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The status of the genus name *Parapodemus* SCHAUB, 1938; new data bearing on an old controversy

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The literature on *Parapodemus* is reviewed and it is shown that the original holotype of *Mus gaudryi* DAMES, 1883 is within the range of variation of the population from which the neotype was chosen. *Parapodemus* is a valid genus, but the diagnosis is revised because the first and second upper molars do not show the same grade of evolution. Analyses of the murines from the Middle Turolian of Düzyayla (C. Anatolia) shows that *Apodemus* is polyphyletic. The International Commission on Zoological Nomenclature is requested to designate the type specimen of *Parapodemus gaudryi*.

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PART 1: *PARAPODEMUS GAUDRYI* AND ITS TYPE SPECIMEN

INTRODUCTION

Few fossil rodent species have been the subject of so many discussions in the literature as *Mus gaudryi* DAMES, 1883, the type species of *Parapodemus*. We therefore hesitate to take up this subject again, but there are compelling reasons to do so. In the first place, dr C. Doukas (Athens) has recently recovered the holotype of *Mus gaudryi*, considered lost since it was figured in Papp (1947), from the collections of the Geology Department of the University of Athens. Secondly, Martín Suárez & Mein (1998) have re-opened the dispute on the status of *Parapodemus* and, in the third place, new material from the Middle Turolian of Düzyayla (near Hafik, C. Anatolia) and Lava (near Servia, Macedonia) that will be discussed below provides information on populations that are transitional between *Parapodemus* and *Apodemus*.

The recovery of the, not very informative, type of *P. gaudryi* after a neotype had been designated (de Bruijn 1976) requires a decision of the International Commission on Zoological Nomenclature on the identity of the type. We therefore summarise the data

relevant for this ruling and formally request a decision on this matter. The measurements of the associations of murid cheek teeth from Düzyayla and Lava 2 are given in the Appendix. All figured specimens except Plate 1, fig. 8 are approximately x19 and illustrated as left cheek teeth. If the original is from the right side its number on de plate has been underlined.

Concise historical review of the genus name *Parapodemus* SCHAUB, 1938, its type species *Mus gaudryi* DAMES, 1883 and its holotype

1883 Dames describes a complete lower dentition of a murid from the classic locality Megaloremma near Pikermi (Attika, Greece) as *Mus* (?*Acomys*) *gaudryi*.

1926 Schaub refers a partial Murinae skull from Samos (Greece) with a dentition that is worn and therefore does not show any detail to *Mus gaudryi*.

1938 Schaub in a monograph on fossil Murinae describes material from Polgárdi (Hungary) and refers it to *Mus gaudryi*. In the same paper he defines the genus *Parapodemus* as murinae similar to *Apodemus*, but with an M1 and M2 that lack the t7 and designates *Mus gaudryi* as the type species of this new genus. This unfortunate action implicates that the generic characteristic (absence of the t7) cannot be observed in the holotype of the type species. In the same paper Schaub assigns a second species, *P. lugdunensis* from Mollon (France) to *Parapodemus*.

1947 Papp studies and figures the (then damaged) type mandible with m2, m3 dext. and m2 sin. from Megaloremma and compares it with the material from Polgárdi studied by Schaub. He reaches the conclusion that the morphology of the Polgárdi material differs from the type of *P. gaudryi* and therefore represents a different species which he names *Parapodemus schaubi*. Papp does not designate a holotype for his species and suggests to regard it as the type species of *Parapodemus*.

1958 Schaub follows this erroneous action and mentions *P. schaubi* PAPP, 1947 as the type species of *Parapodemus*.

1976 De Bruijn describes a collection of isolated rodent teeth from the locality Pikermi-Chomateri, which is situated 3.5 km NE from the Megaloremma locality that yielded the type of *Parapodemus gaudryi*. The dominant rodent in this assemblage is a species of *Parapodemus*. Since the type of *gaudryi* could not be found in 1976, direct comparison of the Chomateri material with the type was impossible. Comparison of the *Parapodemus* teeth from Chomateri with the ones from Polgárdi showed a striking morphological similarity and a large overlap in size (De Bruijn 1976: fig. 1). Although some of the teeth from Polgárdi are somewhat larger than the ones from Chomateri, he (= De Bruijn) concluded that they represent the same species, synonymized *P. schaubi* PAPP and *P. gaudryi* (DAMES) and designated a neotype (M1) for *P. gaudryi* from the Chomateri assemblage (no. 171, Plate 3, fig. 8).

1978 Mein criticizes De Bruijn (1976) on many points. Relevant here is that he considers the neotype designated for *P. gaudryi* not valid because:
(1) It is not certain that the localities Megaloremma and Chomateri are coeval.
(2) It is not certain that the neotype belongs to the same species as the (lost) type.
(3) Schaub (1938) based the genus name *Parapodemus* on characteristics observed in *P. schaubi*. Mein therefore considers *schaubi* as the type species of *Parapodemus* and reaches the conclusion that the name *P. gaudryi* 'doit être rayé des tablettes de la nomenclature zoologique'.

