MAMMALIAN FOSSILS OF SAMOS AND PIKERMI. PART 1. THE TUROLIAN RODENTS AND INSECTIVORES OF SAMOS

CRAIG C. BLACK

Research Associate, Section of Vertebrate Fossils

LEONARD KRISHTALKA

Assistant Curator, Section of Vertebrate Fossils

NIKOS SOLOUNIAS[1]

ABSTRACT

Seven species of small mammals have been recovered from a Turolian locality in the Mytilinii Formation on Samos, Greece—the insectivore *Galerix atticus* (Erinaceidae); and the rodents *Spermophilinus* cf. *S. bredai* (Sciuridae), *Byzantinia hellenicus*, *Pseudomeriones pythagorasi*, *Pliospalax* cf. *P. sotirisi* (Cricetidae), *Occitanomys*? *provocator* (Muridae), and *Hystrix primigenia* (Hystricidae). Only three of these species—the erinaceid, murid, and hystricid—occur at Pikermi. The Samos micromammalian locality appears to represent a paleosol; the microfaunal remains may have been deposited in owl pellets. The rodents suggest a drier, more open habitat than that in which the Pikermi small mammals lived.

INTRODUCTION

The Turolian (late Miocene) bone beds of Samos Island, Greece, are world famous for their large quantities of well preserved fossil mammals. Notable is the abundance of skulls and complete bones, although partial or complete skeletons are uncommon. The fauna of Samos is

[1] Address: Department of Geology, University of Colorado, Boulder, Colorado 80203. Submitted 8 May 1980.

very similar to the fauna of Pikermi, another well known Turolian locality in Greece. Both localities have been repeatedly excavated since the early part of the nineteenth century and the fossils are now distributed in many European and North American museums. The species diversity at Samos and Pikermi is one of the largest known for the Eurasian late Miocene (Solounias, 1981).

Micromammals, while not common at these Turolian localities, have been found at both Pikermi and Samos (Dames, 1883; Schaub, 1926; Abu Bakr, 1959; Freudenthal, 1970; de Bruijn, 1976). At Samos Quarry A, Forsyth-Major's 1887 main excavation, two small mammals were found among nearly 3,000 bones of large mammals. These were a skull of *Parapodemus gaudryi* (Schaub, 1926) and a complete skull and jaw of *Samonycteris majori* (Revilliod, 1922). Barnum Brown's 1924 Quarry 4 yielded approximately four hundred specimens of larger mammals but only one maxilla of *Byzantinia hellenicus* (Freudenthal, 1970; de Bruijn, 1976).

Recently, the Dutch and Greek teams from Utrecht and Athens universities recovered a few micromammals at a new Pikermi locality (Homateri), 8 m above an unexcavated bone bed (Rumke, 1976; de Bruijn, 1976; Martinez, 1976).

GEOLOGY

The Turolian Samos fauna is recovered from the Mytilinii Formation of the Eastern Basin (Fig. 1). Several older formations within the Eastern Basin, which had not previously been prospected for vertebrate fossils, are being studied at present. Twelve of the fifteen bone beds occur in the uppermost part of the Mytilinii and span no more than 100 m of section; three minor fossiliferous horizons occur in the lower part of the Mytilinii. The Mytilinii contains abundant tuffs which, according to K-Ar dates of Van Couvering and Miller (1971), are approximately 8.5 Ma old (Turolian); the total thickness of the Mytilinii (290 m) probably accumulated in no more than 0.5 Ma.

The sediments of the Mytilinii Formation accumulated along the eastern foot of the uplifted marble basement and the older Neogene formations. The Mytilinii is subdivided into a number of distinct units. The lowest unit, the Old Mill Beds, contain uniformly bedded alternating tuffs, marls, and volcaniclastic sediments. Basement gravels occur throughout these beds, which have been interpreted as channel and overbank deposits. The next unit, the massive Gravel Beds, is composed of Neogene and basement pebbles. It is similar to the Old Mill Beds, but with more channels and less overbank deposits. The White Beds consist of limestones, indurated marls, and massive breccia deposits. The breccia contains primarily reworked Hora limestone rubble fragments and could be similar in origin to the bone beds. The
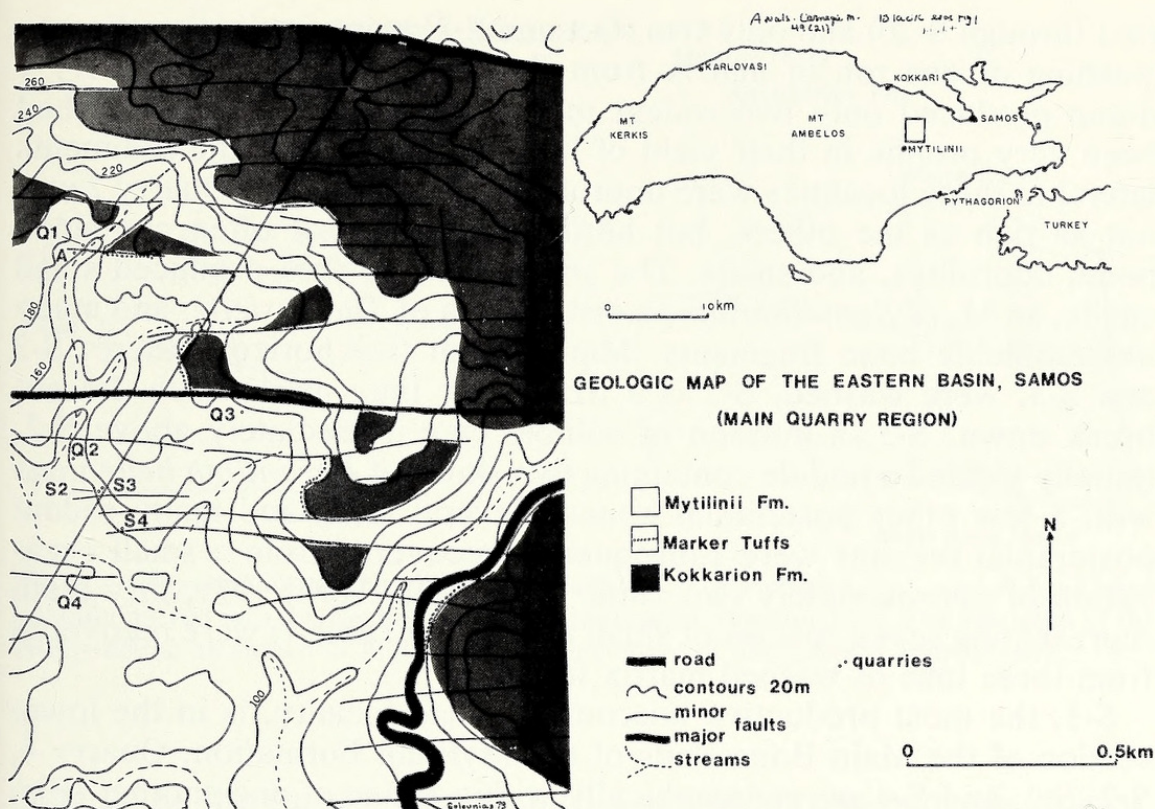
Fig. 1.—Geologic map of the Eastern Basin, Samos (main quarry region). Most faults taken from Meissner (1976).

