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Titel der Diplomarbeit

A Revision of the Murinae (Rodentia, Mammalia) of Kohfidisch (Upper-Miocene, Burgenland, Austria)

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To Thomas
To My Mother

Contents

Abstract

The Upper Miocene fossil locality of Kohfidisch, situated in the south of Burgenland (Austria) was discovered in the mid 1950's. From this time onwards the cave and fissure system has been depleted in annual excavations for almost 30 years until the mid 1980's by two of the great palaeontologists of that time, Friedrich Bachmayer and Helmuth Zapfe. The fossil site yielded a multitude of different vertebrate and invertebrate taxa. Among the most abundant forms were the murines, which yielded an estimated number of 1800 mandibular and maxillary fragments and about 5500 single teeth, but only few postcranial remains. Murines are known from Kohfidisch with two species, namely *Apodemus lugdunensis* and *Progonomys woelferi*, for the latter of which Kohfidisch is the documented type locality. The intensive study of this group of small mammals especially in south-western Europe in the past decades did not only lead to the description of many new taxa, but also revealed their importance for terrestrial biostratigraphy. These new developments in the study of murines, made a revision of the murine fossils of Kohfidisch due, especially since prior examinations dealt only with small portions of the material.

The following study is aimed at achieving better estimations of the true range of variation of the occurring species including more detailed descriptions and more pictures at a higher resolution using electron microscopy. The revision of the murines revealed the occurrence of a third species *Progonomys* cf. *hispanicus* in addition to the two already established ones. *Progonomys* cf. *hispanicus* has not been documented for the site of Kohfidisch prior to this study and it is so far the only locality in Austria yielding this species.

Another objective was to examine the material from the different finding points within the cave system with regards to potential differences. A morphological analysis of character states in combination with multivariate statistical methods showed some irregularities that however did not reveal any patterns, which might have allowed drawing any final conclusions about possible age differences of the separate fissures within the cave system.

Zusammenfassung

Die Obermiozäne Fossilfundstelle Kohfidisch, die sich im Süden des Burgenlandes (Österreich) befindet wurde Mitte der 50ger Jahre entdeckt. Ab diesem Zeitpunkt wurde das Höhlen- und Spaltensystem bis in die Mitte der 80ger für mehr als 30 Jahre im Zuge jährlicher Geländearbeiten, von zwei der großen Paläontologen ihrer Zeit, Friedrich Bachmayer und Helmuth Zapfe, begraben. Die Fundstelle lieferte eine Vielzahl an verschiedenen Vertebraten- und Invertebratentaxa. Unter den häufigsten Formen waren die Murinae deren Fossilien sich auf geschätzte 1800 Mandibel- und Maxilarfragmente sowie 5500Einzelzähne, jedoch lediglich auf wenige postcraniale Fragmente belaufen. Sie sind von Kohfidisch mit zwei Arten dokumentiert, nämlich Apodemus lugdunensis und Progonomys woelferi – für letztere ist Kohfidisch die dokumentierte Typuslokalität. Die intensive Erforschung dieser Gruppe von Kleinsäugern, speziell in Südwesteuropa, in den vergangen Jahrzehnten führten nicht nur zu einer Vielzahl neu beschriebener Taxa, sondern konnte auch ihre Relevanz für die terrestrische Biostratigraphie verdeutlichen. Die neuen Entwicklungen in der Erforschung der Murinae ließen eine Revision des Materials von Kohfidisch an der Zeit erscheinen, ganz besonders da früheren Studien nur ein kleiner Teil des gesamten Materials zu Grunde lag. Ziel der vorliegenden Arbeit war es dieses Material zu überarbeiten und eine genauere Erfassung der Variationsbreite der beiden vorkommenden Arten zu erzielen sowie detailliertere Beschreibungen und mehr Bilder mit höherer Auflösung mittels Elektronenmikroskopie zu liefern. Durch die Revision konnte das Auftreten einer dritten bisher aus Kohfidisch nicht bekannten Art, *Progonomys* cf. *hispanicus* nachgewiesen werden. Kohfidisch bekannt ist bisher die einzige Fundstelle in Österreich aus der diese Spezies dokumentiert werden konnte.

Ein weiteres Ziel der vorliegenden Studie war es, das Material der einzelnen Fundpunkte bezüglich potenzieller Unterschiede zu untersuchen. Eine morphologische Merkmalsanalyse in Kombination mit multivariaten statistischen Methoden zeigte Unregelmäßigkeiten, die aber keine Muster erkennen ließen, welche endgültige Schlüsse über z. B. eventuelle Altersunterschiede der einzelnen Spalten zugelassen hätten.

1. Introduction

1.1 Situation of the outcrop

The outcrop of Kohfidisch is situated in the south of Burgenland in the district of Oberwart. It lies on the western slope of the Hohensteinmais-mountain (345m high), south of the village Kohfidisch, in the forest that belongs to the estate of Kohfidisch. The lowermost point of the excavation site is at about 298m (sea level). The system of caves and fissures though extends to about 302m.

The excavation site is located on top of the road leading from Kirchfidisch to Punitz, just before the point at which the latter crosses a forest aisle, leading from a little hunting lodge to the Point 268 (d.Kte. 1:50.000) (Bachmayer & Zapfe, 1969: 126)
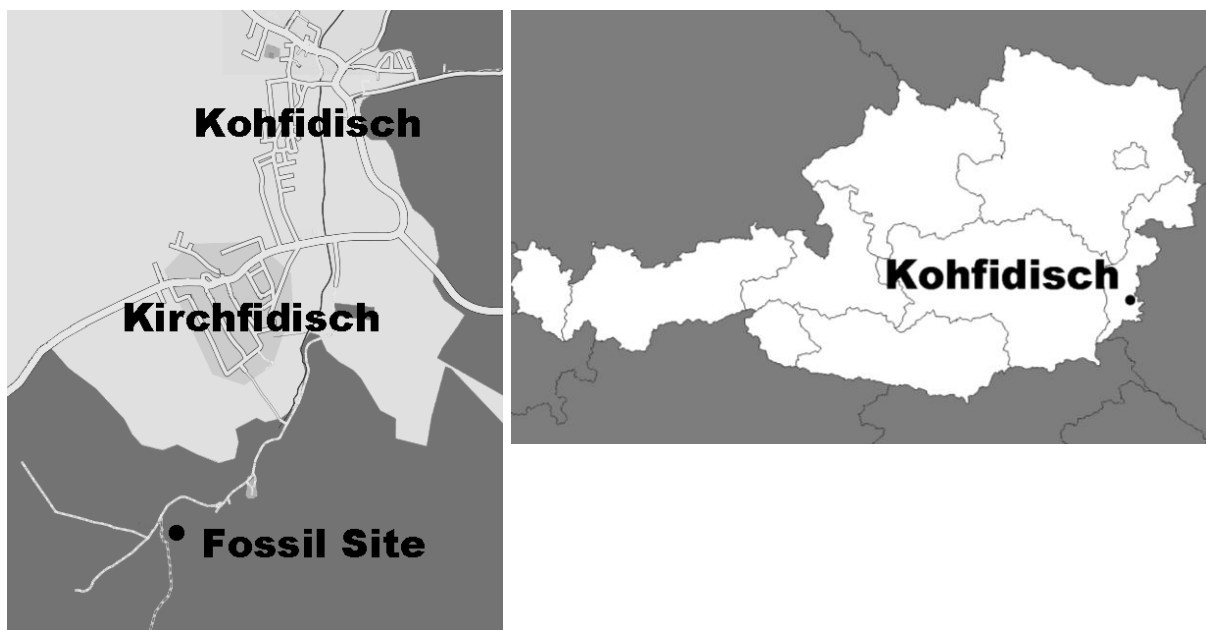
Fig. 1: Location maps of Kohfidisch

1.2   Geology and Lithology

The Hohensteinmaisberg is part of the "Südburgenländischen Schwelle" (South Burgenland Swell) (Bachmayer & Zapfe, 1969: 126), separating the Styrian basin in the west from the Small Hungarian lowlands in the east (Schönlaub, 2000: 10), both of which belong to the Pannonian basin system.

