The late Turolian muroid rodent succession in eastern Spain

Jorge AGUSTÍ and Manel LLENAS

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Abstract. In this paper we present a review of the muroid succession in the late Turolian basins of Spain. The basins of Fortuna, Mula and Teruel, as well as isolated localities like Almenara-M, are taken into account in this analysis. Five main events, recording the entry of *Stephanomys, Parasaidomys, Paraethomys, Protatera* and aff. *Protatera* sp., are recognized. The new genus *Parasaidomys* is described for the new species *P. kowalskii* and other populations of large murids that are found in the lowermost late Turolian levels of the Fortuna and Teruel basins. The dispersal events in the Spanish late Turolian are the result of the commingling of two major zoogeographic realms. The first, of mainly northern Palaearctic character, includes the dispersals of *Apodemus, Rhagapodemus, Pseudocricetus* and perhaps *Paraethomys*. The second, corresponding to an Afro-Asiatic province, includes the entry of *Parasaidomys* in the very early late Turolian and the entry of *Protatera, Myocricetodon, Pseudomeriones, Calomyscus* and others at the end of this mammal stage.

Key words: Rodents, murid, gerbillid, Turolian, Messinian, Late Miocene

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I. INTRODUCTION

Increasing knowledge of the late Turolian, Messinian equivalent, continental faunas in the Mediterranean area has shown the resulting zoogeographic pattern to be much more complicated than initially thought (JAEGER et al. 1977; AGUSTÍ 1989; MEIN et al. 1990). This is especially true in the case of the Iberian peninsula, where the commingling of Iberian, Central European, Asiatic and African faunal elements is evident in several basins and localities (AGUILAR et al. 1984; AGUSTÍ 1990). The sequence of dispersal events responsible for this faunal mixture has not yet been fully established. This is clearly seen from the fact that the late Turolian was initially defined as a single MN mammal unit in MEIN's biochronological subdivision of the Neogene (MN 13; MEIN 1975). Later, AGUILAR (1981) subdivided this unit into three subunits, but recent work in the Teruel and Levant areas has shown that this phase was even more complex (MEIN et al. 1990; MEIN & AGUSTÍ 1990). However, a congruent picture emerges from intensive sampling carried out in these basins, especially in the case of those series in contact with marine beds of Messinian age. This is the case, for instance, of the Fortuna basin, whose results are contrasted in this paper with those of Teruel (MEIN et al. 1990) and Librilla (AGUSTÍ et al. 1990), as well as with isolated localities (Alcoy,

Almenara-M, Salobreña). The joint analysis of this information permits the recognition of a number of dispersal events of different zoogeographical origin, that allow for a subdivision of the upper part of the Turolian stage (Figs 1 & 2).
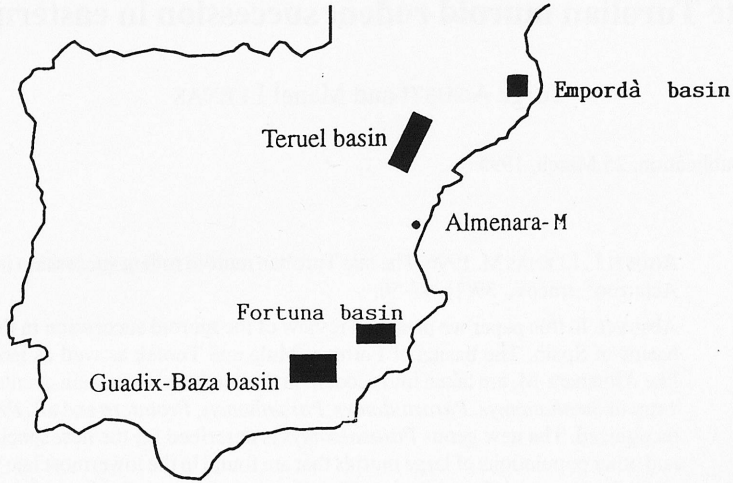
Fig. 1. Location of the main basins and localities mentioned in the text.

