NEOGENE AND QUATERNARY MAMMALS OF THE PALAEARCTIC

PAPERS IN MAMMAL PALAEONTOLOGY HONORING KAZIMIERZ KOWALSKI

Edited by

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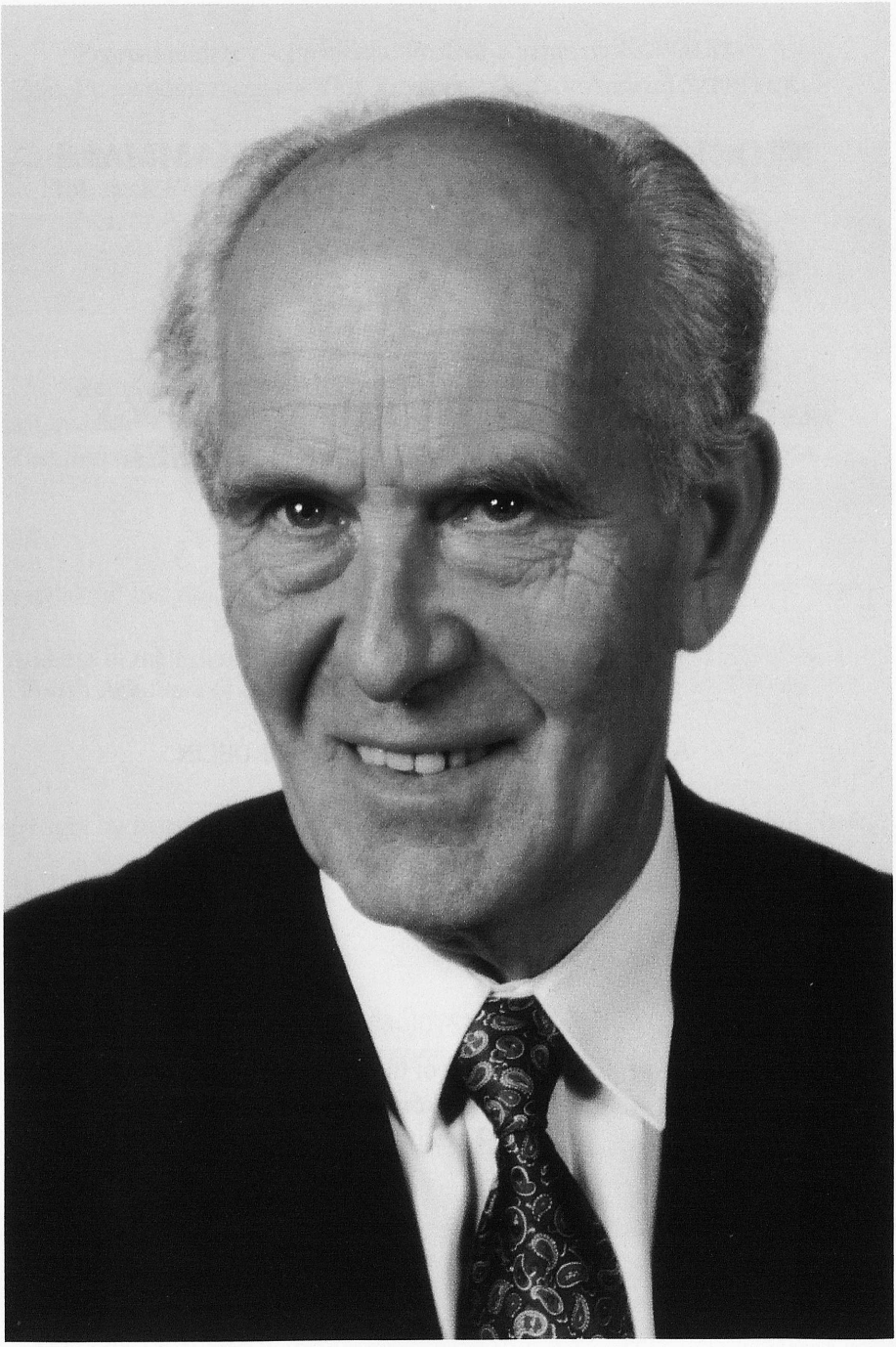

K. Konrelshi

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PREFACE

The conference 'Neogene and Quaternary mammals of the Palaearctic' that we see the printed results of in this volume originated as a tribute to the scientific activities of Kazimierz KOWALSKI. It was developed as one offshoot of the European Science Foundation network on 'Quaternary Mammalian Faunas', which in the years 1991-1993 organised three workshops dealing with important aspects of the evolution of mammalian faunas during the Quaternary. The conference was held in Kraków, 17-21 May, 1994. It included 101 participants from 26 countries.

On the first day a special ceremonial session took place celebrating Kazimierz KOWALSKI's almost 50 years of service to the field of mammalian paleontology. During the subsequent sessions, a total of 39 oral presentations were made and 57 posters presented. There was no central theme to the conference other than that indicated by the title, and papers were presented on mammalian systematics, evolution, taphonomy, palaeoecology and biostratigraphy in the Neogene and Quaternary. In addition, three round-table discussions on specified themes were organised: 'Evolutionary dynamics and classification of phyletic series' (conveners: R. MARTIN and L. WERDELIN), 'The *Allophaiomys* problem and early stages of *Microtus* evolution (convener: J. AGUSTÍ) and 'Biostratigraphic and chronostratigraphic correlation of the Neogene and Quaternary mammal localities of the Palaearctic' (conveners: R. DAAMS, O. FEJFAR, E. VANGENGEIM).

Papers discussing systematics and/or new taxa form 31% of the total, while papers that are regional surveys of mammalian palaeofaunas represent 27%. Articles on mammalian evolution form 19% of all papers, while biostratigraphic problems (11%), palaeoecology (6%), taphonomy (3%) and new methodologies (3%) make up the rest.

Some 62 scientific papers related to the conference are published here. Not all were presented in Kraków; some contributors who were unable to attend were invited to contribute to this volume and to thus honour Kazimierz KOWALSKI. Taken as a whole the contents of this volume make a forceful statement concerning the importance of mammalian palaeontology to studies of the biology of mammals and also show the dynamic state of the field.

After the conference a one-day scientific excursion was organized. It took the participants to karst localities with Neogene and Quaternary mammals in the Kraków-Częstochowa upland.

The following colleagues assisted in the compilation of this volume by reviewing papers: J. AGUSTÍ, P. BRUNET-LECOMTE, J. CHALINE, R. DAAMS, C. DENYS, V. EISENMANN, M. ERBAJEVA, V. FAHLBUSCH, O. FEJFAR, F. FLADERER, A. FORSTEN, M. FORTELIUS, L. GINSBURG, G. HAYNES, G. DAXNER-HÖCK, L. L. JACOBS, W. v. KOENIGSWALD, L. KORDOS, K. KOWALSKI, A. LISTER, A. MARKOVA, R. MARTIN, E. MARTIN-SUAREZ, J. MICHAUX, A. NADACHOWSKI, G. RABEDER, J. REUMER, B. RZEBIK-KOWALSKA, B. SALA, R. SAVAGE, A. SHER, G. STORCH, E. STWORZEWICZ, D. TORRE, A. TURNER, T. VAN KOLFSCHOTEN, L. WERDELIN and M. WOLSAN.

