

A NEW RODENT FROM QUATERNARY DEPOSITS OF THE CANARY ISLANDS AND ITS RELATIONSHIPS WITH NEOGENE AND RECENT MURIDS OF EUROPE AND AFRICA

by

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ABSTRACT

A peculiar new rodent, *Malpaisomys insularis* nov. gen., nov. sp., is described from subfossil deposits of the eastern Canary Islands. The species shows some highly specialized skull features although its molars exhibit a mixture of primitive and derived characters among which a partial stephanodonty is most notable. A comparison of the new rodent with several Miocene to Holocene Muridae shows that *Malpaisomys* possibly shares a common ancestor with *Acomys* and *Uranomys*.

RESUME

Malpaisomys insularis nov. gen., nov. sp. est un rongeur Muridé original trouvé dans des dépôts récents des îles Canaries orientales. Il possède des structures craniennes très spécialisées et ses molaires présentent une combinaison de caractères primitifs et dérivés dont, parmi ces derniers, une structure stéphanodonte. La comparaison de ce nouveau rongeur avec des Muridés néogènes et actuels montre qu'il partage probablement un ancêtre commun avec *Acomys* et *Uranomys*.

RESUMEN

Malpaisomys insularis nov. gen., nov. sp. es un roedor Múrido peculiar hallado en depósitos recientes de las Islas Canarias orientales. Pose estructuras craneanas muy especializadas y sus molares presentan una combinación de caracteres primitivos y derivados, entre estos últimos, una estructura estefanodonta. La comparación del nuevo roedor con los Múridos neógenos y actuales muestra que posiblemente comparte un antecesor común con *Acomys* y *Uranomys*.

INTRODUCTION

The Canary Islands comprise seven larger islands and a number of islets in the Atlantic Ocean west of the coast of southern Morocco. They are of volcanic origin and date back from 2 to 35 Mio. years (Abdel-Monem *et al.*, 1967). The mammalian fauna of these islands is not yet fully known, and only recently a new species of shrew was discovered (Hutterer *et al.*, 1987). Among the rodents, two species of extinct giant rats were described: *Canariomys bravoï* CRUSAFONT-PAIRO & PETTER, 1964, and *Canariomys tamaranis* LOPEZ-MARTÍNEZ & LOPEZ-JURADO, 1987. The former lived on Tenerife, the second on Gran Canaria. No fossils of endemic rodents have ever been found before in one of the eastern Canary Islands, Lanzarote and Fuerteventura. It was therefore a great surprise when in 1979 an archaeological excavation of a Prehispanic site in Fuerteventura (Garralda *et al.*, 1981) yielded numerous remains of an unknown rodent apparently not related to any of the *Canariomys* species. Recent fieldwork by the first author, together with S. Lenné and F. Hutterer, added seven new localities in Fuerteventura, Lanzarote and the islet Graciosa where remains of the same rodent were found. This first account serves to describe and name the new murid and to evaluate its possible origin.

DESCRIPTION OF LOCALITIES AND MATERIALS

The known localities of the new murid are shown in fig. 1. A short description of each of them follows including notes on the associated mammal fauna. The material obtained at each site is shown in brackets and expressed as the "Minimum Number of Individuals" (MNI); the MNI was calculated from the left and right maxillae and mandibulae; the actual number of specimens is therefore five to ten times larger.

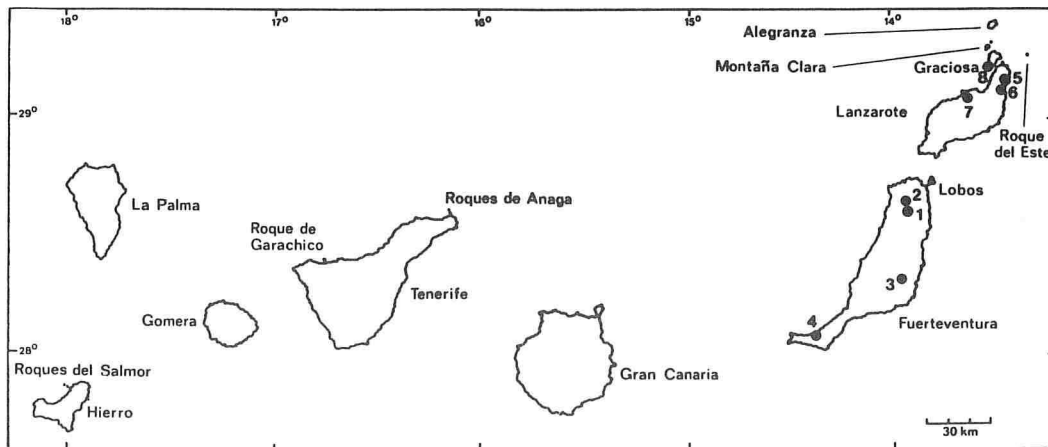


Fig. 1. Map of the Canary Islands with the localities where remains of *Malpaisomys* nov. gen. were found.

Locality 1. Fuerteventura, Cueva Villaverde (MNI = 944 + uncounted material). A cave of volcanic origin which was inhabited by Prehispanic men. The cave deposits were excavated by a team of Spanish archaeologists from 1979 to 1987 (see Garralda *et al.*, 1981; Meco Cabrera *et al.*, 1982; Hernández & Sanchez, 1986) and their activities yielded an extremely rich vertebrate fauna. Sixty samples containing microfauna were obtained, 40 from inside the cave, and 20 from outside. Seven levels of different age have been distinguished in the cave. Radiocarbon dates are available for the uppermost level (surface; 1070 ± 50 B.P.) and for one of the deeper levels (level 3; 1730 ± 50 B.P.). Additional small mammals in this site are *Crocidura canariensis* and *Mus musculus*. The house mouse is dominant in the upper levels but almost absent in the lowermost levels (Carrascosa & López-Martínez, 1988).

Locality 2. Fuerteventura, Malpais de Arena (MNI = 20). A small section of a collapsed lava tube with a compact sediment filling of 5 to 20 cm thickness. A section of 1 x 1 m was screened in 1987 by R. Hutterer and S. Lenné (also loc. 3 and 4). It contained also bones of *Crocidura canariensis*, *Mus musculus* and *Oryctolagus cuniculus*. Goat and pieces of pottery were also found. No datation of this site is yet available, but the presence of *Oryctolagus* indicates a younger age than locality 1.

Locality 3. Fuerteventura, Malpais Grande (MNI = 7). Bones were screened from the sediment which filled small caves in the malpais, some were found on the surface. *Crocidura* and *Mus* were also present. The age of these recent lava flows is around a few thousand years (Afonso Perez, 1980).

Locality 4. Fuerteventura, Jandia Peninsula, north coast at 150 m a.s.l.; (MNI = 2). A hanging dune consisting of compressed white sand yielded a rich bird fauna but only few rodent bones. No other mammal was found in this site. Judged from the geological situation this site might be older than the preceding ones.

Locality 5. Lanzarote, Malpais de Corona (MNI = 10). Bones screened from sediment in fissure and cave fillings in the malpais by R. and F. Hutterer in 1987 (all Lanzarote localities). Access to sediment was only possible at road cuts. Other mammals found are *Crocidura*, *Mus*, *Rattus* and *Oryctolagus*. The presence of *Rattus* and *Oryctolagus* indicates a young age of this site. The age of the Malpais de Corona was estimated as ca. 3000 - 5000 years (Bravo, 1964; Hernandez-Pacheco, 1909).