FAD	LAD	Fortuna (Agustí et al. 1985)	Librilla (Agustí et al. 1990)	Teruel (Mein et al. 1990)	Empordà	Other localities
	Calomyscus Myocricetodon					Almenara M
Calomyscus Myocricetodon Protatera						Salobreña
		La Hornera	Librilla 2A, 2C	Celadas 2	Romanyà	La Alberca
		Molina de Segura 7,8,9	Sifón 6,7	Arquillo 4		Venta del Moro
Paraethomys			Sifón 2B	Arquillo 1	Bàscara	
			Sifón 1	Villastar		
	Parasaidomys	Molina de Segura 1		La Gloria 6		
Apodemus Stephanomys Parasaidomys		Molina de Segura D				
	Huerzelerimys	Casa del Acero		Los Mansuetos	Camallera	

Fig. 2. Correlation of the late Turolian from several basins of Spain, based on rodents.

II. THE *STEPHANOMYS* EVENT

Stephanomys ramblensis, the first *Stephanomys* species in the Spanish basins, is the most characteristic late Turolian taxon in this area. The zoogeographic range of this species is limited to western Europe, the French locality of Lissieu being the northernmost site with this genus in the Late Miocene (MEIN 1988). The origin of *Stephanomys* seems to lie very close to *Occitanomys adroveri*, a species widely distributed in the middle Turolian of Spain. In fact, some morphotypes of this species could easily be seen as primitive *Stephanomys* specimens. However, the most primitive member of the genus, *Stephanomys stadii*, has been described in the French locality of Cucuron (MEIN & MICHAUX 1979) and up till now there is no record of this species in the rich faunal collections of the Iberian basins. At Cucuron, *S. stadii* coexists with *Occitanomys adroveri*. In the basins where the transition from the middle to the late Turolian is present, as in the case of Teruel and Fortuna, *Stephanomys* is abundantly represented in association with a small *Occitanomys* species. *Occitanomys alcalai*, in levels in which *Huerzelerimys turoliensis* is already extinct. In any case, the sudden widespread abundance of *Stephanomys* in the late Turolian is a very consistent event, even if its appearance is the result of evolution *in situ* and not the consequence of a dispersal process. However, if *Stephanomys* derives from the middle Turolian species *Occitanomys adroveri*, this transition appears to have been a very rapid one given the absence of intermediate populations and the coexistence of the two species at Cucuron.

III. THE *APODEMUS* EVENT

After *Stephanomys*, *Apodemus* is the most characteristic murid element of the late Turolian. What is more, it is also an element of correlation between western and eastern European localities. In the Teruel basin, the first *Stephanomys ramblensis* are still associated with *Parapodemus* cf. *barbarae*, but some *Apodemus* specimens are already present (MEIN et al. 1990). In the Librilla section, *Parapodemus* is already absent from the lowermost levels of the series and *Apodemus gudrunae* is the species accompanying *Stephanomys ramblensis* (AGUSTÍ et al. 1990). In the Fortuna basin, *Apodemus* is a very scarce element in the various levels of the Molina de Segura section (AGUSTÍ et al. 1985). In the Empordà basin, recent finds in the late Miocene of Romanyà indicate that the first "*Apodemus*"-like species to enter the basin was not *Apodemus gudrunae* but *Rhagapodemus* aff. *lissiensis*, as in the French localities of Castelnou 1 and Lissieu. From this confusing set of data, the following scheme is composed:

– *Apodemus gudrunae* is an eastern immigrant in the late Turolian of Western Europe, coexisting with the last *Parapodemus barbarae* populations in the Teruel basin.

– Independently, a separate "*Apodemus*-like wave", represented by the *Rhagapodemus* lineage, settles in the continental areas of western Europe, its southern limit being northern Spain (Romanyà d' Empordà).