White Beds represent deposits from small pools of standing water, as well as flood plain and paleosol deposits. The Main Bone Beds are approximately 100 m thick and are primarily fine silts and clays, representing flood plain deposits. Angular conglomerates represent small ephemeral stream deposits. The tuffs were reworked before deposition. Most of the quarries occur within the Main Bone Bed unit, primarily in individual flood cycle overbank deposits; in a few cases, they occur in paleosol deposits. The Marker Tuffs form the uppermost part of the Mytilinii. This series of tuffs occurs throughout the basin and interfingers with the Kokkarion Formation to the southeast. The Kokkarion is primarily freshwater limestones laterally equivalent to and overlying the Mytilinii Formation.

Of the 15 bone beds known within the Mytilinii Formation on Samos (Solounias, 1981), most have been worked extensively over the last 100 years and are no longer productive. Quarry 4 of 1887, where *Samonycteris* and *Parapodemus* were discovered, was excavated by the Germans until 1920 and the region is now covered by a dense pine forest with undergrowth. Examination of ant hills in the area was unproductive.

During the 1976 field season, approximately 20 sites were sampled

(S-1 through S-20) and only two (Q-1 and S-3) were productive. Screen washing of one ton of matrix from Barnum Brown's 1924 Quarry 1 dump produced only two rodent incisors. Quarries A, 1, and 5 had been very prolific in their yield of large mammals, but the sediments lateral to these localities were unproductive. In contrast, Quarry 2 was not as rich as the others, but horizons lateral to it often contained bone, coprolites, and snails. The surface of one area produced small snails, an M_3 of *Samotherium*, a distal fibula of *Thalassictis*, and many unidentifiable bone fragments. Matrix from two horizons there, S-2 and S-3, were washed. S-2 is a freshwater limy marl which did not break down. S-3, a horizon of soluble clay immediately above S-2, initially yielded a nodule containing two skulls of *Byzantinia hellenicus* with a few other postcranial bones. Several teeth and many rodent postcranial remains were subsequently recovered from a small excavation of approximately two cubic meters. In April, 1979, fifty teeth representing seven species of small mammals (Table 1) were recovered from three tons of washed matrix from S-3.

S-3, the most productive micromammalian locality, is in the lower section of the Main Bone Beds of the Mytilinii Formation. Quarry 4, S-2, S-3, and S-4 are geographically within 300 m of one another (Fig. 1). Due to minor compressional and extensional block faulting and folding, and the absence of marker horizons, the exact stratigraphic position of S-4 is not known. Nevertheless, it is no more than 10 m higher or lower than S-3. Barnum Brown excavated two horizons at Quarry 2, but the collection at The American Museum of Natural History does not distinguish between them. Most of the fossils probably came from the upper Q-2 horizon (John Skaros, personal communication). S-3 is approximately 4 m higher than that upper horizon and 35 m away, whereas S-2 is approximately at the same level as the upper Q-2 horizon.

A number of lithologies occur in the Main Bone Beds in the Potamies District (Figs. 2 and 3): (a) the most common lithology is poorly sorted volcaniclastic marls and mudstones from 50 to 150 cm thick. The bedded gravels and pebbles within these marls are largely erosional debris from the Hora limestones with occasional clay casts and pumice pebbles; (b) unstratified marls and mudstones of similar thickness as (a) showing little bedding and differing from (a) in being better sorted. These units in particular are highly fossiliferous (Quarry 2) but, as was previously mentioned, exposed bone beds have been exhausted; (c) clay nodule horizons within (a) and (b) are only one nodule in thickness (3–10 cm) and are not laterally continuous for more than 6 to 8 m. In some cases the clay nodule horizons seem to be in a thin, indurated limy bed that was partly eroded, and clay films have been observed on a few of the nodules. Most clay nodules are composed of the same
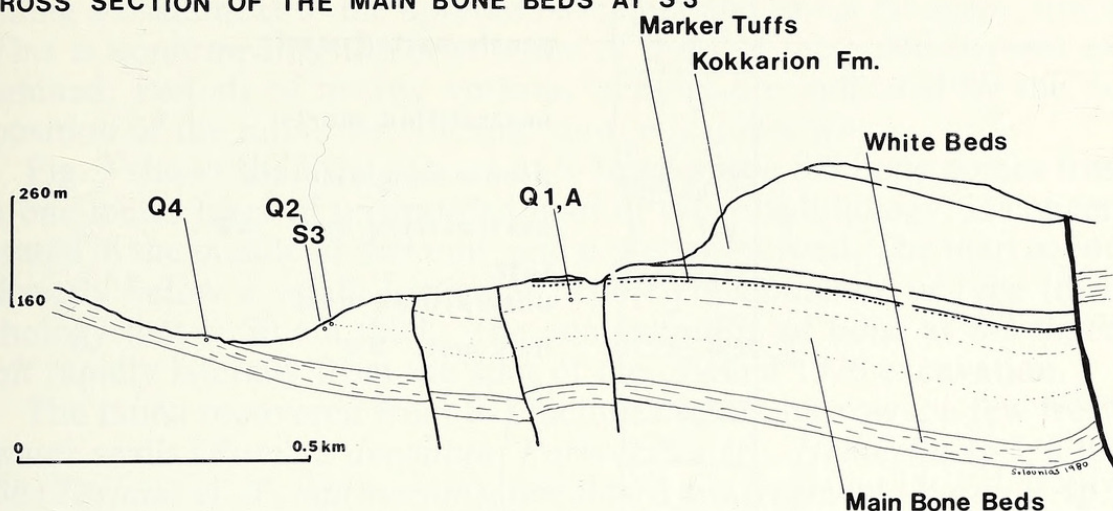
CROSS SECTION OF THE MAIN BONE BEDS AT S3