This threshold was formed due to different subsidence rates of the basins mainly during Carpathian and Sarmatian, but formation continued up to the Pontian.

The South Burgenland Swell stretches from the Hohensteinmaisberg in the northeast as far as St. Anna in the southwest and is composed primarily of phyllitic shales, green shales and limestone shales in the Silurian and carbonates in the Devon (Schönlaub, 2000: 35). These Palaeozoic layers are widely covered transgressively by Neogene and Pleistocene brackish to freshwater sediments (Flügel & Heritsch, 1968 quoted from Tempfer, 2004: 7)
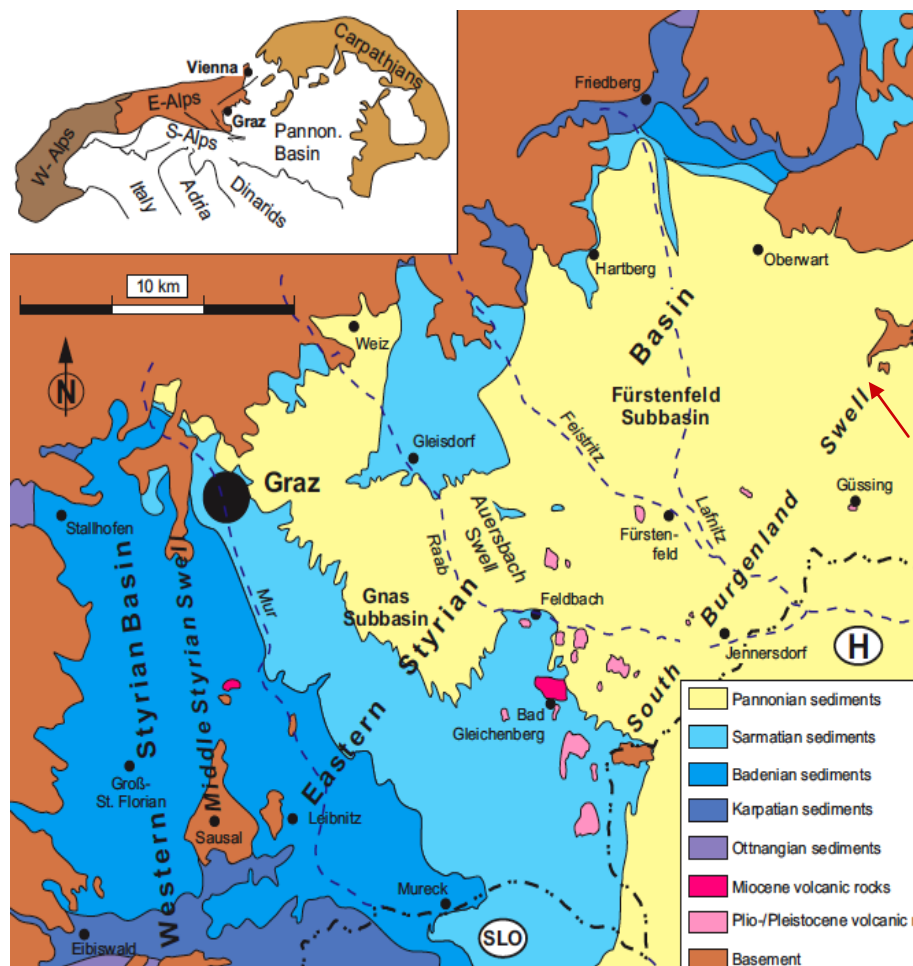
Fig. 2: Geological overview of the Styrian basin, locality of Kohfidisch indicated by red arrow (modified after Gross et al., 2007)

The Hohensteinmaisberg is one of the Palaeozoic horsts emerging from these surrounding tertiary sediments. It consists mainly of grey to dark grey dolomitc calcites and dolomites, but also sericite shales.

The cave and fissure system of Kohfidisch is located in this complex, but its rocks have been converted into a detrital mass, full of holes, in which dripstones, crusts of sinter and solitary purely dolomitc rocks represent the only components of hard consistency. Bachmayer & Zapfe (1969: 126-127) suggest that soaring mineral waters, that ascended only after the caves were filled, could have been the cause of this alteration.

Dr. Ing. Wieden (Chemical Laboratory of the Bundesversuchs- und Forschungsanstalt Arsenal) investigated the fossil-bearing cave and fissure sediments petrographically and was able to detect a significant participation of volcanic material (bentonite) in the cave loam. Bachmayer and Zapfe inferred that there had to be a sour volcanism in the distant vicinity before the replenishment of the cave and fissures (Bachmayer & Zapfe 1969: 128)

1.3 History of the discovery

The cave and fissure system of Kohfidisch was discovered by the bailiff Sepp Wölfler, who led the geologist Friedrich Kümel to the outcrop in 1955, as he was nearby because of geological field mapping. The view fossil remains, which Kümel brought to the Museum of Natural History of Vienna, already revealed the importance of these tertiary terrestrial deposits (Bachmayer & Zapfe, 1969: 123, 124). From 1956 onwards, two scientist of the museum, namely Friedrich Bachmayer and Helmut Zapfe organized annual excavations, which were only terminated in 1984(Bachmayer & Wilson, 1990: 1). During this period a vast number of mammals, reptiles and amphibians where found and described. Kohfidisch is up to date one of the richest Miocene terrestrial deposits found in Austria.

1.4   Finding Points

The first fossils were found at the a little outcrop where the excavation commenced. In 1957 further exploration into the depth revealed a little opening that was widening as it descended. During the years 1958 and 1959 the base of the excavation could be recessed until a whole rock face including the entrance of a cave was uncovered. This spot was marked as finding point I (see fig. 8 and 9). As the excavation descended the concentration of fossils decreased, so the bedrock of the cave was never reached, not even when drilling 3 meters deep from the bottom of the excavation.

Instead of digging deeper the excavation was extended to the southeast of the original finding point I. There, fossil bones were frequently found inside a little fox burrow or the earth in front of it. This finding spot was marked II (see fig. 8 and 9). At this point the excavation revealed a system of fissures and kolks in the karsts/rock that were filled with fossil bearing loam (Bachmayer & Zapfe, 1960: 22)

During the years from 1961 to 1969 the main digging activity shifted to the space between finding points I and II, where the rock was characterised by the vast abundance of fissures and hollow spaces. This section was called finding point III.

In the year 1964 even a fourth finding point was exploited south of finding point I. At this finding point VI, a former lime pit, fossil remains were rather scarce (Bachmayer & Zapfe, 1969: 130-131)

Fig. 3: Photograph of finding point I

Fig. 4: Photograph of finding point II

Fig. 5: Valorisation of finding point III.

