. Seen from the labial and lingual sides, all reentrant folds are filled with cement on their two third upper part while their one-third lower part has no cement. The occlusal surface has a triangular shape, with a generally wide distal edge; however, the distal edge may be less wide in some specimens. The ratio width/length varies from 0.77 to 1.17 with an average of 1.03 (n, 14). The occlusal surface is cut by two labial and one lingual persistent folds. The hypoflexid is wide but not deep; it does not reach the longitudinal axis of the tooth. The protoflexid is narrow

and deep. The paraflexid is placed symmetrical to the protoflexid, but it is more transverse. The mesoflexid is variable in importance: it is deep (three specimens), shallow (one specimen) trace (one specimen) or absent (nine specimens). Its occurrence is not related to the age of the individual or to the degree of attrition since it occurs all along the shaft. In specimens with a trace or no mesoflexid, the metaconid-entoconid complex forms a wide surface. The anteroconid is the most variable part of the p3 pattern. It is more or less widened. The number of folds on the anteroconid is variable: one specimen has two folds filled with cement; five specimens have only one labial fold and another one has only one lingual fold with cement; on nine specimens, there are labial and lingual grooves but the former is sharper. These folds and grooves are continuous all along the shaft.

p4, m1 and m2 are formed of two lophids (trigonid and talonid) joined with cement. The trigonid is losange-shaped while the talonid has a triangular occlusal outline. The shafts of these teeth are not curved.

m3 has an almost triangular occlusal outline. It is narrower than the preceding teeth. Its shaft is curved backward.

COMPARISON

The Çalta ochotonid is a small species in comparison to other members of this family. However, it is quite variable in size since it displays about 30% of difference between the smaller and larger individuals (see p3 on table 1), but no bimodality in the dimensions of teeth. The occlusal morphology of cheek teeth also displays some variation, but with all intermediate states. For these reasons, the Çalta ochotonid population is considered to represent a single species. This species shares many dental pattern characters with the following taxa.

COMPARISON WITH *Ochotona* Link, 1795

This is the unique extant genus of Ochotonidae. Its present day distribution covers the areas from Iran to southeastern Russia, and northwestern North America. Erbajeva (1988, 1994) retains, as belonging to this genus, twenty-two living and twenty fossil species. The oldest representatives

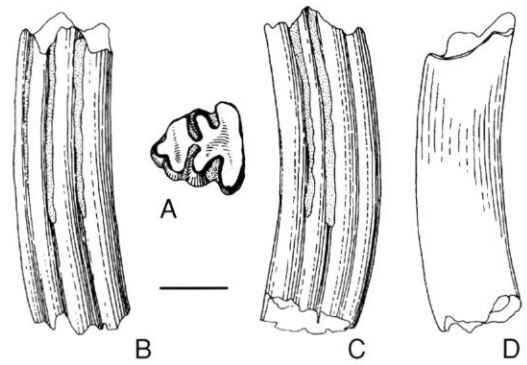


FIG. 5. — *Ochotonoma anatolica* n.g. n.sp. from Çalta, left p3 (ACA-1015) in occlusal (A), labial (B), lingual (C) and distal (D) views. Scale bar: 1 mm.

of *Ochotona*, *O. lagreli* Schlosser, 1924 and *O. minor* Bohlin, 1942 are known from the latest Miocene of China. During the Pliocene and Pleistocene, several species are recognized in Asia and some others in Europe (see Erbajeva 1988, 1994). The species referred to this genus are small-, to middle-sized, with p3 of simple occlusal pattern. Indeed, on this tooth, the anteroconid is generally small, triangular or rounded in shape, and it lacks cemented flexids that occur in *Ochotonoides* and *Ochotonoma* n.g. However, some species of *Ochotona*, such as *O. lagreli* Schlosser, 1924 from the Late Miocene of China, *O. antiqua* Pidoplichko, 1938 from the late Pliocene of Odessa catacombs and the Central Asian extant species *O. alpina* (Pallas, 1733) have on the p3 anteroconid some labial and occasionally lingual depressions, as on some specimens from Çalta. Qiu (1987: 388) mentioned that in *O. lagreli* "about 24% of specimens show a small but visible persistent fold in the anterior part of the anteroexternal fold". Nevertheless, if some species of *Ochotona* have anteroexternal and/or anterointernal folds on the anteroconid, it is in fact a shallow groove not filled with cement. In the species referred to the new genus *Ochotonoma*, these folds may be deep and filled with cement.