Locality 6. Lanzarote, Arrieta, ca. 3 m a.s.l. (MNI = 18). Fissure fillings of an ancient malpais covered by about 2 m of alluvial sediments. The site was accessible for a few days during the construction of a building pit. The small mammal fauna includes *Crocidura* and *Mus*.

Locality 7. Lanzarote, Casa de la Caldera (MNI = 4). A few bones were screened from a cave sediment in a remnant malpais area. *Crocidura*, *Mus* and *Oryctolagus* were also present.

Locality 8. Graciosa, Montaña Amarilla (MNI = 2). Bones were screened from a fissure filling. *Crocidura*, *Mus* and *Oryctolagus* were also present.

In addition to the mapped localities (fig. 1), we found small samples of *Malpaisomys* nov. gen. at La Vegueta and at Costa Teguisse, Lanzarote. Further material from Mozaga, Lanzarote, was studied by us in the Museo Insular, Santa Cruz de Tenerife. Additional material was also collected in Fuerteventura by A. Alcover (pers. comm.)

METHODS

For the evaluation of the characters of *Malpaisomys insularis* nov. gen., nov. sp., we selected 10 recent and 13 extinct species of murids as follows:

Apodemus sylvaticus (LINNÉ, 1758)

Rattus rattus (LINNÉ, 1758)

Mus musculus (LINNÉ, 1758)

Acomys cahirinus (DESMAREST, 1819)

Arvicanthis niloticus (DESMAREST, 1822)

Dasymys incomtus (SUNDEVALL, 1847)

Grammomys dolichurus (SMUTS, 1832)

Oenomys hypoxanthus (PUCHERAN, 1855)

Thamnomys venustus THOMAS, 1907

Uranomys ruddi DOLLMAN, 1909

Canariomys bravoii CRUSAFONT & PETTER, 1964

Canariomys tamarani LOPEZ-MARTÍNEZ & LOPEZ-JURADO, 1987

Progonomys cathalai SCHAUB, 1938

Occitanomys adroveri (THALER, 1966)

Occitanomys montheleni AGUILAR & MICHAUX, 1986

Stephanomys donnezani (DEPÉRET, 1890)
 "Paraethomys" *miocaenicus* JAEGER, MICHAUX & THALER, 1975
 "Paraethomys" *meini* (MICHAUX, 1969)
Paraethomys darelbeidae JAEGER, 1975
Parapodemus lugdunensis SCHAUB, 1938
Karnimata darwini JACOBS, 1978
 "Parapodemus" *vireti* SCHAUB, 1938
Anthracomys majori SCHAUB, 1938

Initial comparisons were also made with specimens of *Castillomys crusafonti* MICHAUX, 1969, *C. magnus* SEN, 1977, *Occitanomys brailloni* MICHAUX, 1969, *Occitanomys* sp. from Calta (Sen, 1977), *Paraethomys* cf. *filifilae* PETTER, 1968, *P. cf. anomalus* DE BRUIJN, DAWSON & MEIN, 1970, *P. ras* JAEGER, 1975, and *Valerymys ellenbergeri* (THALER, 1966). For the final analysis we used only 17 taxa. The initial comparison started with 4 mandibular and 46 dental characters, of which only 20 were used for the phylogenetic analysis to reduce the number of highly convergent characters.

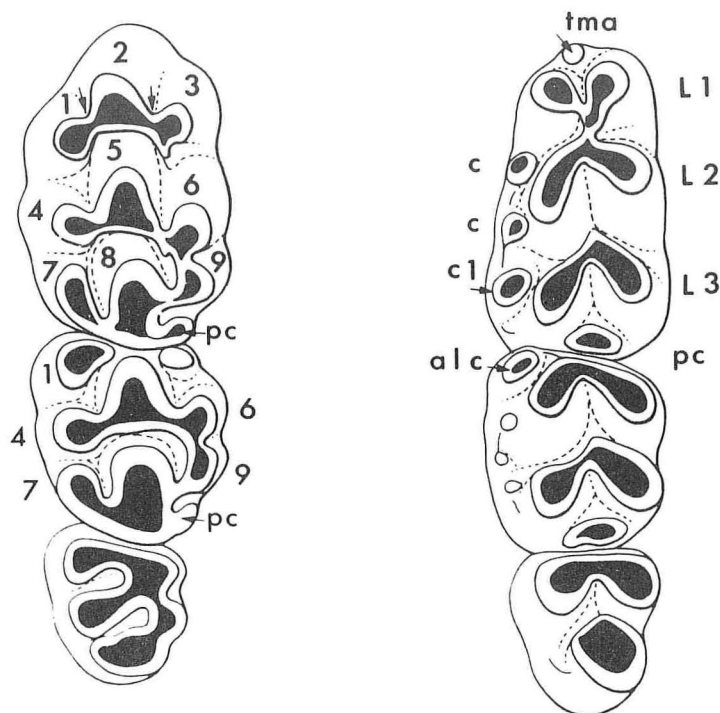


Fig. 2. Abreged nomenclature of dental structures : a diagram of upper and lower molars in *Apodemus*. Upper molars : cusps are numbered according to Miller's (1912) scheme and cusps (or tubercles) are referred to in the text with the prefix t; pc : posterior cingulum; arrows indicate the position respectively of t 1bis and t 3bis . Lower molars : L1, L2, L3 are respectively the first, the second and the third (or posterior) lobes; alc : anterolabial cusp on second lower molar; c1 : cusplet on the side of postero external cusp of first and second lower molar; c accessory cusplets on the external border of the lower molar; pc : posterior cingulum.

We used a cladistic approach for phylogenetic analysis. Cladograms have been obtained using a Phylip 2.8. program of J. Felsenstein (1985), and a manual procedure of a stepwise elimination of the most convergent characters (López-Martínez, 1978). Some tables have been made with the MacClade 2.1 program of W. Maddison and D. Maddison (1987).

Nomenclature used for dental description is given in fig. 2. Occlusal structures of murid teeth have received various names. For upper molars (fig. 2A) the nomenclature is the one proposed by Michaux (1971) which is derived from Miller's nomenclature. Lower molars (fig. 2B) which play a lesser role in phylogenetical studies than the upper ones are here described using a simplified nomenclature derived from the one of Michaux (ibid.). The accessory cusps in front of the anterior lobe (L1) of the first lower molar is called the tma, and c1 is the cusplet located on the side of the external cusp of the posterior lobe or third lobe (L3) of the first and second lower molars.

DESCRIPTION OF THE NEW RODENT

RODENTIA: MURIDAE

MALPAISOMYS NOV. GEN.

Type species: Malpaisomys insularis nov. sp.

Diagnosis: As for the type species.

Etymology: The generic name is formed by combining the Greek mys for mouse with "malpaís", the Canarian name for rough lava fields.

Malpaisomys insularis nov. sp.

Holotype: Partial skull of an adult specimen with the anterior part well preserved but lacking most of the braincase (fig. 3), CV-188.1, deposited in the Department of Paleontology, Universidad Complutense, Madrid.

Type locality: Cueva Villaverde near La Oliva (22°38'10"N, 10°12'30"W), Fuerteventura, Canary Islands. The age of the type level (CV-A1 surface) is 1070 ± 50 B.P.