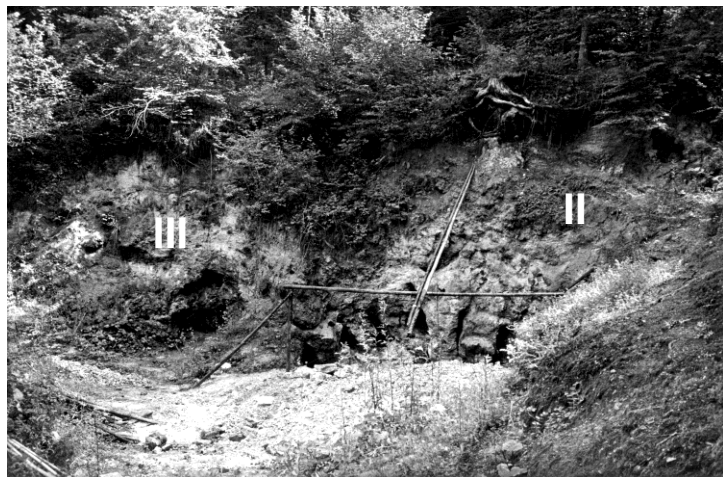Fig. 6: Photograph of finding point II (right) and III (left)
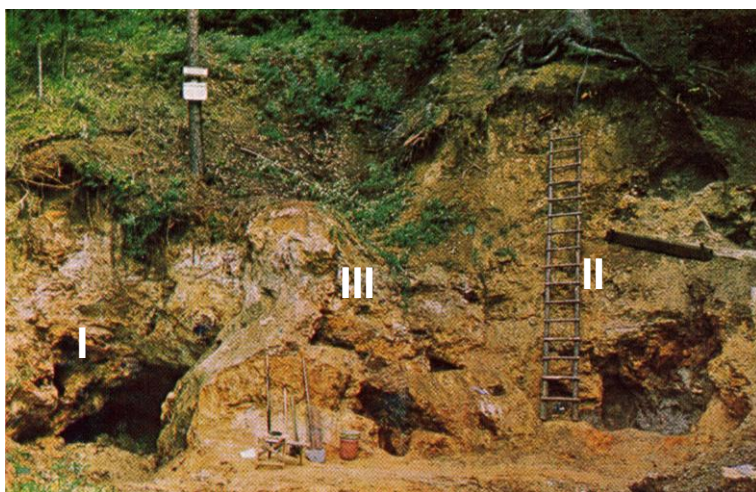

Fig. 7: Overview over the finding points
(modified after Bachmayer & Zapfe, 1969)
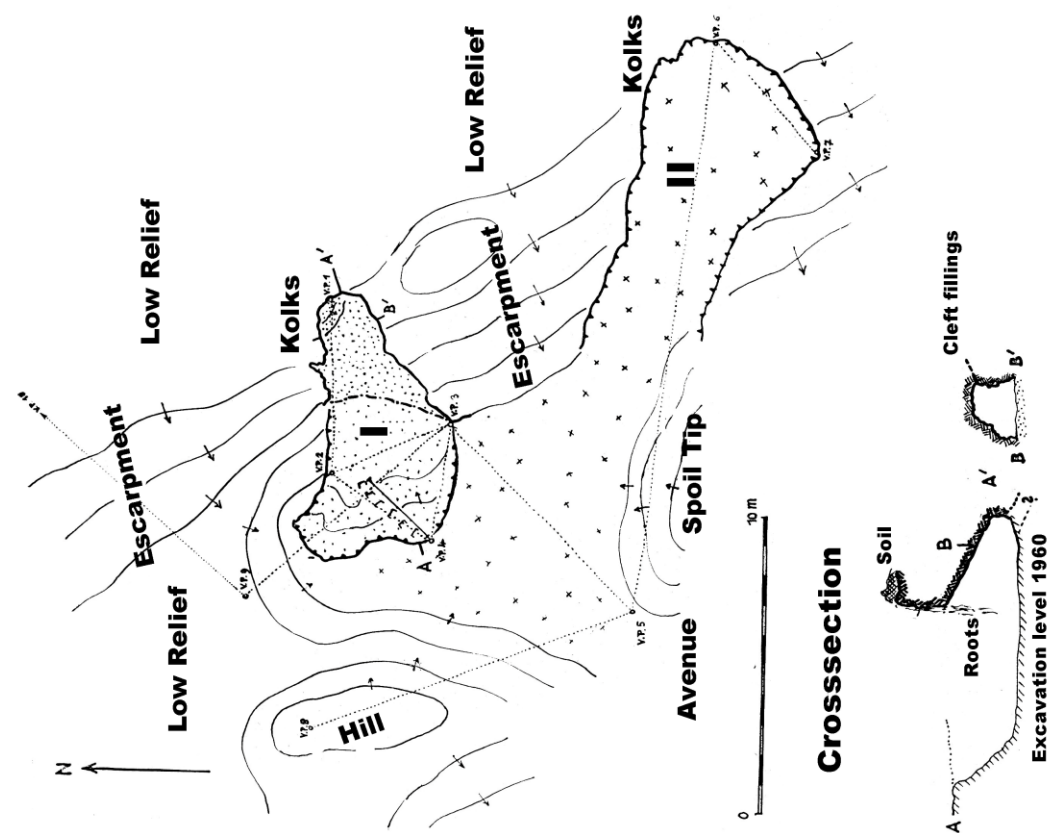
Fig. 9: Sketch of the excavation site (modified after Bachmayer & Zapfe, 1969)

Fig. 8: Sketch of the excavation site (modified after Bachmayer & Zapfe, 1960)
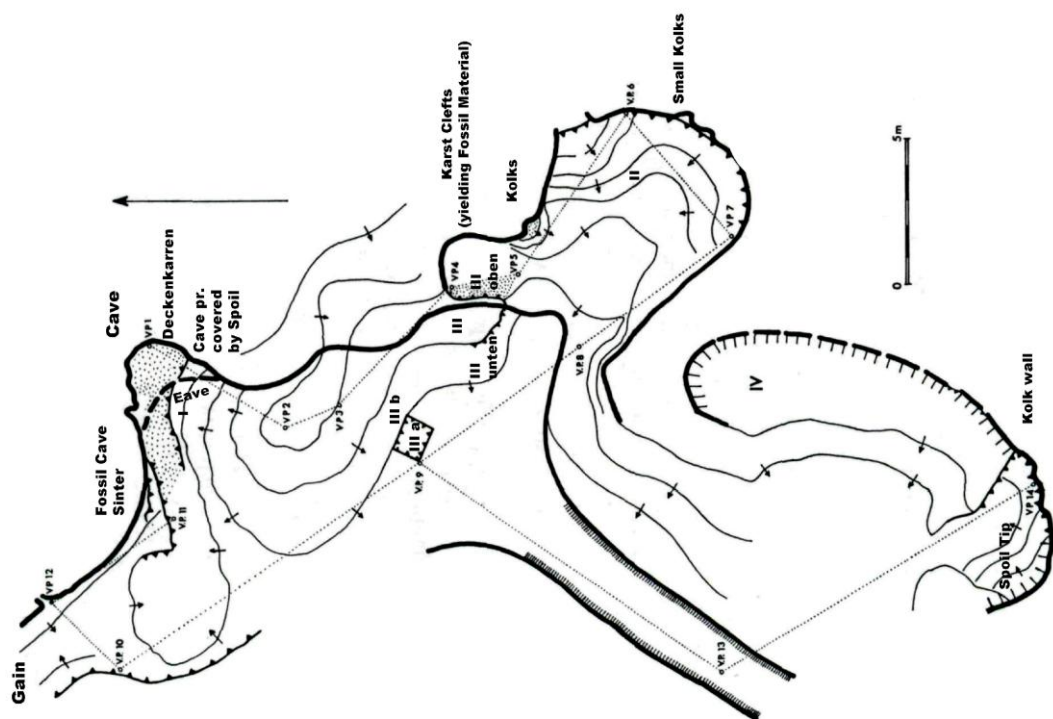
1.5   The Age of the fauna of the cave and fissure fillings

When viewing the fossils of Kohfidisch it soon became clear to the investigators that they represented a typical Hipparion fauna and were therefore no older than latest Mid Miocene (=Pannonian) (Bachmayer & Zapfe, 1969: 123)

In the earlier literature (older than 1979) the outcrop of Kohfidisch is described as early Pliocene. This may be somewhat confusing, but is not due to a change in the dating of the sediments, but rather because the Pannonian used to be attributed to the Pliocene and only after 1979 was attributed to Miocene (Tollmann, 1985: 510)

Later the description of the age of the material is refined to Pannon F (Papp, 1951) because of several reasons, among which the following seem to have been the most important.
From the Top of the Hohensteinmaisberg at 340m Kümel (1957: 22, quoted from Bachmayer & Zapfe, 1969: 135) described blue-green marly clays (= Tegel) yielding freshwater snails, which he put into Pannonian zone G. This means that during this time the Hohensteinmaisberg was covered by lake Pannon or only protruded as a little island, in which case the caves would have been covered by water. As there is no evidence that early high stands of lake Pannon were considerably lower, it was inferred that the caves where only dry and inhabitable during its lowest stands. Exactly these were only described for zones A and F (Papp, 1951: 189 in Bachmayer & Zapfe, 1969: 136). The fauna found in the sediments of Kohfidisch though strongly contradicts a classification into zone A. Bachmayer and Zapfe in 1969 therefore assigned the cave and fissure deposits as lower Pannonian, zone F.