Another characteristic of *Ochotonoma* is the shorter diastema of the mandible. The index "length of the diastema/length of the p3-m3 alveoli", cal-

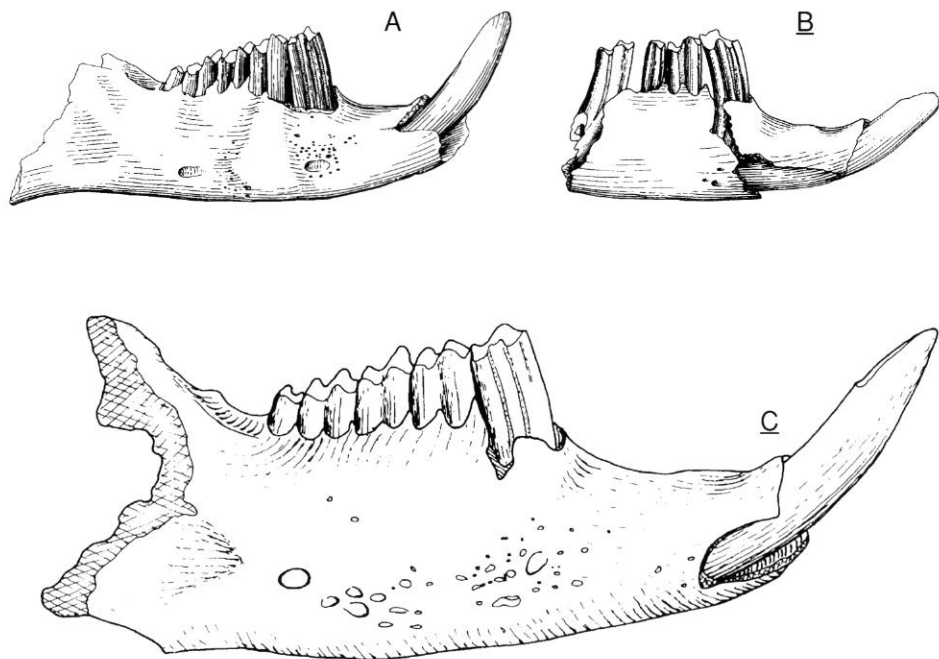


FIG. 6. — Comparison of mandibles; **A, B**, *Ochetonoma anatolica* n.g. n.sp. from Çalta (A, ACA-1001; B, ACA-1003); **C**, *Ochotonoides complicidens* (Boule et Teilhard, 1928) from Shamar, Mongolia (coll. M. Erbaeva, No. 970/500). Scale bar: 1 cm.

culated on ten different extant species, varies between 0.56 in *O. koslovi* (Büchner, 1894) to 0.85 in *O. alpina*, both Asiatic living species. This index is calculated on the type specimen of *Ochetonoma anatolica* n.sp. as 0.52. This indicates that the Çalta species has a shorter snout than is usual in *Ochetonoma*.

COMPARISON WITH *Proochotona* Khomenko, 1914

Khomenko (1914) erected the new taxon *Proochotona eximia* from the late Miocene (MN12) of Taraklia, Moldavia, because of the similar pattern of p3 to *Ochetonoma*, but its great age with respect to all previously known species of this genus. Later on, Lungu (1981) described *P. kalfense* from Kalfa (MN9) in Moldavia, and Erbaeva (1988) referred to *P. eximia* some remains from the late Miocene localities of Gucinii Perelet and Kanal Irtysh in Kazakhstan. There are no notable differences between the dental morphology of *Proochotona* species and those of *Ochetonoma*. For example, the pattern of

p3 is identical in *P. eximia* (type species) and *Ochetonoma antiqua* from the Odessa catacombs. In any case, the species referred to *Proochotona* differ from *Ochetonoma* n.g. in the simple pattern of their p3 anteroconid.

COMPARISON WITH *Pliolagomys* Erbaeva, 1983

The type species of this genus is *Proochotona gigas* Argyropoulos et Pidoplichka, 1939 from the late Pliocene of Odessa catacombs, Ukraine. Erbaeva (1988) also included in this genus *Ochotonoides kujalnikensis* Topachevski et Skorik, 1977 and *Ochotonoides danubicus* Topachevski et Skorik, 1977 from late Pliocene localities of southern Ukraine. Agadjanian & Erbaeva (1983) described some other materials from northern Kazakhstan as *Pliolagomys* cf. *kujalnikensis*. This genus is characterized by its p3 with triangular shaped anteroconid, connected to the protoconid. In *Proochotona*, *Ochotonoides*, *Ochetonoma* n.g. and *Ochetonoma*, the anteroconid is generally connected centrally to the protoconid-metaconid junction, and thus the protoflexid and paraflexid