Fig. 2.—Cross-section of the Main Bone Beds at S-3. Quarries 4, 1, 2, and A have been laterally moved into this section to show stratigraphic relationships. The direction of the cross-section as shown in Fig. 1. The displacement of the faults is approximate.

material as the surrounding rock. S-4 and other one-bone-thick accumulations occur within the clay nodule horizon; (d) well-defined lenticular gravel and pebble conglomerates, from 4 to 5 m thick, are mainly unsorted angular Hora limestone fragments, and are often imbricated; (e) pumice tuffs are 50 to 150 cm thick and are well bedded. Certain tuffs change laterally into sands and eventually into conglomerates. Most tuffs fine upward and their lower contact is often transitional with the marl below; however, the upper contact of a tuff with a marl or another tuff is abrupt. The tuffs have been interpreted as water lain. The marls and tuffs alternate in a random sequence and the gravel and the conglomerates occur almost always within the marls rather than the tuffs. Unlike the upper section of the Main Bone Beds, where bone occurs only at the Quarries L, 1, 3, 5, and 6, the lower section is productive throughout, yielding bone, root casts, insect burrows, coprolites, and snails.

Lithologies (a) and (b) have been interpreted as overbank vertical accretionary deposits of sediment which have rapidly [(a) lithology] or slowly [(b) lithology] settled from a waning current. Such deposits are usually formed near the river channel on a flood plain. The clay nodule horizons have been interpreted as parts of paleosols that may have been saturated with standing water. The gravel and pebble conglomerates resemble recent small channels and have been interpreted as such. Since most pebbles are unsorted and angular, they appear to represent ephemeral stream and flash flood deposits. Bone beds would be formed in a similar fashion when flash floods accumulate bones and

poorly sorted marl

unstratified marl

pebble conglomerate

unstratified marl   S3

tuff

unstratified marl

limy marl   S 2

marls, tuffs, conglomerates

5 m

mudstones
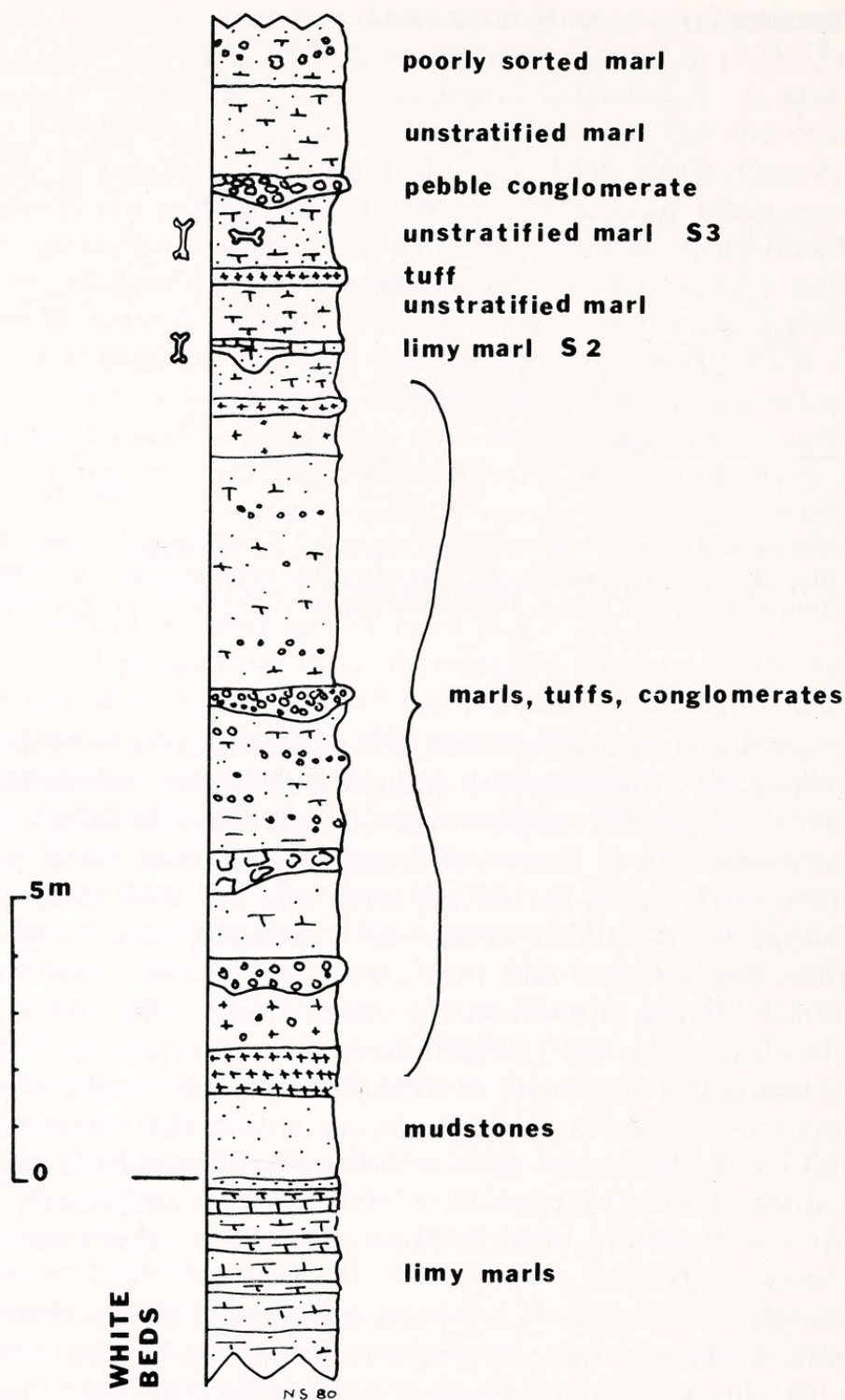
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limy marls

WHITE BEDS

N S 80

Fig. 3.—Stratigraphic section at S-3.

carcasses. Most of the channels are narrow and deep and probably developed after droughts, when new streams cut deeply into the strata but were not well developed laterally. Repetition of these depositional events produced cycles that record flood plain and flash flood deposits,

filling a basin next to the uplifted basement and lower Neogene strata. This is confirmed by the orientation of most of the paleocurrents examined. Periods of nearby volcanic activity are indicated by the deposition of the tuffs; the volcanic source is unknown.

