

Progonomys Schaub, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in Western Europe

P. Mein, E. Martín Suárez & J. Agustí

Mein, P., E. Martín Suárez & J. Agustí. *Progonomys* Schaub, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in Western Europe. — Scripta Geol., 103: 41-64, 6 figs., 1 pl., Leiden, April 1993.

In this paper the various species and populations attributed to the genus *Progonomys* Schaub, 1938 are revised.

Valerymys Michaux, 1969 is considered to be synonymous with *Occitanomys* Michaux, 1969, since the type-species *V. ellenbergeri* (Thaler, 1966) was included in *Occitanomys* by Aguilar et al. (1986a). Other species from Western Europe that had been included in *Valerymys* cannot be transferred to *Occitanomys*. They are the descendants of *Progonomys cathalai*, for which we create the new genus *Huerzelerimys*, that includes the known species *H. vireti* (Schaub, 1938), *H. turoliensis* (Michaux, 1969) and *H. oreopitheci* (Engesser, 1989), and the new species *H. minor*.

Key words: Rodentia, evolution, Neogene, Western Europe.

En este trabajo se aborda una revisión de las distintas poblaciones y especies atribuidas al género *Progonomys* Schaub, 1938.

Valerymys Michaux, 1969 es sinónimo de *Occitanomys* Michaux, 1969, ya que la especie tipo *V. ellenbergeri* (Thaler, 1966) ha sido incluida en *Occitanomys* por Aguilar et al. (1986a). Otras especies de Europa Occidental, que habían sido incluidas en *Valerymys*, no pueden ser consideradas *Occitanomys*. Se trata de descendientes de *Progonomys cathalai* que incluimos en el nuevo género *Huerzelerimys*, al que pertenecen: *H. vireti* (Schaub, 1938), *H. turoliensis* (Michaux, 1969) y *H. oreopitheci* (Engesser, 1989), además de *H. minor* sp. nov.

Palabras clave: Rodentia, evolución, Neógeno, Europa Occidental.

P. Mein, Centre des Sciences de la Terre, Université Claude Bernard, 27-43 Bd. 11 Novembre, F-69622 Villeurbanne Cédex, France; E. Martín Suárez, Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain; J. Agustí, Instituto de Paleontología 'Miquel Crusafont', Escola Industrial 23, E-08201 Sabadell, Spain.

Introduction	42
Genus <i>Progonomys</i> Schaub, 1938	43
Genus <i>Huerzelerimys</i> gen. nov.	49
Conclusions	61
References	62

Introduction

In the past decades the fossil record of murids in Europe has increased considerably. Basically this has been a quantitative increase: more localities, more populations, more species. On the other hand there has hardly been an increase of qualitative knowledge: the newly discovered populations were put into known species, or new species were created, but no fundamental progress was achieved in the fields of supraspecific taxons and their phylogenetic relationships. The generally adopted classification of the family Muridae (like in other rodents) is a 'horizontal' one, specially in the case of *Progonomys*: almost all Vallesian Muridae have been allocated to this genus. Nevertheless, already in the Early Vallesian (zone MN9) various lineages of Muridae may be distinguished; e.g. in the locality Jalalpur in Pakistan (Cheema et al., 1983) an association of two murid species is found, none of which – in our opinion – is related with *Progonomys*. In Can Llobateras too, a murid is found that is not related with *Progonomys*, although it was classified as *P. cathalal* (Hartenberger & Thaler, 1963; Michaux, 1971), because that was the only 'available' species. Also in the locality Buzhor in Moldavia (Lungu, 1981, and new, unpublished data) two lineages of Muridae are found, related to *Parapodemus* and *Mus* respectively, and certainly not related with *Progonomys*. In the material from the locality Sinap Tepe 1 in Anatolia (Sen, 1990) we have recognized two lineages of Muridae, related with *Parapodemus* and *Progonomys* sensu stricto, respectively. In the Late Vallesian '*Progonomys hispanicus*' is known from many localities (Michaux, 1969), and in some of these it coexists with *P. cathalal* (van de Weerd, 1976). Yet another example is the coexistence of '*Progonomys clauzoni*', *Progonomys woelferi* and *Parapodemus* sp. (Aguilar et al., 1986b). The largest diversity of Muridae recorded in the Late Vallesian is found in the locality Dionay (Mein, 1984).

So, *Progonomys* in its current concept, is clearly a paraphyletic genus, since it houses species that have been brought together on the mere basis of sharing plesiomorphic characters, like the absence of a connection between t6 and t9 in M¹ and M². If one accepts that all Muridae are derived from a common ancestor like an archaic form of *Antemus*, the separation of t6 and t9 is a symplesiomorphy of all archaic Muridae. But this character should not be the only one used in the classification. First of all, because this leads to a subdivision in clearly paraphyletic taxons. And, secondly, because a large variety of Muridae from SE Asia, and the majority of African Muridae have conserved the separation t6-t9 even in the present.

In our opinion the species that have been included in *Progonomys* do not form

a homogeneous group. In the first part of this paper we will present a revision of this genus and propose a new classification for those species that formerly had been included in *Progonomys*.

The second part of this paper is dedicated to the descendants of *Progonomys cathalal* in W. Europe among which, in our opinion, are various species, that had been grouped in the genus *Valerymys*.

Aguilar et al. (1986a) described the new species *Occitanomys montheleni* from the locality Mont-Hélène; its differential diagnosis (op. cit., p. 133) says: 'espèce plus petite que l'*Occitanomys ellenbergeri* de Sète...' This means, that the type-species of the genus *Valerymys*, *V. ellenbergeri*, was transferred to the genus *Occitanomys*. We agree with that classification, and *Occitanomys* and *Valerymys* fall into synonymy (both genera were defined by the same author in the same paper, see Michaux, 1969). In agreement with art. 24 (Principle of the first reviser) of the International Code of Zoological Nomenclature (Ride et al., 1985) we propose to maintain the name *Occitanomys* Michaux, 1969, and consider *Anthracomys ellenbergeri* Thaler, 1966 as a valid species within this genus.

However, several other species, that had been included in *Valerymys*, cannot be considered to belong to *Occitanomys*: *V. vireti* (Schaub, 1938), *V. tuoliensis* Michaux, 1969, and *V. oreopithec*i Engesser, 1989. For these species, and for others that were not included in *Valerymys*, we propose the new generic name *Huerzelerimys*.

Acknowledgements

We wish to express our thanks to all those who allowed us to carry out direct comparisons with their collections, original specimens or casts, even unpublished material: Drs R. Ameur, H. de Bruijn, G. Daxner-Höck, L. Jacobs, A. N. Lungu, A. Ruiz Bustos, S. Sen, and G. Storch.

We thank Dr M. Freudenthal for his computer programs, his scientific suggestions, his aid in the interpretation of the ICZN, and for translating the text into English.

The photographs were taken on the Zeiss 950 Digital Scan Microscope of the University of Granada. The drawings were made by Isabel García.

This study was carried out within the framework of Project PB90/0575 of the DGICYT; the travel expenses were covered by the 'acciones integradas hispano-francesas' for 1992 and 1993.

Genus *Progonomys* Schaub, 1938

Type-species — *Progonomys cathalal* Schaub, 1938.

Original diagnosis — No diagnosis was given in the original publication.

Remarks — The genus *Progonomys* was created by Schaub (1938) on the basis of a species of small size, in the molars of which there is no connection between t6 and t9, and there is no tma. The author does not give a diagnosis of the genus, but compares

with other Muridae (*Parapodemus*, *Apodemus* and *Micromys*).

Diagnosis — Muridae with lengthened and slender molars, without longitudinal connections between the tubercles, and slightly larger than those of the extant *Mus musculus*. M^1 with an almost elliptical outline, with the t1 in an anterior position (not placed backwards) and without t1bis. t4 united to t5 by a high connection, and with a tendency to fuse with t8 by a low crest, that never forms a t7. Upper molars with t6 and t9 generally separated. M_1 with a reduced or absent tma; the anteroconid-metaconid connection is generally absent, except in very much worn specimens. Upper molars with one single lingual root. M_1 with two main roots and a small central one.

Distribution — Vallesian and earliest Turolian of Europe, South Asia and maybe North Africa.

Attributed species

Progonomys cathalai Schaub, 1938

Progonomys woelferi Bachmayer & Wilson, 1970

Progonomys sp. from Sinap Tepe 1 (Sen, 1990)

Progonomys cathalai Schaub, 1938

Fig. 1a-f.

Original reference — *Progonomys cathalai* Schaub, 1938, p. 19-21.