Bachmayer & Wilson (1970: 538-542) compare Kohfidisch with several other European localities and in time place it after Gaiselberg-bei-Zisterdorf (Austria), Vösendorf (Austria), La Grive-St. Alban (France) and Montredon (France), but before Eichkogel (Austria) Csákavar (Hungary), Polgárdi (Hungary), Rousillon (Hungary), Alcoy (Spain), Sète (France) and Nimes (France).

Bachmayer & Wilson (1978: 133, 134) confirm the previous suspicion of Bachmayer and Zapfe that the Kohfidisch fauna is slightly older than the one at Eichkogel. They also presume it to be rather of early Turolian than of latest Vallesian age.

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In the same work, the authors for the first time stress the important role of the murines in the correlation of faunas over wide areas.

Mein (1975, enclosed Table) ranks the Kohfidisch fauna in the newly established "Biozonation of the Mediterranean Neogene on the basis of Mammals" (see also: Fahlbusch, 1976) and assigns it to the MN zone 11.

Later Bachmayer & Wilson (1980: 381) adopt this classification and also assign Kohfidisch to MN zone 11, but still do not revise their prior classification into Pannonian zone F.

Papp & Steininger (1979: 164, 165) put Kohfidisch into Pannonian zone H in a table of their publication, without referring to this change of Position in the Text.

Bachmayer & Wilson (1984: 305, 307) discuss the stratigraphic position of Götzendorf, which is, though not with a very high certainty, zone F. They argue that because of this evidence, the assignment of Kohfidisch to the same Zone is in all likelihood wrong, since the fauna of Götzendorf is a much more primitive one.
In a later publication they grant that Götzendorf and Kohfidisch could only be time equivalent, if environmental and burial influences played a more important role in the Vienna basin than specific zone indicators (Bachmayer & Wilson, 1985)

According to a unification of the West European classification widely introduced shortly before (cf. e. g. Fahlbusch, 1981; Steininger & Papp, 1979), Bachmayer & Szyndlar, (1985: 80) change the age description of Kohfidisch from Lower Pliocene to Upper Miocene.

Only a few months after the senior authors death the last publication of Bachmayer and Wilson appears. Once more they treat the age and stratigraphic position of Kohfidisch and argue that the latter and Götzendorf (of which the assignment to zone F is now certain) could indeed be time equivalent. They explain that according to Zapfe, it is possible that a more primitive fauna was able to survive in Götzendorf because of very favourable environmental conditions. They concede that this solution would also agree much better with the view of Geologists, who have argued that the locality cannot be as old as its faunal list would suggest.
This perception would also explain, why Kohfidisch is more similar to the fauna of Eichkogel than to that of Götzendorf (Bachmayer & Wilson, 1990: 3-4).

De Bruijn et al. (1992: 74) revise the biochronological zonation of the continental Neogene of Europe and Western Asia (MN zonation). They put Kohfidisch into the uppermost part of the Zone MN10, which would be equivalent with the Papp zone of Pannon G, and correlate it with the reference locality Masia del Barbo (Van de Weerd, 1976).

Also Rögl et al. (1993: 517, 518) in their report on further results of the site of Götzendorf (Pannon zone F, border of MN9/MN10;) argue that the faunas of the latter and Kohfidisch are too different to have the same age and also put Kohfidisch into the uppermost Vallesian, that is Papp zone G and MN zone 10.

Although they mention that the early Turolian (MN 11) is characterised by the first appearance of *Apodemus lugdunensis,* Rögl & Daxner-Höck (1996: 52, 53) place Kohfidisch in the upper most MN 10, as *Kowalskia fahlbuschi* and *Progonomys woelferi* are still abundant and compare the locality to other MN 10 localities like Soblay (France) and Lefkon (Greece).

Daxner-Höck (1996: 6,7) still positions Kohfidisch into the upper MN zone 10. In her publication she stresses the great faunal changes during the ending Vallesian and debates the changing Paratethys as an underlying cause. The eastward retreat of the central Paratethys, her fragmentation into partial/sub- basins and the aggradation of the margin areas might have opened up possibilities for immigrations from East- and Southeast Europe into the Pannonian and Vienna basins and further into Western Europe.

Daxner-Höck (2001b: 28-32) lines up the Austrian vertebrate localities in accordance with the correlation charts for the **G**eomagnetic **P**olarity **T**ime **S**cale (GPTS) and marine and continental biozonations (Steininger, 1999: 14, 15) commonly used in Central Europe, and furthermore compares them to the ones used in Spain (cf. Daams et al. 1999; Agusti et al. 2001; Agusti, 2001) in which the numerical ages for MN-boundaries differ up until the lower boundary of zone MN 9. She still puts Kohfidisch into MN 10 but grants that it is indeed very similar to the fauna of the Eichkogel (MN 11) and that "discussion is still going on".

In accordance with the reworked MN zones (Agustí et al. 2001) Daxner-Höck (2003: 38, 39) changes the position of Kohfidisch to earliest Turolian (=lowest MN 11, upper Pannon zone G) because of its faunal composition characterized by the FAD of *Hystrix parvae*, *Epimeriones austriacus*, *Vasseuromys pannonicus*, *Kowalskia fahlbuschi*, *Apodemus lugdunensis* and *Progonomys woelferi* (Daxner-Höck, 2009: 381).

Also in further publications (q.v. Daxner-Höck, 2004: 7; Vislobokova & Daxner-Höck, 2004; Vislobokova, 2005, Daxner-Höck 2009) this classification of Kohfidisch is maintained and is until today the valid specification of the age of the fauna. Magnetostratigraphic calibrations for the zone MN11 result in a base at the base of Chron C4r.2r and a top at the base of Chron C4n.2n (Steininger in Rössner & Heissig, 1999: 19). According to geochronologic calibrations the zone MN 11 has its base at 8.7 Ma and its top at 8.0 Ma, which results in a duration of 0.7 Ma, in and consequently an estimated age of Kohfidisch of 8.6 - 8.5 Ma.

1.6   Ecology

The low frequency of intact and complete bones, the many fragmented bones and bone chips as well as characteristic damages on the bones made it almost certain that the cave and fissure system of Kohfidisch served as home for the predators *Percrocuta* and *Ictitherium*. That these animals really lived inside the caves was also deduced from the calcareous coprolites, the size of which rather corresponds to *Ictitherium*. In addition the fossils of *Ictitherium* were much more abundant than *Percrocuta* which is probably due to the fact that all of the cavities, apart from the bigger cave I, were to small for *Percrocuta*, but suitable for the only fox-sized ictitheres. Probably also tortoises, snakes and porcupines, at least temporarily lived in the fissures.