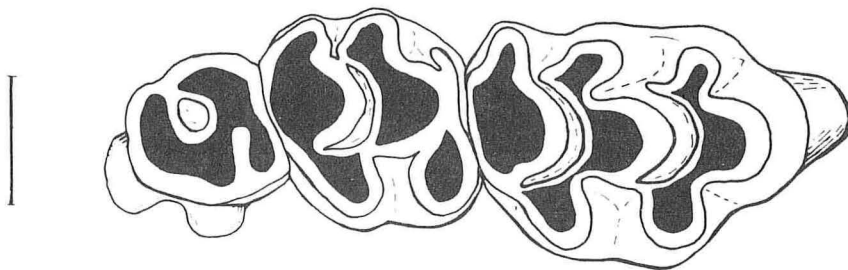


Fig. 3. Upper M1-3 of the holotype of *Malpaisomys insularis* nov. gen., nov. sp. (CV. 188-1).

Paratypes: Numerous cranial and skeletal elements from level 1 to 3 of the type locality representing 944 individuals. Paratypes are deposited in the Departamento de Paleontología, Universidad Complutense, Madrid; in the Museo Nacional de Ciencias Naturales, Madrid; the Museo Canario, Las Palmas de Gran Canaria; the Museo Insular de Ciencias Naturales de Santa Cruz de Tenerife; the Departamento de Zoología, Universidad de La Laguna, Tenerife; the Museum National d'Histoire Naturelle, Paris; the Laboratoire de Paléontologie des Vertébrés, the Université de Montpellier; and the Museum Alexander Koenig, Bonn.

Other material: Specimens representing 65 individuals from Fuerteventura (localities 2-4), Lanzarote (loc. 5-7) and Graciosa (loc. 8), deposited in the respective collections of Bonn, Montpellier, Madrid, Santa Cruz de Tenerife, and La Laguna de Tenerife.

Diagnosis: A small-bodied terrestrial rat characterized by the following combination of characters: skull stout with wide zygomatic arches and an extremely narrow interorbital constriction; incisive foramina long, their distal tips reaching the intermolar space at the middle of M1 sup.; palate extending posteriorly and covering most of the mesopterygoid fossa with bone; bulla small; mandible with a prominent alveolar crest which passes almost to the distal part of the condyle; the condyle sigmoid-shaped in lingual view; first upper molar with cusp t1 placed in a rather distal position; cusps t6 and t9 separated far from each other; cusps t1-t5 and t6-t9 frequently connected by a crest.

Measurements: Tables 1-4.

Etymology: Named because the species is only known from islands.

Distribution: Known from subfossil deposits in Fuerteventura, Lanzarote and Graciosa, Canary Islands. The species got extinct in historical times.

Description: The skull and dentary of *Malpaisomys insularis* are shown in figs. 4 and 5. Its distinct shape, namely the wide zygomatic arches and the extremely narrow interorbital, recalls at once the skull of *Nesoryzomys*, a genus of lava-dwelling rats endemic to the Galapagos Islands (see Patton & Hafner 1983, fig. 2). The dorsal profile of the skull is convex; the rostrum and nasals are of moderate size, the nasals are slightly broadened in their proximal parts; the zygomatic arches are very wide, their

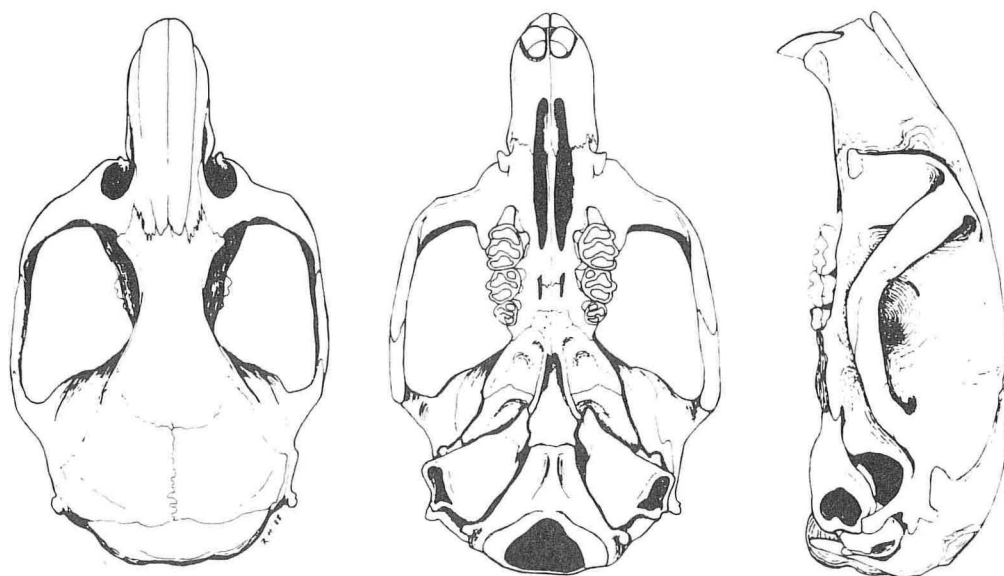


Fig. 4. Skull of *Malpaisomys insularis* nov. gen., nov. sp. in dorsal, ventral and lateral view, based upon an almost complete specimen from Fuerteventura (loc. 2).