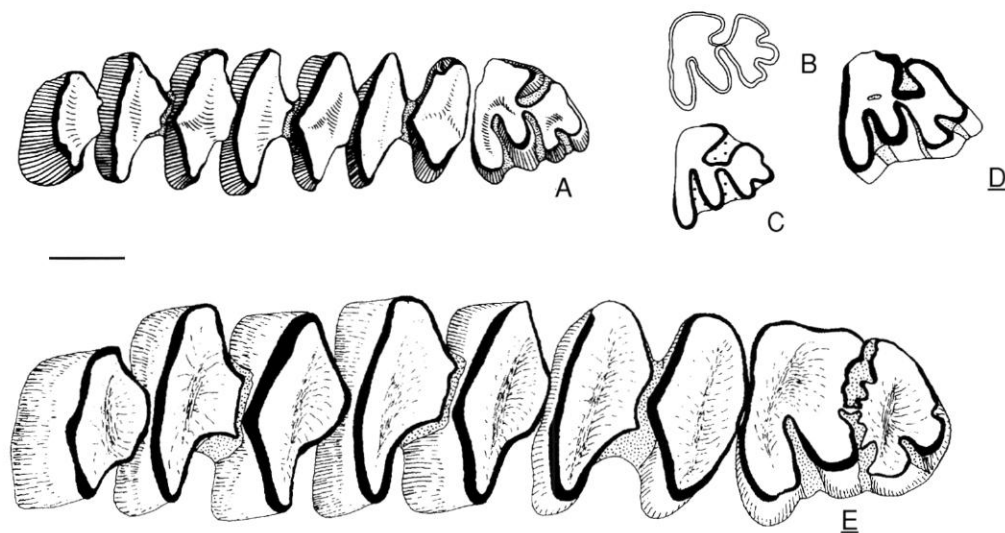


FIG. 7. — Comparison of lower premolars and molars of species attributed to *Ochotonoma* n.g. and *Ochotonoides* Teilhard et Young, 1931; **A**, *Ochotonoma anatolica* n.g. n.sp. from Çalta, p3-m3, (ACA-1001, holotype); **B**, *Ochotonoma csarnotanus* from Csarnota-2, p3 (holotype, after Kretzoi 1962); **C**, *Ochotonoma anatolica* from Ciurpereni-2, p3 (after Terzea & Boroneant 1979); **D**, *Ochotonoma* sp. from Apolakkia, p3 (after Van de Weerd et al. 1982); **E**, *Ochotonoides complicidens* from Shamar, Mongolia, p3-m3 (coll. M. Erbajeva, No. 970/500). Scale bar: 1 mm.

are equal in depth. In *Pliolagomys*, the anteroconid-trigonid connection is labial, and consequently, the protoflexid is very reduced while the paraflexid is deep and often V-shaped. However, *Pliolagomys kujalnikensis* shares a derived character with *Ochotonoma* in having labial and lingual depressions (or even some flexids filled with cement) on p3 anteroconid. This feature seems to be a parallelism that appears in several lineages.

COMPARISON WITH *Ochotonoides* Teilhard et Young, 1931

The type species of this genus *O. complicidens* (Boule et Teilhard, 1928) is a large-sized species quite common in late Pliocene and early Pleistocene localities of East Asia (China, Mongolia and eastern Russia). Its p3 has a complicated pattern in having widened anteroconid with a labially-developed "second colonette" and thus forming an independent lophid, plicated enamel along the protoflexid and also often along the paraflexid, one or two deep flexids on the anteroconid, and the lack of the mesoflexid. From this species, I measured one p3 from Shamar (4.55×4.47) and two others from

Beregovaya (4.66×4.47 ; 4.33×4.47), both localities in the Transbaikalian area (Fig. 7E).

Several other species were reported to this genus. Among them *O. bohlini* Erbajeva, 1988 from the late Pliocene of Kirgiz Nur-2 in Mongolia is notably smaller (p3, 2.7×2.5 in Erbajeva 1988: 82) than *O. complicidens*. The unique p3 illustrated by this author has a trefoil-shaped anteroconid because of the presence of two deep flexids filled with cement, as in *O. complicidens*. However, there is no labial development of the anteroconid, nor enamel plication along the protoflexid and paraflexid. This is obviously a primitive species of the *Ochotonoides* lineage. From the late Pliocene of Kiikbay locality in Kazakhstan, Agadjanian & Erbajeva (1983: 63, fig. 13) referred some specimens to *Ochotonoides complicidens*. However, the material they illustrated seems to be heterogeneous since it contains one p3 (*op. cit.*, fig. 13-1) having the typical characters of *O. complicidens*, but four other p3 (*op. cit.*, figs 13-4 to 7) are much smaller and have a less complicated occlusal pattern (narrow anteroconid and gently plicated protoflexid and paraflexid). These last four p3 cannot be attributed to *O. complicidens*. From the same locality,