Other important elements in the caves are the small vertebrates emanating from the pellets of owls, which also nested in the caves. However previous studies could neither rule out nor prove that some of the rodents and insectivores sojourned/visited the caves, at least from time to time. The described bats though most certainly belong to the primary fauna of the cave (Bachmayer & Zapfe, 1060: 21; Bachmayer & Zapfe, 1969: 131-132).

1.7   Murinae: systematics, evolution, Immigration and dispersal in Europe

Mostly, Murinae together with Gerbillinae, Deomyinae, Leimacomyinae, Lophiomyinae and Otomyinae (depending on whether viewed as an independent group or comprised inside the murines) form a monophyletic clade and are generally classified into the family

Muridae (Wilson & Reeder, 2005; Jansa & Weksler, 2004). Other authors (e.g. de Bruijn, 2010; McKenna & Bell 1997) interpret this family in a much wider sense comprising a set of subfamilies[1] that in other systems (like the prior one mentioned) are separated into different families. In this kind of classification (McKenna & Bell, 1997) the family Muridae is probably best comparable to the superfamily Muroidea used in the other type of classification systems (e.g. Wilson & Reeder, 2005).

The differences of the two groups of classification systems (set aside differences in the assignment of certain single species or genera to a given subfamily) lie in the level at which the plenitude of different subfamilies is grouped. Systems that focus on extant taxa (for which molecular information is at hand) are able to group the subfamilies into different families (clades with closer relations) under the supertaxon Muroidea. This approach however is not very practical for the various subfamilies only known from fossils, because their relations among each other are not yet or may never be able to be resolved. This is probably the reason why taxonomic systems that include the fossil groups tend to be more unifying on the family level and subsume all muroid subfamilies (but not the Dipodidae) under the family Muridae.

While exact numbers depend on the Taxonomy used and the individual views of various authors generally the Murinae comprise over 100 genera with more than 500 species and are by far the largest and most widely spread group of mammals (Freudenthal & Martín-Suárez, 1999: 401). Their recent representatives natively inhabit Asia, Africa, Europe and Australia and have been introduced by men all over the world, with the extreme Polar Regions being the only exception. They occupy a wide variety of habitats and have adjusted to a vast spectrum of ecological niches. Their cosmopolitan occurrence, as much as their extreme adaptability and rapid rate of evolution have made them a popular studying object over centuries for various disciplines.

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[1] Pappocricetodontinae Tong, 1997; Paracricetodontinae Mein & Freudenthal, 1971; Eucricetodontinae Mein & Freudenthal, 1971; Pseudocricetodontinae Engesser, 1987; Adelomyarioninae Ünay-Bayraktar, 1989; Tachyoryctoidinae Schaub, 1958; Melissiodontinae Schaub, 1925; Heterocricetodontinae Ünay-Bayraktar, 1989; Cricetopinae Matthew & Granger, 1923; Platacanthomyinae Alston, 1876; Eumyarioninae Ünay-Bayraktar, 1989; Anomalomyinae Schaub, 1925; Spalacinae Gray, 1821; Copemyinae Jacobs & Lindsay, 1984; Megacricetodontinae Mein & Freudenthal, 1971; Cricetodontinae Schaub, 1925; Cricetinae Fischer von Waldheim, 1817 (including Trilophomyidae Kretzoi, 1969); Lophiomyinae Milne-Edwards, 1867; Murinae Illiger, 1811; Arvicolinae Gray, 1821; Microtoscoptinae Kretzoi, 1955; Myospalacinae Lilljeborg,1866; Rhizomyidae Winge, 1887; Gerbillinae Gray, 1825; Myocricetodontinae Lavocat, 1961; (after de Bruijn, 2010)

Despite the great advances in research over the past decades, the evolution and origin of the murines as well as the phylogeny of fossil lineages remain poorly understood until this day.

Currently the most complete list of fossil murine genera is the one published by de Bruijn in 2010 (in Fortelius, 2011). It lists 30 fossil genera that are indisputably acknowledged up to date, but the number is likely to increase in the course of time when more information and material of this group (especially of Asian populations) becomes available.

The earliest occurrence of fossils commonly accepted as murines, belong to the species *Antemus chinjensis* (Jacobs, 1977) from the Mid Miocene Siwalik deposits of Northern Pakistan. *Antemus primitivus*, described by Wessels et al. in 1982 was considered even more primitive and an ancestor of *Antemus chinjensis*, but was moved to the new genus *Potwarmus* (Lindsay, 1988), which in turn was included in the Subfamily Dendromurinae (formerly considered part of the Cricetidae, sconce 2004 Nesomyidae (Jansa & Weksler). (Lindsay, 1988) or placed inside the myocricetodontines (Tong & Jaeger, 1993). Although the dispute over which family *Potwarmus* should be grouped into does not matter to the understanding of general evolutionary trends in this group of rodents and the stage-in-evolution-concept, it can be significant to finding the true ancestor of the murines. Because if *Potwarmus* is indeed a Myocricetodontine, the link between Murines and gerbillines, as suggested by genetic studies, would also be supported by fossils, since Myocricetodontines are the postulated ancestors of the gerbils (Jaeger, 1997; Wilson & Reeder 2005;).

Independent of the subfamily the genus *Potwarmus* is grouped into, almost all authors generally agree that *Potwarmus primitivus* is an ancestor to *Antemus chinjensis* (Lindsay, 1988; de Bruijn et al. 1996;). However, Freudenthal & Martín-Suárez (1999) concede that: " this does not necessarily mean that *Antemus* is derived from *Potwarmus*, and that the Muridae are derived from the Dendromurinae, but it may mean that we have come as close as possible to the origin of the Muridae, and that taxa more primitive than *Antemus* will be arranged in other families than the Muridae." Also de Bruijn et al. (1996) suggest that "Assignment to subfamily of the teeth in the two middle rows (note: figure shows *Antemus*, *Potwarmus*, *Dakkamys*, *Primus* and Myocricetodontinae and Muroidea gen. indet.) remains more or less a matter of taste at this stage."

Whatever the taxonomical details may be – fact is that the oldest murines are found in southern Asia, which is also one of the centres of greatest abundance and diversity today. This makes southern Asia the most probable area of origin of murids. While during Oligocene and for most of the Miocene rodent assemblages where still dominated by Cricetids, during the late Miocene the newcomers – murines, supersede them and until today remain the dominating element in small mammal communities.

Although many of the Early Vallesian populations have been excluded from the genus *Progonomys* (Mein et al. 1993), it was the extinct genus *Progonomys* or forms at the *Progonomys*-stage-in-evolution, to be the first murines to migrate out of Asia and into Europe and Anatolia during the early Vallesian. However, already the early Vallesian murines are quite diversified and three lineages (*Mus*, *Apodemus* and *Progonomys*) can be distinguished.

2. Material and Methods

2.1 Material

The Material of this work was provided by the department of Geology and Palaeontology of the Natural History Museum Vienna, where it is stored.

Separate divisions of the fossils were kept in a multitude of little glass tubes and plastic bags and boxes etc., labelled with finding points. These labels did not always correspond to the finding points recorded in the detailed sketch of the outcrop, which is why the fossils had to be assigned to finding points on the sketch and hence assembled into larger groups. Another reason for the grouping was to obtain larger sample sizes necessary for additional statistics.

Finding points recorded in the sketch are: I, II, III, IIIa, IIIb, III unten (below), III oben (above) and IV.

Material labelled with I, Ia, was grouped into finding point I.

Material labelled with II, IIa, II/1, II/2, II/3, was grouped into finding point II.

Material labelled with III, III Mitte (Middle), III Mitte Spalte (middle cleft), III rechts (right), III/2, III/3, III/6 where grouped into finding point III.

Material labelled with III unten (below), III unten Spalte (below cleft), III rechts unten (right below), III links unten Spalte (left below cleft), III links unten (left below) were grouped into finding point III unten (below).