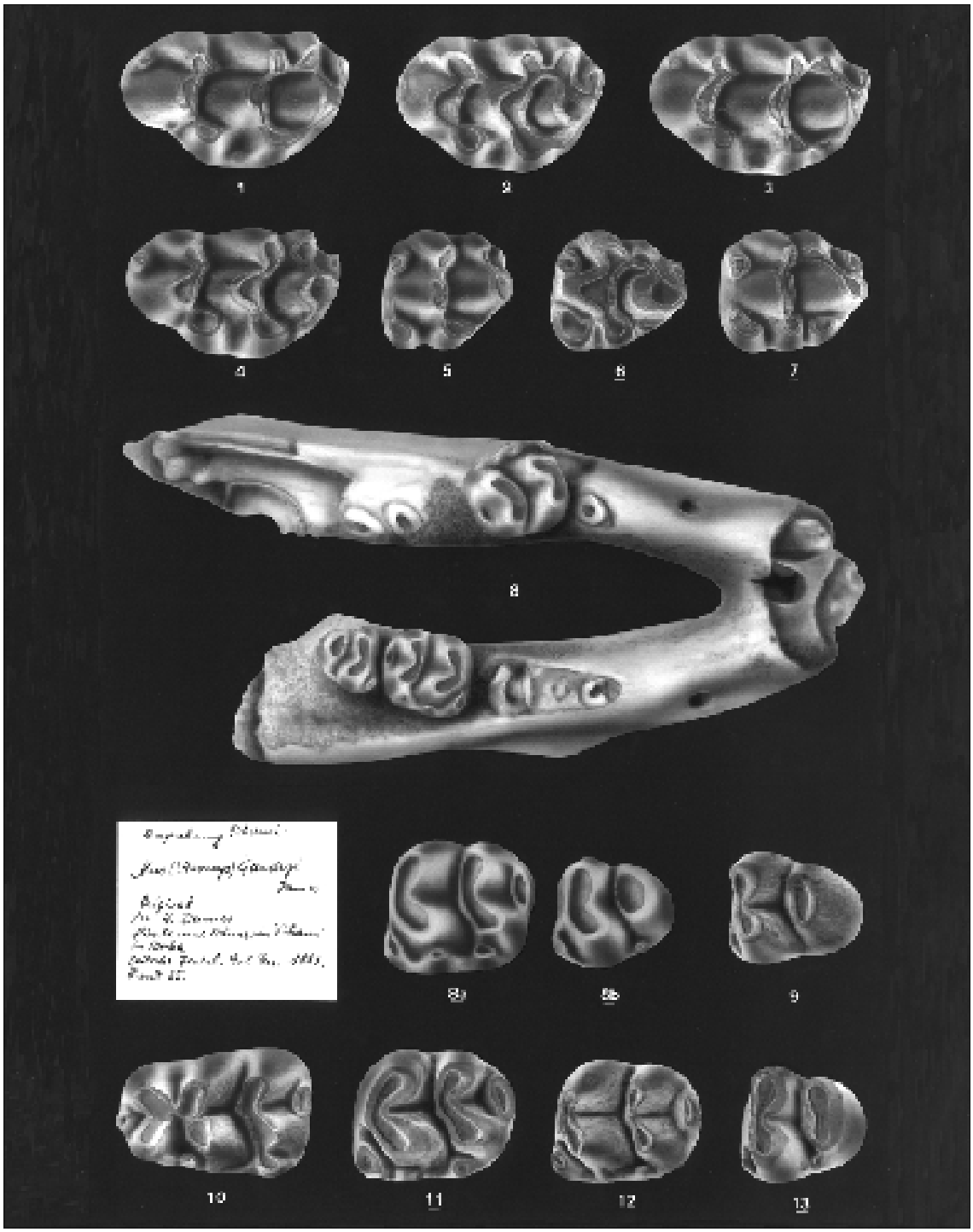

PLATE I *Parapodemus gaudryi* (DAMES, 1883). Figs. **1-4**: M1, figs. **5-7**: M2, fig. **10**: m1, figs. **11** and **12**: m2, and figs. **9** and **13**: m3; all from Chomateri. Fig. **1** is the neotype. Fig. **8** is the holotype mandible from Megaloremma with m2 sin. and m2 and m3 dext. Figs. **8a** and **8b** are the reversed m2 and m3 of the holotype figured at the same scale as the isolated cheek teeth from Chomateri.

1978 Van de Weerd & De Bruijn in a reaction on Mein (1978) argue that:
(1) Schaub explicitly designated *P. gaudryi* as the type of *Parapodemus*.
(2) The exact locality where the type mandible was found is known.
(3) The Megaloremma and Chomateri localities are in the same formation.
(4) The differences between the Polgárdi and Megaloremma material noted by Papp (1947) are based on the undiagnostic m2.
They further observe that designation of *P. schaubi* as the type of *Parapodemus* is not in accordance with the The International Code Zoological Nomenclature (I.C.Z.N.) and recommend that *P. gaudryi* be recognized as the valid type species.

1998 Martín Suárez & Mein analyze the literature reviewed above and write (p. 88): 'it is not our intention to revive an old polemic on this subject' (= the status of the genus name *Parapodemus*). New in their discussion are some of the reasons to reject the neotype designated by de Bruijn (1976). These are:
(1) De Bruijn (1976) designates a neotype without any justification (Art. 75c, I.C.Z.N.).
(2) De Bruijn (1976) fails to give evidence that the localities Megaloremma and Chomateri represent the same geological horizon (Art. 75d, 5, I.C.Z.N.)
(3) De Bruijn (1976) gives no evidence that the neotype belongs to the same genus and species as the lost type mandible of *P. gaudryi* (Art. 75d, 4, I.C.Z.N.)

DISCUSSION

About the first objection made by Martín Suárez & Mein (1998) one can say that the description of the variation in the Pikermi 4 sample, the figures, the emended diagnosis and the designation of a neotype given in 1976 have ascertained the unambiguous use of the genus name *Parapodemus* for twenty two years. In retrospect this seems to justify the designation of the neotype.

The second objection by Martín Suárez & Mein (1998) is partly correct. Sections in the Neogene continental deposits near Pikermi show a series of fluviatile sandy red-beds at the base that grade upwards into grey lacustrine marls. From west to east the lacustrine part of the section increases in thickness suggesting that part of the red-bed deposits in the Megaloremma area is the lateral equivalent of part of the lacustrine series near Rafina. Since the quarry Chomateri is situated some 3.7 km east of Megaloremma and the level with the small mammals is situated in the lower part of the lacustrine beds (Bachmayer *et al.* 1982) the two localities are expected to represent roughly the same horizon. This assumption is supported by the occurrence of a level rich in large mammal remains in the Chomateri quarry at about 12m. below the level with the small mammals. The association of large mammals from that level is very similar to the one from Megaloremma (Fig. 8). We therefore consider these faunas to be of about the same age. Moreover, the test samples collected between the level with large mammals and the one of Pikermi 4 are all similar. This suggests that the rate of sedimentation was high relative to the rate of faunistic change. We therefore are of the opinion that the Pikermi 4 level meets condition 75, d, 5 of the I.C.Z.N.: '*Evidence that the neotype came as nearly as practicable from the same level as the original name-bearing type*'.

The third objection raised is correct, or rather, was correct until the holotype of *P. gaudryi* had been recovered. Comparison of the figures of the holotype in Papp (1947) on Plate 1 (figs. 8a and 8b) shows a number of differences. Peculiar is that the incorrect figures given by Papp are accompanied by a description that is consistent with these figures. Papp (1947, last paragraph of p. 372) writes: (our abbreviated translation from German) 'Comparison of the remains from Polgárdi and *Mus gaudryi* from Pikermi shows that the two species are not related.