Holotype — An isolated M^1 dext., Montredon 584, deposited in the 'Naturhistorisches

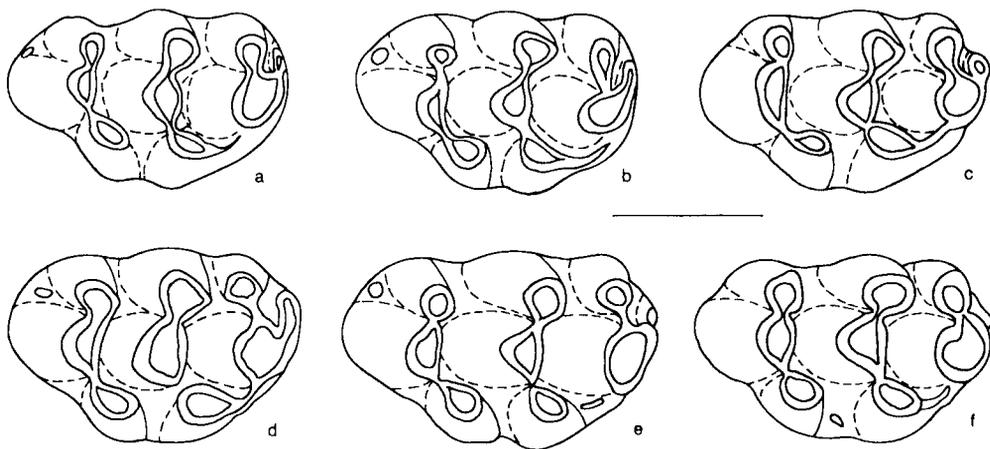


Fig. 1. *Progonomys cathalai* from various localities. a: Biodrak; b: Bayraktepe II; c: Montredon (type-locality); d: Masía del Barbo 2B; e: Soblay; f: Ambérieu 1. Drawings based on original material or casts kept in Lyon. Scale represents 1 mm.

Museum', Basel (Schaub, 1938, pl. 1, fig. 8).

Type locality — Montredon, niveau Depéret (Hérault, France).

Selected references

Progonomys cathalai from Ravin de la Pluie (de Bonis & Melentis, 1975).

P. cathalai from Masía del Barbo B, Peralejos 4 and Peralejos A (van de Weerd, 1976).

P. cathalai from Biodrak (de Bruijn, 1976).

P. cathalai from Freiria do Rio Mayor (Antunes & Mein, 1979).

P. cf. cathalai from Bayraktepe II (Ünay, 1981).

P. cathalai from Soblay and Ambérieu 1 (Farjanel & Mein, 1984).

N.B.: In the locality of Farafra in Egypt (Heissig, 1982) a faunal association typical of the latest Aragonian has been found, in combination with a murid, that has been classified as *Progonomys cathalai*; this is the next oldest record of Muridae after *Antemus* Jacobs, 1978. A decision on the taxonomical position of this species requires a revision of the material, which we have not yet been able to do.

The following populations are excluded from this species:

Can Llobateres 1 (Michaux, 1971) and Can Llobateres 2 (new collections). This is a murid of larger size than *Progonomys cathalai* from its type-locality. In the M¹ the labial tubercles are very voluminous, and t4 and t8 are separated by a valley (Fig. 2). In our opinion this population represents a different lineage, that we will study when more material becomes available.

Buzhor 1 (Lungu, 1981). As we have said in the introduction, this locality contains two lineages of Muridae (Fig. 2), not related with *Progonomys*, but with *Mus* and *Parapodemus* (reason why the latter cannot be a descendant of *Progonomys cathalai* in

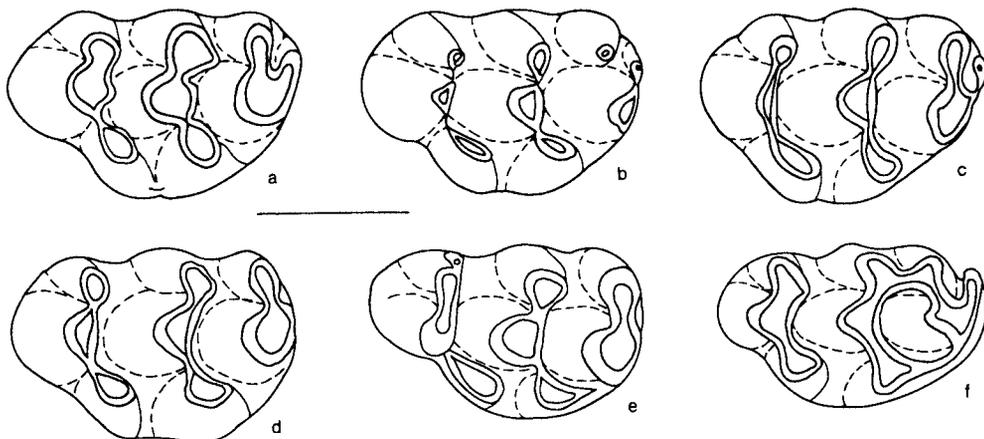


Fig. 2. Specimens from populations that have been excluded from *Progonomys cathalai*. a: Can Llobateres; b: Bou Hanifia; c: Sidi Salem; d: Kastellios Hill KA3; e & f: Buzhor. Scale represents 1 mm.

W. Europe, but must be an immigrant in our region during the latest Vallesian).

'*Progonomys cathalai*' from Kastellios KA-3 (de Bruijn et al., 1971; de Bruijn & Zachariasse, 1981) is excluded because of the absence of a connection between t4 and t8; the absence of t12 in the upper molars (Fig. 2); the great development of the labial cingulums, and the absence of a third root in the M₁.

Ubeidiya (Haas, 1966). Under the name of *Progonomys* digested teeth of *Apodemus sylvaticus* were described, that show the alteration, typical of rests that have passed through the digestive tract of predators.

'*Progonomys cathalai*' from Oued Zra (Jaeger, 1977) and Bou Hanifia (Ameur-Chehbeur, 1988). In our opinion this is not *P. cathalai*, because of the tendency towards an isolated t9 in M¹; the weak connection t4-t8 (Fig. 2); the great development of the cingular margin of the lower molars, with very voluminous c1 and c2 in M₁. On the other hand, it cannot be the ancestor of *P. chougrani* Ameur-Chehbeur, 1988 (= *P. mauretanicus* Coiffait-Martin, 1991), since the latter has a much more reduced cingular margin, without c2, the t9 of M¹ much more backwards, and it misses the small accessory root of the M₁, that is present in some M¹ from Bou Hanifia (Ameur-Chehbeur, 1988); this means, that *P. chougrani* (= *P. mauretanicus*) has more primitive characters than the species from Oued Zra.

Progonomys woelferi Bachmayer & Wilson, 1970
Fig. 3a-d.

Original reference — *Progonomys woelferi* Bachmayer & Wilson, 1970, pp. 576-578.

Holotype — Maxillary fragment with M¹-M², No. 1970/1395, coll. Natural History Museum, Vienna, Div. Geol. Pal.

Type locality — Kohfidisch, southern Burgenland (Austria).

Selected references

Karnimata darwini Jacobs, 1978.

Progonomys aff. *cathalai* Torrent de Febulines, Trinxera Sur Autopista II, Trinxera Nord Autopista II, Can Perellada (Agustí, 1981; Agustí & Gibert, 1982).

Parapodemus sp. in Jacobs (1978, pp. 46-49).

Progonomys woelferi from Kastellios Hill in de Bruijn et al. (1971), de Bruijn & Zachariasse (1981).

P. woelferi from Lo Fournas 6 in Aguilar et al. (1986b).

P. woelferi from Kohfidisch in Bachmayer & Wilson (1980).

Discussion — In our opinion *Progonomys darwini* is a junior synonym of *P. woelferi*. The upper molars are identical (Fig. 3); in the lower molars of the population from 182A the tma is more frequent and the labial cingulums are somewhat more reduced than in the type-population from Kohfidisch.

Progonomys sp. from Kastellios Hill is somewhat larger than the rest of the

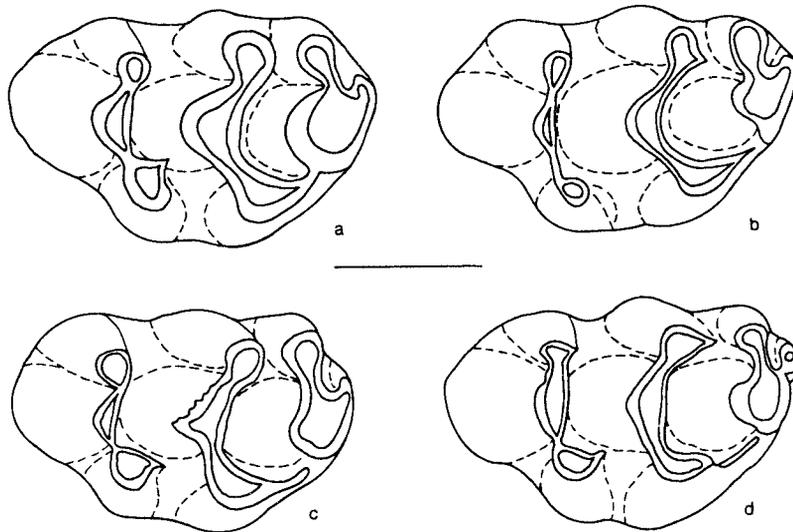


Fig. 3. *Progonomys woelferi* from various localities. a: Kastellios Hill; b: Kohfidisch; c: Torrent de Febulines; d: YGSP 182A. Scale represents 1 mm.

populations attributed to this species. Its morphology too is somewhat more advanced with regards to the development of the posterior crests of t1 and t3 in the M^1 (Fig. 3). The age of this locality is still under study (van der Meulen, pers. comm.): it appears, however, to be more recent than 8.5 Ma BP (S. Sen, pers. comm.); this means that it should be dated as somewhat earlier than the Vallesian-Turolian limit, and not in the Early Vallesian as supposed before.