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KAZIMIERZ KOWALSKI: A BIOGRAPHICAL SKETCH

Kazimierz KOWALSKI was born in Cracow 15 March, 1925 into the family of Jagiellonian University professor Tadeusz KOWALSKI and Zofia MEDWECKA, a medical doctor. He attended high school (gymnasium) before the Second World War, and completed his studies by 1943, passing courses in secret. Immediately after, he began attending classes in biology at the Jagiellonian University, officially closed under German occupation, but secretly working underground. He graduated from this University in 1947 and obtained his PhD in 1949. His thesis was based on the description of daily activity rhythms in two common rodents and their dependence on lighting conditions.

From 1948 to 1954 he worked as a research assistant and instructor at the Department of Animal Psychology and Ethology at the Jagiellonian University, and was interested in the ecology and biology of small mammals. In 1954 Dr. KOWALSKI changed his job and continued his research in the Cracow Branch of the Institute of Zoology of the Polish Academy of Sciences (now the Institute of Systematics and Evolution of Animals). From that time onward his career has been linked to this Institute.

In 1962 Dr. KOWALSKI became professor of zoology. He was appointed as the director of the Institute and served in this capacity for many years (1960-1978, and again in 1985-1987) and also headed its Department of Vertebrates. Under his direction the Institute became an independent research unit of the Academy (1960). This long stay in the Institute was interrupted only for 5 years (1978-1983) when Professor KOWALSKI went to Algeria, where he lectured in zoology at the University of Oran and studied the mammalian fauna of this country.

The scientific interests of Kazik KOWALSKI (as he is known to his friends) are well known to zoologists, paleontologists and speleologists. As a zoologist he studied the ecology of forest rodents and their activity rhythms. He studied the distribution and migration of bats and the ecological conditions of their hibernation. One of the results of these studies was a book: "Our bats and their protection" (1954), which was later translated into English (1969). Kazik was also interested in the morphological characteristics of mountain rodents and contributed to research on the mammal fauna of selected regions and national parks. This interest in the mammal fauna of Poland was later extended, and was summarized in "Keys to vertebrates of Poland. V. Mammals" (1964). Professor KOWALSKI had initiated this series, and was the editor of the part devoted to Mammals, of which he wrote half the text. He participated in the next two editions of this book.

KOWALSKI's interest in living mammals was revived many years later, when he worked in Algeria (1978-1983). He collected more than 5000 specimens, published several papers on the adaptation of mammals to living in subtropical climates and above of all, prepared a monograph (together with his wife Barbara RZEBIK-KOWALSKA) on "Mammals of Algeria" (1991). This was based on studies lasting 12 years and gave an up to date summary of the recent mammal fauna of Algeria, its origin and evolution.

The editors wish to express their appreciation to all the contributors and reviewers, who have worked so hard to pay a worthy tribute to our friend and colleague Kazimierz KOWALSKI. We are grateful to the staff of Acta zoologica cracoviensia and espècially to Zygmunt BOCHEŃSKI and Ewa ŻYCHOWSKA for the support and assistance that has made it possible to publish these proceedings.

We wish to dedicate this volume to Kazimierz KOWALSKI in acknowledgement of his achievements as a scientist, his devotion to natural history and his efforts on behalf of our scientific community.

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Poland and abroad, including Acta Theriologica, Folia Biologica, Evolutionary Theory (USA), Paleovertebrata (France), and Quartärpaläontologie (Germany).

Kazik KOWALSKI enjoys traveling immensely and has visited many countries in Europe, Africa, America and Asia. These trips include study tours or longer stays as visiting professor as well as scientific expeditions. He was the head of the first Polish- Mongolian Expedition to the Gobi Desert (1964), organized from the Polish side by the Institute of Paleobiology in Warsaw. He also organized and headed a zoological expedition to some countries of the Near East in 1977. Kazik has represented Poland at many conferences and congresses, including the first four International Theriological Congresses. All these visits abroad have been connected with collecting new material and bringing it to the Institute in Cracow, or the investigation of already existing museum collections. This usually resulted in new publications, frequently prepared together with colleagues from the countries he visited. These study tours increased KOWALSKI's knowledge of the recent and fossil mammal fauna of the world and brought about new scientific contacts, co-operation and friendships. Several of these collegues have described new taxa in his honour.

Unlike university professors, Kazik has not had to teach students when working in the research institute. In several cases he has, however, acted as a supervisor of master's and PhD theses. He is also frequently appointed as a reviewer of theses in mammalogy, presented at various universities or research institutes, and has also acted as appraiser of the scientific output of several mammalogists in Poland. The fact that he does not regularly teach in the classroom situation does not mean that he has no contact with students. He trained students of biology at summer field courses, and spend 5 years in Algeria devoting himself mainly to lecturing in zoology. However, Kazik's main contribution to teaching has been his books. As co-author of the handbook of "Vertebrate Zoology" (1979) he is responsible for sections on "mammals" and "zoogeography". He wrote a textbook of mammalogy ("Mammals. An outline of theriology" 1971) that has been translated into English (1976) and Spanish (1981).

Professor KOWALSKI plays a very important part in the scientific life of Poland. Polish mammalogists know that the Theriological Section of the Polish Zoological Society was organized in 1962 on his initiative. It was also chaired by him for the first few years. Kazik actively participates in several committees and commissions of the Polish Academy of Sciences and on scientific boards of some institutes and national parks. He was scientific secretary (1958-1969) and chairman (1984-1987) of the Committee for Zoology PAS, deputy Scientific Secretary or presidium member of the Cracow Branch of PAS. He served for two terms as a member of the Central Qualification Commission, a body which accepts scientific degrees and professorial nominations in Poland. Recently, Kazik has been very active in re-starting the activities of the Polish Academy of Arts and Sciences in Cracow. He undertook the responsibility of organizing of the scientific Station of PAAS in New York.

Kazik KOWALSKI's scientific achievements have been well recognized by the community of Polish zoologists and paleontologists, who nominated him for membership in the Polish Academy of Sciences. In 1971 he was elected corresponding member, and in 1986 full member of this Academy. After restoring the activities of the Polish Academy of Arts and Sciences (1990) he was also elected an active member and played an important role in its governing body (deputy chair).

In 1994 Professor KOWALSKI was elected President of the Polish Academy of Arts and Sciences.

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After his move from the Jagiellonian University to the research institute of the Polish Academy of Sciences, Kazik KOWALSKI's studies took a change in direction. After 1954 he became more and more involved in the systematics and evolution of mammals and began investigating fossil mammals, predominantly rodents from Tertiary and Quaternary deposits. This was soon to become his main area of study. It would be difficult for me to summarize in detail all of his work in this field, and I can offer only a very brief recapitulation of his most important results. Kazik discovered and studied mammal faunas from many Miocene to Holocene sites in Poland and described 24 new taxa of fossil shrews, bats and rodents. He investigated the evolution of mammal faunas and various larger groups of arvicolids, glirids, gerbillines, zapodids and sciurids. This rich material enabled him to formulate important conclusions concerning paleoclimatic changes in Poland. A succession of mammal faunas from Paleolithic sites enabled him to reconstruct the environmental conditions of the oldest human occupation of Poland. During his study tours abroad he investigated the fossil mammal faunas of other countries. He prepared monographs on Pleistocene rodents of Great Britain (together with A. SUTCLIFFE) and Japan (together with Y. HASEGAWA), participated in the investigation of the Bacho Kiro Cave in Bulgaria, as well as deposits in Czechoslovakia, Jugoslavia, China, Japan and Mongolia.