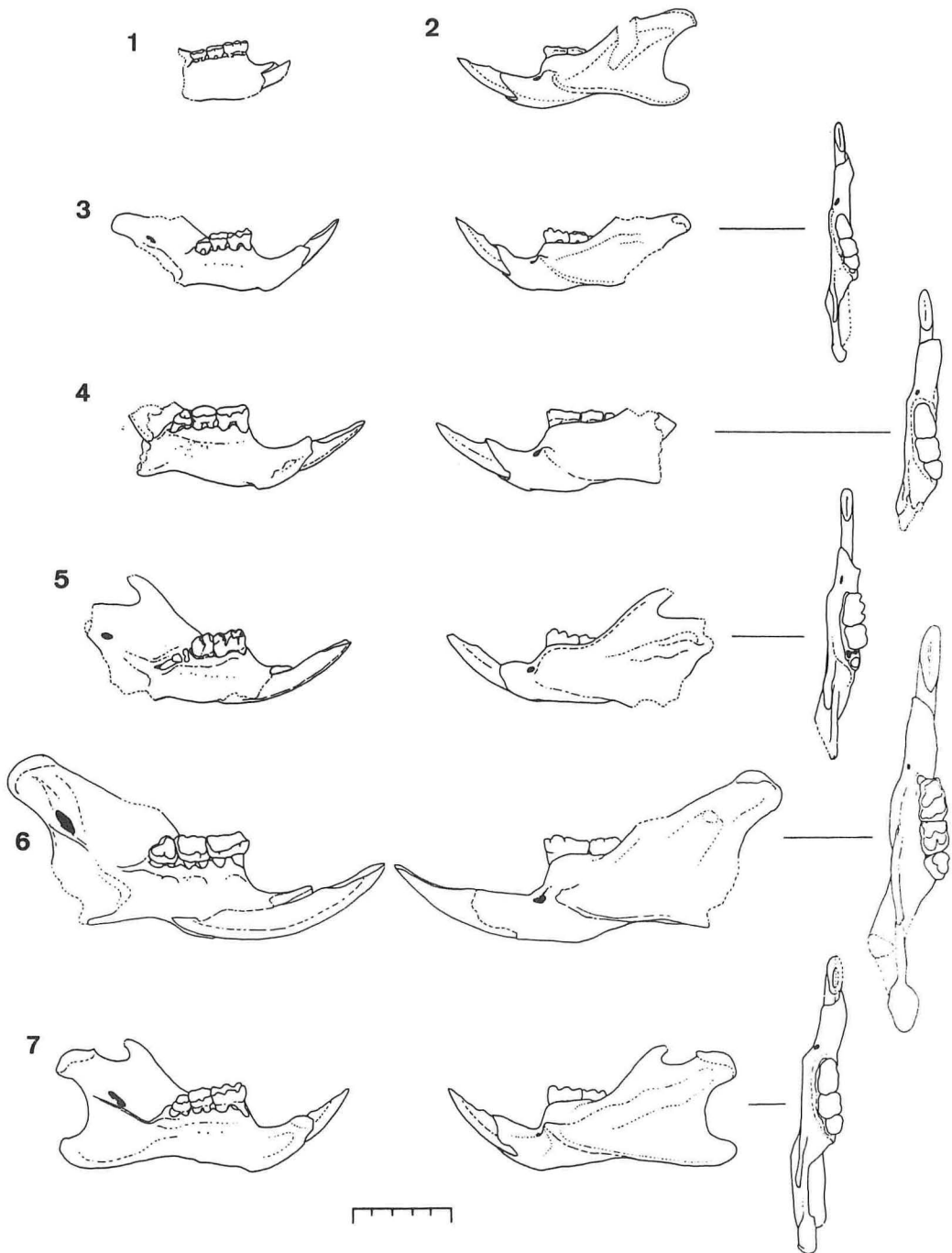


Fig. 5. Mandibular fragments of *Progonomys*, *Occitanomys* and *Paraethomys* compared with a dentary of *Malpaisomys*.

1. *Progonomys cathalai* (Montredon sup., France).
 2. "*Paraethomys*" *miocaenicus* (Hellin, Spain, see Calvo *et al.*, 1978).
 3. *Occitanomys adroveri* (Algora, Spain)
 4. *Occitanomys montheleni* (Mt H el ene, France)
 5. *Paraethomys meini* (Mt H el ene, France)
 6. *Paraethomys ras* (Doukkala-2, Morocco)
 7. *Malpaisomys insularis* (Cueva Villaverde, Fuerteventura)
- Specimens in the collections of Montpellier and Madrid.

width being 57% of the total skull length; the zygomatic plate is wide and its anterior margin is almost vertical; the frontal bones are very narrow so that the interorbital breadth counts 10,8% of the total skull length; the frontal and parietal ridges are very faint; the braincase is high, its height being almost constant from the middle of the frontal to the end of the parietal bones, then at the relatively small interparietal bone the braincase gently slopes down to the occipital bone; the incisive foramina are long and wide and extend past the middle of the first upper molars; the palatal bridge is narrow but extends far beyond to the back of the third molars, palatinum and pterygoid fossa are fused so that most of the mesopterygoid fossa is covered by bone (a similar condition is known among murids in *Acomys* and *Uranomys*, see Ellerman, 1941); the bullae are relatively small and of triangular shape, each is separated from the squamosum by a wide postglenoid vacuity; the bone of the eustachian tube is rather long; the mandible is massive; its dorsal curvature of the diastema is sharply angulated (fig. 5); the mental foramen is situated externally to the line of the molar row; the upper margin of the articular process is of sigmoid shape; the coronoid process is small; the angular process is short and rounded; a prominent alveolar ridge is running from the distal end of the alveolar row to the lower margin of the condyle.

The teeth of *Malpaisomys insularis* are brachyodont (plate 1). The first upper molar shows three roots, the internal one being a large one looking as if it was made of two fused roots. Two roots anchor the first lower molar.

The first upper molar is relatively stout, wider for example than the first upper molar in *Stenocephalemys*. Molars weakly overlap each other. The second upper molar is more or less as wide as long and the third upper molar is not very reduced. The first upper molar consists of three transverse rows of cusps linked together by crests. This tooth is widest at the level of cusp t1. The central cusps are slightly larger than the inner and outer ones. There are two inner and three outer cusps. Cusp t7 and posterior cingulum are absent on both first and second upper teeth. A gentle and shallow fold of the crown can nevertheless be observed on first upper molar between cusp t9 and cusp t8.

Cusp t1 occupies a rather posterior position by comparison with cusps t2 and t3. In this manner, *Malpaisomys* resembles more *Occitanomys* than *Paraethomys*. There is no cusplet t1 bis. On most of the molars a narrow crest of variable length links the cusp t1 and t5 following the lingual flank of cusp t5. A short posterior crest can be seen on cusp t3, like often in *Apodemus*. The second row of cusps (t4, t5, t6) runs more or less parallel to the first one. Cusp t6 slopes weakly in the anterior direction so it offers a long anterior flank. This situation contrasts sharply with the more vertical cusp t3. The relative size difference between cusps t9 and t6 is small and connection between them occurs in half of the cases. Stephanodonty is not completely established in *Malpaisomys*. The second upper molar possesses a large cusp t1 and a small cusp t3. Cusp t1 shows a beak directed labially. In most of the cases, cusps t6 and t9 are isolated and there is no incipient crest linking cusps t1 and t5 as observed on the first upper molar. The third upper molar has a triangular cusp t1 with a short labial beak. This cusp is as big as cusp t4. Cusp t3 is absent. Behind cusp t4 there are two cusps more or less at the same transversal level. The third upper molar is more or less square-shaped. The central cusps, t4, t5 and t6 form an asymmetric row.

The lower first molar shows in half of the cases a rather small anteromedian cusp. First and second lower molars have a relatively reduced posterior cingulum. The external row of cusplets on the first lower molar is weak or absent. The anterior lobe of the first lower molar is wide and shows two equally well differentiated cusps which are centrally linked to the median lobe. No connection occurs between the median and the posterior lobe. The same situation is present on the second lower molar. The anterolabial cusp is rather small on the second lower molar and absent on the third one.

The posterior lobe of the third lower molar is isolated and widened labially.

Measurements of 100 mandibles from Cueva Villaverde (table 2) show a trimodal distribution of mandible length. Distribution has been separated into three age classes: 1 (molars slightly worn), 2 (molars moderately worn) and 3 (molars heavily worn). Bimodality appears separately in both 2 and 3 age classes. This indicates that dimorphism not related with age is present in the mandibular length of *Malpaisomys*. The most probable explanation is the sexual dimorphism. There are no indications of a dimorphism in tooth size. However, there is a trend towards smaller molar measurements in the Lanzarote samples, notably in the upper M 1 (table 3).

Numerous remains of the postcranial skeleton have been recovered. At first sight no special features have been observed which would indicate special adaptations. Some elements are shown in plate 2 and measurements are given in table 4. Apparently there exist significant differences in the size of some skeletal elements between some populations. First, within Fuerteventura, the population from locality 4 seems to be larger. Secondly all the Fuerteventura populations show higher measurements than the Lanzarote populations. As the samples may differ in geological age, it is difficult at this moment to evaluate this variation.

CHARACTER ANALYSIS AND PHYLOGENETIC AFFINITIES

We have selected 20 dental characters for the phylogenetic analysis out of 51 features used in the preliminary comparison. Characters listed below have been rejected because information for all taxa was not available (1) or because they were redundant in relation to other selected characters (2).