Progonomys sp.

Locality — Sinap Tepe 1, Anatolia (Sen, 1990).

Discussion — This locality has yielded a fossil association with two Muridae (unpublished; we have had the opportunity, to study the casts that Dr S. Sen has put at our disposal). In our opinion one of them is a *Progonomys* sensu stricto. In its M_1 the two anterior pairs of tubercles are separated; the relative position of the hypoconid, entoconid and posterior heel leaves room for a very wide posterosinusid. In the upper molars t4 and t8 are connected by a low crest, t6 and t9 are separated. There are no longitudinal connections.

Morphologically this population agrees with our definition of *Progonomys*, but the dental elements are very small.

We believe, that it represents a new species, the oldest one known for this genus. Probably the *Progonomys* from Biodrak is more closely related to this new species than to *P. cathalai*.

Species excluded from this genus

'*Progonomys*' *hispanicus* Michaux, 1971. This is a small-sized murid, with the t1 of M¹ placed very much backwards. It probably is the ancestor of *Occitanomys sondaari*. In fact there are populations in which a generic attribution is difficult, like in the one from Puente Minero (Alcalá et al., 1991), in which the determination is based on frequencies of character states. We transfer this species to the genus *Occitanomys*.

'*Progonomys*' cf. *hispanicus* from Castelnou 1B (Aguilar et al., 1991) is a 'modern' murid, similar to the first *Occitanomys*, but its age coincides with that of *Antemus*. It would be interesting to collect more material, in order to carry out a more complete study.

'*Progonomys*' *clauzoni* Aguilar et al., 1986b. This is a Muridae of very large size, specially the width of the molars is great. The t1 is placed very much backwards, and there are no traces of the formation of a connecting crest between t4 and t8. It should be transferred to the genus *Occitanomys*, or it may be yet another lineage, in which case it should be given a new generic name.

'*Progonomys*' *debruijini* Jacobs, 1978. This is a very small Muridae. In M¹ the t1 and t4 are placed very much backwards, just like in *Mus* and *Proceromys*. The oldest record of this lineage is from the locality of Buzhor 1 (Lungu, 1981), where it was classified as *P. cathalai*.

'*Progonomys*' *yunannensis* Qiu & Storch, 1990 cannot be considered to be *Progonomys* sensu stricto because of the position in chevron of the cusps of the lower molars, the strong longitudinal crest; the development of a t7, and because of the very narrow and high central cusps of the upper molars, that show a markedly V-shaped wear surface (a situation, that we have never observed in European Muridae). This morphology is a combination of characters of *Apodemus* and *Occitanomys* both in the lower and in the upper molars. It represents a group, that is independent of *Progonomys*, and we are inclined to think, that it must be very close to *Yunomys*, even though both are found in the same locality. It may be related with some extant Asiatic genus (see Misonne, 1969).

'*Progonomys*' sp. from Jalalpur (Cheema et al., 1983) is a Muridae of relatively large size; M¹ has the t1 and t4 placed backwards. It probably is more related with the group '*Mus*' than with *Progonomys*.

'*Karnimata darwini*' is, in our opinion, a junior synonym of *Progonomys woelferi*. This means, that the type-species of the genus *Karnimata* is moved to *Progonomys* and that, automatically, the rest of the species attributed to this genus should be placed in *Progonomys* too, or in some other genus. In fact, only *Karnimata* sp. (Jacobs, 1978, p. 61) can be transferred to *Progonomys* on the basis of the morphology of the crown, and because of the number of roots. We consider *Karnimata huxleyi* Jacobs, 1978 not to be related with *Progonomys*, nor are *K. minima* Brandy, 1979; *K. intermedia* Brandy, 1979; *K. hipparionum* (Schlosser, 1924); and *K. inflata* Mein, Moissenet & Adrover, 1990. All these species attributed to *Karnimata* are not even a homogeneous group. Taxonomic decisions in this matter will have to wait for a complete revision of the available material.

Consequently the following species are provisionally labeled as Muridae incertae

sedis: *Karnimata huxleyi* Jacobs, 1978; *K. minima* Brandy, 1979; *K. intermedia* Brandy, 1979; *Mus hipparionum* Schlosser, 1924; and *K. inflata* Mein, Moissenet & Adrover, 1990.

Discussion on the genus Progonomys

The oldest record of *Progonomys* is from the locality of Sinap Tepe 1 of Early Vallesian age (unit MN9 of Mein, 1990; de Bruijn et al., 1992). The next younger localities are Biodrak (Crete; de Bruijn, 1976), Bayraktepe II (Anatolia; Ünay, 1981) and Ravin de la Pluie (Macedonia; de Bonis & Melentis, 1975). All these localities are of earliest Late Vallesian age (unit MN10). In W. Europe the first record known, from the Late Vallesian (unit MN10), is that of Montredon (Schaub, 1938; Michaux, 1971; Aguilar, 1982); this is a locality in which the Cricetidae are still dominant. Subsequently, *Progonomys cathalai* is present in Masía del Barbo (van de Weerd, 1976), the oldest locality where Muridae are numerically dominant, a situation maintained throughout the rest of the Vallesian and the Turolian.

Progonomys cathalai shows size increase in the course of time (Fig. 4) and evolves towards *Progonomys woelferi*, which has a wide geographical distribution throughout the south of the Palaearctic Region: it has been found in various localities of the Vallès-Penedès Basins, like Torrent de Febulines (Fig. 3) and Trinxera Nord Autopista (Agustí, 1981); in France, Lo Fournas 6 (Aguilar et al., 1986b); in Central Europe, in its type-locality; in Pakistan, loc. YGSP 182A (Jacobs, 1978); and in Kastellios Hill (Crete, de Bruijn et al., 1971; de Bruijn & Zachariasse, 1981).

The last records known for this species are from Kastellios Hill (KA-1) in Crete, and YGSP loc. 182A in Pakistan. This means, that *Progonomys woelferi* existed during the entire Late Vallesian in Europe, and until the Early Turolian in SW Asia. The lineage *P. cathalai* - *P. woelferi* shows a considerable size increase, in combination with a great morphological stability. Sure enough, it is not easy to establish a clear separation between these two species, except on the basis of size.

Genus *Huerzelerimys* gen. nov.

Type species — *Parapodemus vireti* Schaub, 1938.

Derivatio nominis — The genus is dedicated to Dr J. Hürzeler (Basel), who discovered the locality of Mollon, where the type-species was found.

Diagnosis — Molars smaller than or similar in size to those of extant *Rattus rattus*, and with a poor development of the longitudinal connections between tubercles. Upper molars without t7, but with t4 and t8 connected by a weak crest. M¹ and M² with a well-developed t9, and with t6 and t9 united in more than 50% of the specimens. M³ without t9. M₁ with a reduced tma, and with a connection between the two anterior pairs of tubercles; three roots; cingular margin moderately developed. Tendency towards a strong size increase in the course of time.