Professor KOWALSKI's most recent interest is concentrated on the Miocene mammals of the Bełchatów brown coal deposits. This is a very rich mammal fauna, which includes, among other taxa, representatives of the genus *Neocometes*, known from the Miocene of Europe and Thailand. These finds suggest an uninterrupted expanse of tropical forest from southeast Asia to Europe. In addition he found mastodont teeth, one of the oldest dated finds of Proboscidea in Europe.

Professor KOWALSKI was an active member of the steering committee of the European Science Foundation network "Quaternary Mammalian Faunas", which promoted research on the evolution of the mammalian fauna of the Quaternary of Europe.

During the last few years Professor KOWALSKI has become very much involved in taphonomy. He has already presented some of his own results and propagated these ideas in several articles.

As a young man Kazik eagerly practiced caving and took part in many expeditions to caves in the Tatra Mountains, as well as many other caves in Bulgaria, Czechoslovakia, France, Cuba and Mexico. As a zoologist, he observed cave animals and collected scientific material for his studies. He investigated bat distribution and ecology, analysed cave sediments, with breccias containing mammal fossils. He soon became an authority on cave faunas and authored an extensive study of the "Cave fauna of Polish Tatra Mts" (1956) and a fundamental three volume monograph "Polish caves" (1952-1954), which contains detailed description of all known caves. Through popular books and many articles and notes (some 80 publications between 1946 and 1961) he promulgated knowledge of the caves and the need for protecting them. Among these publications were such books as "Life in caves" (1956), and "Polish caves" (1965). This writing stimulated further interest in the scientific exploration and protection of caves. Kazik was one of the organizers of caving in Poland, founded the Speleological Section of the Nicolaus Copernicus Society of Naturalists and chaired it for many years.

Professor KOWALSKI has published 11 books and many articles. The total number of publications from his pen is probably about 550, including original books, chapters and papers containing first-hand materials (ca 120), reviews, congress reports and abstracts, popular articles, notes and entries in encyclopedias. Counting the total volume of books (of one edition only), scientific papers and more important articles this is no less than 6000 printed pages! We can see him as an unusually productive and efficient author.

Kazik KOWALSKI has also edited several books (e. g., "Keys to Vertebrates of Poland", 1960-1971, which he initiated, chaired the editorial board of and was the editor of part 5, devoted to mammals, "Small Zoological Vocabulary, Mammals" - 4 editions between 1973-1992, and "History and evolution of the terrestrial fauna of Poland", 1989). He was the editor-in-chief of Acta Zoologica Cracoviensia for 14 years (1971-1984) and he has been the editor of Folia Quaternaria from its inception in 1960. He is a member of several editorial boards of different periodicals in

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KAZIMIERZ KOWALSKI AS THE MOST PROMINENT POLISH SPELEOLOGIST AND CAVER

Professor KOWALSKI is not only an outstanding zoologist and vertebrate palaeontologist, but also a prominent speleologist and caver. These latter activities should be mentioned here because his attainments are of great importance.

Kazimierz KOWALSKI began caving in the vicinity of Cracow as a boy before the Second World War. He began a systematic survey of caves in the Cracow upland during the dangerous times of the War and extended this work to encompass all of Poland just after the war. He published many papers on this subject (KOWALSKI 1950), including the monumental monograph "Caves of Poland" (KOWALSKI 1951a, 1953a, 1954). This monograph contains a complete review of all that is known of karst and caves in this country, with an unrivalled annotated bibliography. However, the value of this monograph lies mostly in the original descriptions and maps of 658 caves. During this work he showed broad interdisciplinary knowledge and penetrating scientific ability, which are seen in the many references to this monograph in subsequent books and papers. This monograph forms the starting point of modern speleology in Poland (cf. WÓJCIK 1981).

K. KOWALSKI had as a zoology student combined his caving interest with biospeleological observations, which gave him material for many papers on cave bats (e. g., KOWALSKI 1951b, KOWALSKI 1953b). During his cave survey, he found new localities of Pliocene and Pleistocene fossil vertebrates in cave deposits, which shifted his scientific activity towards vertebrate palaeontology, and this subject became his main scientific field over the next decades. Here I can mention the discovery of the important Pliocene vertebrate fauna in Podlesice (KOWALSKI 1951c, 1956) and many papers on Pliocene and Pleistocene vertebrates from localities found by other geologists and archaeologists in cave deposits. He concentrated his interest in the at that time poorly known micromammals, which are very important for Cenozoic stratigraphy and palaeoecology. He began very early with broad interdisciplinary collaborations with archaeologists, geologists and geomorphologists, not only as a laboratory expert determining bones of mammals, but also as a careful field collaborator collecting micromammals. Due to this cooperation we have at present very useful data on the Neogene and Quaternary stratigraphy and paleogeography of Poland, which was mostly established by KOWALSKI and his students and collaborators. This knowledge has been summarized and presented at international conferences or in well known papers and monographs several times (e. g., KOWALSKI 1962, 1964, 1989).

K. KOWALSKI has discovered many caves and new cave passages, as well as gained many sportive and technical successes in caving (BARYŁA 1980, 1981, 1985). He gained his first success in cave diving (Zwolinski's Syfon in the Zimna Cave, Tatra Mts.) in 1953. Two times he broke records in vertical caving in Poland: -160 m in 1951 and -213 in 1952 (both in the Miętusia Cave, Tatra Mts.). Moreover, jointly with French cavers he reached a world record in vertical caving in August 1956 (-1122 m) in the Gouffre Berger (France, Isère, Plateau Vercors). This world record

in vertical caving was beaten only 10 years later, since the depth of -1171 m reached in 1956 by French cavers in the cave system Pierre St.-Martin (Atlantic Pyrenees, France and Spain) was partly reached through an artificial EDF tunnel. However, by Polish cavers it was not broken until 1980.

Kazimierz KOWALSKI (nicknames among cavers "Kazik" or "Kowal") was also very active in caving and speleological organizations. He was co-founder of the Cracow Cavers Club in 1950 and of the Speleological Section of the Polish Copernicus Society of Naturalists, where he was the first President (1963-1968). He has been the organizer and leader of many caving and surveying expeditions to Polish caves since the 1950's. When the political conditions after 1955 began to permit caving expeditions to foreign countries, KOWALSKI organized and/or participated in many such expeditions to Slovakia, Hungary and Bulgaria, and since 1956 to France, Cuba and Mexico (Phot. 1). This activity was accompanied by many programmatic papers (written in Polish only) for the mimeographed caving bulletin "Grotołaz" (Caver), e. g., "Speleology and caving in Poland" (1950) and "We are travelling abroad" (1955). It was natural that Kazik was certified as one of the first caving instructors in Poland.

Really it is impossible to imagine the present state of the art in caving and the present state of knowledge of speleology in Poland without the attainments of Professor K. KOWALSKI!

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Phot. 1. Expedition to caves in Mexico, 1969. From right to left: Bronisław KOISAR, Kazimierz KOWALSKI, Maciej KUCZYŃSKI, Ryszard GRADZIŃSKI, Wojciech SKARŻYŃSKI. Phot. B. KOISAR.