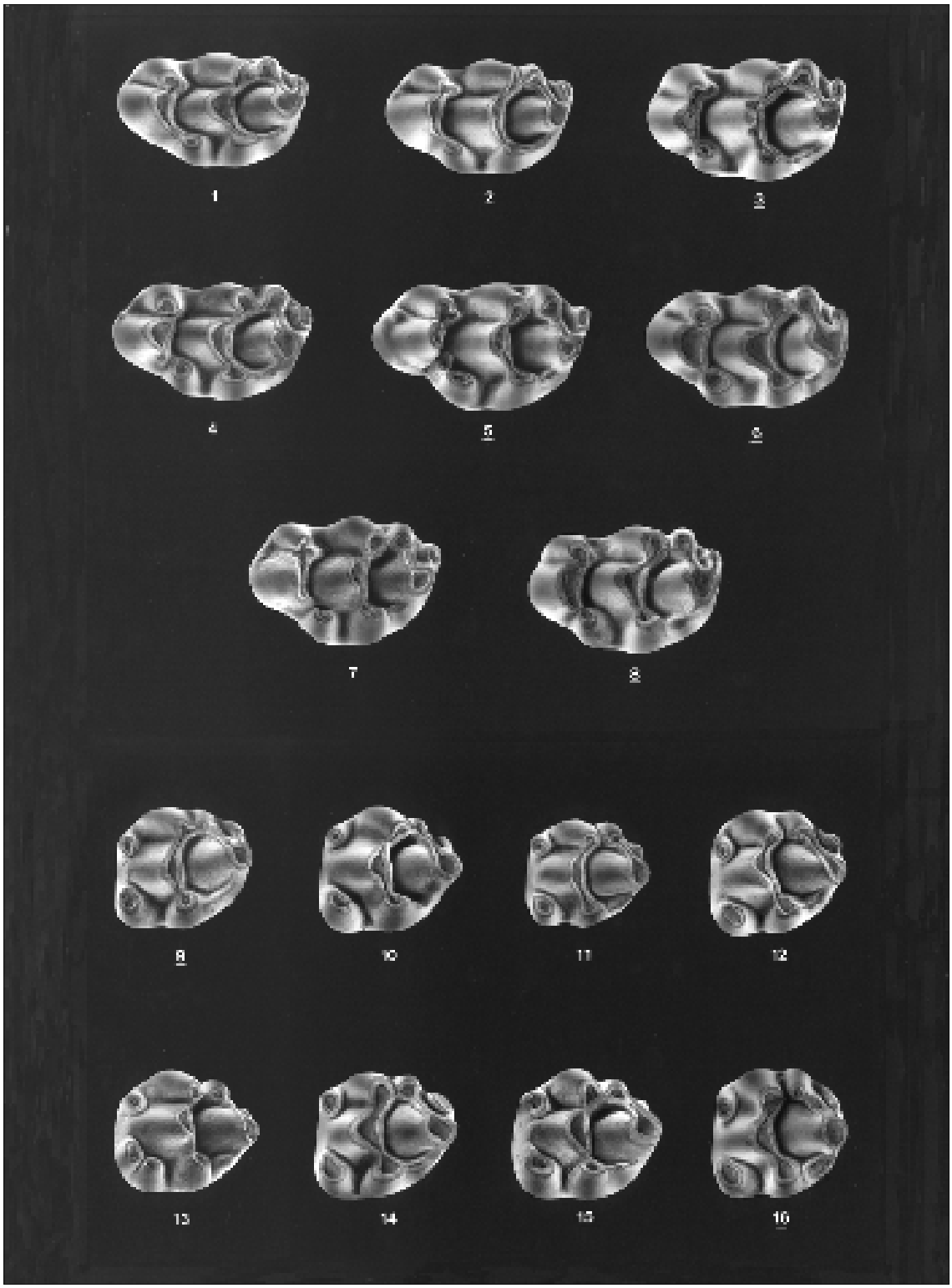

PLATE 2 *Apodemus* sp. 1 from Düzyayla. Figs. **1-8**: M1, figs. **9-16**: M2. The teeth have been arranged in a sequence according to the development of the t7. The frequency distribution of the various morphotypes is given in (text)Figure 3. The M2 of figure 13 is the only specimen with a t1 bis.

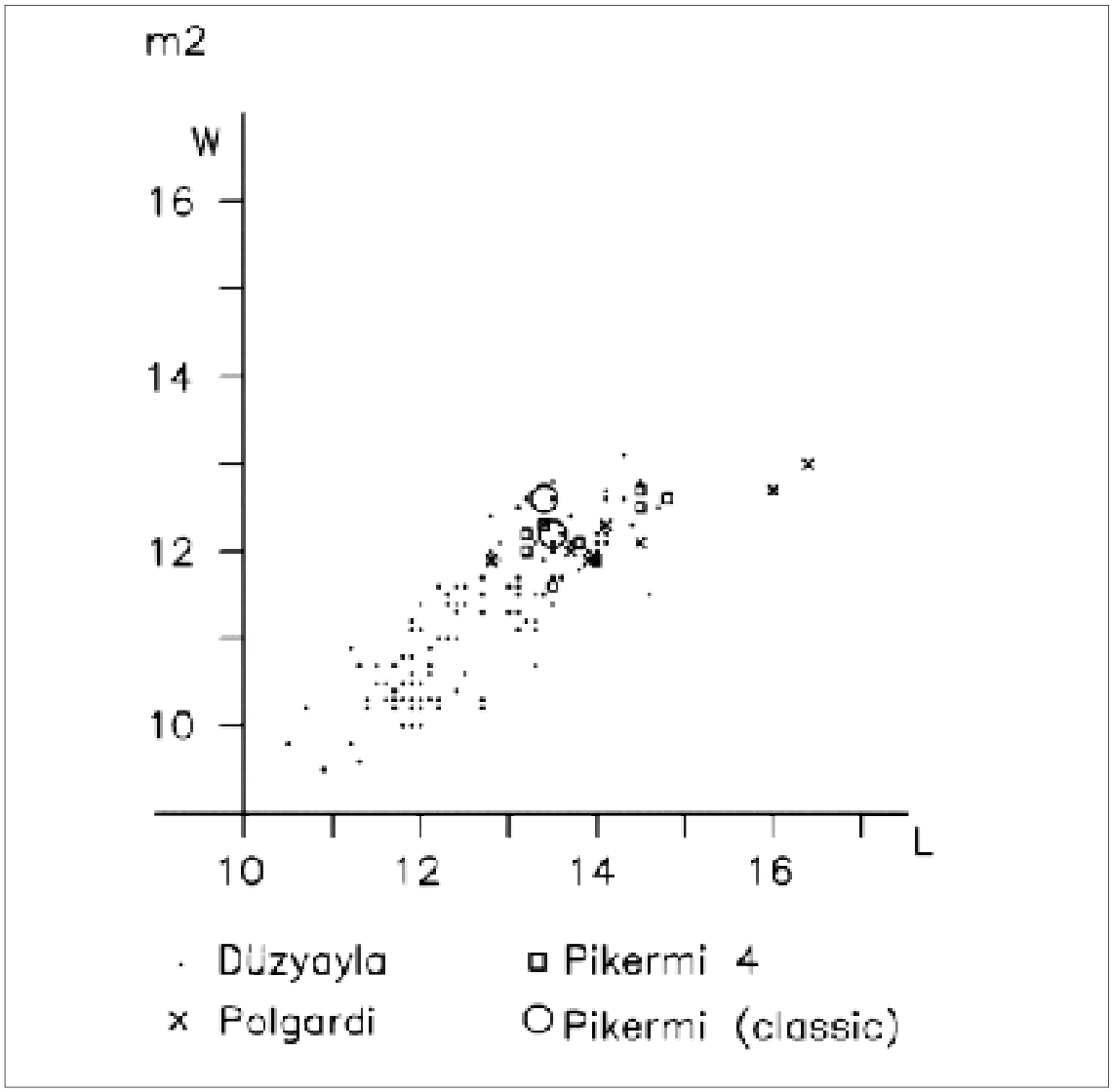

Figure 1 Scatter diagram of the length and width of the *Parapodemus* / *Apodemus* m2 from Pikermi, Polgárdi and Düzyayla.

The m2 of the latter has no extra cusp labially of the hypoconid and the terminal heel is absent'. However, the teeth preserved in the holotype have the banal morphology shared by most *Parapodemus* and *Apodemus* species and fit within the variation of the population from which the neotype was designated (Fig. 1 and Plate 1, figs. 8, 8a, 8b, 9,11, 12 and 13). The neotype was thus designated in accordance with Art. 75, d, 4 of the I.C.Z.N.