Tyut'kova (1992) described a new species as *Ochotonoides progressivus*, and illustrated two p3 (dimensions: length 2.20-2.25, width 2.20-2.25). This author did not mention if the material studied by Agadjanian and Erbajeva (1983) and later by herself (1992) is the same or not. Nevertheless, the attribution of the Kiikbay ochotonid to a new species is justified. In spite of its name, it is clearly less derived than *Ochotonoides complicidens*, in having smaller dimensions, less plicated protoflexid and para-flexid, and only one deep fold on the anteroconid. The general characters of p3 from Kiikbay fit well with *Ochotonoides*, but differ from other ochotonids such as *Ochotona*, *Proochotona*, *Pliolagomys* and *Ochotonoma* n.g.; in all these genera, the size is smaller, the p3 anteroconid is narrower, and the enamel lacks plication along the protoflexid and paraflexid.

COMPARISON WITH OTHER SPECIES ATTRIBUTED TO *Ochotonoma* n.g.

Ochotonoides primitivus Zheng et Li, 1982 from the late Miocene of Songshan (Gansu, China) was considered by Qiu (1987) as a probable junior synonym of *Ochotona lagreli* Schlosser, 1924. Its attribution to *Ochotonoides* is certainly doubtful because of its small size (p3: 1.89 × 1.80), the lack of enamel plication along the protoflexid and paraflexid, its narrower anteroconid, the presence of one tenuous labial flexid on the anteroconid, and the small "second colonette". Moreover, the unique p3 available has a trace of mesoflexid. Qiu (1987: 391) is right in stating that "*Ochotonoides primitivus* does not correspond in principal structures to the diagnosis of *Ochotonoides*". The characters mentioned above fit better with those of *Ochotonoma* n.g., although this species is a little larger than the specimens from Çalta, Csarnóta-2 and Ciuperceni-2. Its synonymy with *Ochotona lagreli* cannot be defended because the latter species is smaller, lacks such a complicated pattern on the p3 anteroconid, and p4, m1 and m2 are less differentiated in size than in *O. lagreli* in which these teeth diminish in size posteriorly. Therefore, this species is tentatively included in the new genus *Ochotonoma*.

One right p3 from Csarnóta-2 (MN15, Hungary, Fig. 7B) was attributed by Kretzoi (1962) to a new species, *Ochotonoides csarnotanus*. Although the drawing of Csarnóta-2 specimen, as given by Kretzoi (1962, fig. 6), is obviously rough, it can be observed that it belongs to a small-sized species (p3: 1.48 × 1.37, after Terzea & Boroneant 1979), the anteroconid is widened and it has two anterior flexids. Despite the paucity of the material from Csarnóta-2, this species cannot be included in *Ochotonoides* because of its small size, lack of plication in the protoflexid and paraflexid and its short second labial "colonette". The characters mentioned above are shared with the new genus *Ochotonoma* to which I attribute this species. However, *O. csarnotanus* differs from the Çalta species in the following characters:

- deep and wide paraflexid, *vs* shallow and narrow one at Çalta;
- deep, transverse protoflexid, *vs* short, posteriorly-directed one at Çalta;
- narrow metaconid-entoconid complex, *vs* a wide one in Çalta p3s;
- lack of mesoflexid, *vs* a variable mesoflexid on some Çalta p3s.

Terzea & Boroneant (1979) and Terzea (1997) referred to this species a few other specimens, including one P2 and three p3, from Ciuperceni-2 (MN15, Romania, Fig. 7C). According to the measurements taken on the illustrations in Terzea (1997), the dimensions of p3 (1.43 × 1.43, 1.37 × 1.39, 1.39 × 1.26) are very similar to that of both Csarnóta-2 and Çalta. On the other hand, the pattern of p3 from Ciuperceni-2 compares better with that of Çalta than Csarnóta-2 because its anteroconid is narrower than at Csarnóta-2, with one labial deep and one lingual shallow flexids, the shape and the depth of protoflexid and paraflexid are similar. I suggest the attribution of the Ciuperceni-2 specimens to *Ochotonoma anatolica* n.g. n.sp.