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PAPERS IN MAMMAL PALAEONTOLOGY HONORING KAZIMIERZ KOWALSKI

Acta zool. cracov., **39**(1): 35-45, Kraków, 15 Aug., 1996

The beginning of the age of Murinae (Mammalia: Rodentia) in southern France

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Abstract. We describe the Murinae found in the localities of Lo Fournas 6 and 7 in southern France. The material includes two new species: *Progonomys castilloae* sp. nov. and *Parapodemus pasquierae* sp. nov. We discuss the diagnoses of the genera *Progonomys* and *Huerzelerimys*. *Progonomys* is geologically the oldest Murinae found in southwestern Europe, but members of the genera *Occitanomys*, *Huerzelerimys* and *Parapodemus* are found in levels older than previously believed. A diversified fauna of Murinae rapidly appears at the beginning of the Late Miocene.

Key-words: Murinae, *Progonomys*, Rodentia, Late Miocene, southern France.

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I. INTRODUCTION

The stratigraphically oldest fossil Murinae to be described from Europe was *Progonomys cathalai* SCHAUB, 1938 from the locality of Montredon in southern France (DEPERET 1895). About sixty years later, a few specimens of a slightly older geological age were found in Spain, at Can Llobateres (HARTENBERGER et al. 1967; THALER 1966). Since then new murid-bearing localities have been discovered in Spain (VAN DE WEERD 1976; DAAMS et al. 1988) and France (AGUILAR et al. 1986, 1991) and more material has been collected at Montredon (MICHAUX 1971; AGUILAR 1982). The present paper describes two new species, *Progonomys castilloae* sp. nov. and *Parapodemus pasquierae* sp. nov., and the Murinae from the localities Lo Fournas 6 and 7 (AGUILAR et al. 1986) previously referred to as *Progonomys hispanicus*, *Progonomys clauzoni*, and *Parapodemus lugdunensis*. These new data provide an opportunity to discuss the recently published diagnoses of the genera *Progonomys* and *Huerzelerimys* (MEIN et al. 1993). Our cusp terminology follows VAN DE WEERD (1976).

A c k n o w l e d g m e n t s. This is publication no. 96-024 de l'Institut des Sciences de l'Evolution (URA 327 C.N.R.S.). The photographs in Plate 1 were taken by Mr. L. DATAS, and the prints were made by Mr. M. PONS.

II. SYSTEMATIC PALAEONTOLOGY

Subfamily Murinae MURRAY, 1821

Genus *Progonomys* SCHAUB, 1938

Progonomys castilloae sp. nov.

Pl. 1, Figs. 1-9

1986 – *Progonomys cathalai* in AGUILAR et al.

D e r i v a t i o n o m i n i s: This species was named after Dr. C. CASTILLO RUIZ, in recognition of her studies of the Murinae.

T y p e l o c a l i t y: Lo Fournas 7 (Roussillon, southern France)

D i a g n o s i s: A *Progonomys* similar in size to *P. cathalai*, but the first lower molar has a simpler morphology.

D i f f e r e n t i a l d i a g n o s i s: *P. castilloae* sp. nov. differs from *P. cathalai* in having no or a reduced tma on M_1, a more reduced cingular margin, and a less developed terminal heel.

H o l o t y p e: M_1 sin. FOU 7 no. 4, Pl. 1, Fig. 1, Université Montpellier II

O t h e r l o c a l i t y: Lo Fournas 14.

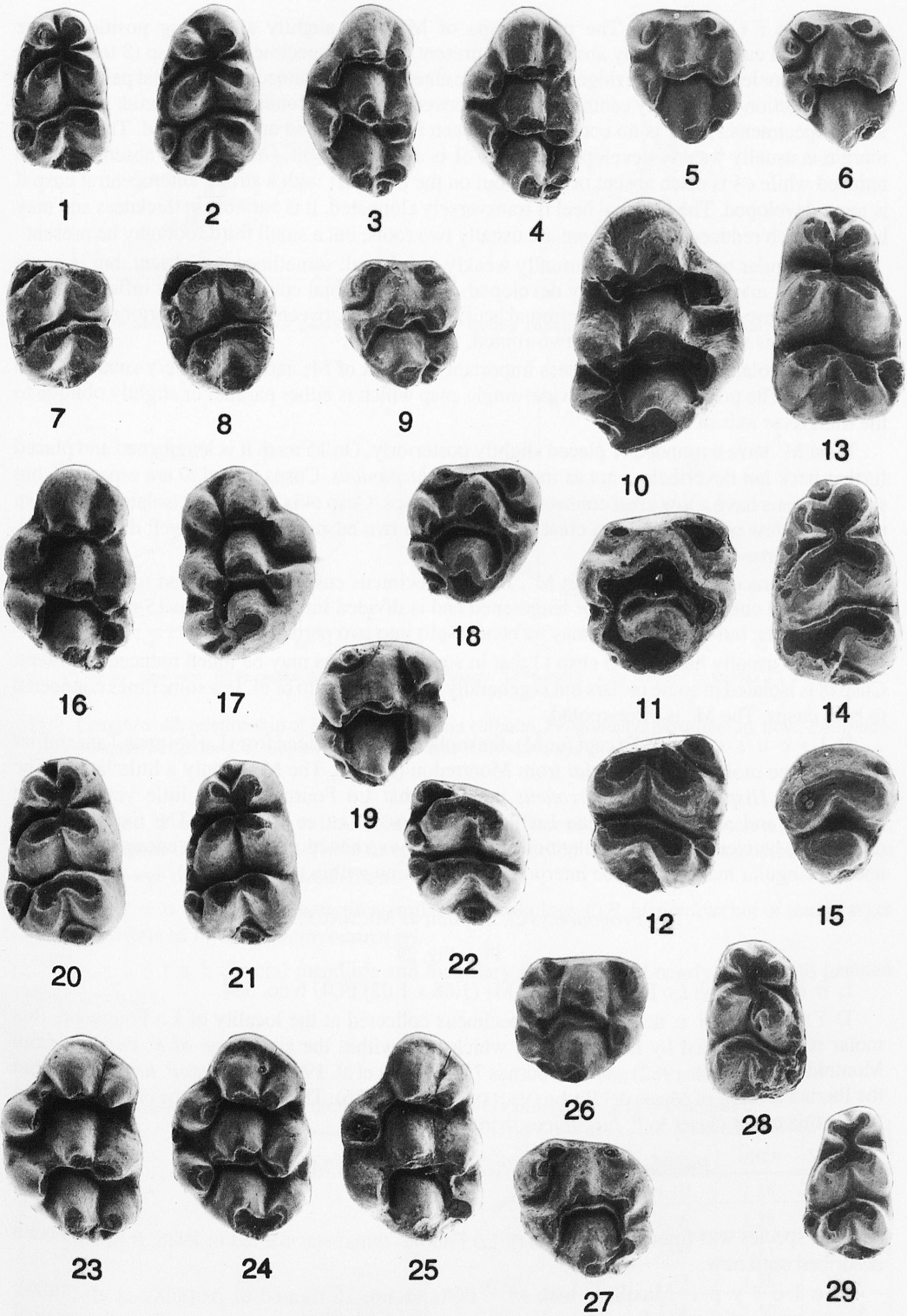
M a t e r i a l: one mandible with M_1-M_2, one maxillary with M^1-M^3, one maxillary fragment with M^1 and numerous isolated teeth FOU 7 nos. 1-180 and nos. 183-353 (Table I).