Fig. 3 shows the local section at S-3. All of the S-3 bone comes from a one-meter layer of unstratified marl of type (b) lithology, is concentrated in the middle of that unit, and is well preserved. The marl occurs directly below a small, lenticular pebble conglomerate of type (d) lithology that is 50 cm thick. The concentration of bone at S-3 tapers off rapidly laterally from the spot of the original 1976 excavation.

The fauna recovered from S-3 includes insect burrows, a few freshwater snails (*Rumina decollata*, *Parmacella* sp., *Hellicella* sp.), a turtle (*Testudo* cf. *T. marmorum*), one lizard jaw fragment (*Varanus* sp.), egg shell fragments (Aves indet.), unidentifiable fragments, as well as a few specimens of larger mammals (*Thalassictis wongii*, *Hyaenictis eximia*, *Hipparion proboscidium*, *Hipparion dietrichi*, *Samotherium boissieri*), many skeletal fragments of small mammals, as well as 52 teeth and two skulls.

The micromammalian accumulation resembles that in owl pellets that have been weathered and slightly dispersed. The two skulls of *Byzantinia hellenicus* are broken behind the orbits and were associated in a nodule containing other, presumably *B. hellenicus*, bones. The preservation in the nodule and the condition of the additional micromammalian skeletal material from S-3 is similar to that found in owl accumulations described by Mellett (1974), Fulk (1976), and Dodson and Wexlar (1979). We have interpreted the fossiliferous layer at S-3 as representing a paleosol.

S-2 is a limy, discontinuous marl and yielded skulls of *Protoryx laticeps* and *Protoryx crassicornis*, fragments of *Gazella* jaw and horn core, and an isolated M$_3$ of *Samotherium boissieri*. The S-2 sediments seem to be the result of deposition in standing muddy water.

S-4 is a layer of bone within a clay nodule horizon. All of the excavated elements were aligned against the current flow indicating a shallow water depositional regime. Jaws and limb elements were coated with indurated marl. The sample from S-4 contains *Protoryx*, *Chilotherium samium*, and *Hipparion proboscidium*.

ACKNOWLEDGMENTS

METHODS

All measurements are given in millimeters (mm). Specimens are housed in the Institute of Geological and Mining Research, Athens, Greece; the Museé Geologique de Lausanne, Switzerland; The American Museum of Natural History (AMNH); the University of Colorado Museum (UCM); and Carnegie Museum of Natural History (CM). Abbreviations used: M, mean; N, number; OR, observed range; L, length; W, width; AW, anterior width; PW, posterior width.
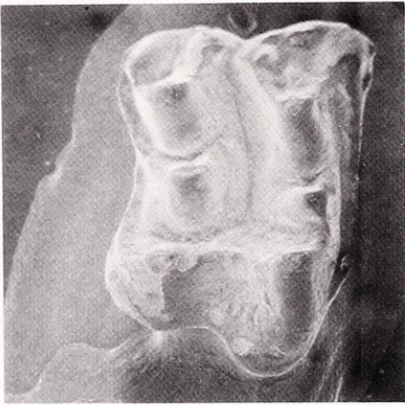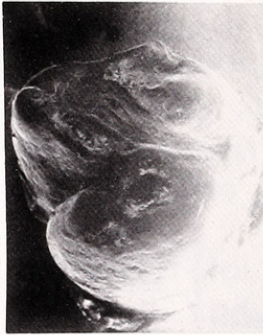
SYSTEMATICS

Order Insectivora
Family Erinaceidae
Galerix Pomel, 1848
Galerix atticus Rumke, 1976
Fig. 6

Material.—CM 38357, RP^4; CM 36286, RM^2; CM 38358, RM$_1$.

Description.—P^4 (L = 2.25; W = 2.9) is essentially rectangular in occlusal view, except for the large and posterolabially projecting metastylar lobe that is partially set off from the remainder of the crown by a deep labial emargination. The anterior border is also emarginate lingual to the small parastyle. The paracone is tall, large, and rounded; the protocone is comparatively much lower and approximately one-quarter the size of the paracone; the hypocone is lower and smaller than the protocone. Conules are absent on P^4.

M^2 (L = 2.2; W = 3.3), also rectangular in crown view, has convex and concave anterior and posterior margins, respectively. The six main cusps are subcrescentic with long lingual slopes, and are aligned labiolingually into two arcuate rows that are parallel to one another and to the anterior and posterior margins of the crown. The paracone, paraconule, and protocone form the anterior row; the metacone, metaconule, and hypocone form the posterior one. A narrow median valley separates the two rows labial to the joined hypocone and protocone. The paracone, slightly taller and more compressed anteroposteriorly than the metacone, occurs more lingually than the latter. The metaconule is more labial on the crown than the paraconule, and approximately twice as large. The protocone, higher and narrower at the base than the hypocone, also slopes farther lingually. Although both cusps share a common lingual wall, they are demarcated lingually by a vertical indentation. The protoconal root is joined to, but approximately twice as large as, the hypoconal one. The protocristae are continuous and aligned anteroposteriorly. The posthypocrista merges with the posterior cingulum, leaving the meta-

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Fig. 4.—*Spermophilinus* cf. *S. bredai*. CM 36299, RM$^{1 \text{ or } 2}$, approx. ×10.

Fig. 5.—*Pliopalax* cf. *P. sotirisi*. a) CM 36286, LM$_2$; b) CM 36301, LM$_3$; approx. ×10.

Fig. 6.—*Galerix atticus*. a) CM 36286, RM^2; b) CM 38357, RP^4; c) CM 38358, RM$_1$; approx. ×10.

conule isolated, whereas the preprotocrista extends to the paraconule. Four stylar cusps occur on the narrow stylar shelf—a conical parastyle and metastyle at the end of the preparacrista and postmetacrista, respectively; and two well-developed and adjacent mesostyles, one on either side of the midline, at the ends of postparacrista and premetacrista.