We conclude that the identity of *Mus gaudryi* DAMES, 1883 is clear and that the genus *Parapodemus* is valid. The size difference between the teeth from Polgárdi and Chomateri (Fig. 1) is not sufficient to warrant two species names, so *P. schaubi* is considered a junior synonym of *P. gaudryi*. Species assigned to *Parapodemus* are:
P. gaudryi (DAMES, 1883)
P. lugdunensis SCHAUB, 1938
P. barbarae VAN DE WEERD, 1976
P. meini MARTÍN SUÁREZ & FREUDENTHAL, 1993

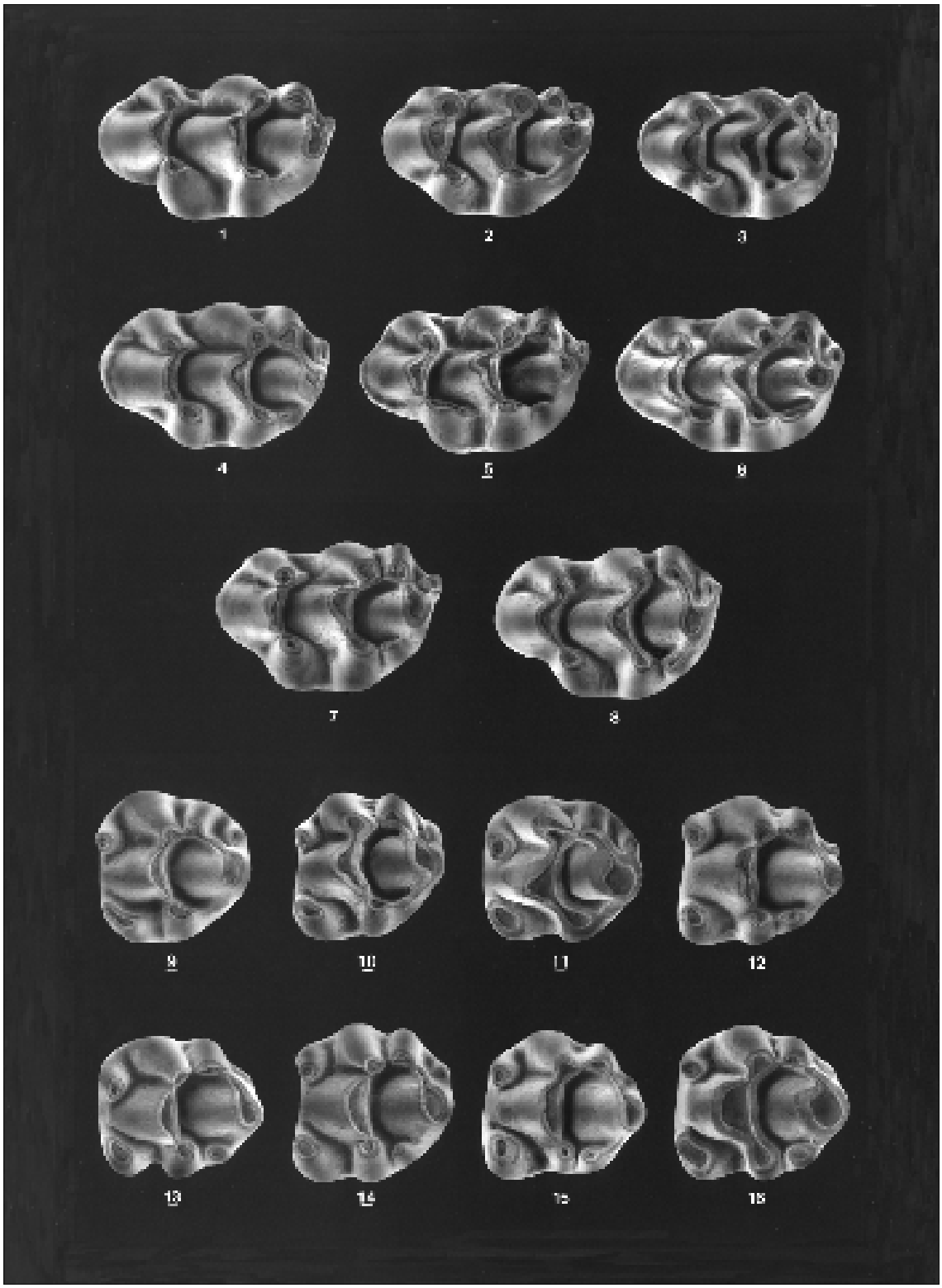

PLATE 3 *Apodemus* sp. 2 from Düzyayla. Figs. **1-8**: M1, figs. **9-16**: M2. The teeth have been arranged in a sequence according to the development of the t7. The frequency distribution of the various morphotypes is given in (text)Figure 3.