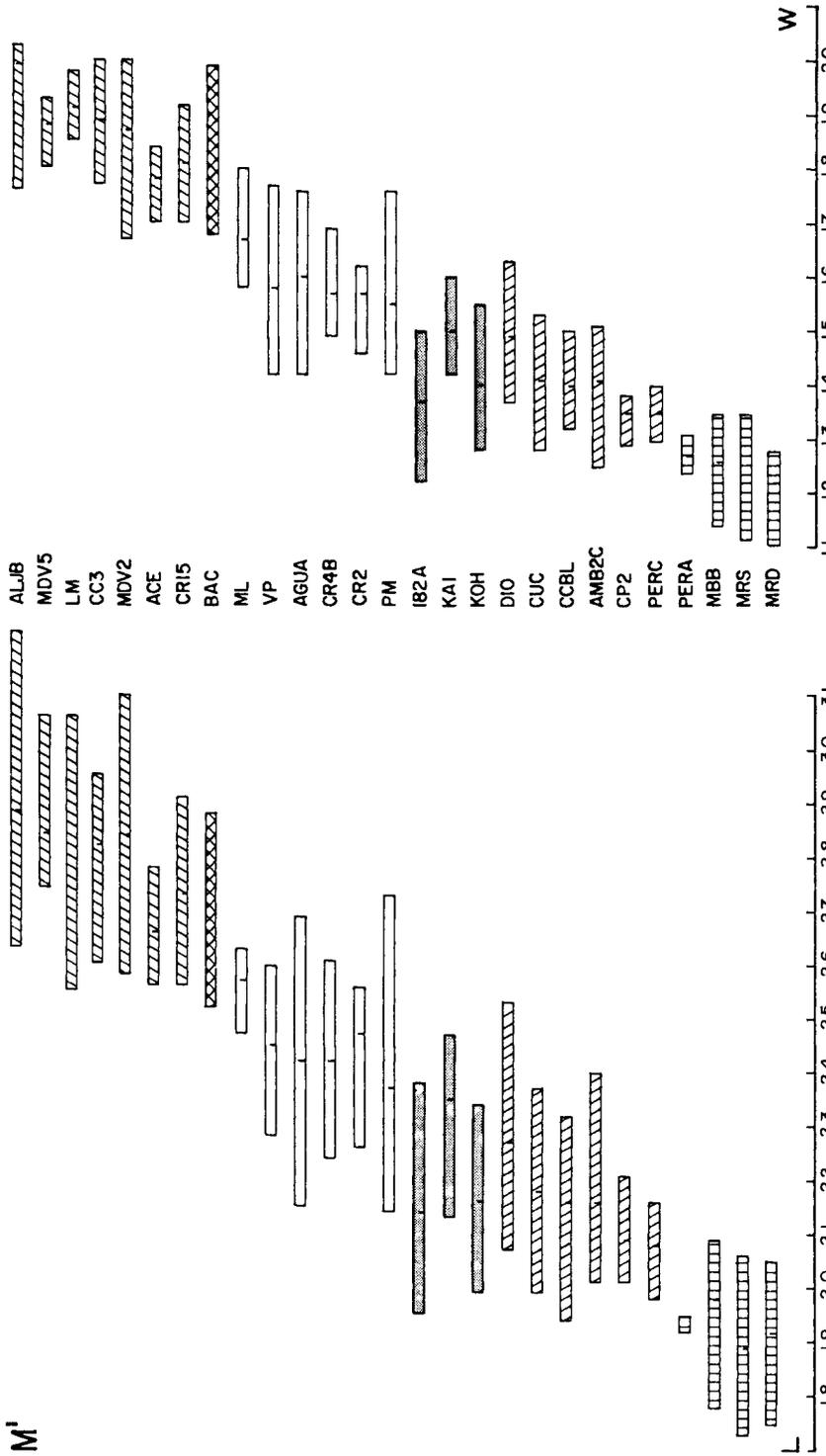


Fig. 4. Size ranges of the M1 of various populations of *P. cathalai*, *P. woelfferi*, *H. minor*, *H. vireti* and *H. turrolensis*. ACE = Casa del Acero; AGUA = Los Aguanaces; ALJB = Aljezar B; AMB2C = Ambérieu 2C; BAC = Baccinello; CC3 = Concud 3; CCBL = Cascante-Cubla; CP2 = Cortijo de la Piedra 2; CR2 = Crevillente 2; CR15 = Crevillente 15; CUC = Cucalón; DIO = Dionay; KAI = Kastellios Hill 1; KOH = Kohfidisch; LM = Los Mansuetos; MBB = Masía del Barbo 2B; MDV2 = Masada del Valle 2; MDV5 = Masada del Valle 5; ML = Molton; MRD = Montredon niveau Depéret; MRS = Montredon niveau supérieur; OZRA = Oued Zra; PERA = Peralejos A; PERC = Peralejos C; PM = Puente Minero; VP = Vivero de Pinos; 182A = YGSP 182A.

Distribution — Late Vallesian and Turolian of SW Europe.

Differential diagnosis — Differs from *Progonomys* by having a connection between the two anterior pairs of tubercles in the M_1 ; t6 and t9 are connected. Differs from *Occitanomys* by the anterior position of t1 in M^1 , and by a larger width of the central tubercles. Differs from *Parapodemus* and *Apodemus* by the presence of a connection t4-t8 and of a well-developed t12 and tma in species of those two genera. Differs from *Paraethomys* by having a M^2 with a well-developed t9.

Attributed species

Parapodemus? vireti Schaub, 1938

Valerymys turoliensis Michaux, 1969

Valerymys oreopitheci Engesser, 1989

Huerzelerimys minor sp. nov.

Huerzelerimys vireti (Schaub, 1938)

Original reference — *Parapodemus vireti* Schaub, 1938, pp. 24-26.

Holotype — An isolated M^1 sin., P.L. 61, deposited at the 'Naturhistorisches Museum', Basel.

Type locality — Mollon (Ain), France.

Selected references

Valerymys vireti from Lobrieu (Mein & Truc, 1966).

V. vireti from Crevillente 1, 2 and 3 (de Bruijn et al., 1975).

V. vireti from Tortajada A (van de Weerd, 1976).

V. vireti from Aguanaces and Vivero de Pinos (Adrover, 1986).

V. vireti from Fosso de la Fittaia (Engesser, 1989).

V. vireti from Puente Minero (Alcalá et al., 1991).

Huerzelerimys vireti from Crevillente 2 and 4B (Martín Suárez & Freudenthal, 1993).

Discussion — In some specimens of *H. vireti* of various populations (Mollon, Lobrieu, Crevillente 2 and 4B, among others) small longitudinal connections may be observed, both in the lower and in the upper molars. These small connections are found already in specimens of *Progonomys cathalai* from Montredon.

Huerzelerimys oreopitheci (Engesser, 1989)

Original reference — *Valerymys oreopitheci* Engesser, 1989, pp. 228-232.

Holotype — Right maxillary fragment with M^1 - M^3 , Bb 55, deposited at the 'Naturhistorisches Museum', Basel.

Type locality — Baccinello V-1 (Tuscany, Italy).

Huerzelerimys turoliensis (Michaux, 1969)

Original reference — *Valerymys turoliensis* Michaux, 1969, p. 23.

Holotype — Left maxillary with M¹ and M², RA 141 (Thaler, 1966 pl. 25, fig. A); deposited in the 'Museo de Paleontología Miquel Crusafont', Sabadell.

Type locality — Los Mansuetos (Teruel, Spain).

Selected references

Valerymys turoliensis from Masada del Valle 5, Conclud 3, Masada del Valle 2 (van de Weerd, 1976).

V. turoliensis from Casa del Acero (Agustí et al., 1981).

V. turoliensis from Aljezar B (Adrover, 1986).

Huerzelerimys turoliensis from Crevillente 15 (Martín Suárez & Freudenthal, 1993).

The populations from El Arquillo 1 (Teruel; Mein, 1990) and from Barranco del Beiro and Los Arcos (Granada; Padiá, 1986) are excluded from this species and included in *Karnimata inflata*.

Huerzelerimys minor sp. nov.

Pl. 1, figs. 1-22.

Derivatio nominis — This species is named 'minor' because it is the smallest species known within this genus.

Holotype — M¹ dext, n° 65898, deposited in the Centre des Sciences de la Terre, Université Claude Bernard, Lyon.

Type locality — Ambérieu 2C (Ain, France), Lambert co-ordinates x = 834.600, y = 111.250; altitude 294 m above sea-level. Farjanel & Mein (1984) give a description of the locality, that is situated at a depth of 3 m in a boring executed in the frame of the mentioned paper; in a later stage the locality was sampled, when it was accessible during excavations carried out for the enlargement of a water reservoir.

Selected references

Parapodemus sp. A in van de Weerd (1976, p. 84), from Peralejos B, C & D (Teruel, Spain).

Progonomys cf. *cathalai* Adrover et al. (1982) from La Roma II (Teruel, Spain).

Apodemus sp. in Sesé (1989), from Cortijo de la Piedra (Granada, Spain).

Diagnosis — *Huerzelerimys* of small size. Upper molars with a t6-t9 connection, that is weak but present in more than 60% of the specimens.

Differential diagnosis — *H. minor* differs from the other species of *Huerzelerimys* by its smaller size; by the greater frequency with which t6 and t9 are separated; by the presence in M¹ of a t12, that is more developed than in the other species.

Stratigraphical distribution — Late Vallesian.

Other localities with H. minor — Dionay (Isère, France), Ambérieu 2A (Ain, France), Cascante-Cubla (CCBL, Teruel, Spain) and Cortijo de la Piedra 2 (CP-2, Granada, Spain) are stratified localities, and Cucalón (CUC, Teruel, Spain) is a fissure-filling.

Measurements — See Table 1.

Description of the material from the type locality

M₁ — Molars with a practically symmetrical anteroconid; both lobes are of the same size, and united in little-worn specimens. In 83% of the specimens there is a minuscule tma in anterolabial position, which may be connected to the labial lobe of the anteroconid. The lingual lobe of the anteroconid is generally united to the metaconid. Protoconid and metaconid are situated almost at the same transverse level. There is no longitudinal connection between the two posterior pairs of tubercles. The labial cingulum is continuous, with a very voluminous c1, a c2 (smaller than c1) attached to the protoconid, and one more cuspid between protoconid and anteroconid. The posterior tubercle is low and oval-shaped. There are two main roots and a trace of a small central root.