Table I

Measurements of the teeth of *Progonomys castilloae* from Lo Fournas 7

	n	Lmin	Lmoy	Lmax	V/√logN	lmin	lmoy	lmax	V/√logN
M_1	51	1.55	1.71	1.90	15.52	0.98	1.06	1.17	13.53
M_2	67	1.18	1.32	1.48	18.92	1.05	1.13	1.25	12.88
M_3	42	0.87	1.05	1.13	20.40	0.84	0.93	1.01	14.42
M^1	47	1.77	1.90	2.09	12.82	1.13	1.22	1.29	10.23
M^2	67	1.24	1.34	1.50	14.05	1.09	1.22	1.34	15.24
M^3	77	0.72	0.90	1.02	25.11	0.81	0.94	1.05	18.79

Plate 1. *Progonomys castilloae* nov. sp. from Lo Fournas 7. 1 – M_1 sin.(1.61 × 1.01) Fou 7 no.4 Type; 2 – M_1 sin.(1.76 × 1.10) Fou 7 no.8; 3 – M^1 sin.(1.90 × 1.21) Fou 7 no.148; 4 – M^1 sin.(1.92 × 1.25) Fou 7 no.165; 5 – M^2 sin.(1.24 × 1.26) Fou 7 no.201; 6 – M^2 sin.(1.41 × 1.27) Fou 7 no.175; 7 – M_2 sin.(1.28 × 1.10) Fou 7 no.83; 8 – M_2 sin.(1.35 × 1.16) Fou 7 no.52; 9 – M^2 sin.(1.29 × 1.20) Fou 7 no.177; *Huerzelerimys vireti* from Lo Fournas 7; 10 – M^1 dext.(2.58 × 1.76) Fou 7 no.361; 11 – M^2 dext.(1.55 × 1.65) Fou 7 no.363; 12 – M_2 dext.(1.65 × 1.43) Fou 7 no.357; 13 – M_1 dext.(2.17 × 1.33) Fou 7 no.354; 14 – M_1 sin.(2.07 × 1.36) Fou 7 no.355; 15 – M_3 dext.(1.42 × 1.29) Fou 7 no.364; *Parapodemus pasquierae* nov. sp. from Lo Fournas 6; 16 – M^1 sin.(1.98 × 1.32) Fou 6 no.537 Type; 17 – M^1 dext.(2.10 × 1.40) Fou 6 no.541; 18 – M^2 dext.(1.50 × 1.36) Fou 6 no.579; 19 – M^2 dext.(1.44 × 1.28) Fou 6 no.573; 20 – M_1 sin.(1.91 × 1.18) Fou 6 no.501; 21 – M_1 sin.(1.85 × 1.21) Fou 6 no.498; 22 – M_2 sin.(1.38 × 1.28) Fou 6 no.523; *Progonomys clauzoni* AGUILAR, CALVET, MICHAUX, 1986; 23 – M^1 sin.(2.03 × 1.37) Fou 6 no.100; 24 – M^1 sin.(2.05 × 1.40) Fou 6 no.114; 25 – M^1 sin.(2.06 × 1.43) Fou 6 no.161; 26 – M^2 dext.(1.43 × 1.37) Fou 6 no.237; 27 – M^2 sin.(1.44 × 1.42) Fou 6 no.239; *Parapodemus* cf. *lugdunensis* SCHAUB, 1938 from Lo Fournas 6; 28 – M_1 dext.(1.61 × 1.04) Fou 6 no.583; *Progonomys* cf. *hispanicus* MICHAUX, 1971; 29 – M_1 sin.(1.68 × 1.02) Fou 6 no.584. All figures are × 16.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D e s c r i p t i o n: The main cusps of M_1 have slightly alternating positions. The anterocentral cusp is generally absent, but is present on a few specimens as a cusp (3 teeth) or as a low, more or less developed ridge (9 teeth). The anteroconid is connected to the first pair of cusps. This connection is generally central or occurs between the anteroconid and metaconid. It is absent in two specimens. There is no connection between the anteroconid and protoconid. The cingular margin is usually weakly developed. Cusplet c1 is always present. Cusplet c3 is absent or much reduced while c4 is often absent or small, but on the three M_1 with a strong anterocentral cusp it is more developed. The terminal heel is transversely elongated. It is variable in thickness and may be very much reduced in size. There are usually two roots, but a small third root may be present.

The cingular margin of M_2 is usually weakly developed; sometimes it is absent, but in some specimens it may be more strongly developed. The anterolabial cusp is not very inflated, and is elongated in most specimens. The terminal heel is elongated between the two posterior main cusps; its thickness is variable. The M_2 is two-rooted.

The anterolabial cusp of M_3 is less important than that of M_2 and may be very small in some specimens. The posterior lobe is a wide, single cusp which is either parallel or slightly oblique to the transverse axis of the tooth.

Most M^1 have a rounded t1 placed slightly posteriorly. On 15 teeth it is lengthened and placed further back but nevertheless not as much as in *P. hispanicus*. Cusps t6 and t9 are separated, but six specimens have a low crest connecting the two cusps. Cusp t4 is most often isolated from cusp t8, but in a few molars there is a crest connecting the two cusps. Cusp t12 is well differentiated. The M^1 is three-rooted.

Most characters of M^2 are as in M^1. In five specimens cusp t6 is connected to cusp t9. The anterolingual cusp is tubercular or lengthened and is divided into two cusps in 15 molars. There are three roots, but the inner one may be nearly split into two parts.

The M^3 usually has a small cusp t3 that in some specimens may be much reduced or absent. Cusp t8 is isolated in some molars but is generally united to cusp t6 or t4. It is sometimes connected to both cusps. The M^3 is three-rooted.

D i s c u s s i o n: Except for M_1, the molars of *P. castilloae* from Lo Fournas 7 are similar in size to the molars of *P. cathalai* from Montredon (Fig. 1). The M_1 is only a little larger. The presence of *Hispanomys mediterraneus* indicates that Lo Fournas 7 is a little younger than Montredon and a little older than Lo Fournas 6 (AGUILAR et al. 1994). The morphological differences between the two populations of *Progonomys* (reduction of both the anterocentral cusp and the cingular margin) may be interpreted as evolution within the lineage.

Progonomys cf. *hispanicus* MICHAUX,1971

Pl. 1, Fig. 29

L o c a l i t y: Lo Fournas 6. One M_1 (1.68 x 1.02) FOU 6 no. 584.

D i s c u s s i o n: Among the specimens collected at the locality of Lo Fournas 6, this molar is characterized by its small size, which falls within the size range of *P. cathalai* from Montredon (AGUILAR 1982) and Lo Fournas 7 (AGUILAR et al. 1994) as well as *P. hispanicus* from the Iberian locality of Masia del Barbo (VAN DE WEERD 1976). The absence of the cingular margin places this molar closer to *P. hispanicus* than to *P. cathalai*.

Progonomys clauzoni AGUILAR, CALVET, MICHAUX, 1986

Pl. 1, Fig. 23-27

This species was found in the fauna of Lo Fournas 6 and was named in 1986. It has not been described until now.

H o l o t y p e: Maxillary with M^{1-2} FOU 6b no. 26 figured in AGUILAR et al. (1986); measurements of the M^1 from the type specimen are 2.04 × 1.41 mm, the width in the original publication being erroneously recorded as 1.21 mm.