– *Apodemus gudrunae* has an irregular distribution in the Iberian basins, its first appearance datum being different in each basin. This can be explained if we assume that *Apodemus gudrunae* was, like the present-day *Apodemus sylvaticus*, a forest dweller. Thus, its presence or absence in a basin would depend on local ecological conditions. This interpretation is backed up by the fact that in the Late Miocene beds *A. gudrunae* appears frequently in association with *Muscardinus*. On the other hand, *Stephanomys* probably was a much more opportunistic element, being widely present both in lacustrine and karstic localities.

IV. THE *PARASAIDOMYS* EVENT

At the base of the late Turolian series of the Teruel and Fortuna basins, *Stephanomys ramblensis* is associated with a murid of large dimensions displaying very broad central cusps (Figs 3 & 4). This large murid was initially assigned to *Valerimys* (AGUSTÍ et al. 1985) and later to *Karnimata* (AGUSTÍ et al. 1989; AGUSTÍ 1990; MEIN et al. 1990). From the shape of the upper molars, with broad t2, t5 and t8, this form seems clearly related to the "*Karnimata*" group. Therefore, the species *Karnimata inflata* was described by MEIN et al. (1990) in the locality of La Gloria-6. In the Fortuna basin a related form is present at the levels of Molina de Segura-D and Molina de Segura-1. However, at both localities this lineage is represented by more derived morphotypes in which the t6-t9 connection is realized. Since we are not sure that the form from Molina de Segura-1 is the direct descendant of *K. inflata* or the result of a new dispersal event, we prefer to assign the material from this locality to a separate species dedicated to Prof. K. KOWALSKI. Moreover, the assignment of both species to the genus *Karnimata* JACOBS seems doubtful. The type species of that genus, *K. darwini*, is in fact a junior synonym of *Progonomys woelferi* (MEIN et al. 1993). "*Karnimata*" *huxleyi* is morphologically closer to the Spanish samples, but some differences still exist. However, "*Karnimata*" *inflata* and "*K.*" *kowalskii* are morphologically close to some large murid species which have also been assigned to *Karnimata*: *K. intermedia* BRANDY and *K. afghanensis* BRANDY. Just as the Iberian forms, these species display enlarged central cusps in the upper molars, large t1 and t4, unreduced t12 and large M3. In fact, *Karnimata inflata* from Teruel could be a junior synonym of *K. intermedia* from the locality of Ghazgay (BRANDY 1981), although more material is necessary to confirm this conclusion. An alternative would be to include this set of species within the genus *Saidomys* JAMES & SLAUGHTER, 1974, which also shares some characteristics with them. However, once again the shape of the lower molars precludes this assignment. Therefore, we have decided to establish the new genus, *Parasaidomys*, for these species, whose relationships to the aforementioned genera are discussed below (the terminology used in the descriptions follows WEERD 1976).

V. SYSTEMATIC PALEONTOLOGY

Parasaidomys n. gen.

T y p e   s p e c i e s. *P. afghanensis* (BRANDY, 1979).

O t h e r   s p e c i e s   i n c l u d e d   i n   t h e   g e n u s. *P. inflatus* (MEIN et al. 1990), *P. kowalskii* n. sp., *P. intermedius* (BRANDY, 1979).

S t r a t i g r a p h i c   r a n g e. Late Turolian (Late Miocene) of Spain and Afghanistan; Early Pliocene of Afghanistan.

D i a g n o s i s. Large murid with enlarged central cusps (t2, t5, t8) in the upper molars. T1 and t4 larger than t3 and t6. Well developed t12. Large M3/ with distinct t9. First lower molar with well developed tma.

D i f f e r e n t i a l   d i a g n o s i s. *Parasaidomys* differs from some species included in the genus *Karnimata* JACOBS (*K. huxleyi* JACOBS) in its well developed t12 and less reduced upper M3. In the lower molars, it differs in its better developed tma and labial cingulum. Moreover, *Parasaidomys* is distinctively larger than species assigned to *Karnimata*. *Parasaidomys* differs from *Saidomys* in its larger t12 and better developed tma. *Parasaidomys* differs from *Parapelomys* in the absence of the characteristic arcuate cusps in the lower and upper molars and its well developed tma. *Parasaidomys* differs from *Huerzelerimys* in its broader t2, t5 and t8 and its large sized t1 and t4. It differs also in its better developed tma.