M₂ — Molars with a big anterolabial cuspid, the apex of which may be isolated or united to the anterolingual wall of the protoconid. There are no longitudinal connections between the two pairs of tubercles, although in one specimen there is a

Plate 1

Huerzelerimys minor sp. nov. from Ambérieu 2C.

Fig. 1. M¹ sin.

Fig. 2. M¹ sin.

Fig. 3. M¹ dext., holotype, n° 65898.

Fig. 4. M² sin.

Fig. 5. M³ sin.

Fig. 6. M₂ dext.

Fig. 7. M₃ dext.

Fig. 8. M₁ sin.

Fig. 9. M₁ dext.

Huerzelerimys minor sp. nov. from Cucalón.

Fig. 10. M¹ sin.

Fig. 11. M² sin.

Fig. 12. M₁ sin.

Huerzelerimys minor sp. nov. from Cascante-Cubla.

Fig. 13. M¹ sin.

Fig. 14. M² dext.

Fig. 15. M₁ sin.

Huerzelerimys minor sp. nov. from

Cortijo de la Piedra 2.

Fig. 16. M¹ sin.

Fig. 17. M² sin.

Fig. 18. M² dext.

Fig. 19. M³ sin.

Fig. 20. M₃ dext.

Fig. 21. M₂ dext.

Fig. 22. M₁ dext.

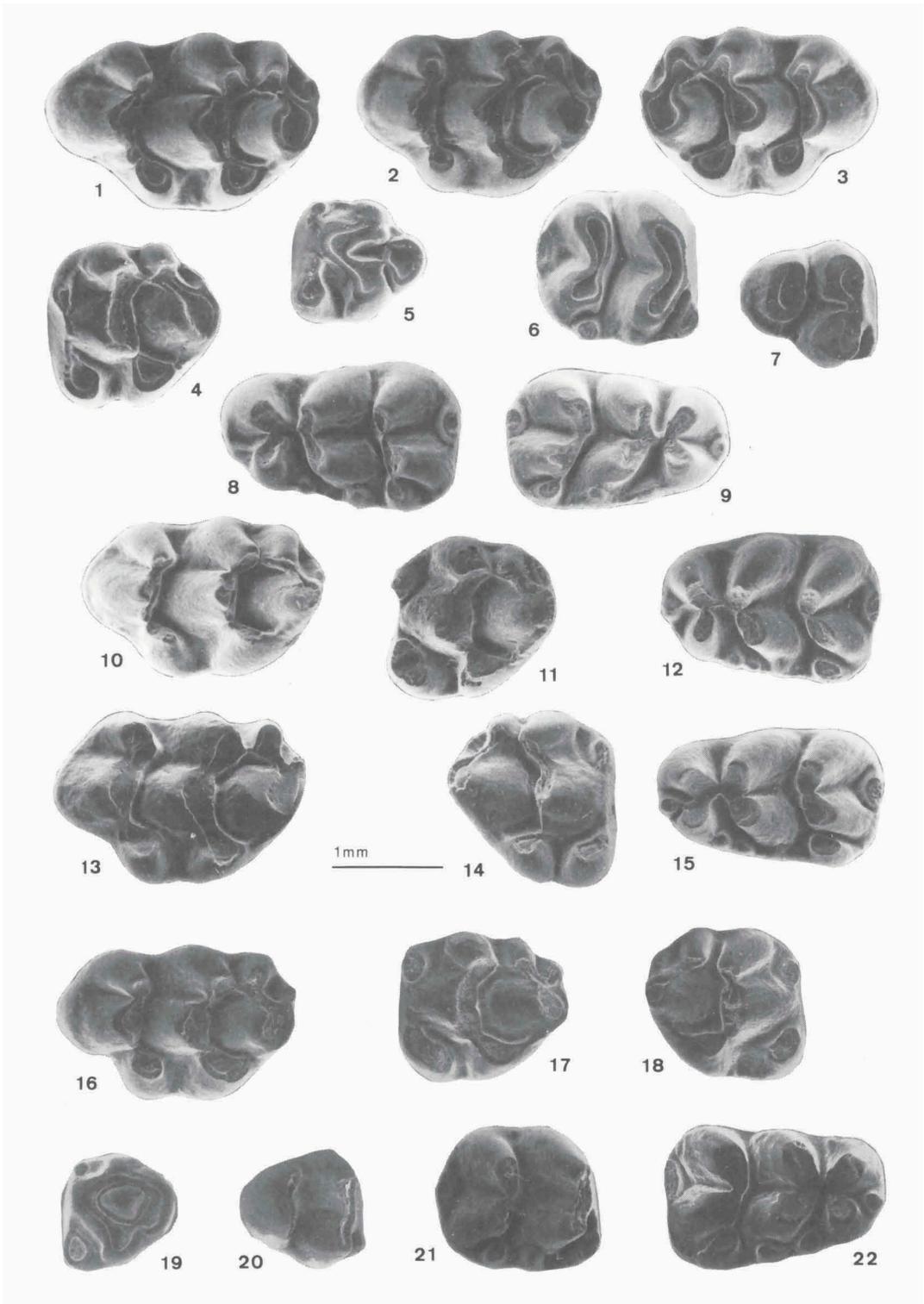


Table 1. Measurements of the molars of *Huerzelerimys minor* sp. nov.

	Length					Width				
	n	min.	mean	max.	V'	n	min.	mean	max.	V'
M₁										
CUC	40	1.81	1.97	2.14	13.20	40	1.16	1.25	1.36	12.54
CCBL	22	1.84	1.96	2.04	8.90	22	1.15	1.21	1.33	12.53
AMB2C	13	1.83	1.95	2.12	13.91	13	1.09	1.20	1.30	16.65
CP-2	8	1.70	1.87	1.96	14.95	8	1.09	1.15	1.24	13.55
M₂										
CUC	43	1.39	1.49	1.62	11.96	43	1.25	1.34	1.47	12.66
CCBL	15	1.39	1.51	1.63	14.66	15	1.27	1.32	1.43	10.93
AMB2C	15	1.37	1.47	1.56	11.96	15	1.20	1.32	1.41	14.84
CP-2	6	1.35	1.38	1.41	4.93	6	1.17	1.24	1.27	9.29
M₃										
CUC	41	1.13	1.24	1.35	13.97	41	0.99	1.10	1.20	15.10
CCBL	14	1.07	1.19	1.32	19.54	14	1.02	1.10	1.17	12.80
AMB2C	14	1.06	1.19	1.28	17.56	14	1.00	1.09	1.17	14.64
CP-2	4	1.04	1.13	1.18	16.25	5	0.97	1.02	1.10	15.02
M¹										
CUC	48	1.99	2.18	2.37	13.44	48	1.28	1.41	1.53	13.72
CCBL	18	1.94	2.16	2.32	15.92	18	1.32	1.40	1.50	11.39
AMB2C	18	2.01	2.16	2.40	15.79	18	1.25	1.41	1.51	16.82
CP-2	9	2.01	2.09	2.21	9.70	9	1.29	1.35	1.38	6.90
M²										
CUC	49	1.35	1.51	1.62	13.99	49	1.33	1.42	1.51	9.75
CCBL	14	1.34	1.54	1.70	22.12	14	1.28	1.41	1.51	15.40
AMB2C	17	1.36	1.50	1.62	15.73	17	1.30	1.40	1.46	10.45
CP-2	5	1.37	1.46	1.49	10.04	5	1.22	1.32	1.36	12.98
M³										
CUC	21	0.98	1.06	1.16	14.63	21	0.99	1.09	1.16	13.75
CCBL	13	0.88	1.02	1.11	21.90	13	0.96	1.06	1.12	14.58
AMB2C	10	0.91	1.07	1.14	22.44	10	0.94	1.06	1.21	25.12
CP-2	6	0.87	0.96	1.02	17.99	5	0.95	1.02	1.07	14.21

trace of a longitudinal spur. The labial cingulum is less developed than in *M₁*; c1 is always present, and a c2, leaning against the protoconid, may be smaller or larger than c1. The posterior tubercle, oval-shaped and broad, closes the posterosinusid (in one specimen it is absent).

M₃ — The anterolabial cuspid is low but always present. The posterior cuspid is displaced towards the lingual side. The c1 is present in 71.4% of the cases.

M¹ — Molars lengthened ($W/L = 0.65$). The t1 is rounded, united to the t2 (except in one specimen) by a small crest, which slightly inflated in two cases. Neither t1 nor t3 present longitudinal spurs towards the t5. The t4 is united to t5 by a crest, that is as high as the connection t5-t6. More than half the specimens have their t4 united to the t8 by a crest. Cusps t6 and t9 are always convergent and generally united, although in 20% of the cases the connecting crest is low. The t12 is always present, in some case it is tubercular. There are three main roots and a trace of a small central one.