On M_1 (L = 2.9; AW = 1.85; PW = 2.0) the trigonid is compressed anteroposteriorly and slightly higher than the talonid. The protoconid, lingually inclined, is subcrescentic and linked by a strong, high paracristid to a labiolingually elongate paraconid. The metaconid is conical, higher than the paraconid, but slightly lower than the protoconid. The talonid is four-cusped. The hypoconid, also subcrescentic, and the entoconid, compressed labiolingually, are subequal, whereas a third, much smaller and lower accessory cuspule occurs in the valley between them (=the second entoconid in Rumpke, 1976). These three cusps are aligned in a labiolingual row parallel to the posterior wall of the trigonid. The fourth cusp, a strong, shelf-like entostylid, forms the posterolingual corner of the talonid and is continuous anteriorly with the entoconid and labially with a broad, ventrolabially sloping postcingulid. The cristid obliqua joins the trigonid below and labial to the apex of the protoconid and the hypocristid ends lingually on the labial face of the accessory cuspule.

Discussion.—*G. atticus,* known previously from Pikermi (Turolian) and possible Biodrak (Vallesian) (Rumpke, 1976), is distinguished from other species of *Galerix* by the structure of the talonid on M_1—a large entostylid, an isolated hypoconid, and an accessory cuspule between the latter and the entoconid—and the presence of well-developed mesostyles, an isolated metaconule, and conjoined protocone and hypocone on M^2.

In contrast to these teeth in *G. atticus,* on M^2 of *G. exilus* the mesostyles are weak or absent, the hypocone is isolated, and the postprotocrista joins the metaconule. M^2 of *G. socialis* also lacks mesostylar development, and M_1 has neither an entostylid nor a cuspule between the entoconid and hypoconid. Instead, the hypocristid extends to the posterior cingulid (Engesser, 1972). *G. moedlingensis* from Pikermi and the Vienna Basin has a P^4 with a less well-separated metastylar lobe, and an M_2 without an accessory cuspule and with a much weaker entostylid. Descriptions of *G. zapfei* from the Kohfidisch Fissures (Bachmayer and Wilson, 1970) imply that, except for a single rather than two-rooted P_2, this species is dentally indistinguishable from *G. atticus.* But, as Rumpke (1976) noted, the figures of *G. zapfei* (Bachmayer and Wilson, 1970; Rabeder, 1973) do not show the degree of development of the molar talonid structures that is distinctive in *G. atticus.*

Family Sciuridae
Spermophilinus de Bruijn & Mein, 1968
Spermophilinus cf. **S. bredai** (v. Meyer, 1848)
Fig. 4

Material.—CM 36299, $RM^{1 \text{ or } 2}$ (L = 1.554; W = 1.95).

Description.—The anterior cingulum is broad, with a low parastyle. The protoloph is complete, but with no distinct protoconule. The metaloph passes diagonally from the

metacone to a clear metaconule which in turn is joined by a thin ridge to the protoconule. There is a very small mesostyle at the buccal base of the metacone.

Discussion.—The tooth is similar to upper molars of *Spermophilinus bredai* from La Grive. This species has been reported from Crete (de Bruijn et al., 1971, 1972) and a larger species, *Spermophilinus giganteus*, has been described from the Maritsa I locality on Rhodes (de Bruijn et al., 1970). Following de Bruijn and van der Meulen (1979), the occurrences on Crete would be older than the Samos find, whereas the Rhodes species of *Spermophilinus* is younger. *Spermophilinus bredai* is known from the early Turolian of Kohfidisch (Bachmayer and Wilson, 1970), a fauna that is very close in age to the Samos assemblage. The suggestion that *S. bredai* existed later in central and southeast Europe than in western Europe (de Bruijn et al., 1971:13) is substantiated by the Samos occurrence. No sciurids are known at present in the Pikermi fauna.

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Family Cricetidae
Subfamily Cricetodontinae Stehlin & Schaub, 1957
Byzantinia de Bruijn, 1976
Byzantinia hellenicus (Freudenthal, 1970)
Fig. 7

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Holotype.—AMNH 29766, RM^1–M^3.

Hypodigm.—UCM 43604 and 43605, partial skulls; CM 36258, LM^1–M^3; CM 36269, RM$_1$–M$_3$; CM 36270, LM$_2$–M$_3$; AMNH 23000, RM$_1$–M$_2$; UCM 43615–43618 and CM 36260, 36261, M$_1$; UCM 43606, 43610, 43619 and CM 36266, 36280, M^2; UCM 43607, M^3; UCM 43620, 43621, 43623 and CM 36274–36276, 36290, M$_1$; UCM 43608, 43609, 43611, 43622, 43624 and CM 36281, 36289, M$_2$; UCM 43612–43614 and CM 36283, M$_3$.

Description.—There are two partial skulls, one preserving parts of the palate, the zygoma, and all cheek teeth, and the other preserving the snout, incisors and palate in a slightly crushed condition. The snout is long and narrow more as in *Cricetodon* and *Democricetodon* than in *Megacricetodon* and *Ruscinomys* (Hartenberger, 1967). The nasals are slender with the nasofrontal suture parallel to the posterodorsal termination of the zygomatic arch. The maxillary-premaxillary suture begins just anterior to the anterior border of the infraorbital (IOF) foramen with the premaxilla forming the medial wall of the anterior portion of the infraorbital canal. The premaxilla passes to the dorsal surface of the skull meeting the frontals at the point of the frontalnasal suture. The maxilla forms the entire dorsal roof of the zygoma and the lateral wall of the IOF. The zygomatic plate is almost vertical to the palatal surface. It sweeps sharply upwards from opposite the middle of M^1 and terminates dorsally in line with the anterior end of M^1. The origin of the lateral masseter is clearly set off by lateral and medial ridges which delimit the zygomatic plate. The plate terminates dorsally in a deep angular notch. The IOF is large and oval. The anterior limit of the origin of the medial masseter is marked by a low ridge on the premaxilla just above and anterior to the opening of the IOF.

The incisive foramina are moderately elongate, terminating opposite the anterior end of M^1. The palate is narrow and the cheek teeth converge posteriorly. The upper incisor is grooved and there is a faint rib on the lower incisor.