Van de Weerd et al. (1982) referred to *Ochotonoides* sp. two upper incisors, one P2 (0.77 × 1.72), two P3 (1.06 × 2.74, 1.00 × 2.27), one P4 (1.23 × 2.33), one M2 (1.42 × 2.22) and one p3 (1.78 × 1.55) from the late Pliocene (late MN15) of Apolakkia, Rhodes Island, Greece. The size of these specimens is

slightly larger than those from Çalta, Csarnóta-2 and Ciurpeni-2, but notably smaller than those of *Ochotonoides* species. P2 from Apolakkia differs from that of *Ochotonoides* in being shorter. In *Ochotonoides complicitens*, the anterior hyperloph of P2 is strongly-developed anteriorly; in contrast the Apolakkia specimen has short anterior hyperloph, as at Çalta and Ciurpeni-2. The unique p3 from Apolakkia (Fig. 7D) is distinguished by its wide anteroconid which has a deep anterolabial fold filled with cement, and its "second colonette" is more developed labially than the protoconid. This last feature is typical for *Ochotonoides*, while in some Çalta specimens there is a trend to extend laterally. However, this p3 differs from *Ochotonoides* in having less folded anteroconid, smooth enamel along the protoflexid and paraflexid and small size. In morphology, upper incisors, premolars and molars share the same characters with the Çalta specimens. The similarities of the Apolakkia ochotonid with that of Çalta are greater than with any *Ochotonoides*. Thus, it is referred to the new genus *Ochotonoma*, and it probably represents a new species of this genus.

The systematics of ochotonids is based on the pattern of p3. For most genera and species, the characters of the skull, mandible and other teeth are not given in the related literature. For these reasons, tentative analyses of the phylogenetic relationships between ochotonid genera (Erbajeva 1988, 1994) only used the p3 characters. Because of the limited nature of information on several taxa, particularly on the species of *Proochotona*, and on *O. csarnotanus* and *O. primitivus*, a new phylogenetic analysis is not undertaken in the present study. However, it is obvious that the new genus *Ochotonoma* shares many characters with *Bellatona*, *Proochotona*, *Pliolagomys*, *Ochotonoides* and *Ochotona*, and is therefore considered as belonging to this group.

CONCLUSIONS

After the present study, the Çalta fauna includes nine species of rodents and one ochotonid lagomorph listed as:

MURIDAE

- Centralomys magnus* (Sen, 1977)
- Occitanomys* sp.
- Apodemus dominans* Kretzoi, 1959
- Orientalomys galaticus* (Sen, 1975)

CRICETIDAE

- Mesocricetus* cf. *primitivus* de Bruijn *et al.*, 1970

GERBILLIDAE

- Pseudomeriones tchaltaensis* Sen, 1977

ARVICOLIDAE

- Mimomys davakosi* van der Meulen, 1979

SPALACIDAE

- Pliospalax macovei* (Simionescu, 1930)

GLIRIDAE

- Dryomimus eliomyoides* Kretzoi, 1959

OCHOTONIDAE

- Ochotonoma anatolica* n.g. n.sp.

This list shows that the number of rodent and lagomorph species at Çalta is only moderately diverse compared to similar age faunas in western, central and northeastern Europe. This is probably related to some environmental and climatic factors, since most Çalta faunal elements indicate grassland and open woodland vegetation and seasonal temperate climate.

This association has a melting-pot composition because it includes species with European and Asiatic affinities together with local forms. The local forms are *Mesocricetus* and *Pliospalax* since their past and present history remains limited to territories between the Balkans and the Middle East. The taxa with European affinities are *Centralomys*, *Occitanomys*, *Dryomimus* and *Mimomys*. Three other genera, *Orientalomys*, *Pseudomeriones* and *Ochotonoma* n.g. are better represented in Asia and/or have affinities with related Asiatic taxa, although these are also known in some European localities. The genus *Apodemus* is apparently ubiquitous since it is frequent both in European and Asiatic faunas. We have also to note that the Çalta small mammal association does not contain any taxon of African origin.

Among rodents, *Pseudomeriones* and *Pliospalax* are dominant, while the murids, cricetids and

glirids are rare. I have in mind that the composition of a small mammalian association is intimately related to the nature, mode of life and preferences of predators. However, the abundance of gerbils and spalacids can only be explained by the presence of grasslands and open environments with contrasting seasonal climate. The ochotonid of Çalta is also well-documented by more than a hundred specimens. Its extant representatives occupy open environments in mountainous plateaus in Asia and North America. They are inhabitants of uneven ground with rocky cover and open grasslands. From this, it can be deduced that the environment of the Çalta rodents and lagomorphs was a grassland and open woodland mixture with a plateau-like ground and seasonal temperate climate.

In a previous paper (Sen 1977), I discussed the age of the Çalta fauna and stated that it is of late Ruscinian age (MN15). Later on, several Ruscinian faunas from Europe and Anatolia have been compared to Çalta, and paleontologists agree with its age. The present study does not offer refinement.

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