M^2 — Molars with a voluminous t1, and without longitudinal connections; in one specimen there is a small t1bis. The t3 is reduced, always smaller than t9. The t4 is united to t8 in 71.4% of the cases. Cusps t6 and t9 are always convergent and united in 64% of the specimens. The t12 is less developed than in M^1 , in some specimens it is a mere enamel fold. There are three roots; the internal one is not subdivided.

M^3 — Molars with a rounded and voluminous t1. The t3 is very much reduced, but present. The t8 is large, and united to t4 or t6, or to both, enclosing a mesosinus. There are three roots.

Comparisons with the material from the other localities — The population from Cucalón (CUC) is much more numerous, as usual in a karstic locality. *H. minor* from CUC is slightly larger in size than the type-population. With respect to the morphology small variations are observed, that are worthwhile mentioning. In the M_1 from CUC the tma is less frequent than in the type-population from AMB-2C, and, when present, it may occupy a central position and be isolated. The c2 is smaller than in the type-population; there are no differences in the pattern of the roots. The M_2 from CUC have a more rounded outline than those from AMB-2C. In the M_3 from CUC the c1 is less frequently present than in the type-population; one specimen has a tubercle in posterolabial position. In the M^1 from CUC one specimen has its t1 united to t5 and another one has its t1 united to the connection t4-t5; like in AMB-2C there are no labial longitudinal connections, but in some case the t3 presents a short posterior spur. The t4 and t8 are connected with the same frequency as in the type-locality. The t6 and t9 are united in 87% of the cases. The t12 is somewhat smaller in the M^1 from CUC. The M^2 from CUC have t6 and t9 united in 80% of the specimens, in one case the t1 has a short posterior spur. The M^3 from CUC have their t3 more reduced than in the type-population; it may even be missing.

The dimensions of the population from Cascante-Cubla (CCBL) are very similar to those of the type-population. There are some morphological differences. The M_1 from CCBL have a somewhat more symmetrical anteroconid than those from AMB-2C, the tma is very frequent and occupies a central position; the trace of the third (central) root is of larger size in CCBL than in the type-population. No differences are observed in the M_2 . In the M_3 from CCBL, the c1 is present in 21% of the cases only. The M^1 from CCBL have a small t1-t5 connection in 13% of the cases, and have t6 and t9 united in 87% of the specimens. 25% of the M^2 from CCBL also have a small t1-t5 connection, and 69% of them have t6 and t9 united. In the M^3 , like in the material from CUC, the t3 may be missing.

The material from CP-2 shows smaller dimensions than the other populations. Morphologically, in the M_1 from CP-2 the tma is less frequent or smaller than in the type-population; if present, it is somewhat displaced towards labial. In the M_2 the anterolabial cuspid always has a free apex, and the c2 is smaller than the c1. In the M_3 from CP-2 there is no c1. In the M^1 , like in the type-population, some specimens have an isolated t1; the t4-t8 connection is low in two specimens, and the t6-t9 connection is less developed than in the type-population. In the M^2 the connections t4-t8 and t6-t9 are somewhat less developed than in the type-population. The M^3 present no differences.

Comparison of these four populations shows, that in the M_1 of the Spanish

populations the tma is less frequent than in the type-population, and when present it occupies a more central position. In M_3 the c1 is more frequent in the French population than in the Spanish ones. In the upper molars of the type-population posterior spurs of the t1 are rare, they have not been found in the population from CP-2, whereas these are present in the other Spanish populations (more frequently in CCBL than in CUC). In the M^3 from AMB-2C the t3 is very small, but always present, in the Spanish populations it may be missing.

The morphology of *H. minor* seems to indicate that Cortijo de la Piedra 2 and Peralejos B, C and D are the older localities; Ambérieu 2C is intermediate in age, Cascante Cubla is later, and more nearer to Cucalón, which is the youngest locality.

Discussion — This new *Huerzelerimys* is known, for the moment, from various French and Spanish localities. The latter are much richer than the French ones. Nevertheless we have chosen the French locality Ambérieu 2C as the type-locality because it is located in a stratigraphical sequence with various fossiliferous levels: Ambérieu 1, 2A, 2B, 2C, and 3 (Farjanel & Mein, 1984). In this sequence *Progonomys cathalai* is found at the oldest level, *Huerzelerimys minor* at the intermediate ones, and *H. vireti* in the youngest locality. This means, that we have a continuous fossil record of this evolutionary lineage.

Huerzelerimys minor is a form, that has the same size as *Progonomys woelferi* from Kohfidisch (Fig. 4) and, presumably, the same age. Still, its morphology is somewhat more primitive than that of *H. vireti* and it is of smaller size.

Comparing *H. minor* with *P. woelferi* from Kohfidisch one may observe, that the relative position of the t1 in M^1 is more forward in *H. minor*. In the upper molars the connection t4-t8 is higher in *H. minor*; t6 and t9 are convergent and are generally united in *H. minor*, while in the KOH material they are divergent and always separated (Fig. 5); the t12 is more developed in KOH. The t3 is reduced in the M^2 of both species. In the M_1 from KOH the anteroconid is isolated or connected by a very low union to the second pair of tubercles; this union is higher in *H. minor*; the labial cingulum is wider in *H. minor* and in some cases it is individualized (not coalescent

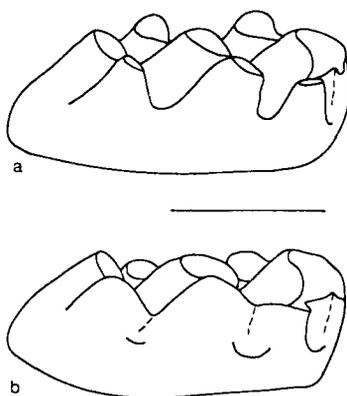


Fig. 5. Labial view of a M^1 of *Progonomys woelferi* from Kohfidisch (a) and of the holotype of *Huerzelerimys minor* from Ambérieu 2C (b). Scale represents 1 mm.

with the protoconid); the small central root is a mere trace in KOH and somewhat larger in *H. minor*. In *Progonomys cathalai* this trace of a third root is found in the largest M^1 only. The foramen incisivum in the KOH species reaches backwards until the lingual root of M^1 or continues farther backwards in between the first molars; in *H. minor* the foramen does not continue backwards beyond the anterior root.

Progonomys cathalai from Ambérieu 1 is smaller, has t6 and t9 separated, and the t3 of the M^2 is larger than in *Huerzelerimys minor* from Ambérieu 2C.

Huerzelerimys vireti has a considerably larger size than *H. minor*, yet the relation W/L of the M^1 is similar in both species. In *H. vireti* there are some rare examples of upper molars with separated t6 and t9; t12 is persistent. In the M_1 the connection between anteroconid and metaconid is higher in *H. vireti* than in *H. minor*. In *H. vireti* from Crevillente 2 there are M_1 with a relatively large tma in central position; in *H. minor* the tma is less frequent, smaller and is displaced towards labial. The small central root of the M_1 , whenever present, is larger in *H. vireti* from CR2.

Species excluded from this genus

Engesser (1989) attributes *Parapodemus vireti* from Lissieu (Huguency & Mein, 1965) to his new species *Valerymys oreopithecii* Engesser, 1989 from Baccinello V-1. We do not agree with this determination because the population from Lissieu is one in which the M_1 have tma, a strong crest of connection t4-t8 in M^1 and M^2 , and none of the M^3 has five roots; in other words it shares none of the diagnostic characters with *H. oreopithecii*. This is understandable because in reality it is a very large species of the genus *Parapodemus*, probably a descendant of *Parapodemus meini* from Crevillente 7 and 8 (Martín Suárez & Freudenthal, 1993).

Another species attributed originally to *Valerymys* is *V. juniensis* Padiál & Ruiz Bustos, 1989. In our opinion this species is a large-sized form of *Parapodemus*, since it has a tma, the labial cingulum shows an extreme vertical development, and the two posterior pairs of tubercles in M_1 are placed in chevron. In the upper molars the stephanodonty (sensu Schaub, 1938) is complete and the t12 is well-developed.

Discussion on the genus Huerzelerimys

As said above, the lineage *Progonomys cathalai* - *P. woelferi* persists in Central Europe until the end of the Vallesian. It shows an important increase in size, and it is quite conservative in the morphological characters of its dentition.

During this same period, in contemporaneous French and Spanish localities, *P. woelferi* is not found (except for the already mentioned Catalan localities), but another species is present, *Huerzelerimys minor*, that finally acquires the same size (Fig. 4), but presents much more derived morphological characters. In other words, in the Ibero-Occitan Province *Progonomys cathalai* follows a different evolution. Not only does it increase in size, but there is also a clear morphological break, that marks the origin of a species, similar in size to *P. woelferi* but with apomorphic characters. So, there is a clear separation of lineages (Fig. 6).