Fig. 3. 1 – Left upper M1, IPS-MS-O1-O1, of *Parasaidomys kowalskii* n. gen. n. sp., from Molina de Segura-1 (Fortuna basin, SE Spain). Holotype; 2 – Right lower M1, IPS-MS-01-04, of *Parasaidomys kowalskii* n. gen. n. sp. from Molina de Segura-1 (Fortuna basin, SE Spain). Scales – 1 mm.
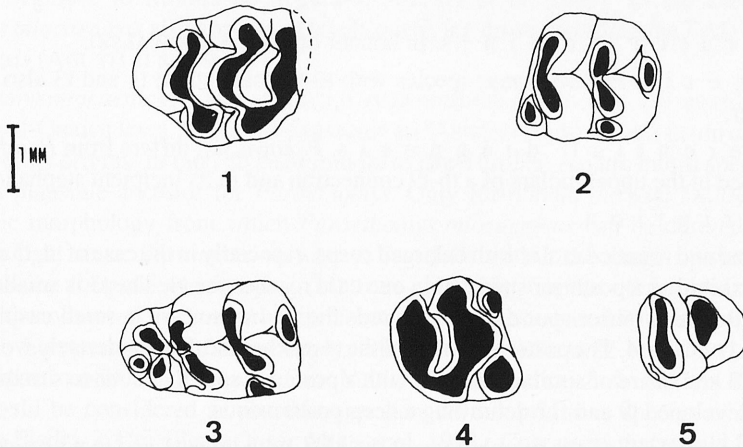

Fig. 4. *Parasaidomys kowalskii* n. gen., n. sp. from the Fortuna basin; 1 – left upper M1, IPS-MS-D-01, from Molina de Segura D; 2 – Left lower M2, IPS-MS-01-07, from Molina de Segura 1; 3 – Left lower M1, IPS-MS-01-05, from Molina de Segura-1; 4 – Right upper M2, IPS-MS-D-02, from Molina de Segura-D; 5 – Left lower M3, IPS-MS-D-05, from Molina de Segura-D.

Parasaidomys kowalskii n. sp.

S y n o n y m y: *Valerimys* aff. *turoliensis* AGUSTÍ et al. (1985)

Karnimata sp. AGUSTÍ (1989)

Karnimata sp. AGUSTÍ (1990)

H o l o t y p e. First upper molar, IPS-MS-01-01, deposited in the collection of the Institut de Paleontologia "M. Crusafont" (Sabadell). Fig. 3(1).

T y p e l o c a l i t y. Locality of Molina de Segura-1 (Fortuna basin, southeast Spain).

O t h e r   l o c a l i t i e s. Molina de Segura-D (Fortuna basin) (see Fig. 4).

M e a s u r e m e n t s: Molina de Segura-1

Measurements Tooth	Length			Width			N
	min	x	max	min	x	max	
M1/	2.57	2.74	2.92	1.78	1.94	2.11	2
M2/		1.79			1.96		1
M/1	2.68	2.71	2.74	1.72	1.76	1.79	2/3
M/2		2.14			1.90		1
M1/		2.93		1.89	1.93	1.97	1/2
M2/	1.78	1.82	1.86		1.95		2/1
M/1		–			1.76		1
M/3		1.65			1.49		

D e r i v a t i o   n o m i n i s. In honour of Prof. K. Kowalski.

D i a g n o s i s. *Parasaidomys* species with t6-t9 connection; t1 and t3 also bear a small posterior spur.

D i f f e r e n t i a l   d i a g n o s i s. *P. kowalskii* differs from *P. inflatus* (Mein) in the presence in the upper molars of a t6-t9 connection and in its incipient stephanodonty.

D e s c r i p t i o n.