The upper molars decrease in size significantly from M^1 to M^3. All cusps and lophs slope posteriorly with the lophs enclosing two deep fossettes on all molars. The anterior lobe of M^1 is composed of two distinct cusps, the buccal cusp being the larger of the
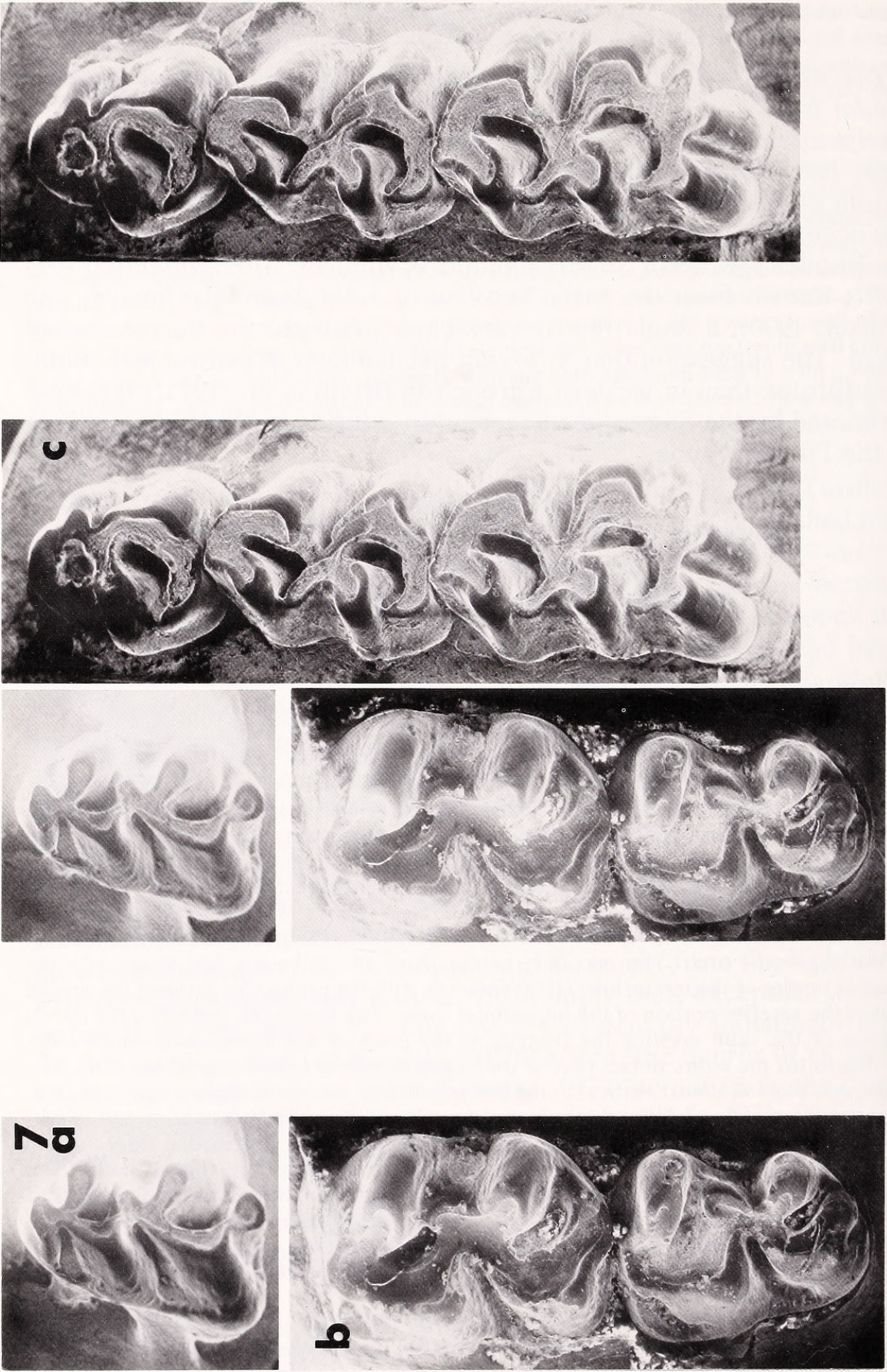
Fig. 7.—*Byzantinia hellenicus.* a) CM 36274, LM₁; b) CM 36270, LM₂–M₃; c) CM 36258, LM¹–M³; approx. ×10.

Table 1.—*Dimensions of teeth of* Byzantinia hellenicus.

Teeth	Characters	B. hellenicus			B. pikermiensis
		N	M	OR	
M¹	L	9	3.61	3.50–3.70	
	W	7	3.42	2.30–2.55	
M²	L	8	2.72	2.55–2.90	2.30–2.40
	W	9	2.10	2.00–2.20	1.80
M³	L	6	2.17	2.15–2.30	1.90–2.10
	W	6	1.81	1.70–1.95	1.60–1.80
M₁	L	7	2.84	2.70–2.95	2.30–2.60
	W	7	1.80	1.70–1.90	1.50–1.65
M₂	L	8	2.78	2.65–2.90	2.45–2.50
	W	8	1.96	1.85–2.10	1.80–1.85
M₃	L	5	2.49	2.40–2.60	2.15–2.40
	W	6	1.83	1.75–1.90	1.60

two. Freudenthal (1970) has given a detailed description of the upper dentition. We would only add that on M^3 the metacone is displaced posterointernally so that there is only a faint groove on the posterior face of the tooth between it and the hypocone.

A description of the lower dentition of *Byzantinia hellenicus* has not been published previously, although a jaw of the species was reported by Abu Bakr as *Cricetodon magnum* (1959). The lower molars are more nearly of equal size with almost no difference in length between M_1 and M_2; M_3 is only slightly shorter. The first lower molar shows a well developed anteroconid connected to the protolophid in the midline of that crest. The major cusps all lean anteriorly and all crests are directed towards the front of the teeth. There is a small short mesolophid on M_1 which closes off the anterior fossettid well below the top of the metaconid. The posterior fossettid is open much longer, only being closed off near the base of the entoconid. The posterior crest from the hypoconid is short and terminates in a distinct hypoconulid. The two external and single internal valleys are very deep.

There is no anteroconid on M_2, but a small shelf is present near the base of the tooth crown on the anteroexternal surface. The metalophid projects sharply anteriorly. The mesolophids and posterolophids are short and a distinct hypoconulid is present. There is only a single external valley, with both the internal and external valleys deep as on M_1.

The posterior half of M_3 is compressed laterally with the entoconid and hypoconid closely appressed and the posterior fossettid opening at the rear of the tooth in a narrow but deep notch. The anterior half of M_3 is basically similar to that of M_2.

Discussion.—de Bruijn (1976) has reviewed the species of *Byzantinia* and has pointed out the dental differences between that genus and *Ruscinomys*. In addition to those differences, the skull of *Byzantinia*, now known for the first time, has a longer and narrower snout and palate than does *Ruscinomys*. The two genera appear to be quite distinct.