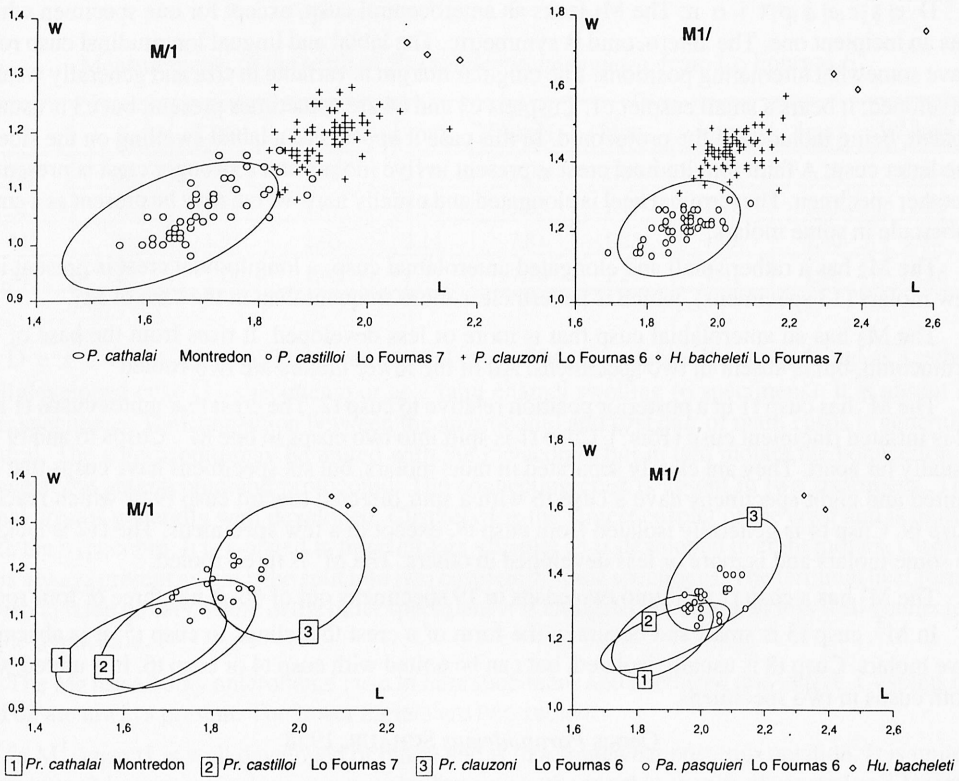

Fig. 1. Length/width relationship of M1 in *Progonomys cathalai*, *Progonomys castilloae* sp. nov., *Parapodemus pasquierae* sp. nov., *Progonomys clauzoni* and *Huerzelerimys vireti*.

T y p e l o c a l i t y: Lo Fournas 6 (three different samples have been taken from the site: Lo Fournas 6a, 6b and 6c. These have since been pooled, as the species associations do not indicate any age difference between them.

D i a g n o s i s: A *Progonomys* similar in morphology to *P. hispanicus* but of much larger size; size nearly as in *Occitanomys adroveri*.

M a t e r i a l: Several mandible and maxillary fragments and nearly a thousand isolated teeth (Table II).

T a b l e II

Measurements of the teeth of *Progonomys clauzoni* from Lo Fournas 6

	n	Lmin	Lmoy	Lmax	V/√logN	lmin	lmoy	lmax	V/√logN
M_1	72	1.82	1.92	2.15	12.20	1.08	1.19	1.28	12.43
M_2	66	1.29	1.42	1.52	12.14	1.18	1.26	1.38	11.59
M_3	40	0.92	1.07	1.22	22.15	0.91	1.00	1.11	15.65
M^1	72	1.89	2.04	2.19	10.79	1.31	1.43	1.58	13.70
M^2	66	1.31	1.44	1.57	13.39	1.25	1.38	1.50	13.48
M^3	42	0.87	0.98	1.09	17.61	0.93	1.03	1.16	17.27

D e s c r i p t i o n: The M_1 lacks an anterocentral cusp, except for one specimen which has an incipient one. The anteroconid is symmetric. The labial and lingual longitudinal cusp rows have somewhat alternating positions. The cingular margin is variable in size and generally weakly developed; it bears a small cusplet c1. Cusplets c3 and c4 are sometimes present, but c3 is usually absent, being included in the protoconid. In this case it appears as a labial swelling on the side of the latter cusp. A faint longitudinal crest is present in five molars and a stronger crest is present in another specimen. The terminal heel is elongated and usually narrow, but may be present as a small tubercule in some molars.

The M_2 has a rather small and elongated anterolabial cusp; a longitudinal crest is present in a few molars (13 specimens), which is nevertheless more frequent than in the case of M_1.

The M_3 has an anterolabial cusp that is more or less developed. It rises from the base of the protoconid, but is absent in two specimens. All of the lower molars are two-rooted

The M^1 has cusp t1 in a posterior position relative to cusp t2. The crest that unites cusps t1 and t2 is inflated (incipient cusp t1bis?). Cusp t1 is split into two cusps in one M^1. Cusps t6 and t9 are usually far apart. They are clearly separated in most molars, but six specimens have cusps that are united and eight specimens have a cusp t6 with a spur directed toward cusp t9 or which reaches cusp t9. Cusp t4 is generally isolated from cusp t8, except in a few specimens. The t12 is lacking in some molars and is more or less developed in others. The M^1 is three-rooted.

The M^2 has a cusp t1 split into two cusps in 19 specimens out of 66. It has three or four roots.

In M^3, cusp t3 is small and occurs in the form of a crest that clings to cusp t5; it is absent in five molars. Cusp t8 is usually isolated, but can be united with cusp t4 or cusp t6. It is united with both cusps in two specimens.

Genus *Parapodemus* SCHAUB, 1938

Parapodemus cf. *lugdunensis* SCHAUB, 1938

Pl. 1, Fig. 28

L o c a l i t y: Lo Fournas 6.

D i s c u s s i o n: One M_1 (1.61 x 1.04 mm), FOU 6 no. 583 which has an anterocentral cusp and well developed cusplets c1 and c2 differs from the *Progonomys* cf. *hispanicus* molar found in the same locality. Molars of *Parapodemus pasquierae* sp. nov. are larger.

Parapodemus pasquierae sp. nov.

Pl. 1, Fig. 16-22

1976 - *Parapodemus* sp. in VAN DE WEERD

1986 - *Parapodemus* sp. in AGUILAR et al.

D e r i v a t i o n o m i n i s: This species has been named after L. PASQUIER in recognition of her studies of Plio-Pleistocene *Apodemus*.

T y p e l o c a l i t y: Lo Fournas 6 (Roussillon, South of France).

D i a g n o s i s: Size intermediate between *P. lugdunensis* and *P. barbarae* from Los Mansuetos.

D i f f e r e n t i a l d i a g n o s i s: Differs from *P. barbarae* in its more reduced anterocentral cusp. The size is the same as *P. barbarae* from Masada del Valle 2, but cusps t6 and t9 are not always united.

H o l o t y p e: M^1 sin. FOU 6 no. 537, Pl. 1, Fig. 16, Université Montpellier II.

P a r a t y p e s f i g u r e d: Pl. 1, Figs. 17-22.

M a t e r i a l: Isolated teeth FOU 6 nos. 497-582 (Table III).