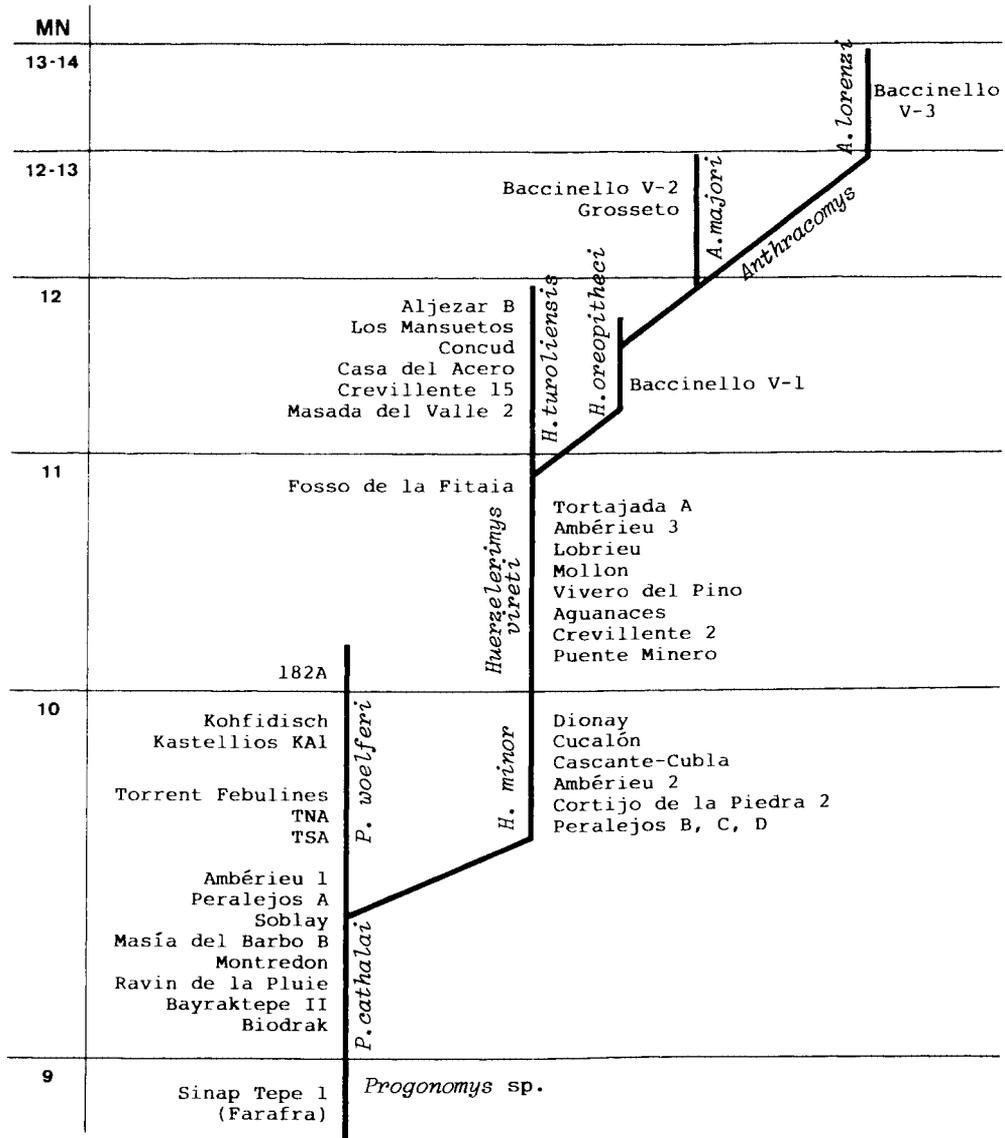


Fig. 6. Chronological distribution and phylogenetic relationships of the populations and species of *Progonomys* and *Huerzelerimys*. *H. oreopitheci* and *Anthracomys* may differentiate from a source population close to the one from Fosso de la Fitaia.

This separation obliges us to give them different names. We reserve the name *Progonomys* for the species with conservative morphology, and propose the new genus name *Huerzelerimys* for the species with derived morphology.

Huerzelerimys includes four species, three of them successive in time: *H.*

minor, *H. vireti* and *H. turoliensis*. The fourth species, *H. oreopithecii* is contemporaneous with the last populations of *H. vireti* or with the first ones of *H. turoliensis*, and it is modified by conditions of insularity (Engesser, 1989); it forms the origin of *Anthracomys*. The various species of this new genus are known from Western Europe only, and have a time distribution from latest Vallesian until the beginning of the Late Turolian (units MN10, 11 and 12).

Conclusions

Progonomys, in its previous concept, was a clearly paraphyletic genus, that included numerous species, brought together on the basis of plesiomorphic characters.

In this paper *Progonomys* has been redefined. It now is a monophyletic genus, that includes three species: *Progonomys* sp. from Sinap Tepe 1, *P. cathalal* Schaub, 1938 and *P. woelferi* Bachmayer & Wilson, 1970, ancestor and descendant respectively. Its first representants appear in Sinap Tepe 1, in the Early Vallesian (unit MN9) and the last ones are reported from YGSP loc. 182A (Jacobs, 1978) in the Early Turolian.

The two named species have a wide distribution in the south of the Palaearctic Region, and constitute a lineage in which there is a marked increase in size, and a long period of morphological stability.

During the Late Vallesian in Western Europe a separation of lineages takes place. On one hand, the lineage *P. cathalal* - *P. woelferi* persists as it is, and on the other there arises a new lineage, which we have denominated *Huerzelerimys*, in which there is also a marked increase in size, and on top of that a clear morphological break in comparison with *Progonomys*.

In the group *Progonomys* - *Huerzelerimys* several common anatomical characters may be observed:

Lower molars without longitudinal crest.

In M_1 tma is reduced or absent.

M_1 with a small central root. In *P. cathalal* this root is not present in the entire population, but only in the larger specimens. In *P. woelferi* the third root is very frequent, but it is much smaller than in the species of *Huerzelerimys*. However, in both groups it may be absent.

Upper molars with a tendency to develop a connection between t4 and t8, and without t1bis.

M^1 with its t1 situated in an anterior position (not backwards).

Progonomys cathalal colonizes Western Europe from the east at the beginning of the Late Vallesian. The record of the group *Progonomys*-*Huerzelerimys* is restricted to the Late Miocene.

Several localities of Early Vallesian age (Jalalpur, Can Llobateras, Buzhor, Sinap Tepe 1) contain Muridae, that are not related with *Progonomys*. So, at the end of the Early Vallesian already, there existed various lineages of Muridae, with morphotypes '*Mus*', '*Parapodemus*', *Progonomys*, and furthermore the Muridae indet. from

Can Llobateras, and the lineage that is represented in Oued Zra in North Africa. None of these lineages has an ancestor-descendant relationship with any of the other ones, but they have a common origin.