It is noteworthy that the material of III below consists only of lower jaws.

Material labelled with III oben links (above left), III oben rechts (above right), III rechts oben Spalte (right above cleft), III oben rechts Spalte (above right cleft), III oben nicht Spalte (above not cleft) is grouped into finding point III above.

Material labelled with o.A. or "ohne Angabe" (meaning without specification) and material that was not labelled at all is referred to as "ohne Angabe" and probably stems from the reinvestigation of the spoil of the excavations.

Although there is no point marked CM on the sketch of the cave, material labelled as such was left together, as this group represented a rather large proportion of the material.

There were also some boxes with mounted single teeth, separated according to and labelled with species names, which comprised almost exclusively upper molars. It seems plausible, that this material was taken from III below, as there were no upper molars labelled with this finding point. However there is no way of knowing for sure since the material separated specieswise did not contain any labels indicating the finding point it was taken from.

Generally, the murine material from Kohfidisch contains a lot more mandibles and lower molars than maxillas and upper molars. This backlog of upper molars fits very well to the observation that the small mammal fauna stems mainly from owl pellets. Although the taphonomy of owl pellets varies greatly with the species, Dodson & Wexlar (1979) showed that generally mandibles are found far more often intact, than the cranium. The authors were able to show, that the cranium of mice is a "site of intense destructibility" and that especially the maxillas and the appurtenant upper molars were frequently missing. The excess of lower molars seems to militate against the deliberation that the mice regularly sojourned the caves but agrees very well with the findings that most small mammal remains were introduced into the cave by owls.

2.2 Pictures

Pictures of characteristic teeth were taken using the scanning electron microscope Philips XL20 at the department of cell imaging and ultra structure research and a Jeol JSM-6400 at the Department of Palaeontology of the Vienna University. They are shown in plates 1-6. Right teeth were mirror imaged to facilitate comparison.

2.3 Measurements

If at disposition, for every one of the 12 molars present in a murine jaw, 50 specimens were measured of out of every finding point (I, II, III, III unten, III oben, CM, and o.A.).

Measurements were taken using images of the teeth taken with the Leica stereomicroscope MZ12 and a Sony 3CCD-camera (Model: DXC-950).

Measurements were taken on the computer using the Sony camera adaptor, the program KSRun 3.0 and a measuring macro, kindly written by Kai-Uwe Hochhauser (Department of Palaeontology, University of Vienna).

This little program allowed adjusting a rectangle to the picture of the occlusal view of the molars on a computer screen, so that the inner margin would just touch, but not cover the outer margin of the tooth. With this technique it was possible to get a perfect accuracy because one is able to focus on different levels of depth and so perfectly adjust the measuring rectangle. The computer then measured the length and width of the rectangle and transferred the numbers into Excel tables.

2.5 Orientation

Orientation is the major source of error when measuring small mammal teeth. Since the Orientation guidelines for measuring murid teeth described by van de Weerd (1976) do not give any reference points, to help orient teeth in a standardised way, I decided to use the specifications of reference points developed by Martín-Suárez & Freudenthal (1993: 66-68).
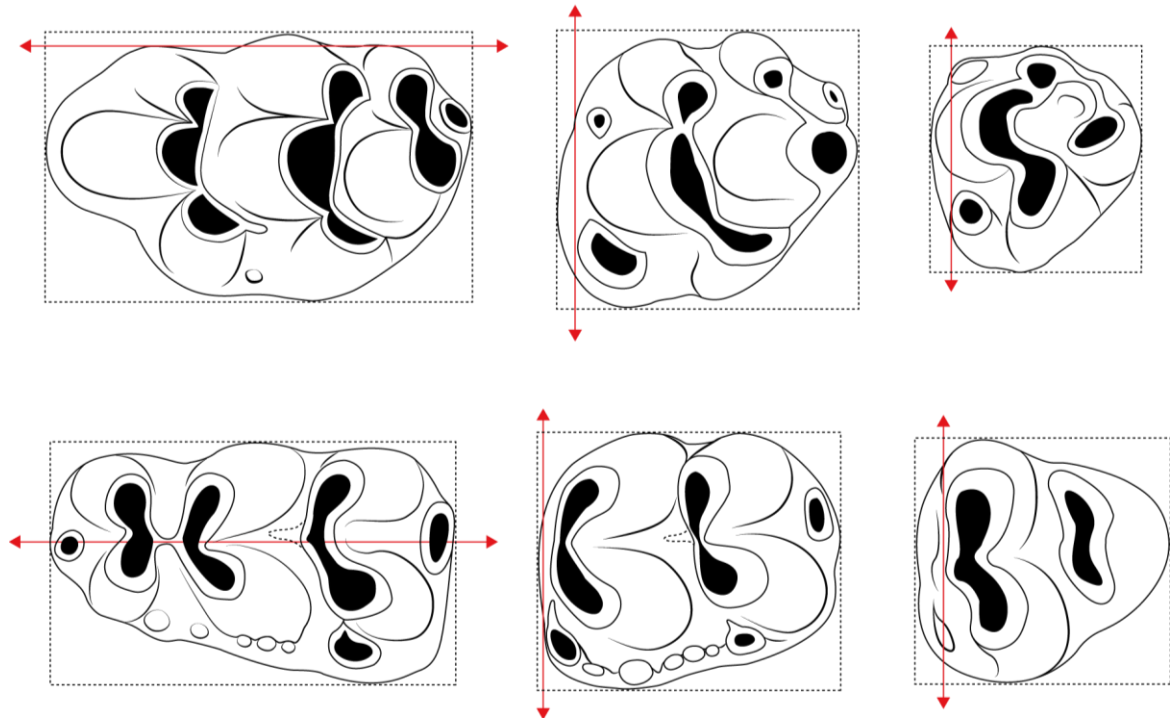
Fig. 10: Sketch illustrating the measuring method after Martín-Suárez & Freudenthal (1993); reference lines are indicated by red arrows.

Essentially the first upper molars were turned into a position such that the row of middle cusps 2, 5 and 8 was as horizontally a possible. In the second and third upper molars the reference line is a vertical tangent to the anterior border.

Also in the first lower molar the reference line is horizontal through the middle of the posterior wall and the anteroconid-protoconid-metaconid connection. In the second and third lower molars the anterior wall (in M_2 and M_3) was taken as horizontal guideline.

2.4   Statistics

Relative Frequencies of the occurring species within the samples of the different finding points were compared with the use of Pearson's Chi^2 and Fisher's exact test.

The length and width distributions of the different tooth positions were utilized to compare variations between the finding points with the help of MANOVA. The design of the MANOVA was an unbalanced one using the type III sum of Squares. The assumptions of multinormality and homogeneity of variances of MANOVA were tested using Mardia's test and Box-test respectively. Post hoc procedures