Table III

Measurements of the teeth of *Parapodemus pasquierae* from Lo Fournas 6

	n	Lmin	Lmoy	Lmax	V'√logN	lmin	lmoy	lmax	V'√logN
M_1	22	1.68	1.83	2.00	15.00	1.09	1.18	1.28	13.84
M_2	13	1.24	1.41	1.53	19.83	1.17	1.25	1.33	12.13
M^1	26	1.95	2.03	2.14	7.81	1.25	1.32	1.40	9.52
M^2	25	1.24	1.42	1.53	17.70	1.21	1.31	1.45	15.26

D e s c r i p t i o n: The anterocentral cusp of M_1 is variable. It may be found as a rather well developed cusp (11 specimens) or as a faint enamel swelling (6 specimens). It is absent in four specimens. The connection between the anteroconid and first pair of main cusps is generally central. The anteroconid may be united with the metaconid, but in two molars the connection is between the anteroconid and protoconid. The connecting crest is absent in two specimens. The labial crest is generally well developed. Cusplet c1 is the largest cusplet of the crest and is united with the hypoconid. It is isolated in three molars. Cusplet c3 is developed in eight molars. Cusplet c4 is always present and may be split into two cusplets in some specimens. The terminal heel forms a cusp in three molars, while in the other specimens it is elongated and more or less well connected to the hypoconid.

The M_2 has a bulky anterolabial cusp in nine specimens and a reduced one in five. Cusplets c1 and c2 are always present. The lower molars are two-rooted.

In M^1, cusp t1 is well developed or bulky and is in a somewhat posterior position. It is united with cusp t2 by a more or less strong crest. In two specimens this cusp is elongated and located nearer cusp t4. Cusp t3 is smaller than cusps t1 and t2. It is located at the level of cusp t2 and a narrow groove separates the two cusps. Cusp t6 is larger than cusp t9. These two cusps are always united, with the exception of one specimen. Cusp t4 and cusp t8 are usually united by a more or less well developed crest. These cusps are separated in three out of 26 specimens. The posterior cingulum is well developed. There are three roots.

The M^2 has a cusp t1 that is clearly larger than cusp t3. Cusp t9 is sometimes very much reduced. The connection between cusps t6 and cusp t9 is present in seventeen specimens and absent in eight. Cusp t4 is sometimes united with cusp t8 by a well developed crest (23 out of 25 specimens), but the connection is absent in two teeth. There are usually three roots, the inner one being very large and nearly split into two parts. One specimen has four roots.

D i s c u s s i o n: *Parapodemus pasquierae* differs in size (Fig. 1) and morphology from the other Murinae of Lo Fournas 6. It is very similar to *Parapodemus* sp. A from the locality of Peralejos C (VAN DE WEERD 1976). The latter population has been attributed to *Huerzelerimys minor* by MEIN et al. (1993). Two characters clearly differentiate between *Parapodemus* sp. A from Peralejos C and *H. minor*: *Parapodemus* sp. A. is smaller and has a stronger anterocentral cusp. *P. pasquierae* is larger than *P. lugdunensis* from Mollon and Tortajada A (VAN DE WEERD 1976) and smaller than *P. barbarae* from Los Mansuetos.

P. lugdunensis and *P. barbarae* (MICHAUX 1971; VAN DE WEERD 1976) were previously considered as two consecutive members of a lineage characterized by an increase in size and some minor changes in morphology. The occurrence of the two latter species in the localities of Lobrieu and Andance in France (DEMARCQ et al. 1989) was the first argument against the single lineage hypothesis. The fauna of Lo Fournas 6 supplies a second argument, since *P. pasquierae* sp. nov. is a plausible ancestor for *P. barbarae*.

Genus *Huerzelerimys* MEIN, MARTIN SUAREZ & AGUSTÍ, 1993

Huerzelerimys vireti (SCHAUB, 1938)

Pl. 1, Fig. 10-15

1986 – *Progonomys woelferi* in AGUILAR et al.

Material and measurements: isolated teeth FOU 7 no. 354-364.

3 M_1 (2.17 1.33; 2.07 × 1.36; 2.11 × 1.34); 3 M_2 (1.65 × 1.43; 1.48 × 1.37; 1.42 × 1.31); 1 M_3 (1.42 × 1.29); 3 M^1 (2.39 × 1.60; 2.58 × 1.76; 2.32 × 1.64); 1M^2 (1.55 × 1.65).

Discussion: A few molars from Lo Fournas 7 are referred to *Huerzelerimys vireti*. They are very similar to the teeth of *H. vireti* from Crevillente 2 and 4B (MARTIN SUAREZ & FREUDENTHAL 1993). The presence of *Huerzelerimys vireti* at Lo Fournas 7 can be used to address the relationships of *H. vireti* as advocated by MEIN et al. (1993), with *H. minor* (Ambérieu 2) as the ancestor of *H. vireti* (Ambérieu 3). Lo Fournas 7 is older than Ambérieu 1, 2 and 3, all of which include *Parapodemus lugdunensis* (FARJANEL & MEIN 1984), while Lo Fournas 6 (AGUILAR et al. 1994) is as old as Ambérieu 1. As *H. minor* from Ambérieu 2 (MEIN et al. 1993) is younger than *H. vireti* from Lo Fournas 7, our data suggest that *H. minor* may be an independent lineage parallel to that of *Huerzelerimys vireti*. Characters used in the differential diagnosis of the genus *Huerzelerimys* by MEIN et al.(1993) are subject to rather large variation: the connection between cusps t4 and t8, the size of cusp t12 and of the tma, the connection between the anterior lobe of M_1 and the first pair of cusps. These characters are difficult to use in any diagnosis. This was also the conclusion of the study of *P. cathalai* from Montredon.

III. EARLY UPPER MIOCENE MURINAE IN SOUTHERN FRANCE

The definition of the genus *Progonomys*

A diagnosis of the genus *Progonomys* and a revised list of species included within that genus have been presented by MEIN et al. (1993). According to this diagnosis, the material from Montredon (the type locality of the type species of the genus) is heterogeneous and should be referred to different species and genera. Descriptions of the Montredon populations of *P. cathalai* have all stressed the morphological variation in many characters of potential use in a diagnosis. To the previous descriptions of *P. cathalai* from Montredon (MICHAUX 1971; AGUILAR 1982), it is possible to add the following observations. Cusp t1 on M^1 can be more (Fig. 2d) or less (Fig. 2e) anteriorly placed, but not as much as in *P. hispanicus*. Cusp t4 is isolated from cusp t8 in a few specimens, but is most often united with cusp t8 by a crest. This crest, usually low, may sometimes be rather high. Cusps t6 and t9 on M^{1-2} are generally separated (Fig. 2e) but a connecting crest is present (Fig. 2d) in 10% to 30% of the teeth (see diagram in AGUILAR 1982 Fig. 2). Some M^1 have a small t12. The anterocentral cusp on M_1 is present in half of the specimens and its size is variable (Fig. 2a-c). When there is a connection between the two anterior pairs of cusps, the connection may be central (15 teeth) (Fig. 2f), between the anteroconid and metaconid (17 teeth) (Fig. 2g), or between the anteroconid and protoconid (3 teeth) (Fig. 2h). The connection may be absent or very faint (4 teeth) (Fig. 2i). The M_1 is two-rooted but sometimes may exhibit a third very small central root. This variability is at the origin of divergent interpretations when populations are known from a few specimens. This occurred with the *Progonomys* populations from Kastellios (DE BRUIJN et al. 1971; DE BRUIJN & ZACHARIASSE 1971), Can Llobateres 1, Oued Zra and Bou Hanifia, which according to MEIN et al.(1993) do not belong to *P. cathalai*. We have re-examined the material of Bou Hanifia 2 (Algeria) and Oued Zra (Morocco) stored in the collections of Montpellier University. The latter was first considered to be *P. cathalai*, and recently has been referred first to *P. chougrani* (AMEUR CHEHBEUR 1988), then to *P. mauretanicus* (COIFFAIT-MARTIN 1991). Cusp