M1/: Broad and rounded molar with enlarged cusps, especially in the case of t2, t5 and t8. Large, rounded t1 exhibiting a posterior spur that in one case reaches the t4. The t3 is smaller than the t1 and also exhibits a posterior spur directed towards the t6. In one case, a small cuspule is present between the t1 and the t4. The posterior corner of the t4 reaches the t8 in moderately worn specimens (Fig. 3: 1). T3 and t6 are of similar sizes. T6 with a posterior spur that connects to the t9 at a high level. Well developed t9 and t12 delimiting a deep posterosinus.

M2/: This tooth follows the morphology of the M1/, with large t1 and t6 with a posterior spur. As a difference from the M1, this posterior spur only reaches the t9 in highly worn specimens.

M/1: Symmetric anteroconid, in which the labial and lingual lobes are isolated. Well developed tma, almost reaching the size of the anteroconid lobes. The posterior wall of the labial lobe of the anteroconid is directed backwards. Besides a moderate c1, two labial cuspules are also present close to the labial wall of the protoconid. The posterior heel is elongated and separated from the hypoconid and the entoconid.

M/2: A prominent anterolophid is present, isolated from the protoconid. The only cingulum cusp is the c1, its size being smaller than that of the anterolophid. A very tiny cingular formation descends from the anterolophid towards the c1. Oval posterior heel, isolated from the hypoconid and the entoconid.

M/3: Broad transverse cusps. A small anterolophid is present.

D i s c u s s i o n. *Parasaidomys kowalskii* is probably a descendant *in situ* of *P. inflatus* that developed t6- t9 connections. In its turn, *P. inflatus* seems very close to *P. intermedius* from Ghazgay (Afghanistan) and is certainly an immigrant in the late Turolian of the Spanish basins of

Teruel and Fortuna. This event must have been of very short duration, since it is not recorded in other continuous series, such as Librilla.

V. THE *PARAETHOMYS* EVENT

Paraethomys was first considered to be a taxon with African affinities because of the association between *Paraethomys anomalus* (BRUIJN, DAWSON & MEIN) and gerbils in the Mio-Pliocene transitional beds of eastern Spain (Alcoy and Caravaca; DE BRUIJN 1974). This African character was later questioned by JAEGER et al. (1975), who recognized a more primitive species, *Paraethomys miocaenicus*, in the localities of Khendek-el-Ouach and Librilla. These authors advocated an Asiatic origin for *Paraethomys miocaenicus*, a species which would have simultaneously colonized both shores of the Mediterranean during the late Turolian. In fact, given that both Librilla and Khendek-el-Ouaich can be correlated with the Messinian, an obvious scenario would result from a single eastern immigration across the Mediterranean basin during the Messinian salinity crisis, as suggested by MOYÀ-SOLÀ et al. (1984) for other late Turolian mammals. Despite this, the phylogenetic relationships of *Paraethomys miocaenicus* remain an unsolved question. In the Iberian basins, *Paraethomys* appears to be an immigrant in the upper part of the late Turolian. In the Fortuna basin, *P. miocaenicus* is found in levels overlying those with *Parasaidomys kowalskii* (Molina de Segura-2 to Molina de Segura-9; AGUSTÍ et al. 1985). In the Librilla section, *Paraethomys miocaenicus* also appears in levels overlying those recording the FAD of *Stephanomys ramblensis* (AGUSTÍ et al. 1990).