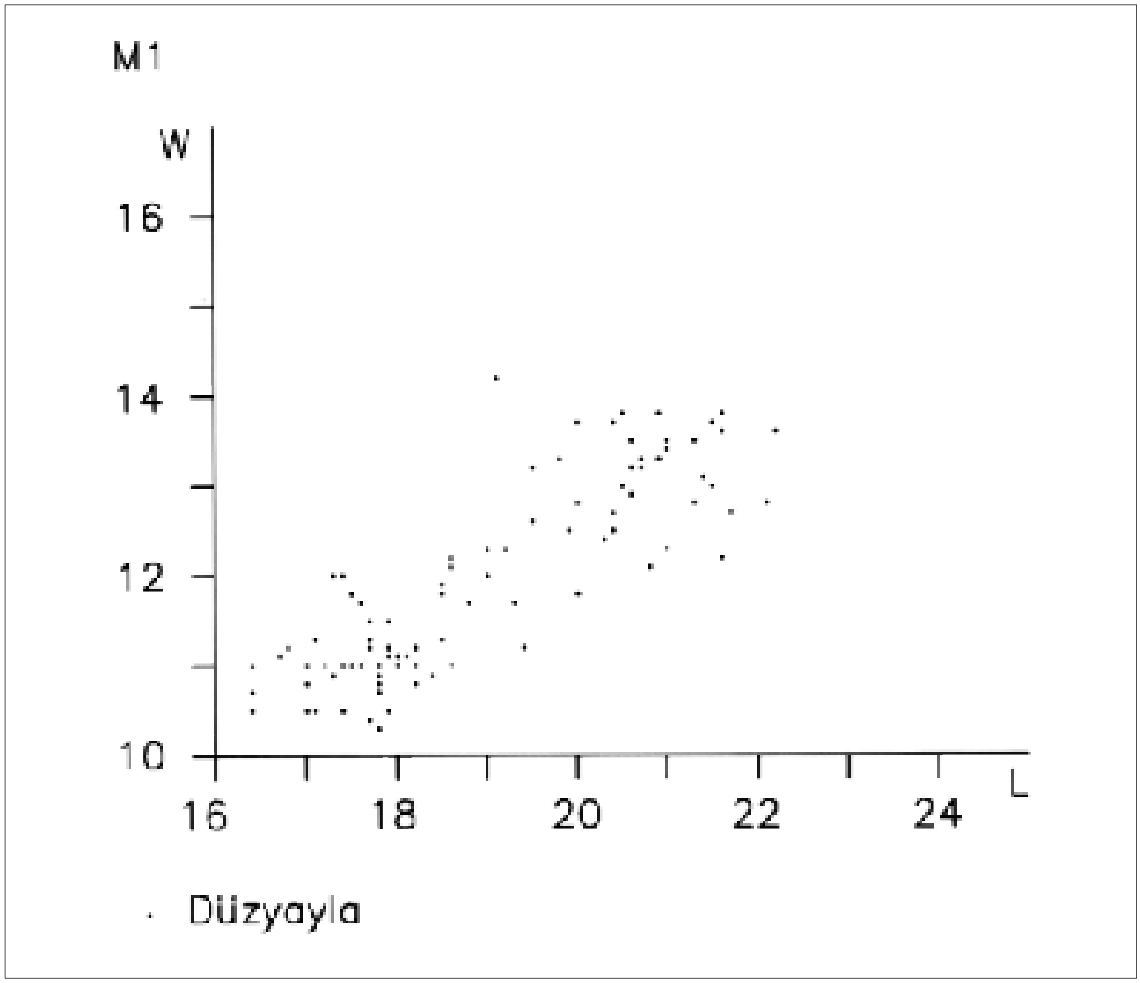

Figure 2 Scatter diagram of the length and width of the *Parapodemus* / *Apodemus* M1 from Düzyayla showing two slightly overlapping clusters indicating the presence of two species.

PART 2: THE MURINAE FROM THE MIDDLE TUROLIAN LOCALITIES DÜZYAYLA (C. ANATOLIA) AND LAVA (MACEDONIA)

INTRODUCTION

The Murinae from Düzyayla and Lava are of interest for understanding populations with a mixture of *Parapodemus* and *Apodemus* morphotypes in the M1 and M2. In Düzyayla there are two species of different size (Fig. 2) showing this transitional stage represented in the same level (Plate 2, figs. 1-16; Plate 3, figs. 1-16). The assemblages from Düzyayla and Pikermi 4 are similar in that they both contain *Hansdebruijnia neutrum* (Plate 4, figs. 19-22) and '*Karnimata*' *provocator* (Plate 4, figs. 15-18), but they differ in the stage of evolution of the *Parapodemus* / *Apodemus* populations (Fig. 3). The use of the genus name *Karnimata* here does not imply that we do not agree with Mein *et al.* (1993) who synonymize *K. darwini* JACOBS, 1978, the type species of *Karnimata*, with *Progonomys woelferi* BACHMAYER & WILSON, 1970. The problem is that there is no genus name available for the species formerly assigned to *Karnimata* and that does not fit *Progonomys*, *Huerzelerimys* MEIN *et al.* 1993 or *Castromys* MARTÍN SUÁREZ & FREUDENTHAL,

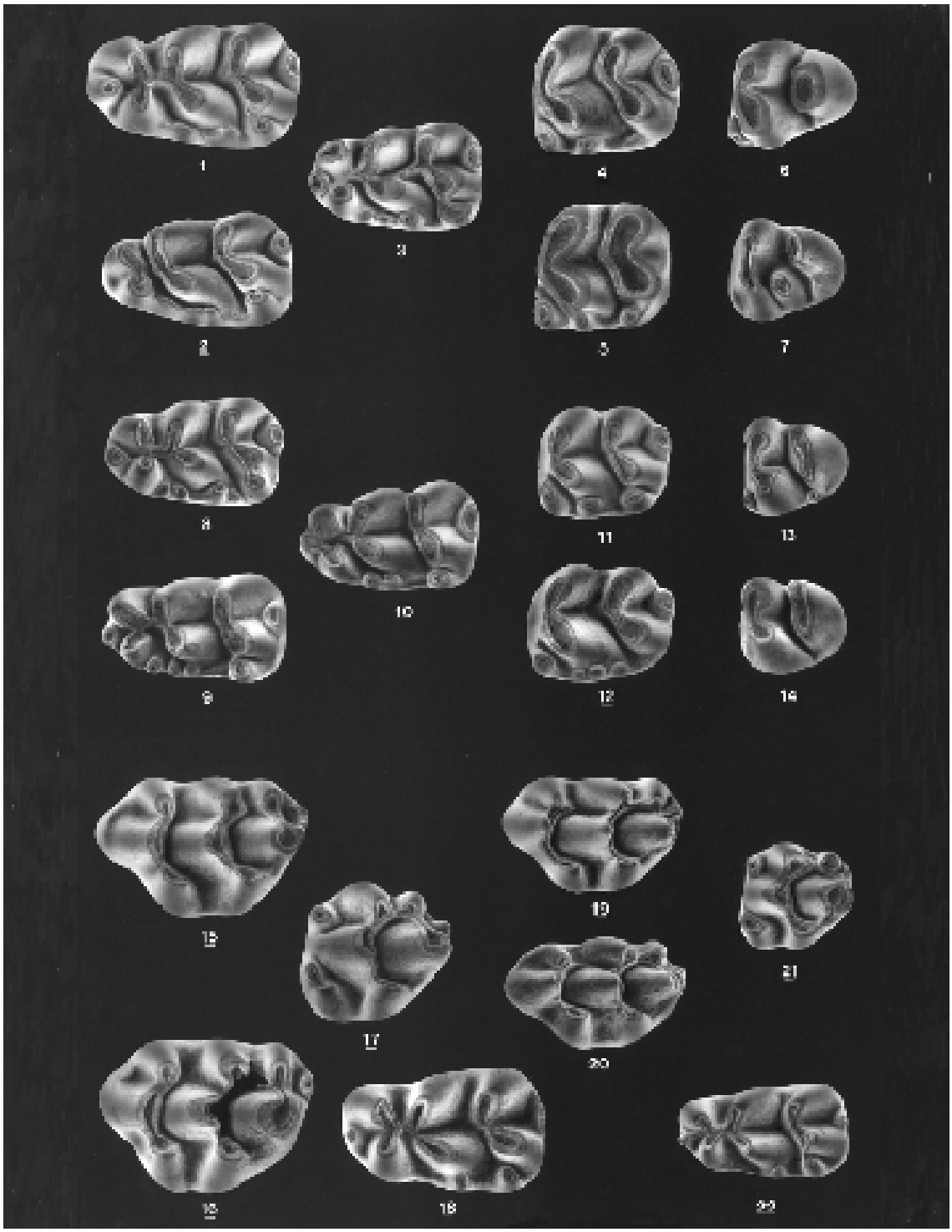

PLATE 4 *Apodemus* sp. 2 from Düzyayla. Figs. **1-3**: m1, figs. **4-5**: m2, figs. **6-7**: m3. The m1 of fig. 2 is the only specimen without the anterocentral cusp., and fig. 3 shows the only m1 with a strong longitudal crest. The m3 of fig. 7 is considered to be an aberrant specimen. *Apodemus* sp. 1 from Düzyayla. Figs. **8-10**: m1, figs. **11-12**: m2, figs. **13-14**: m3. "*Karnimata*" *provocator* (DE BRUIJN, 1976). Figs. **15-16**: M1, fig. **17**: M2, fig. **18**: m1. *Hansdebruijnia neutrum* (DE BRUIJN, 1976). Figs. **19-20**: M1, fig. **21**: M2, fig. **22**: m1

1994. Since the revision of the species in this category is beyond the scope of this study we provisionally assign the species *K. huxlei* JACOBS, 1978, which seems to be a junior synonym of ?*Occitanomys provocator* DE BRUIJN 1976, to '*Karnimata*'.