Byzantinia hellenicus is considerably larger than *B. pikermiensis* (Table 1), but the two are nearly identical in dental morphology.
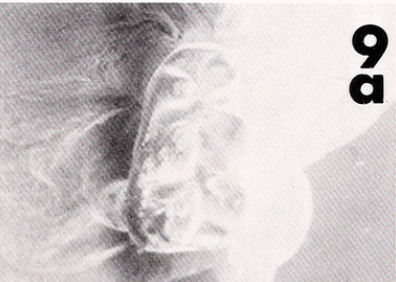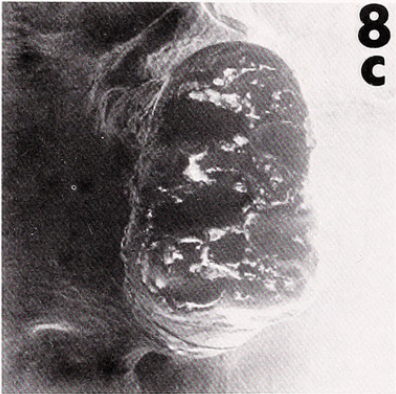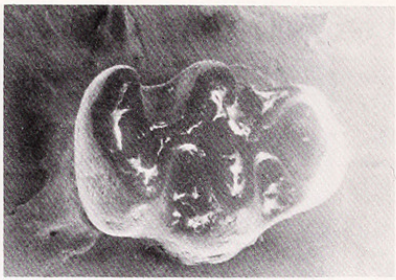
Table 2.—*Dimensions of teeth of* P. pythagorasi.

| Teeth | Characters | P. pythagorasi | | | P. abbreviatus |
		OR	M	N	M
M¹	L	2.35–2.50	2.44	4	3.05
	W	1.60–1.70	1.67	4	1.68
M₁	L	2.20–2.25	2.22	3	2.57
	W	1.35–1.50	1.44	3	1.55

Subfamily Gerbillinae
Pseudomeriones Schaub, 1934
Pseudomeriones pythagorasi, new species
Fig. 8

Holotype.—CM 36305, RM₁.
Hypodigm.—CM 36303, 36304, 36307, 36284, M¹; CM 36306, 36298, M₁.

Diagnosis.—Smaller than *Pseudomeriones abbreviatus* by about 20%; posterior arm of the hypoconid stronger than in *P. abbreviatus*; the cusps of $M^1/_1$ are more alternate than in *P. abbreviatus* and $M^1/_1$ are not as narrow.

Description.—The first upper and lower molars are elongate, but not as narrow in proportion to length as those of *P. abbreviatus* (Table 2). The cusps are only slightly alternate and the central longitudinal crest connecting the transverse crests is narrow. On M¹ the posterior arm of the hypocone is short but distinct. All trace of this arm is lost with wear. On M₁ the posterior hypoconid arm is distinct and remains so until the tooth is well worn. There is a prominent crest on M₁ which passes posterobuccally from the anteroconid closing off a portion of the anterobuccal reentrant.

Discussion.—*Pseudomeriones* was first described from China with original material named *Lophocricetus abbreviatus* (Teilhard de Chardin, 1926) and *Gerbillus matthewi* (Young, 1927). Schaub (1934) established the genus *Pseudomeriones* for this material. *Pseudomeriones abbreviatus* was later reported from the Isle of Rhodes, Greece, by de Bruijn et al. (1970) from the locality Maritsa I. Later *Gerbillus*? sp. was reported by de Bruijn (1976) from Kalithies, Rhodes. We believe the Kalithies specimen, a lower first molar, is referrable to *Pseudomeriones* and, based on its size, most probably belongs in *P. pythagorasi*. Sen (1978) recorded *Pseudomeriones abbreviatus* from Calten,

←

Fig. 8.—*Pseudomeriones pythagorasi,* new species. a) CM 36303, RM¹; b) CM 36284, RM¹; c) CM 36305 holotype, RM₁; approx. ×10.

Fig. 9.—*Occitanomys*? *provocator*. a) CM 36285, LM₁; b) CM36302, RM¹; approx. ×10.

Ankara, Turkey, a fauna of Pliocene age said to be younger than the Maritsa I fauna of Rhodes, but older than the fauna of Tourkobounia-I from outside Athens (de Bruijn and van der Meulen, 1975). More recently, Armour-Brown et al. (1979:619) have recorded *P. abbreviatus* from Ano Metochi 3 in Eastern Macedonia, a locality believed to be of late Turolian age. No measurements or descriptions have yet been published for these specimens, but they may also be referrable to *P. pythagorasi* rather than the younger *P. abbreviatus,* or they may be transitional between the two species.

Daxner-Höck (1972) described a new genus, *Epimeriones,* which she assigned to the Subfamily Gerbillinae. *Epimeriones* differs from *Pseudomeriones* and modern gerbils in that the molars, when unworn, show a multitude of small crests and shallow basins on their occlusal surfaces (Daxner-Höck, 1972: plate 1). The second and third molars are also not as shortened in *Epimeriones* as in *Pseudomeriones* and modern forms.

In overall occlusal morphology and proportions, the dentition of *Pseudomeriones* is much closer to that of *Meriones* than is that of *Epimeriones.* Whether the latter genus has any true relationship to the Gerbillinae is, we believe, open to serious question. We would agree with de Bruijn et al. (1970:563) that *Pseudomeriones* is the earliest member of the subfamily discovered to date.

The first gerbilline known in North Africa is from Amama 2, Algeria (Jaeger, 1977:88). This form, described as *Protatera algeriensis,* is of late Turolian age and clearly belongs in the *Tatera-Gerbillus* group of gerbils which are quite distinct dentally from the *Meriones-Psammomys* group. Jaeger (1977:117–119) makes a strong case for the derivation of at least the *Tatera*-like gerbils from an African *Myocricetodon* stock through the loss of the longitudinal crests connecting the transverse crests of the molars. In the *Meriones* group a central longitudinal crest is a dominant occlusal feature on all molars.

The presence of both types of gerbilline dentitions during the Turolian, one in North Africa and the other in the eastern Mediterranean, suggests very early separate centers of origin for the *Meriones* and *Tatera* groups; the former perhaps in Asia or the Middle East, the latter in North Africa. Other members of the *Tatera*-like group are known, but as yet undescribed, from the Langebaanweg faunas of South Africa (Pocock, 1976) which are some 4 to 5 million years old.