2.6 Nomenclature of morphological characters

Jacobs (1978: 25-30) has in the authors view best applied the Cope-Osborn nomenclature to murid teeth. In his work he also gives a detailed summary of the different other systems in use throughout the history of the study of small mammals. Although I agree with his view of the application of the Cope-Osborn nomenclature I believe that the system of Miller (1912) as applied by Van de Weerd (1976: 16, figure 9) and many others is easier to use and more flexible in its application. Therefore the nomenclature of cusps was used according to van de Weerd, with the exception of the accessorial cusps, where it was supplemented with a numeration for all possible positions. Where possible this numeration was tried to be kept in accordance with the numeration used by Wessels (2009) but some positions where not taken into consideration in their system and had to be added.
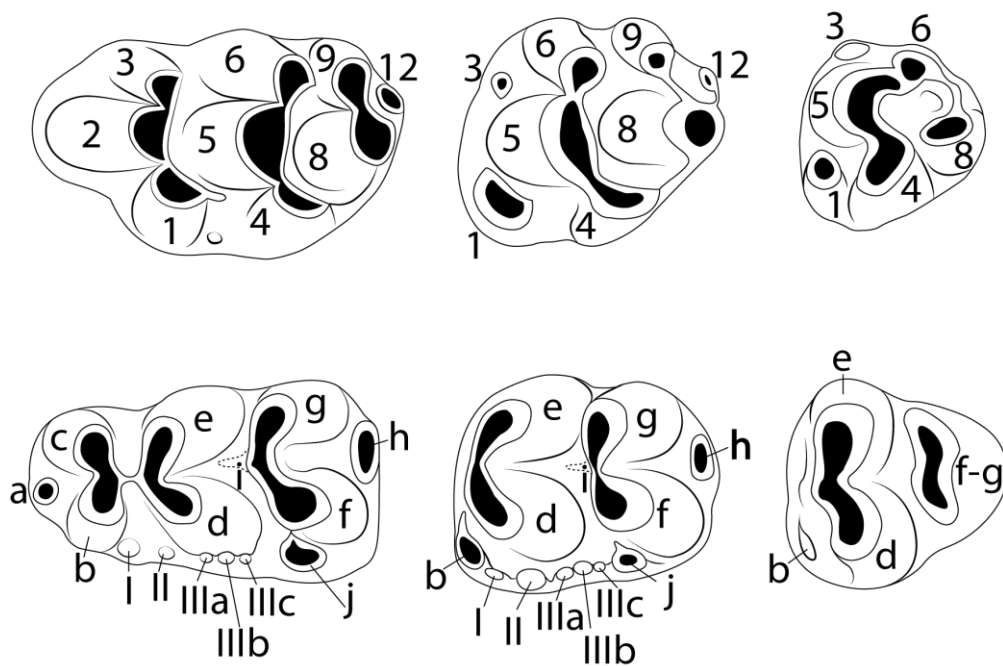
Fig. 11: Cusp terminology (on a morphotype scheme of left molars of *Progonomys woelferi*); Lower molars: a=tma/anterocentral cusp, b=anterolabial cusp, c=anterolingual cusp, d=protoconid, e=metaconid, f=hypoconid, g=entoconid, h=posterior heel/posterior cusp, i= longitudinal spur, Roman numbers indicate accessorial cusps on the labial cingulum; Upper molars: are numbered according to Miller's system;

3. Comparison of Finding Points

3.1 Comparison of relative abundances at the different finding points with a Chi² test.

The comparison of the different finding points based on the relative abundances (max. individual counts) of the two most common murine species with a Chi² test gave a Chi² of 119,48 (df: 6), significant at the 0,001 level. This highly significant Chi² was mainly caused by the residuals from the finding point III unten, but also finding point I and o.A. yielded high partial Chi²s. While in the latter two finding points there is a slight overhang of *Progonomys woelferi* compared to the overall distribution, in III unten there is a large excess of *Apodemus lugdunensis* compared to the other finding points.
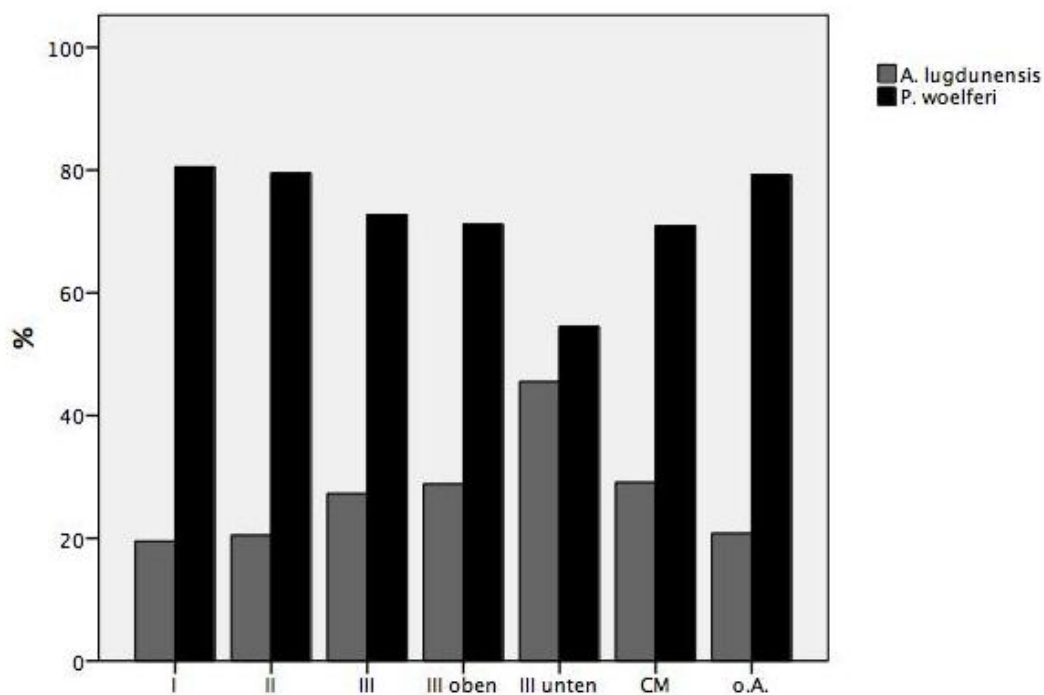
Fig. 12: relative sample frequencies of *Apodemus lugdunensis* and *Progonomys woelferi* within the different finding points; based on max. individual counts (all tooth positions);

3.2 Comparison of size distributions at the different finding points with MANOVA

		M^1			M^2			M^3		
		F	p	df	F	p	df	F	p	df
Progonomys woelferi	Pillai's V	0,75	0,610	6	5,42	<0,001	6	3,29	0,012	4
	Wilk's Λ	0,75	0,612	6	5,62	<0,001	6	3,33	0,011	4
	Hotelling's T^2	0,74	0,614	6	5,80	<0,001	6	3,38	0,010	4
	Box's M	2,89	0,002	9/300014	0,97	0,465	9/103783	1,50	0,175	3/20447
	Findingpoints	I, IIIunten, o.A., CM			I, IIIunten, o.A., CM			I, IIIunten, CM		
Apodemus lugdunensis	Pillai's V	0,91	0,487	6	1,80	0,13	4	4,116	0,003	4
	Wilk's Λ	0,91	0,486	6	1,82	0,13	4	4,288	0,003	4
	Hotelling's T^2	9,10	0,486	6	1,83	0,13	4	4,455	0,002	4
	Box's M	1,40	0,182	9/50937	0,029	0,94	6/4610	0,403	0,877	6/21178
	Findingpoints	I, IIIunten, o.A., CM			I, IIIunten, CM			I, IIIunten, CM		

Table 1: Results of the MANOVA (upper molars); F= F-value, p= probability, df= degrees of freedom;

|		m_1			m_2			m_3		
		F	p	df	F	p	df	F	p	df
Progonomys woelferi	Pillai's V	9,73	0,465	10	5,15	<0,001	12	3,76	<,001	8
	Wilk's Λ	9,73	0,465	10	5,21	<0,001	12	3,87	<,001	8
	Hotelling's T^2	9,73	0,465	10	5,26	<0,001	12	3,98	<,001	8
	Box's M	1,41	0,133	15/45576	1,53	0,71	18/6127	2,93	<,001	12/61169
	Findingpoints	I, II, III, IIIunten, CM, o.A.			I, II, III, IIIoben, IIIunten, CM, o.A.			I, IIIoben, IIIunten, CM, o.A.		
Apodemus lugdunensis	Pillai's V	1,10	0,361	12	0,820	0,629	12	0,670	0,752	10
	Wilk's Λ	1,09	0,369	12	0,819	0,631	12	0,670	0,751	10
	Hotelling's T^2	1,08	0,377	12	0,817	0,633	12	0,670	0,751	10
	Box's M	1,25	0,217	18/1002	0,953	0,513	18/612	0,572	0,898	15/1470
	Findingpoints	I, II, III, IIIoben, IIIunten, CM, o.A.;			I, II, III, IIIoben, IIIunten, CM, o.A.;			I, III, IIIoben, IIIunten, CM, o.A.;		