Paraethomys miocaenicus is also an immigrant in northern Africa, since no record exists before the Khendek-el-Ouaich level. However, to assume an "Asiatic origin" for this taxon does not solve the problem of its origins. In fact, no clear middle to late Turolian Asiatic murid species could be considered a plausible ancestor for *Paraethomys*. Only *Karnimata darwini* JACOBS displays a plesiomorphic morphology from which *Paraethomys miocaenicus* can be derived. This is not surprising though, since *Karnimata darwini* in fact falls within the range of variation of the European species *Progonomys woelferi* (MEIN et al. 1993). On the other hand, some of the synapomorphies observed in *Paraethomys miocaenicus* are also shared by some primitive populations of the European genus *Huerzelerimys* MEIN, MARTIN-SUAREZ & AGUSTÍ. Thus, some samples assigned to *Huerzelerimys minor* MEIN, MARTIN-SUAREZ & AGUSTÍ and *H. vireti* (SCHAUB) could be considered as possible ancestors of this primitive species of *Paraethomys* (Cortijo de la Piedra-2, Crevillente-2, see MEIN et al. 1993). Characters that would favour such a relationship are the presence of a voluminous t1, the absence of a clear t4-t8 connection (or its presence at the base of the tooth, in contrast with other populations of *Huerzelerimys*) and the shape of the upper M3. In turn, *P. miocaenicus* from the type locality retains primitive characteristics such as the persistence of a small tma and the lingual connection between the anteroconid and the metaconid. However, *H. vireti* has a distribution restricted to western Europe, while the range of *H. minor* is even smaller. On the other hand, *Progonomys woelferi*, the supposed direct ancestor of both species, displays a very large range, from Spain (Torrent de Febulines, Vallès-Penedès basin) to the the Siwaliks (*Karnimata darwini* in JACOBS 1978).

VI. THE *PSEUDOCRICETUS* EVENT

Associated with *Stephanomys ramblensis* and *Paraethomys miocaenicus*, the most common cricetid in the late Turolian beds of eastern Spain is a medium sized species commonly referred to as *Pseudocricetus kormosi* (type locality: Polgardi, Hungary). Although there remain some doubts

about the specific identity of the Spanish and Central European populations, the presence of this species in the Iberian peninsula is clearly the result of a dispersal event rather than a case of evolution *in situ*. Thus, in the Fortuna basin, the level of Casa del Acero is characterized by the presence of a small *Kowalskia* species (*K. adroveri*), with reduced M3, which cannot be the ancestor of the *P. kormosi* samples that appear at the level of Molina de Segura-9 (Agustí et al. 1985). In this basin, the FAD of the latter species is placed between the LAD of *Parasaidomys kowalskii* and the FAD of *Paraethomys miocaenicus*. However, in the Librilla section (Mula basin), *Pseudocricetus* cf. *kormosi* is found at the levels of Librilla 2A and 2C, above the levels of Sifón-6 and -7 in which *P. miocaenicus* is already present (Agustí et al. 1990). In the Teruel basin, the sequence is quite similar to that of Fortuna, *P. kormosi* being already present in the lower beds with *Stephanomys ramblensis* and *P. miocaenicus* missing. These apparently contradictory data in areas that are very close to each other geographically suggest a strong ecological component controlling the presence or absence of this species, as proposed for *Apodemus gudrunae*.

VII. THE *PROTATERA* EVENT(S)

A number of late Turolian-early Ruscinian sites are characterized by medium sized gerbils close to the genus *Protatera* Jaeger: Almenara-M (=Casablanca-M), Alcoy (Brandy 1979 and unpublished data), Botardo and Gorafe 1 and 4 (Guadix-Baza basin; Agustí 1986). The species from Almenara-M displays peculiar characteristics with respect to the others and was described as a new species, *P. almenarensis* (Agustí 1990). The upper molars of this species are similar to those of the late Miocene *Protatera algeriensis* Jaeger from Amama-2, but the upper M3 is much more reduced. In this respect, *Protatera almenarensis* seems closer to *Protatera kabulense* Sen from the late Miocene site of Pul-e Charké (Afghanistan), although the lower molars are very different from those of the previously described species, with a broad anteroconid and an enlarged anterolophid that almost attains the size of the anteroconid. A very tiny longitudinal spur can be recognized at the base of the sinusids. This character is more developed in the lower M2. Because of their broad anteroconid, the lower molars of *Protatera almenarensis* display a superficial resemblance to the extant *Tatera indica*. On the other hand, an ancestor-descendant relationship between *P. algeriensis* and *P. almenarensis* seems rather probable. The transition from one population to the other could have occurred through a reduction of M3 and the development of an enlarged anterolophid in the lower M1.

