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

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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 *Huerzelerimus*, 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.


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

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. cathalai (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 Also in the locality Buzhor in Moldavia (Lungu, 1981, and new, unpublished data) two lineages of Muridae are found, related to Parapodemus and Mus respectively, and certainly not related with Progonomys.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. cathalai (van de Weerd, 1976). Yet another example is the coexistence of ‘Progonomys clazuoni’, 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
Mein et al., *Progonomys* and *Huerzelerimys*, Scripta Geol. 103 (1993)

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 cathalai* 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 montheleini* 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. tuolienis* Michaux, 1969, and *V. oreopitheci* Engesser, 1989. For these species, and for others that were not included in *Valerymys*, we propose the new generic name *Huerzelerimys*.

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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.

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**Genus *Progonomys* Schaub, 1938**

*Type-species* — *Progonomys cathalai* 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
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.


Holotype — An isolated M\(^1\) dext., Montredon 584, deposited in the ‘Naturhistorisches
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 taxonomic 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 M\(^1\) 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

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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.


*Type locality* — Kohfidisch, southern Burgenland (Austria).

*Selected references*

**Karnimata darwini** Jacobs, 1978.


**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
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 M1 (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 M1 the two anterior pairs of tubercles are separated; the relative position of the hypoconid, entoconid and posterior heel leaves room for a very wide posterinusid. 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’ debruijni 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

**Discussion on the genus Progonomys**

The oldest record of *Progonomys* is from the locality of Sinap Tepe 1 of Early Vallesiian 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 Weerdt, 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.
Huerzelerimys toroiensis (Michaux, 1969)
Huerzelerimys cathalaí Schaub, 1938
Huerzelerimys vireti (Schaub, 1938)
Huerzelerimys minor sp. nov.
Huerzelerimys oreopithec (Engesser, 1989)
Progonomys woelferi Bachmayer & Wilson, 1970
Fig. 4. Size ranges of the $M_1$ of various populations of *P. cathalai*, *P. woelferi*, *H. minor*, *H. vireti* and *H. turoliensis*. ACE = Casa del Acero; AGUA = Los Aguamaces; ALJB = Aljezar B; AMB2C = Ambérieu 2C; BAC = Baccinello; CC3 = Concut 3; CCBL = Cascante-Cubla; CP2 = Cortijo de la Piedra 2; CR2 = Crevillente 2; CR15 = Crevillente 15; CUC = Cucalon; DIO = Dionay; KA1 = Kastellios Hill 1; KOH = Kohfidisch; LM = Los Mansuetos; MBB = Masía del Barbo 2B; MDV2 = Masada del Valle 2; MDV5 = Masada del Valle 5; ML = Molion; 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 M₁; t₆ and t₉ are connected. Differs from *Occitanomys* by the anterior position of t₁ in M₁, 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 t₉ in species of those two genera. Differs from *Paraethomys* by having a M₂ with a well-developed t₉.

**Attributed species**
- *Parapodemus? vireti* Schaub, 1938
- *Valerymys turoliensis* Michaux, 1969
- *Valerymys oreopithecii* Engesser, 1989
- *Huerzelerimys minor* sp. nov.

*Huerzelerimys vireti* (Schaub, 1938)


**Type locality** — Mollon (Ain), France.

**Selected references**
- *V. 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 Aguanaes 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 oreopithecii* (Engesser, 1989)


**Holotype** — Right maxillary fragment with M₁-M₃, Bb 55, deposited at the ‘Naturhistorisches Museum’, Basel.
Type locality — Baccinello V-1 (Tuscany, Italy).

*Huerzelerimys turoliensis* (Michaux, 1969)


*Holotype* — Left maxillary with $M^1$ and $M^2$, 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, Concud 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; Padial, 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* — $M^1$ 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 M:\(^1\) 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**

*M:\(^1\)* — 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.

*M:\(^2\)* — 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

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**Plate 1**

*Huerzelerimys minor* sp. nov. from Ambérieu 2C.
- Fig. 1. M:\(^1\) sin.
- Fig. 2. M:\(^1\) sin.
- Fig. 3. M:\(^1\) dext., holotype, n° 65898.
- Fig. 4. M:\(^2\) sin.
- Fig. 5. M:\(^3\) sin.
- Fig. 6. M:\(^3\) dext.
- Fig. 7. M:\(^3\) dext.
- Fig. 8. M:\(^3\) sin.
- Fig. 9. M:\(^3\) dext.

*Huerzelerimys minor* sp. nov. from Cascante-Cubla.
- Fig. 13. M:\(^1\) sin.
- Fig. 14. M:\(^2\) dext.
- Fig. 15. M:\(^1\) sin.

*Huerzelerimys minor* sp. nov. from Cortijo de la Piedra 2.
- Fig. 16. M:\(^1\) sin.
- Fig. 17. M:\(^2\) sin.
- Fig. 18. M:\(^3\) dext.
- Fig. 19. M:\(^3\) sin.
- Fig. 20. M:\(^3\) dext.
- Fig. 21. M:\(^2\) dext.
- Fig. 22. M:\(^2\) dext.
Table 1. Measurements of the molars of _Huerzelerimys minor_ sp. nov.

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<th>Length</th>
<th>Width</th>
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<td>min.</td>
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<tr>
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<td><em>M2</em></td>
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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 poserosinusid (in one specimen it is absent).

_M1_ — The anterolabial cusp is low but always present. The posterior cusp is displaced towards the lingual side. The c1 is present in 71.4% of the cases.

_M2_ — 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.
M² — 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 M¹, in some specimens it is a mere enamel fold. There are three roots; the internal one is not subdivided.

M³ — 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 M₁ 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 M₂ from CUC have a more rounded outline than those from AMB-2C. In the M₃ from CUC the t3 is less frequently present than in the type-population; one specimen has a tubercle in postero-labial position. In the M¹ 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 M¹ from CUC. The M² from CUC have t6 and t9 united in 80% of the specimens, in one case the t1 has a short posterior spur. The M³ 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 M₁ 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 M₂. In the M₃ from CCBL, the c1 is present in 21% of the cases only. The M¹ 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 M² from CCBL also have a small t1-t5 connection, and 69% of them have t6 and t9 united. In the M³, 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 M₁ 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 M₂ the antero-labial cusp always has a free apex, and the c2 is smaller than the c1. In the M₃ from CP-2 there is no c1. In the M¹, 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 M² the connections t4-t8 and t6-t9 are somewhat less developed than in the type-population. The M³ present no differences.

Comparison of these four populations shows, that in the M₁ 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 $M_1^1$ of *Progonomys woelferi* from Kohfidisch (a) and of the holotype of *Huerzelerimys minor* from Ambérieu 2C (b). Scale represents 1 mm.](image-url)
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 Ambéreu 1 is smaller, has t6 and t9 separated, and the t3 of the M\(^2\) is larger than in *Huerzelerimys minor* from Ambéreu 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 (Hugueney & Mein, 1965) to his new species *Valerymys oreopitheci* 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. oreopitheci*. 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* Padial & 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).
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. oreopithecis* 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. cathalai* Schaub, 1938 and *P. woelferi* Bachmayer & Wilson, 1970, ancestor and descendant respectively. Its first representatives 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. cathalai - 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 M1 tma is reduced or absent.
- M3 with a small central root. In *P. cathalai* 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.
- M1 with its t1 situated in an anterior position (not backwards).

*Progonomys cathalai* 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


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