- 1 – Alveolar ridge of mandible (1)
- 2 – Articular process (1)
- 3 – Mental foramen (1)
- 4 – Diastema of the mandible (1)
- 5 – Overlap of the upper molars (1)
- 6 – Slope of the molar cusps (1)
- 7 – Roots of the lower first molar (2)
- 8 – Shape of the upper second molar (2)
- 9 – Posterior cingulum of the second upper molar (2)
- 10 – Relative size of t9 in the first upper molar (2)
- 11 – Cusp t7 on upper molars (not present in the compared species)
- 12 – Connection between t6-t9 in second upper molar (2)
- 13 – Connection between t1-t5 in second upper molar (2)
- 14 – Connection between t3-t5 in second upper molar (2)
- 15 – Relative position of t6 and t8 on the third upper molar (1)
- 16 – Posterior cingulum of the second lower molar (2)
- 17 – Width of the anterior lobe of the first lower molar (2)
- 18 – Position of the anterior cusps of the first lower molar (2)
- 19 – Connection between the two lobes of the second lower molar (2)
- 20 – Antero-labial cusp of the third lower molar (2)
- 21 – Width of the posterior lobe of the third lower molar (1)
- 22 – Number of cusps at the posterior part of the third lower molar (1)
- 23 – Shape of the third upper molar (1)
- 24 – Size of cusp t1 in the third upper molar (1)
- 25 – Shape of cusp t1 in the third upper molar (1)
- 26 – Shape of the medial lobe in the third upper molar (1)

Remaining characters have been analysed previously with the Lequesne method in search of the *a priori* less convergent characters. The number of combinations of character states was controlled for each pair of characters in all the selected species. The presence of the four possible combinations of the two main states (primitive and derived) of two characters indicates that one of the features, at least, is convergent or, in the Lequesne terminology, has not been uniquely derived.

After statistical calculation, the characters concerning the stephanodonty showed the smallest number of combinations, indicating that they are *a priori* less frequently subject to convergence. On the contrary, the characters listed below, and frequently cited in the literature as relevant features for the phylogenetic and systematic studies, showed the highest number of combinations. Therefore, they have been rejected because they introduce noise in the phylogenetic information. The remaining features may have also convergences, but they show *a priori* not a random distribution.

- 1 – Relative size of cusp t9 in the second upper molar
- 2 – Anterio-external beak of cusp t1 in the second upper molar
- 3 – Divergence of cusps t3 and t6 in the first upper molar
- 4 – Size of cusp t3 in the second upper molar
- 5 – Presence of cusp t3 in the third upper molar.

The characters selected for the phylogenetic analysis are defined below. Code (0) indicates our view of the primitive state. The species *Antemus chinjiensis* JACOBS, 1978 has been used as the outgroup for this purpose.

- 1 – Tooth morphology: brachyodont (0) or semi-hypsodont (1)
- 2 – Enamel differentiation: thickness of the enamel slightly differentiated (0); almost not differentiated (1) strongly differentiated (2). The two evolved states have probably derived independently.
- 3 – Width of the first upper molar: position of the maximum width at t4 (0); similar width at the t4 and t1 (1); or maximum width at t1 (2)
- 4 – Number of roots of the first upper molar: lower than 5 (0) or 5 or more (1)
- 5 – Position of the t1 at the first upper molar: strongly backwards as in *Acomys* (0); less backwards as in *Apodemus* (1) or at the level of t3 like in *Dasymys* (2)
- 6 – Accessory cusps t1bis and t3bis on the anterior lobe of the first upper molar: absent (0), variable (1) or present (2)
- 7 – Connection of t1 with t2 or t4 with t5 on the first upper molar: absent (0) or present (1)
- 8 – Cusps t2-t3 and t5-t6 of the first upper molar: connected but clearly individualized (0) or fused (1)
- 9 – Connection of t6 with t9 at the first upper molar: absent (0), variable (1) or present (2)
- 10 – Connection of t1 with t5 at the first upper molar: absent (0), incomplete (1) or present (2)
- 11 – Connection between cusps t3-t5 at the first upper molar: as in number 10
- 12 – Connection between t4-t8 at the first upper molar: as in number 9
- 13 – Posterior cingulum at the first upper molar: large (0), small (1) and absent (2)

- 14 – Relative size of the third upper molar: ratio length M3/ length M2/ between 0.7 and 0.8 (0); ratio lower than 0.7 (1) or above 0.8 (2). Values have been calculated for the two morphotypes of Jacobs (1978, p. 79) the intermediate state being considered as primitive
- 15 – Anterior median cusps (tma) at the first lower molar: absent (0), variable (1) and present (2)
- 16 – Posterior cingulum at the first lower molar: large (0), reduced (1) or absent (2)
- 17 – External cingular margin at the first lower molar: with one or two additional cusps (0); with no cusps (1) or with more than two cusps (2). The cusp named C1 and another anterior one are usually present in murids and therefore this condition is considered to be primitive. Derived states are divergent
- 18 – Anterior lobe of the first lower molar: asymmetrical weak connection as in *Stephanomys* and *Progonomys* (0); isolated as in *Rattus* (1), or strong central connection like in *Mus* (2). The only well-preserved M1 of *Antemus chinjiensis* (see Wessels *et al.* 1982, pl. 2, fig. 7) presents the character state most common among murids, and therefore regarded as primitive. Derived states are divergent
- 19 – Posterior lobe of the first lower molar: isolated from the median lobe (0); incompletely linked (1) or completely linked (2)
- 20 – Anterolabial cusp of the second lower molar: large (0), or reduced or absent (1).

The data matrix of the character states' distribution in the selected taxa is shown in table 5. The aim of the phylogenetic analysis is to select one of the possible trees constructed by manual or automatic technics. The phylogenetic tree must have as few convergences as possible; but the problem of character reversion has to be considered.

In the Camin-Sokal procedure, reversions are not allowed; all the evolutionary steps are considered irreversible. On the contrary, the Wagner procedure allows reversions for all characters; steps 0>1 and 1>0 are equally probable.

In the case of murids, reversions have been documented in some species lineages. For example, *Stephanomys donnezani*–*S. minor* illustrate reversion of the character 17 (Bachelet, pers. comm.); *Apodemus gudrunae*–*A. jeanteti* illustrate reversion of the character 15 (Michaux, 1967). For other characters, as the enamel differentiation (n°1), acquisition of the semi-hypsodonty (n° 2) and tooth-size reduction (n° 14), it seems unlikely that reversion has occurred in the evolution of mammals in general. The characters 13 and 16 are considered as not reversible.

Fig. 6 shows one of the cladograms constructed under these above mentioned conditions. The total number of steps for this cladogram is 86, and includes as much as 54 convergences and 6 reversions. The high number of necessary convergences indicates that it cannot be taken as a definitive phylogenetic tree. Nevertheless it shows some clusters which were previously recognized by some authors using also characters other than molars, whereas our cladogram is exclusively based on molar characters.

Malpaisomys groups with *Acomys* and *Uranomys*; all three share the derived characters 16 and 18. This cluster is close to the group including all the highly stephanodont taxa: *Stephanomys*, *Occitanomys*, "*Paraethomys*" *darelbeidae*, and *Oenomys*. *Malpaisomys*, *Acomys* and *Uranomys* share one additional character in the extension of the palatal bridge (see fig. 4), a unique feature among murids, according to Ellerman (1941). Also the incisive foramina extend far past the middle of the first upper molars in these three genera, which is a character not frequently encountered in murids. On the other hand, *Malpaisomys* shows a sharply angulated diastema in the mandible

(fig. 5), a character not shared by the two other genera.