<div align="center">

Subfamily Spalacinae Thomas, 1896
Pliospalax Kormas, 1932
Pliospalax cf. P. sotirisi (de Bruijn, Dawson, and Mein, 1970)
Fig. 5

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Material.—CM 36300, LM_2 (L = 2.25, W = 2.10) and 36301, LM_3 (L = 2.00, W = 1.90).

Description.—Based upon size and wear stage, these two teeth probably came from the same individual. M_2 is slightly worn, while M_3 is unworn. M_2 has a crown height of approximately 3.0 mm, whereas M_3 has a crown height of 3.2 mm. On M_2 there is a small circular fossettid at the anterobuccal margin of the occlusal surface which represents the remnant of a short shallow anterior reentrant fold. This reentrant is still preserved on M_3 but would be lost with minimal wear. The central lingual reentrant on M_2 is slightly bifurcate with the long arm passing anterobuccally between the metaconid and protoconid. The posterior arm is short and terminates in the middle of occlusal surface. On M_3 there is a shallow anterobuccal reentrant anterior to the metaconid. The main lingual reentrant on M_3 is deep and long, passing across the crown anteriorly between the protoconid and metaconid. The buccal median reentrant on M_2 and M_3 is deep but short. On M_3 there is a shallow pit between the median reentrant and the entoconid. On M_2 the reentrant between the entoconid and the posterior arm of the hypoconid is long and deep internally but it is shallow at the internal margin and soon would be isolated as a fossettid.

Discussion.—de Bruijn and van der Meulen (1975:330) distinguish *Pliospalax* from *Spalax* and *Prospalax* on the presence of two lingual and two buccal reentrant folds on unworn M_1 of *Pliospalax*. No lower first molars are yet known from Samos but the Samos M_2 is close to that figured as *P. sotirisi* (de Bruijn et al., 1970: plate 6, fig. 1a) which shows a small anterobuccal fossettid. The Samos *Pliospalax* M_2 is slightly larger than that of *P. sotirisi* but they are quite similar in morphology. No spalacine has been reported from Pikermi.

<div align="center">

Family Muridae
Occitanomys Michaux, 1969
Occitanomys? provocator de Bruijn, 1976
Fig. 9

</div>

Material.—CM 36302, RM^1 (L = 1.90; W = 1.25); CM 36285, LM_1 (L = 1.85; W = 1.10); partial skull (snout to rear of palate) with RM^1–M^2, LM^1–M^3 in the collection of the Museé Geologique in Lausanne.

Description.—On M^1 t1 and t4 are distal to t3 and t6, respectively, and there are no posterior spurs from t3 and t6 to t4 and t9. Both t1 and t4 are rounded. There is no t4 to t9 connection. There is no t1 bis. Z is present. On M_1 there is no Sm, but there is a small anterior shelf. All lingual cusps are set ahead of their buccal counterparts. S1, Sv, Epd, and Eod are joined in the midline of the occlusal surface through a low, thin crest. There is no longitudinal crest from the posterior cusps. Two cingular cusps, Cv3 and Cv5, are moderately developed. The posterior shelf bears a Z cusp. The skull (Schaub, 1926) preserves the snout and palate in relatively undistorted condition. The snout is elongate and slender, the palate is narrow, and the incisive foramina are very long. The lateral and dorsal borders of the infraorbital foramina are missing as is most of the zygomatic plate. The dentition of this specimen is so worn as to be almost indeterminate; however, there is no indication of t7 on M^1. The absence of this cusp and the crest from t4 to t9 suggests that the skull is that of *O.? provocator* rather than representing *Parapodemus gaudryi* (de Bruijn, 1976: table 1).

Discussion.—de Bruijn (1976) referred with question material from Pikermi to two new species of *Occitanomys?*, *O. neutrum*, and *O.? provocator*. He noted that the Pikermi specimens differed from other

Table 3.—*Rodents and insectivores of Samos and Pikermi, Greece.*

Taxa	Samos	Pikermi
Insectivora		
Talpidae		
Desmanella dubia	—	x
Erinaceidae		
Galerix moedlingensis	—	x
Galerix atticus	x	x
Rodentia		
Sciuridae		
Spermophilinus cf. *S. bredai*	x	—
Cricetidae		
Byzantinia pikermiensis	—	x
Byzantinia hellenicus	x	—
Kowalskia aff. *K. lavocati*	—	x
Pseudomeriones pythagorasi	x	—
Pliospalax cf. *P. sotirisi*	x	—
Muridae		
Parapodemus gaudryi	—	x
Occitanomys? *neutrum*	—	x
Occitanomys? *provocator*	x	x
Gliridae		
Myomimus cf. *dehmi*	—	x
Muscardinus sp.	—	x
Hystricidae		
Hystrix primigenia	x	x

Occitanomys in not possessing either t1 bis, posterior t1 and t3 spurs on M^1, or a longitudinal crest on M_1; but, nevertheless, he believed it was premature to erect a new genus for this material. We follow him in this decision.

The Samos specimens are too large to be referred to *O.? neutrum.* They agree in almost all respects with the teeth of *O.? provocator.*

<div align="center">

Family Hystricidae
Hystrix Linnaeus
Hystrix primigenia Wagner, 1848

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Material.—AMNH 20551, an almost complete skull; AMNH 23030, left mandible with roots of P_4–M_2, partial M_3.

Discussion.—This material was described by Abu Bakr (1959) and has not been seen by us. He indicates that *Hystrix primigenia* is found also at Pikermi but this was not mentioned by de Bruijn (1976).

SUMMARY

The small mammal fauna of the Turolian of Samos differs from that of Pikermi (de Bruijn, 1976) in a rather striking fashion (Table 3). Of the seven Samos species, three are found at Pikermi—*Galerix atticus, Occitanomys? provocator* and *Hystrix primigenia. Byzantinia* occurs in both faunas but different species are involved. The other three Samos species all suggest a dry, open steppe environment at Samos. *Spermophilinus* cf. *S. bredai* was most probably a ground squirrel, whereas the gerbil and the spalacine indicate an open, rather dry environment. These three species have not been reported from Pikermi. Instead, there are five other rodents known from Pikermi which together suggest a wetter, more closed environment. These include two species of murids, two door mice, and the cricetid *Kowalskia* aff. *K. lavocati.*

While samples from both localities are quite small, the difference in species composition suggests a distinct difference in at least the two local habitats. The microfauna from Samos would appear to have been taken from a dry, open steppe habitat, while that from Pikermi appears to come from a more moist and perhaps densely vegetated region.

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