Curiously, the large gerbil species found in early Ruscinian localities such as Alcoy, Gorafe or Caravaca, referred either to *Protatera* or *Gerbillus*, presents a morphology which is very different from that of *Protatera almenarensis*: oval anteroconid with small anterolophulid in the lower M1 and tendency to develop a longitudinal spur. However, the two species seem closely related, sharing a direct common ancestor (probably *P. algeriensis*). From the presence of these gerbils in the late Turolian-early Ruscinian Pliocene of Spain arises the question of their origin. As we have seen, the early Ruscinian populations from Alcoy, Caravaca or Gorafe-1 cannot be derived from *Protatera almenarensis* from Almenara-M, because of its oval anteroconid and longitudinal spur. Thus, the presence of these two gerbil species indicates the existence of at least two different phases of settlement at the Mio-Pliocene boundary. In the first phase, *Protatera almenarensis* is accompanied by several elements with Afro-Asiatic affinities: *Myocricetodon* cf. *parvus*, *Pseudomeriones abbreviatus*, *Calomyscus* sp., *Blancomys* sp. and others (Almenara-M). The presence of this assemblage in localities such as Almenara-M and Salobreña has been explained on the basis of the existence of a steppic Afro-Asiatic belt extending from Afghanistan to northern Africa (Agustí 1989). The climatic shifts during the Messinian and the subsequent dessiccation of the Mediterranean probably allowed this fauna to move towards higher latitudes, and thus to enter the Iberian peninsula.

VIII. CONCLUSIONS

According to the data presented above, the late Turolian rodent succession in eastern Spain appears punctuated by five main events: expansion of *Stephanomys*, dispersal of *Parasaidomys*, dispersal of *Paraethomys*, dispersal of *Protatera* and dispersal of aff. *Protatera* sp. (the latter in the very early Ruscinian). The first appearance of taxa such as *Apodemus*, *Rhagapodemus* and *Pseudocricetus* is subject to some discrepancies in the investigated basins. According to the evidence from the Teruel basin, the entry of *Apodemus* could be associated with the *Parasaidomys* dispersal event. With regard to *Rhagapodemus lissiensis*, dispersal seems also associated with very primitive populations of *Stephanomys ramblensis*, but correlation with some of the cited events in southeast Spain is difficult. With respect to *Pseudocricetus kormosi*, the main evidence from the Teruel, Fortuna and Mula basins suggests an entry datum close to the *Paraethomys* event. However, in the lower part of the Molina de Segura section, the level of Romeral-2D, which is without *Paraethomys*, yielded some teeth of a large cricetine.

From a zoogeographical perspective, we can classify the above mentioned faunal elements into the following categories: autochtonous, Central European, Central Asiatic and African. Clearly authoctonous is *Stephanomys*, which is derived from advanced populations of *Occitanomys adroveri* somewhere in western Europe. Evidence of a Central-European influence is supported by the dispersals of *Rhagapodemus*, *Pseudocricetus*, *Apodemus* and, perhaps, *Paraethomys*. Except for the last genus, all these forms indicate wetter, forested conditions, since they are commonly associated with *Muscardinus*, *Glirulus* or even flying squirrels. In fact, they probably belong to a northern Palearctic forested realm of which the Central European region represents the eastern margin.

As discussed in previous papers, no real evidence of typical African elements exists in the Spanish basins. All the genera previously cited as such are in fact faunal elements common to northern Africa and Central Asia (*Protatera*, *Myocricetodon*), thus delimiting an Afro-Asiatic steppic belt (AGUSTÍ 1989). In fact, the presence *Pseudomeriones* and *Calomyscus* in Almenara-M strongly supports the idea of a direct Central and even eastern Asian influence. Therefore, during the Messinian, entry of Asian elements is detected in at least two different phases: the first, at the very beginning of the late Turolian, with *Parasaidomys*, the second at the end of the Turolian with the entry of *Pseudomeriones*, *Calomyscus*, *Protatera*, *Myocricetodon* and others.

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