Another cluster is formed by *Arvicanthis*, *Rattus* and "*Canariomys*" *tamarani*. *Karnimata darwini* cannot be clustered because of its low number of derived characters. At the basis of the tree, the branches are supported by few derived characters, but the general grouping seems congruent with the "rat-mouse" dichotomy of Jacobs (1978, p. 83, fig. 35). *Progonomys* appears related to the group including *Mus* and *Acomys*, as Jacobs proposed (1978, p. 83, fig. 37).

This group includes also several large-sized murids like *Canariomys bravoii*, and *Oenomys*. Both share a high degree of stephanodonty and the presence of some accessory cusps in the lower first molar (characters 15 and 17).

The two species of *Canariomys* (López-Martínez & López-Jurado, 1987) appear in two separate clusters. This is mainly the consequence of different states in the characters numbers 3, 4 and 20. At this stage of our study it seems premature to draw conclusions, but our result might indicate that the two species are not as closely related as previously thought. The same applies to the two species of *Paraethomys* included in our study. The high number of taxa described in the genus *Paraethomys* (Jaeger, 1975, Michaux, 1969; de Bruijn *et al.*, 1970; Jaeger, 1975, Jaeger *et al.*, 1975) deserves a careful re-examination before any phylogenetic interpretation can be drawn.

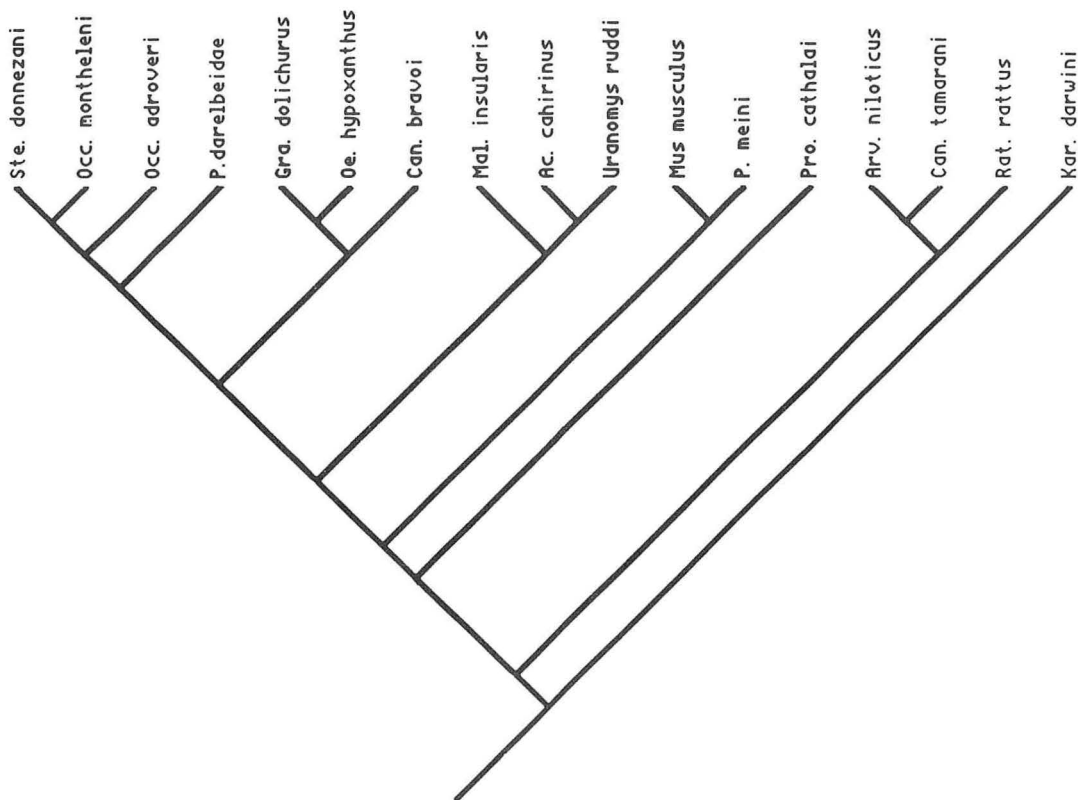


Fig. 6. One cladogram obtained from the data matrix given in table 5. The first three branchings are based on one derived character.

Other cladograms gave sometimes different results in the position of *Malpaisomys*, indicating a closer relationship with either *Paraethomys* or *Mus*. However, none of these alternative solutions fits with additional skull characters like the *Malpaisomys* - *Acomys* - *Uranomys* hypothesis, which we therefore prefer.

CONCLUSIONS

As mentioned earlier, the skull of *Malpaisomys* (fig. 7) is highly specialized in its extremely narrow interorbital region and the wide zygomatic arches. Such a skull configuration is also known from other island endemics, like *Nesoryzomys* of the Galapagos Islands (Patton & Hafner, 1983). The species of *Nesoryzomys* are large-eyed, soft-furred nocturnal rats (see Brosset, 1963, for a photograph of *Nesoryzomys narboroughi*) which live in all available habitats, from the coasts to the summits of the volcanoes (four out of five island populations are extinct; Clark, 1984). Much of the habitat available in the Galapagos corresponds to the malpaís of the Canary Islands. A further example of convergent skull features are the giant rats of the two archipelagos. The Galapagos *Megaoryzomys* (see Steadman & Ray, 1982, for an illustration) is very similar in skull shape to the Canarian *Canariomys* (see López-Mártinez & López-Jurado, 1987, for an illustration). In addition, the skulls of

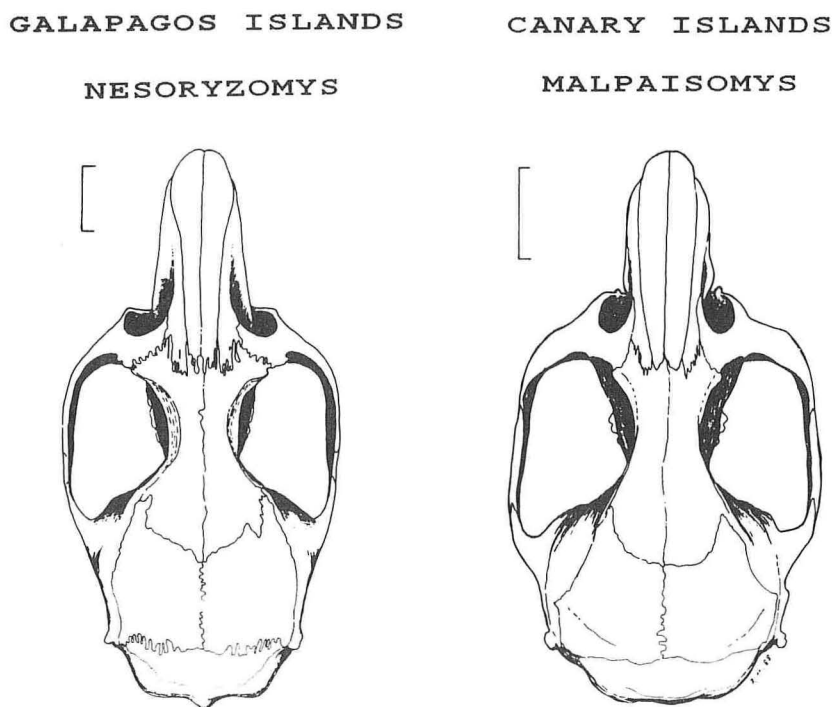


Fig. 7. Dorsal aspects of the skull of *Nesoryzomys narboroughi*, a cricetid, and of *Malpaisomys insularis*, a murid, to show similarities in skull shape which are due to parallel evolution. Both rodents shared the same type of habitat (volcanic islands). Illustrations are based on specimens in the Museum Alexander Koenig, Bonn. The scales represent 5 millimetres each.

both resemble *Crateromys*, a genus of arboreal giant rats of the Philippines (Musser *et al.*, 1985). Apparently the three-dimensional creviscular malpais claims largely the same morphological adaptations as thick bush or trees.