The locality of Düzyayla is situated in the east slope of an abandoned lignite mine just NE of the village of Düzyayla. The continental deposits containing the lignite unconformably overlie a thin section of littoral limestones of Early Miocene age (J.C. Guezou pers. comm. 1995). There are two superposed fossiliferous levels: a greenish-gray clay bed and the overlying laminated lignite bed. Both levels are rich in mollusk remains and show considerable variation in thickness laterally and both contain remains of large as well as of small mammals. Since the local miners collected the large mammals, the provenance of individual fossils is not known. Unfortunately the collection was not donated to a scientific institution and is therefore only partly available for study. The collections of small mammals from the clay and the lignite have been kept separate. Since the preservation of the teeth in the lignite is poor the sample from the clay is much larger. All specimens figured and used to calculate the frequency distribution of the various morphotypes are from the clay. The composition of the rodent associations from the clay and from the lignite is rather different (Fig. 4). We hesitate to interpret these differences in terms of biotope because the mode of accumulation of the fossils seems to have been different.

The locality of Lava is situated close to the edge of the basin in the south western corner of the Lava lignite mine (near Servia, Macedonia). The fossiliferous silts and sands were deposited around large boulders of Mesozoic limestone that seem to have fallen into the basin during the sedimentation. The remains of fish and small mammals occur concentrated on foresets and bedding planes within an irregular sand body of several meters thick.

Localities	Species		*Parapodemus*		*Apodemus*			N. Specimens	% *Parapod.* morphotypes	% *Apodemus* morphotypes
			Morphotypes							
			1	2	3	4	5			
Chomateri	*P.gaudryi*	M1	0	58	0	17	25	12	58	42
		M2	0	50	0	17	33	6	50	50
DUzyayla	*Apodemus* sp.1	M1	4	35	34	10	17	52	40	60
		M2	7	13	15	25	39	61	20	80
	Apodemus sp.2	M1	7	22	13	41	17	46	29	71
		M2	3	11	8	31	47	38	14	86
Lava 2	*Apodemus* sp.3	M1	0	14	0	19	67	21	14	86
		M2	0	5	5	10	80	20	5	95

Figure 3 The relative abundance of the five morphotypes recognized in the M1 and M2 of four different species from three localities. Morphotypes 1 and 2 represent the *Parapodemus* morphology and morphotypes 3, 4 and 5 the *Apodemus* morphology. In each of the four species the percentage of specimens with the *Apodemus* morphology is higher in the M2 than in the M1.

localities / Rodentia	Düzyayla (clay)		Düzyayla (lignite)		Samos main bone beds	Pikermi Chomateri
Keramidomys sp.	68	10.1	1	1	-	-
Spermophilinus bredai	82	12.2	20	18	+	-
Pliopetaurista n. sp.	4	0.6	-	-	-	-
Hylopetes macedoniensis	7	1	1	1	-	-
Glirulus lissiensis	7	1	-	-	-	-
Myoximus aff. *dehmi*	-	-	1	1	-	+
Eozapus intermedius	14	2.1	-	-	-	-
Dipodides sp.	1	0.2	-	-	-	-
Byzantinia hellenicus	-	-	9	8	+	+
"*Blancomys*" sp.	2	0.4	+	+	-	-
Pliospalax sp.	1	0.2	3	3	+	+
Pseudomeriones pithagorasi	3	0.5	+	+	+	-
Apodemus sp. 1	258	38.2	13	12	-	-
Apodemus sp. 2	203	30.2	33	30	-	-
Hansdebruijnia neutrum	15	2.2	2	2	-	+
"*Karnimata*" cf. *provocator*	6	0.9	2	2	+	+
cf. *Castromys* sp.	-	-	5	5	-	-
n total	672			92		
- = absent + = present	n	%	%	n	-	+

Figure 4 Complete list of the rodents collected from the clay and from the lignite of Düzyayla as well as the relative abundance of the taxa in these two levels. N refers to the number of M1 + M2 and m1 + m2. The specimens referred to as "*Blancomys*" represent a large high-crowned muroid which teeth have flat wear surfaces. Similar specimens have become known from a number of new localities of Late Miocene age in Turkey. The affinity of this group is not known, but the teeth are reminiscent of *Blancomys*. In the columns Samos (main bone beds) (Black *et al.* 1980) and Pikermi (Chomateri) only those species are indicated that occur in one of the levels of Düzyayla.

The *Apodemus* association from the Düzyayla clay

The scatter diagram of length and width of the M1 with *Parapodemus* and *Apodemus* morphology (Fig. 2) shows that there are two species represented in this level that show a small overlap in size. Since the morphological difference between the two species is small (Plate 2, figs. 1-16; Plate 3, figs. 1-16; Plate 4, figs. 1-14) it cannot be excluded that a few of the specimens of intermediate size have been assigned to the wrong species. Fortunately the total number is large, so possible mis-identification of single specimens does not affect the relative abundance of the morphotypes much. Figure 3 shows the relative abundance of the five morphotypes recognized in the M1 and M2 in each species. Allocation of morphotypes '1'and '2' to *Parapodemus* and of morphotypes '3', '4', and '5' to *Apodemus* follows tradition. Two conclusions can be drawn from Figure 3:

(1) *Apodemus* sp. 2 has a more advanced grade of evolution than *Apodemus* sp. 1.
(2) In both species the grade of evolution is more advanced in the M2 than in the M1, a phenomenon that occurs in the *P. gaudryi* assemblage from Los Aguanaces (van Dam 1997: 64) also.

This means that the definition of what should be called *Parapodemus* and what *Apodemus* has to be based on either M1 or M2. We suggest to choose the M1 and to stipulate that a minimum of ten specimens is required. If more than fifty percent of these have the *Parapodemus* morphology the species is called *Parapodemus* and vice versa. We redefine *Parapodemus* SCHAUB, 1938 as follows:

> Murinae with a dental pattern closely resembling *Apodemus* but lacking the t7 in the majority of the M1. A minimum of 10 M1 should be available in order to distinguish *Parapodemus* from *Apodemus* in any assemblage of M1 showing a strong t4-t8 connection.

The occurrence of two species of *Apodemus* that differ in size and in grade of evolution in the same bed shows beyond doubt that the genus *Apodemus* is polyphyletic. This could never be demonstrated, but was long since suspected on the basis of fossil evidence from Spain where populations transitional between *Parapodemus* and *Apodemus* are only known in the group of larger species (*P. barbarae*, *A. gudrunae* (VAN DE WEERD 1976). The smaller *A. dominans*, seems to be an immigrant in Spain (Martín Suárez & Mein 1998). Moreover, the relationship of *P. barbarae* and *A. gudrunae* on the one hand and *P. gaudryi* and *Apodemus* sp.1 on the other hand is not clear at all. It is of interest that the polyphyly of *Apodemus* has been a point of discussion among zoologists also (Musser *et al.* 1996).

level	Düzyala 1 (clay)	Düzyala 1 (lignite)
Lagomorpha	n	n
Alilepus turolensis	1	1
Prolagus sp.	-	1

Figure 5 Composition of the lagomorph assemblages collected from the clay and from the lignite of Düzyayla.

level	Düzyayla 1 (clay + lignite)
Insectivora	n
Schizogalerix cf. *zapfei*	1
Amblycoptus	3
Archaeodesmana	1
Petenyia hungarica	24
Soricid indet.	1
Permenella	24

Figure 6 Composition of the insectivore assemblages collected from the clay and from the lignite of Düzyayla.