References

- Adrover, R., 1986. Nuevas faunas de Roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico. — *Inst. Estudios Turolenses*: 1-423.
- Adrover, R., L. Alcalá, J. Paricio, P. Mein & E. Moissenet, 1982. Dos nuevos yacimientos de vertebrados terciarios continentales: La Roma II (Alfambra, Teruel) y Búnker de Valdecebro (Teruel). — *Teruel*, 67: 7-21.
- Aguilar, J.P., 1982. Contributions à l'étude des micromammifères du gisement Miocène supérieur de Montredon (Hérault). 2. Les rongeurs. — *Palaeovertebrata*, 12, 3: 81-117, 2 pls.
- Aguilar, J.P., M. Calvet & J. Michaux, 1986a. Description des rongeurs pliocènes de la faune du Mont-Hélène (Pyrénées-orientales, France), nouveau jalon entre les faunes de Perpignan (Serrat-d'en-Vacquer) et de Sète. — *Paleovertebrata*, 16, 3: 127-144, 2 pls.
- Aguilar, J.P., M. Calvet & J. Michaux, 1986b. Découvertes de faunes de micromammifères dans les Pyrénées Orientales (France) de l'Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l'étalement des échelles continentale et marine. — *C. R. Acad. Sc. Paris*, II, 303, 8: 755-760.
- Aguilar J.P., M. Calvet & J. Michaux, 1991. Présence de *Progonomys* (Muridae, Rodentia, Mammalia) dans une association de rongeurs de la fin du Miocène moyen. — *Géobios*, 24, 4: 503-508.
- Agustí, J., 1981. Roedores miomorfos del Neógeno de Cataluña. — *Doctor's Thesis Univ. Barcelona*: 1-288, 3 pls.
- Agustí, J. & J. Gibert, 1982. Roedores e insectívoros (Mammalia) del Mioceno Superior de Can Jofresa y Can Perellada (Vallès-Penedès, Cataluña). — *Paleont. Evol.*, 17: 29-41, 1 pl.
- Agustí, J., J. Gibert & S. Moyà-Solà, 1981. Casa del Acero: nueva fauna turolense de vertebrados (Mioceno superior de Fortuna, Murcia). — *Butll. Inf. Inst. Paleont. Sabadell*, 12, 1-2: 69-87, 1 pl.
- Alcalá, L., C. Sesé, E. Herráez & R. Adrover, 1991. Mamíferos del Turolense inferior de Puente Minero (Teruel, España). — *Bull. Real. Soc. Esp. Hist. Nat., Sec. Geol.*, 86, 1-4: 205-251.
- Ameur-Chehbeur, A., 1988. Biochronologie des formations continentales du Néogène et du Quaternaire de l'Algérie. Contribution des micromammifères — *Doctor's Thesis Univ. Oran*: 1-480, 33 pls (unpublished).
- Antunes, M.T. & P. Mein, 1979. Le gisement de Freiria do Rio Mayor, Portugal, et sa faune de mammifères; nouvelle espèce de *Rotundomys*; conséquences stratigraphiques. — *Géobios*, 12, 6: 913-919, 1 pl.
- Bachmayer, F. & R.W. Wilson, 1970. Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch fissures of Burgenland, Austria. — *Ann. Naturh. Mus. Wien*, 74: 533-587, 13 pls.
- Bachmayer, F. & R.W. Wilson, 1980. A Third Contribution to the Fossil Small Mammal Fauna of Kohfidisch (Burgenland), Austria. — *Ann. Naturh. Mus. Wien*, 83: 351-386, 3 pls.
- Bonis, L. de & J. Melentis, 1975. Première découverte de Muridés (Mammalia, Rodentia) dans le Miocène de la région de Thessalonique. Précision sur l'âge géologique des Dryopithécinés de Macédoine. — *C. R. Acad. Sci. Paris*, D, 280: 1233-1236.
- Brandy, L.D., 1979. Rongeurs nouveaux du Néogène d'Afghanistan. — *C. R. Acad. Sci. Paris*, D, 289: 81-83, 2 pls.
- Bruijn, H. de, 1976. Vallesian and Turolian rodents from Biota, Attica and Rhodes (Greece). — *Proc. Kon. Ned. Akad. Wetensch.*, B, 79, 5: 361-384, 5 pls.
- Bruijn, H. de, R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein & J. Morales, 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. — *Newsl. Stratigr.*, 26, 2/3: 65-118.

- Bruijn, H. de, P. Mein, C. Montenat & A. van de Weerd, 1975. Corrélations entre les gisements de rongeurs et les formations marines du Miocène terminal d'Espagne méridionale (prov. de Alicante et Murcia). — Proc. Kon. Ned. Akad. Wetensch., B, 78, 4: 282-313, 4 pls.
- Bruijn, H. de, P.Y. Sondaar & W.J. Zachariasse, 1971. Mammalia and Foraminifera from the Neogene of Kastellios Hill, Crete, a correlation of continental and marine biozones. — Proc. Kon. Ned. Akad. Wetensch., B, 74, 5: 1-22, 4 pls.
- Bruijn, H. de & W.J. Zachariasse, 1981. The correlation of marine and continental biozones of Kastellios Hill reconsidered. — Ann. Géol. Pays Hellén., H. S. (VII RCMNS Congr. Athens, 1979), 1: 219-226, 1 pl.
- Cheema, I.U., S. Sen & L.J. Flynn, 1983. Early Vallesian small mammals from the Siwaliks of Northern Pakistan. — Bull. Mus. Natl. Hist. Nat., C, 4, 5, 3: 267-280.
- Coiffait-Martin, B., 1991. Contribution des rongeurs du Néogène d'Algérie à la biochronologie mammalienne d'Afrique nord-occidentale. — Doctor's Thesis Univ. Nancy I: 1-389, 7 pls (unpublished).
- Engesser, B., 1989. The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia). — Boll. Soc. Pal. Ital., 28, 2/3: 227-252.
- Farjanel, G. & P. Mein, 1984. Une association de mammifères et de pollens dans la formation des 'Marnes de Bresse' d'âge Miocène supérieur, à Ambérieu (Ain). — Géol. France, 1984, 1-2: 131-148.
- Haas, G., 1966. On the vertebrate fauna of the Lower Pleistocene site Ubeidiya. — Israel Acad. Sci. Hum.: 1-68.
- Hartenberger, J.L. & L. Thaler, 1963. Sur les rongeurs fossiles du Vallésien (Miocène supérieur) de Can Llobateres (Sabadell, Espagne). — C. R. Acad. Sc. Paris, 256: 3333-3336.
- Heissig, K., 1982. Kleinsäuger aus einer obermiozänen (Vallesium) Karstfüllung Ägyptens. — Mitt. Bayer. Staatssamml. Paläontol. Hist. Geol., 22: 97-101.
- Hugueney, M. & P. Mein, 1965. Lagomorphes et rongeurs du Néogène de Lissieu. — Trav. Lab. Géol. Fac. Sci. Lyon, N. S., 12: 109-123, 3 pls.
- Jacobs, L.L., 1978. Fossil Rodents (Rhizomyidae and Muridae) from Neogene Siwalik Deposits, Pakistan. — Mus. North. Arizona Press, Bull., 52: 1-103.
- Jaeger, J.J. 1977. Les rongeurs du Miocène moyen et supérieur du Maghreb. Paleovertebrata 8, 1: 1-166, 7 pls.
- Lungu, A.N., 1981. Gipparionovaya fauna srednego sarmata Moldavii (nasekomoyadnyye, zaytseobraznyye i grysuny) [The middle Sarmatian *Hipparion* fauna of Moldavia (insectivores, lagomorphs and rodents)]. — Shtiintsa, Kisheniv, MSSR: 1-140.
- Martín Suárez, E. & M. Freudenthal, 1993. Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). — Scripta Geol., 103: ??
- Mein, P., 1984. Composition quantitative des faunes de Mammifères du Miocène moyen et supérieur de la région Lyonnaise. — Paléobiol. Continent., 14, 2 (RCMNS Interim-Coll. Mediterranean Neogene continental paleoenvironments and paleoclimatic evolution, Montpellier, 1983): 339-346.
- Mein, P., 1990. Updating of MN zones. In: E.H. Lindsay, V. Fahlbusch & P. Mein (eds). European Mammal Chronology. — NATO ASI Series, A, 180: 73-90.
- Mein, P., E. Moissenet & R. Adrover, 1990. Biostratigraphie du Néogène supérieur du bassin de Teruel. — Paleont. Evol., 23: 121-139.
- Mein, P. & G. Truc, 1966. Faciès et association faunique dans le Miocène supérieur continental du Haut-Comtat Venaissin. — Trav. Lab. Géol. Lyon, N. S., 13: 273-276.
- Michaux, J., 1969. Muridae (Rodentia) du Pliocène supérieur d'Espagne et du Midi de la France. — Palaeovertebrata, 3: 1-25, 2 pls.
- Michaux, J., 1971. Muridae (Rodentia) Neogènes d'Europe Sud-occidentale. Évolution et rapports avec les formes actuelles. — Paléobiol. Contin., 2, 1: 1-67.
- Misonne, X., 1969. African and Indo-Australian Muridae. Evolutionary trends. — Kon. Mus. Midden-Afrika, Ann., IN-8, Zool. Wetensch., 172: 1-220, 27 pls.

- Padial Ojeda, J., 1986. Estudio de los roedores y lagomorfos del Mioceno continental de la depresión de Granada. — Doctor's Thesis Univ. Granada: 1-303.
- Ride, W.D.L., C.W. Sabrosky, G. Bernardi & R.V. Melville, 1985. International Code of Zoological Nomenclature. — International Trust Zool. Nomenclature, London: 1-338.
- Schaub, S., 1938. Tertiäre und Quartäre Murinae. — *Abh. Schweiz. Pal. Gesellsch.*, 61: 1-39.
- Sen, S., 1990. Stratigraphie, faunes de mammifères et magnétostratigraphie du Néogène de Sinap Tepe, province d'Ankara, Turquie. — *Bull. Mus. Hist. Nat. Paris*, 4, 12, 3/4: 243-277.
- Sesé, C., 1989. Micromamíferos del Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada). In: M.T. Alberdi & F.P. Bonadonna (eds) *Geología y Paleontología de la cuenca de Guadix-Baza*. — *Trab. Neog.-Quatern.*, 11: 185-214.
- Thaler, L., 1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. — *Mém. Mus. Natl. Hist. Nat.*, C, 17: 1-295, 27 pls.
- Ünay, E., 1981. Middle and Upper Miocene Rodents from the Bayraktepe section (Çanakkale, Turkey). — *Proc. Kon. Ned. Akad. Wetensch.*, B, 84, 2: 217-238.
- Weerd, A. van de, 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. — *Utrecht Micropal. Bull., Spec. Publ.*, 2: 1-217, 16 pls.

Manuscript received 18 January 1993.