The above-mentioned genera belong to different families. Therefore the skull features they have in common certainly developed by parallel evolution. This indicates a rather long, independent evolution of *Malpaisomys* in the Canary Islands. In our search for its phylogenetic relationships we therefore disregarded these peculiar features. It is for this reason that we tried to use mainly dental characters and cranial features which we supposed not to be adaptive. However, the phylogenetic study showed that even within these selected characters convergences occur rather frequently. For that reason we finally used only 20 characters out of 51. We arrived at the conclusion that *Malpaisomys* may share a common ancestor with two African genera, *Acomys* and *Uranomys*. Many species of *Acomys*, most of them of unsettled status, occur in Africa, Arabia, and Asia (Honacki *et al.*, 1982; Petter, 1984). East Africa houses the highest number of species. Along the Atlantic coast of NW-Africa only members of the *A. cahirinus* group occur. The distributional range of *Uranomys* is limited by southern Senegal in the north and by Mozambique in the south. Only one species, *U. ruddi*, is currently recognized in this genus (Honacki *et al.*, 1982).

There exists no fossil record of *Uranomys*, and that of *Acomys* is very poor. Wesselman (1984) referred a single first upper molar from the Shungura Formation, Upper Pliocene of Ethiopia, to *Acomys* sp., which was quite similar to the modern species of the genus. Material from Laetoli, Pliocene of Tanzania, also exhibits modern traits (Denys, 1987). Further fossils of *Acomys* were reported by De Graaf (1961a, b) from Makapansgat and Kromdraai, Pleistocene of South Africa. All the fossil material of *Acomys* resembles modern species and therefore contributes little to the understanding of the evolution of that genus. Jacobs (1978) postulated that *Acomys* derived from the "*Progonomys* stock". According to our results, we must claim that the common ancestor of *Malpaisomys*, *Acomys* and *Uranomys* lived between 11Ma (branching of the *Progonomys* -"mouse group") and Pliocene times.

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TABLES 1 to 5

Locality :	2	2	2	1	1	2	1	1
Age class :	1	1	1	2*	2	3	3	3
Measurement :								
Greatest length of skull	—	—	—	—	—	31,5	—	—
Zygomatic breadth	—	—	—	—	—	18,0	—	—
Breadth of braincase	—	—	—	—	—	14,1	—	—
Height of braincase	—	—	—	—	—	10,3	—	—
Interorbital breadth	3,5	3,6	3,6	3,6	4,1	3,4	3,5	3,2
Length of nasals	12,2	13,4	—	12,2	—	13,9	13,4	—
Breadth of zygomatic plate	3,9	4,0	4,1	3,9	—	4,1	4,0	4,1
Length of diastema	8,1	7,7	8,2	8,1	7,3	8,0	7,7	8,2
Length of palate	15,2	15,1	16,2	15,2	14,8	16,2	15,1	16,2
Length of incisive foramina	8,3	8,1	8,5	8,3	7,4	8,3	8,1	8,5
Breadth of incisive foramina	3,1	2,9	2,5	3,1	2,4	3,0	2,9	2,5
Breadth of palatal bridge at M1/	2,6	2,4	2,4	2,6	2,6	3,0	2,4	2,4
Breadth of palatal bridge posterior to M3/	4,4	4,5	4,1	4,4	4,1	4,5	4,5	4,1
Length of bulla	—	—	—	—	—	7,2	—	—
Alveolar length of M1-3/	5,9	6,1	6,7	6,0	6,1	7,0	6,6	6,7
Crown length of M1-3/	5,4	5,6	5,8	5,3	5,6	—	5,8	5,8

* holotype

Table 1. *Malpaisomys insularis* n. g., n. sp., skull measurements of specimens from Fuerteventura (localities 1 and 2; see fig. 1).

Locality	Age class 1	Age class 2	Age class 3
Upper tooththrow length			
Fuerteventura			
Loc. 1	5,44 ± 0,19 (25)	5,44 ± 0,16 (50)	5,37 ± 0,17 (16)
Loc. 2	5,60 ± 0,08 (4)	5,61 ± 0,13 (6)	5,90 ± 0,10 (3)
Loc. 4	–	–	5,85 (2)
Lanzarote			
Loc. 5	5,52 ± 0,19 (4)	5,65 (2)	5,90 (1)
Loc. 6	5,62 ± 0,05 (4)	5,67 ± 0,05 (7)	5,67 ± 0,13 (4)
Lower tooththrow length			
Fuerteventura			
Loc. 1	5,37 ± 0,14 (25)	5,39 ± 0,15 (25)	5,34 ± 0,17 (17)
Loc. 2	5,35 ± 0,13 (4)	5,49 ± 0,12 (7)	–
Loc. 3	5,30 (2)	5,50 (1)	5,60 ± 0,26 (3)
Loc. 4	–	–	5,60 (1)
Lanzarote			
Loc. 5	5,20 (1)	5,40 (2)	5,20 (2)
Loc. 6	5,43 ± 0,10 (6)	5,47 ± 0,06 (3)	5,55 (2)
Mandible length			
Fuerteventura			
Loc. 1	16,68 ± 0,60 (25)	18,18 ± 0,62 (50)	18,58 ± 0,52 (25)
Loc. 2	16,75 ± 0,45 (4)	17,26 ± 0,44 (5)	18,00 ± 0,75 (3)
Loc. 3	17,00 (1)	18,10 (1)	19,60 (1)
Lanzarote			
Loc. 6	17,07 ± 0,92 (4)	–	–

Table 2. *Malpaisomys insularis* n.g., n. sp.; crown length of upper and lower tooththrow and length of mandible without incisor. Measurements separate for age class 1 (no or little wear), 2 (teeth moderately worn) and 3 (heavily worn). Mean, standard deviation and sample size indicated.