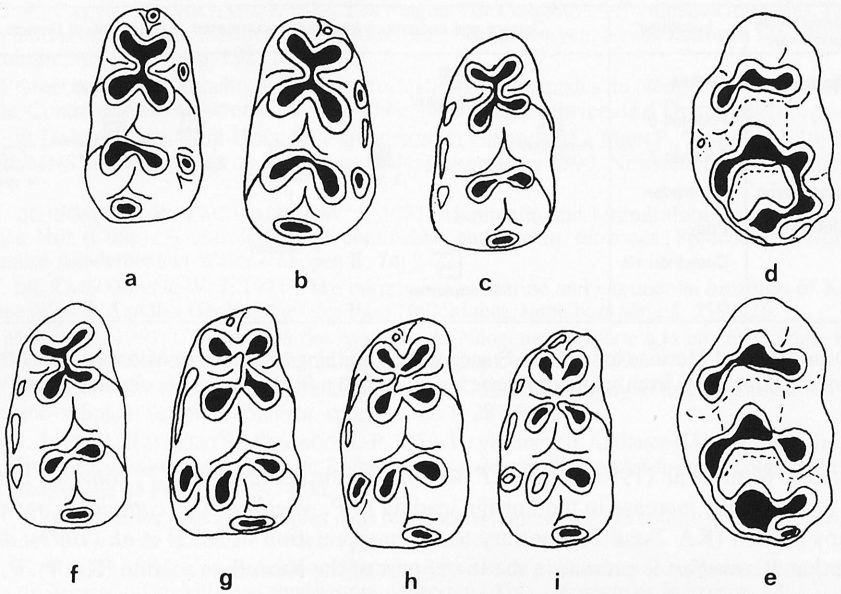

Fig. 2. Morphological variation (Upper and Lower M1) in the population of *Progonomys cathalai* from Montredon (France). a – M_1 dext. MTN no.1242; b – M_1 dext. MTN no.1259; c – M_1 sin. MTN no.1263; d – M^1 sin. MTN no.1351; e – M^1 sin. MTN no.1368; f – M_1 sin. MTN no.1263; g – M_1 sin. MTN no.1249; h – M_1 sin. MTN no.1237; i – M_1 sin. MTN no.1252. All × 20.

t9 is well connected to cusp t6, and t4 is linked to t8 by a low crest on the two M^1 of Bou Hanifia. As the drawing given by MEIN et al. (1993, Fig. 2b) refers to another specimen, this provides direct evidence of the morphological variation within the population. The M^{1-2} of Oued Zra have rather separated cusps t6 and t9. Only one M^2 shows t6 and t9 very close to one another. Nine out of 20 M^1 show cusp t4 united with cusp t8 by a more or less developed crest. Cusplet c2 on M_1 is rather large in four out of 22 teeth. In the other specimens this cusplet is less prominent. Characters of M^1 shown by the population of Kastellios (DE BRUIJN et al. 1971; MEIN et al. 1993) are also present in the population of Montredon. It is the same for M^2, which has a well developed t12. One of the two M^1 from Can Llobateres has a strong t4-t8 connection, the other one shows no connection. In conclusion, there are no definitive arguments to remove these populations from *P. cathalai*.

MEIN et al. (1993) also suggest moving the species *P. hispanicus* and *P. clauzoni* into the genus *Occitanomys*. The distinction between the genera *Progonomys* and *Occitanomys* was initially based on the connection between cusp t6 and cusp t9, which is present in more than 50% of the M1 in *Occitanomys* (VAN DE WEERD 1976). Although cusp t1 is more or less in the same posterior position in *P. hispanicus* and *Occitanomys*, the outline of the M^1 in occlusal view is ovoid in *Progonomys* and more trapezoidal in *Occitanomys*. Because of the strong morphological variation in the molar occlusal pattern, it is not possible to find clear-cut differences in the characters to place a species in either the one or the other genus. The simplest character for this use is the connection between t6 and t9. For this reason, we prefer put the species *hispanicus* and *clauzoni* together with the species *cathalai* in the genus *Progonomys*. The *Occitanomys* morphology is clearly recognizable in southern France only in the species *O. sondaari* (known at Pertuis, AGUILAR 1981) and *O. faillati* at Lo Fournas 7 (AGUILAR et al. 1986).

P. castilloae sp. nov. is a good candidate as a descendant of *P. cathalai*. Such a lineage is characterized by disappearence of the tma in M_1, simplification of the cingular margin, and a slight

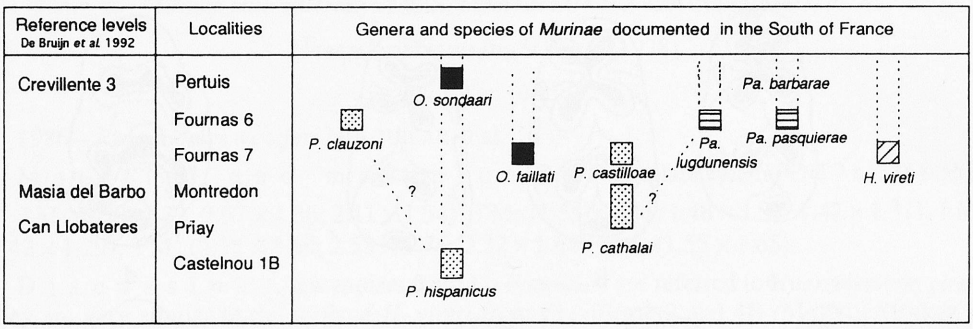

Fig. 3. Distribution of Murinae in southern France at the beginning of the Upper Miocene. Localities used as reference and localities from southern France are given in the first and second column, respectively.

size increase. MEIN et al. (1993) propose *P. woelferi* as the descendant of *P. cathalai*. In this case, there is a strong size increase in the lineage leading to *P. woelferi*. If *P. cathalai* is present in the Kastellios section (KA 2 and 3), contrary to the interpretation of MEIN et al. (1993), it must be stressed that *P. woelferi* is present in the lower part of the Kastellios section (KA 1). *P. woelferi* may consequently be a lineage independent of *P. cathalai*.

The lineages of Murinae in southern France

The geologically oldest Miocene Murinae in France are *P.* cf. *hispanicus* and *P. cathalai*. The former is present at Castelnou 1B, a locality which belongs to a time interval including the upper part of MN8 and the lower part of MN9. *P. cathalai* is known from Montredon but has been found in a slightly older locality outside southern France, Priay near Lyon (WELCOMME et al. 1991) which may be as old as Can Llobateres 1. Seven lineages of *Murinae* are then recognized in the two subsequent chronological levels, documenting a rapid diversification. The species present in these levels have not reached the same evolutionary level. Some are referred to *Progonomys*, but others, morphologically more evolved, are referred to the genera *Occitanomys*, *Parapodemus* and *Huerzelerimys* (Fig. 3). If the evolution of *P. hispanicus* toward *Occitanomys* is likely, the diversification of the lineages in this group cannot be yet described. If *P. cathalai* and *P. castilloae* represent a lineage, the relationship of the two *Parapodemus* species (*P. lugdunensis* and *P. pasquierae*) to the former lineage is obscure. The relationships of *P. cathalai* are also obscure, because there is currently no agreement regarding the definition of *P. cathalai*, and because there are more possible descendants of this species.

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