The *Apodemus* association from Lava

Comparison of the scatter diagrams of length and width of the M1 from Lava (Fig. 7) and from Düzyayla (Fig. 2) shows that the majority of the specimens from Lava are within the size range of *Apodemus* sp.1. A few larger ones seem to represent a species different from *Apodemus* sp.3. However, the small sample size and the general morphological similarity of *Apodemus* cheek teeth do not allow the unambiguous recognition of two species. The relative abundance of the morphotypes of the M1 and M2 from Lava given in Figure 3 therefore refers to all the available specimens.

Remarks on the classification of *Apodemus* of Martín Suárez & Mein (1998)

Now that we have rehabilitated *Parapodemus* and have established that *Apodemus* originated at least twice, it is of interest to review the reasoning behind the incorporation of all species of *Parapodemus*, except *P. gaudryi*, into *Apodemus* as suggested by Martín Suárez and Mein, (1998). These authors argue that: (1) 'The generic differences (between *Parapodemus* and *Apodemus*) were based upon the degree of development of different character states, which may present a problem in intermediate populations; (2) 'Taking into account that the holotype of the type spe-

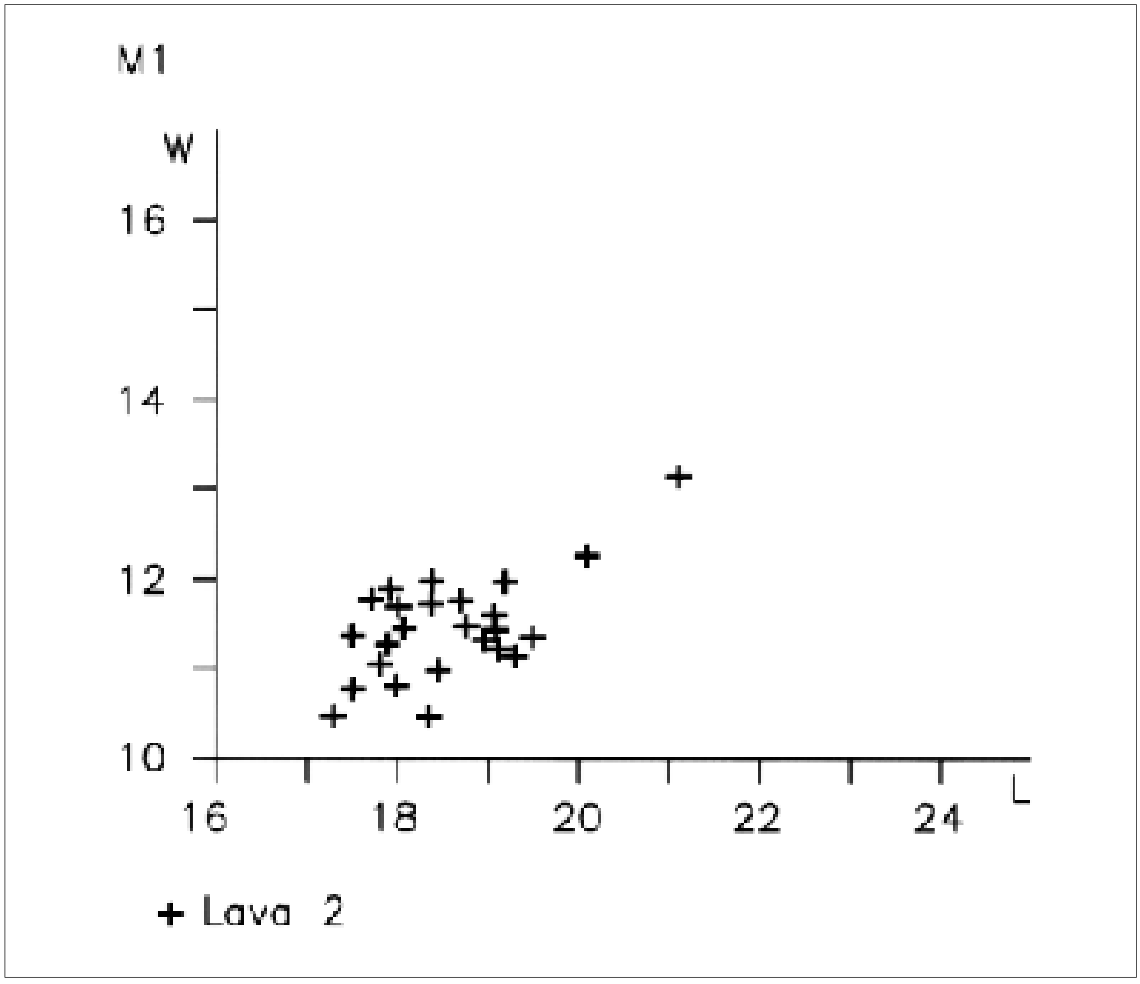

Figure 7 Scatter diagram of the length and width of the M1 of *Apodemus* sp.3 from Lava 2.

localities large mammals	Pikermi Chomateri	Pikermi Megaloremma
Mesopithecus pentelicus	X	X
Hystrix primigenia	X	X
Metailurus parvulus	X	X
Choerolophodon pentelicus	X	X
Hipparion mediterraneum	X	X
Chalicotherium goldfussi	X	X
Microstonyx erymanthius	X	X
Pliocervus pentelicus	X	X
Palaeotragus rouenii	X	X
Gazella capricornis	X	X
Tragoportax gaudryi	X	X
Prostrepsiceros rotundicornis	X	X
Palaeoreas lindermayeri	X	X

Figure 8 The similarity in composition of the associations of large mammals from Pikermi (Chomateri) and Pikermi (Megaloremma). The list is restricted to the species that are known from the not fully studied Chomateri locality. Data for Chomateri are after Marinos & Symeonidis (1974), Symeonidis (1978), Bachmayer *et al.* (1982), and Roussiakis (1996). Data for Megaloremma are after Gaudry (1862-1867), Butler (1965), Solounias (1981), Geraads (1988), and Roussiakis (1996).

cies of the genus *Parapodemus* is lost, we think that the best solution for the stability of the nomenclature is to include in the genus *Apodemus* those species that, in our opinion, form one evolutionary lineage with several ramifications of related species'.

We have serious objections against both these considerations because all fossil species and genera of mammals are based on differences in stage of evolution. If we were to adapt formal nomenclature each time we find populations that are transitional between two taxa we soon create chaos in nomenclature. The second statement, now in part obsolete because the holotype has been recovered, suggests that their classification is based on their 'personal opinion' that it groups closely related species. Taking into account that parallel and convergent evolution is very common in rodents, assuming monophyly for *Apodemus* on the basis of European material only seems not wise.