Locality	M1/ Length	M1/ Width	M/1 Length	M/1 Width
Fuerteventura				
Loc. 1	2,80±0,10 (70)	1,96±0,08 (59)	2,46±0,08 (33)	1,65±0,07 (33)
Loc. 2	2,82±0,24 (21)	1,96±0,09 (21)	2,50±0,08 (24)	1,67±0,09 (25)
Loc. 3	2,80±0,14 (3)	1,92±0,11 (3)	2,48±0,09 (9)	1,61±0,07 (9)
Loc. 4	2,90 (2)	1,90 (2)	2,56 (1)	1,68 (1)
Lanzarote				
Loc. 5	2,72±0,06 (9)	1,91±0,10 (10)	2,44±0,10 (9)	1,56±0,06 (9)
Loc. 6	2,69±0,08 (16)	1,90±0,08 (16)	2,45±0,06 (21)	1,62±0,08 (21)
Loc. 7	2,75±0,02 (3)	1,95±0,06 (3)	2,56 (2)	1,64 (2)
Loc. 8	2,68 (2)	1,84 (2)	–	–
Locality	M2/ Length	M2/ Width	M/2 Length	M/2 Width
Fuerteventura				
Loc. 1	1,88±0,07 (71)	1,87±0,06 (71)	1,69±0,08 (33)	1,66±0,06 (33)
Loc. 2	1,90±0,08 (20)	1,86±0,07 (20)	1,72±0,09 (26)	1,71±0,09 (26)
Loc. 3	1,96 (1)	1,88 (1)	1,73±0,03 (9)	1,63±0,07 (9)
Loc. 4	1,85 (2)	1,88 (2)	1,80 (1)	1,76 (1)
Lanzarote				
Loc. 5	1,87±0,09 (9)	1,81±0,07 (9)	1,68±0,06 (8)	1,61±0,07 (8)
Loc. 6	1,85±0,07 (16)	1,83±0,06 (16)	1,76±0,07 (20)	1,65±0,07 (20)
Loc. 7	1,90 (2)	1,82 (2)	1,83±0,04 (4)	1,73±0,11 (4)
Loc. 8	1,84 (2)	1,78 (2)	–	–
Locality	M3/ Length	M3/ Width	M/3 Length	M/3 Width
Fuerteventura				
Loc. 1	1,43±0,08 (69)	1,36±0,07 (69)	1,32±0,05 (33)	1,31±0,06 (33)
Loc. 2	1,43±0,06 (14)	1,32±0,06 (14)	1,28±0,07 (17)	1,30±0,06 (15)
Loc. 3	–	–	1,30±0,05 (5)	1,23±0,07 (5)
Loc. 4	1,50 (2)	1,40 (2)	1,40 (1)	1,44 (1)
Lanzarote				
Loc. 5	1,42±0,08 (7)	1,34±0,06 (7)	1,21±0,02 (6)	1,27±0,03 (6)
Loc. 6	1,44±0,06 (12)	1,32±0,05 (12)	1,35±0,09 (13)	1,29±0,06 (13)
Loc. 7	–	–	1,36 (1)	1,36 (1)

Table 3. *Malpaisomys insularis* n.g., n. sp., molar measurements; mean, standard deviation and sample size given.

Locality	Total length	Length without epiphysis	Minimum diameter
Humerus			
Fuerteventura			
Loc. 1	16,47 ± 0,60 (9)	14,75 ± 0,78 (32)	1,31 ± 0,10 (41)
Loc. 2	16,00 ± 0,62 (3)	14,67 ± 1,34 (10)	1,32 ± 0,13 (13)
Loc. 3	–	15,10 ± 0,17 (3)	1,30 ± 0,10 (3)
Loc. 4	–	15,8 (1)	1,30 (1)
Lanzarote			
Loc. 5	–	14,50 ± 0,63 (4)	1,42 ± 0,10 (4)
Loc. 6	14,9 (1)	14,62 ± 0,49 (4)	1,32 ± 0,08 (5)
Femur			
Fuerteventura			
Loc. 1	24,56 ± 0,99 (8)	21,67 ± 1,13 (61)	1,84 ± 0,13 (69)
Loc. 2	23,05 (2)	21,26 ± 1,00 (11)	1,76 ± 0,13 (13)
Loc. 3	–	20,95 ± 1,47 (4)	1,85 ± 0,06 (4)
Loc. 4	–	24,15 ± 1,14 (6)	1,95 ± 0,08 (6)
Lanzarote			
Loc. 5	–	19,5 (2)	1,65 (2)
Loc. 6	–	19,19 ± 1,22 (10)	1,75 ± 0,07 (10)
Loc. 7	–	18,8 (1)	1,6 (1)
Loc. 8	–	20,8 (1)	2,1 (1)
Ulna			
Fuerteventura			
Loc. 1	19,41 ± 1,38 (30)	–	0,66 ± 0,06 (30)
Loc. 2	19,06 ± 1,69 (11)	–	0,67 ± 0,04 (11)
Tibia			
Fuerteventura			
Loc. 1	–	24,81 ± 1,65 (30)	1,23 ± 0,09 (30)
Loc. 2		24,84 ± 2,45 (9)	1,20 ± 0,11 (9)

Table 4. *Malpaisomys insularis* n. g., n. sp. ; measurements of some postcranial elements. Mean, standard deviation and sample size indicated.

Characters	1	3	5	7	9	11	13	15	17	19													
Taxa	2	4	6	8	10	12	14	16	18	20													
<i>Can. bravoii</i>	0	1	2	0	2	0	1	0	2	2	2	0	2	1	0	0							
<i>Can. tamarani</i>	1	1	0	1	0	0	1	0	0	0	0	2	2	2	0	1	0	0	1				
<i>Mus. musculus</i>	0	0	2	0	0	0	1	0	0	0	0	0	0	2	1	0	0	1	2	0	1		
<i>Rat. rattus</i>	0	1	1	2	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	
<i>Mal. insularis</i>	0	0	2	0	1	0	1	0	1	2	1	1	2	0	1	1	1	2	0	0	0	0	
<i>Gra. dolichurus</i>	0	0	2	1	1	0	1	0	2	1	0	2	0	0	2	0	2	1	1	0	0	0	
<i>Oe. hypoxanthus</i>	0	2	2	1	1	2	1	0	2	1	2	1	1	2	2	0	2	1	1	0	0	0	
<i>Arv. niloticus</i>	0	1	0	1	2	0	1	1	0	0	0	2	2	0	2	0	0	0	0	1	0	0	
<i>Ac. cahirinus</i>	0	0	2	0	0	0	1	0	0	0	0	1	1	0	0	1	0	2	0	1	0	2	0
<i>Uranomys ruddi</i>	0	0	2	0	0	0	1	0	0	0	0	2	0	0	1	0	2	0	0	0	0	0	0
<i>P. darelbeidae</i>	0	0	0	0	1	0	1	0	2	1	1	2	2	0	0	2	0	1	0	0	0	0	0
<i>P. meini</i>	0	0	1	0	1	0	1	0	2	0	0	0	1	0	0	1	0	1	0	1	0	1	0
<i>Occ. adroveri</i>	0	0	2	0	0	2	1	0	2	1	1	2	1	0	0	1	2	1	1	0	0	0	0
<i>Occ. montheleni</i>	0	0	2	0	0	2	1	0	2	2	1	2	1	0	0	1	2	1	1	0	0	0	0
<i>Pro. cathalai</i>	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0
<i>Ste. donnezani</i>	1	0	2	0	0	2	1	0	2	2	2	2	2	0	0	1	0	1	2	0	0	0	0
<i>Kar. darwini</i>	0	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0

Table 5. Matrix of the taxa and characters used for the phylogenetic analysis.

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LEGENDS OF PLATES

PLATE 1

Upper and lower molars of *Malpaisomys insularis* n. g., n. sp.

1. Upper toothrow (Lanzarote, loc. 6)
2. Upper toothrow (Fuerteventura, loc. 2)
3. Upper toothrow (Fuerteventura, loc. 2)
4. Lower toothrow (Fuerteventura, loc. 2)
(specimens in the Museum Bonn).

PLATE 2

Some skeletal elements of *Malpaisomys insularis* n. g., n. sp. from Fuerteventura (loc. 2).

1. Atlas ; a, caudal view ; b, dorsal view
2. Axis ; a, cranial view ; b, dorsal view
3. Lumbar vertebra ; a, caudal view ; b, lateral view
4. Sacrum ; a, dorsal view ; b, ventral view
5. Scapula ; a, distal view ; b, dorsal view
6. Humerus ; a, anterior view ; b, medial view
7. Ulna ; a, lateral view ; b, anterior view
8. Pelvis ; lateral view
9. Femur ; a, anterior view ; b, lateral view
10. Tibia ; a, lateral view ; b, posterior view
(Specimens in the Museum Bonn).