Biostratigraphy

The occurrence in the eastern Mediterranean of two lineages of *Parapodemus* / *Apodemus* that differ in stage of evolution in the same locality and that both seem to attain a fully developed *Apodemus* dental pattern within MN12, potentially provides a sophisticated tool to determine the relative ages of rodent faunas in that unit. Unfortunately, the number of associations available in collections is too limited to test the accuracy of this method. The *Parapodemus* / *Apodemus* material from

localities / large mammals	Samos mainbonebeds	Pikermi Megaloremma	Pikermi Chomateri	Düzyayla
Adcrocuta exima	X	X	-	X
Choerolophodon pentelicus	X	X	X	X
Deinotherium giganteum	X	X	-	X
Ceratotherium neumayri	X	X	-	X
Microstonyx erymanthius	X	X	X	X
Helladotherium duvernoyi	X	X	-	X
Dioceros wegneri	X	-	-	X
Gazella "gaudryi"	X	-	-	X

Figure 9 The large mammals from Düzyayla that have been identified to species level (identifications by Drs. Tanju Kaya and Vahdet Tuna, Aegean University, Izmir). Absence or presence of these species in the localities Samos (Main bone beds), Pikermi (Megaloremma) and Pikermi (Chomateri) is given for comparison. Data for Samos after Solounias (1981). Data for Chomateri and Megaloremma from the same sources as in Figure 8. The reason that *G. "gaudryi"* is in quotation marks is that this name is preoccupied.

Pikermi, Düzyayla and Lava discussed above nevertheless suggests that Pikermi is the older and Lava the younger of the three associations.

The two rodent associations of Düzyayla coming from two directly superposed beds share ten of the eighteen species that are present in the combined Düzyayla sample (Fig. 4), while the association from the Düzyayla clay shares four species with Samos and only two species with Pikermi 4. For the association from the Düzyayla lignite these numbers are five and two, respectively. This suggests that the age of the locality Düzyayla is closer to Samos (M) than to Pikermi (4). Comparison of the large mammal assemblage from Düzyayla, Samos (M) and Pikermi (Megaloremma) and Pikermi (Chomateri) (Fig. 9) reveals the great similarity of Düzyayla and Samos (M) and therefore supports the conclusion that these faunas are about the same age.

The rodent association from Lava contains ten species (Fig. 10). Apart from *Apodemus* sp.3 all these species are represented by a few teeth only. Some species have very long ranges: *Leptodontomys catalaunicus*, *Prospalax petteri*, *Glis minor*, not a single species has originally been described from a fauna assigned to MN12 and three species are known from faunas that are assigned to MN13/14. Moreover, the Lava rodent assemblage (Fig. 10) does not share a single species with Düzyayla, Pikermi or Samos. This suggests that the Lava locality is younger than these MN12 faunas and fits best in MN13. Since immigrants of African and Asiatic origin are absent, the Lava fauna seems to be pre-Messinian and is best assigned to the lower part of MN13.

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Lava 2
Leptodontomys cf. *catalaunicus*
Spermophilinus sp. (larger than *turolensis*)
Pliopetaurista sp. (larger than *dehmi*)
Hylopetes cf. *hungaricus*
Blackia woelfersheimensis
Glis cf. *minor*
Muscardinus cf. *vireti*
Kowalskia browni
Prospalax aff. *petteri*
Apodemus sp. 3
Pliopentalagus sp.

Figure 10 The species of rodents and lagomorphs found in the locality of Lava.

attention to the occurrence of fossil mammals in the Düzyayla lignite mine. Mrs. A.E. de Bruijn - Dudok van Heel and Mr. C. Theocharopoulos helped collecting. Part of the material from the lignite bed was collected by Dr. E. Güleç (Ankara), Dr. T.D. White (Berkeley) and students from the University of Ankara. The S.E.M. photo's were made by Mr. W. den Hartog and the figures were computer drawn by Mr. T. van Hinte. Mr. J. Luteyn drew the holotype of *Parapodemus gaudryi*, retouched the S.E.M. photo's and made the plates. Mrs. M. van der Tol typed the manuscript. We thank Drs. D.F. Mayhew and A.J. van der Meulen for critically reading the text. The hospitality of Mr. C. Varvoutis in Vevi and the consistent support of the General Directorate of the M.T.A. (Ankara) and the Faculty of Earth Sciences (Athens) made our research possible.

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APPENDIX Measurements

Measurements in 0.1 mm units of "*Karminata*" *provocator* from Düzyayla

M1	20.3 x 14.0	19.3 x 12.8
M2	13.9 x 12.4	
m1	18.3 x 11.5	18.7 x 11.2

Measurements of in 0.1 mm units *Hansdebruijnia neutrum* form Düzyayla

M1	16.9 x 10.7	16.5 x 11.3	16.0 x 10.5		
M2	11.1 x 10.2	11.6 x 10.3			
m1	15.2 x 9.0				
m2	11.0 x 9.5	11.0 x 9.6	10.8 x 9.2	10.0 x 8.7	9.5 x 9.0
	10.0 x 9.1	10.1 x 8.9	10.5 x 9.5	11.5 x 9.0	

APPENDIX Measurements (continued)

Measurements in 0.1 mm units of *Apodemus* sp. 1 from Düzyayla

	length			width	
	range	mean	n	mean	range
M1	16.5 19.4	17.7	53/55	11.1	10.3 – 12.1
M2	11.0 – 13.8	12.2	60	11.2	10.0 – 12.5
M3	7.8 - 9.7	8.5	44	8.6	7.5 - 9.5
m1	15.3 – 17.7	16.5	65	9.7	8.7 - 11.0
m2	10.4 – 13.9	12.1	76	10.6	9.3 - 12.1
m3	8.0 - 10.4	9.4	59	8.8	8.0 - 9.9

Measurements in 0.1 mm units of *Apodemus* sp. 2 from Düzyayla

	length			width	
	range	mean	n	mean	range
M1	18.5 – 22.2	20.5	48/53	13.0	11.7 – 14.2
M2	13.3 – 15.8	14.3	42/41	13.1	12.0 –14.5
M3	9.2 - 11.2	10.2	36	9.9	9.0 – 10.7
m1	16.5 20.2	18.6	56/	11.3	10.0 – 12.6
m2	12.2 – 14.7	13.7	48	12.1	11.2 – 13.1
m3	10.2 – 12.6	11.2	46	10.2	9.4 - 11.2

Measurements in 0.1 mm units of *Apodemus* sp.3 from Lava 2

	length			width	
	range	mean	n	mean	range
M1	17.4 – 21.6	18.6	25/27	11.5	10.5 – 13.2
M2	11.3 – 14.8	12.3	21	11.4	10.7 – 13.2
M3	8.8 - 8.9	8.9	2	9.4	9.0 - 9.3
m1	15.2 – 20.8	17.0	18	10.0	9.2 - 11.9
m2	11.4 – 14.7	12.3	16	11.6	10.0 – 12.8
m3	9.7 - 10.9	10.3	7	9.4	9.2 - 9.9