Table 2: Results of the MANOVA (lower molars); F= F-value, p= probability, df= degrees of freedom;

MANOVA was used to compare the size distributions of *Progonomys woelferi* and *Apodemus lugdunensis* from the different finding points. Unfortunately a multifactorial design was not possible because of the different abundances and thus sample sizes of the two species. Mardia's test was used to test the assumption of multinormality. The test showed non-significant results for all tooth positions except three (*P. woelferi*: M^1, m_2;

A. lugdunensis: m_3;). However in each of the three cases the significance level could be pushed to over 0,5 by removing only one mild outlier (<3IQR), which why the distribution of the population was assumed to normal nonetheless. The homogeneity of variances, another assumption of the MANOVA, was tested with Box-test. In the case of a significant result of the Box-test, unfortunately only those finding points with roughly equal sample sizes could be included, in order not to decrease the reliability of the test statistics. It should be noted however that in the case of violation of the criterion of homogeneity of variances, the results of the MANOVA are shown in Tables 1 and 2. The last line indicates the finding points included in the analyses for the different tooth positions. The test statistics are ordered according to their statistical power under the circumstances (Field, 2009: 601-605).

It can be seen that the sizes of samples of *Apodemus lugdunensis* from the different finding points do not differ significantly, which is in accordance with the results of morphological analyses, which showed the teeth of *A. lugdunensis* to be very uniform and only have a very narrow range of variation. The picture we get from *Progonomys woelferi* however, is a different one. The samples from the different finding points differ significantly in the dimensions of the second and third lower and upper molars.

In the M^2 significant differences could be detected in the distributions of the widths of finding points I and o.A, III unten and CM and CM and o.A. The results of all applied Post hoc procedures proofed to be very consistent and delivered similar p values.

In finding points I and CM mean widths were smaller than in finding points III unten and o.A., of which the latter yielded the largest mean width values.

In the M^3 Post hoc comparisons only showed significant results for the length of the tooth but not the width. However again, differences between I and III unten, CM and III unten proofed to be significant. Again, the mean of the finding point III unten is significantly larger than the means of the other two finding points included in the analyses.

In the m_2 both width and length differences contributed to the significant results of the overall MANOVA. In this tooth position, contrary to the results of the upper molars the means of both width and length of finding point I are significantly larger than those of all other finding points, except II and III.

In the lower m_3 again only the widths showed significant differences. The mean of the finding point I proofed to be significantly larger than those of the finding points II, III oben and CM.

Unfortunately the Post hoc procedures for the different tooth positions did not reveal any clear larger patterns, except that the lower molars of *Progonomys woelferi* are significantly larger in finding point I.
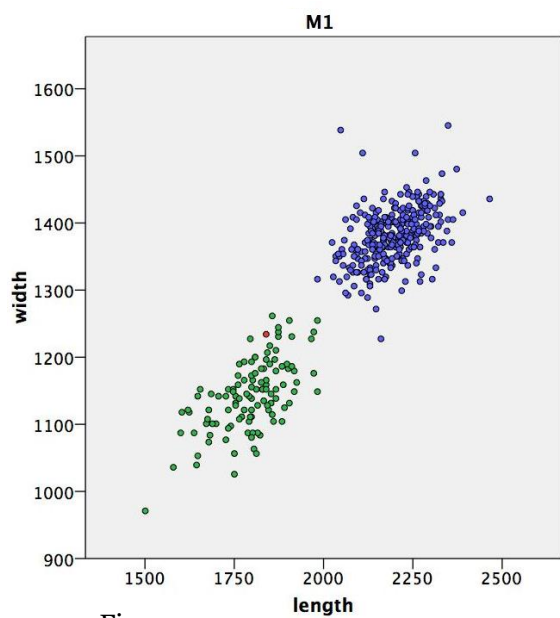
Fig. 13
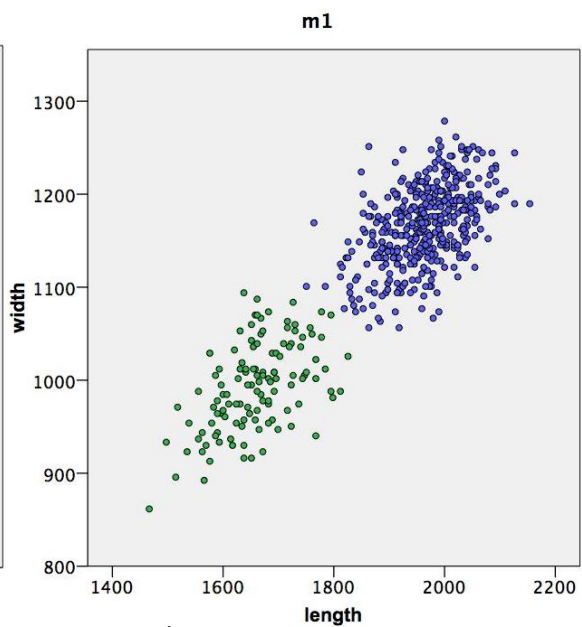
Fig. 14
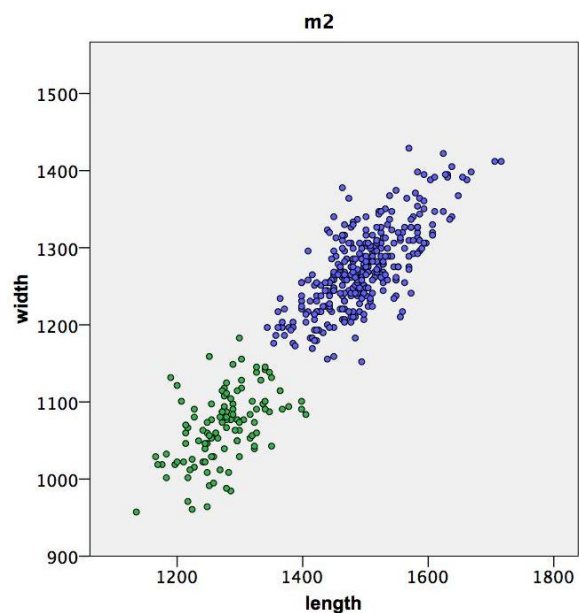
Fig. 15
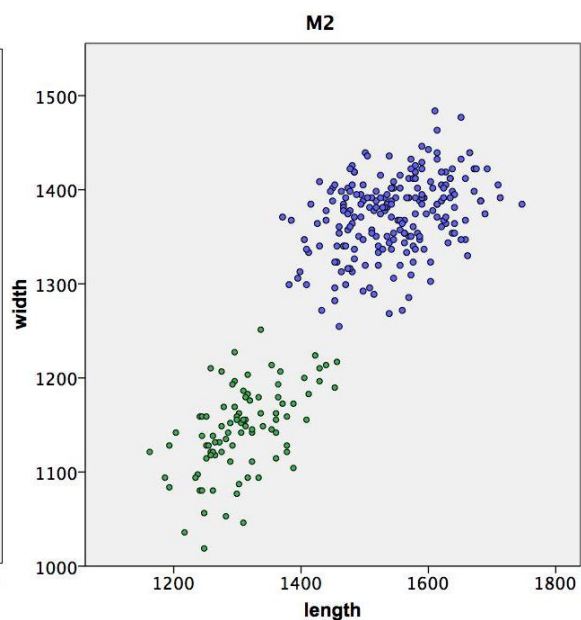
Fig. 16
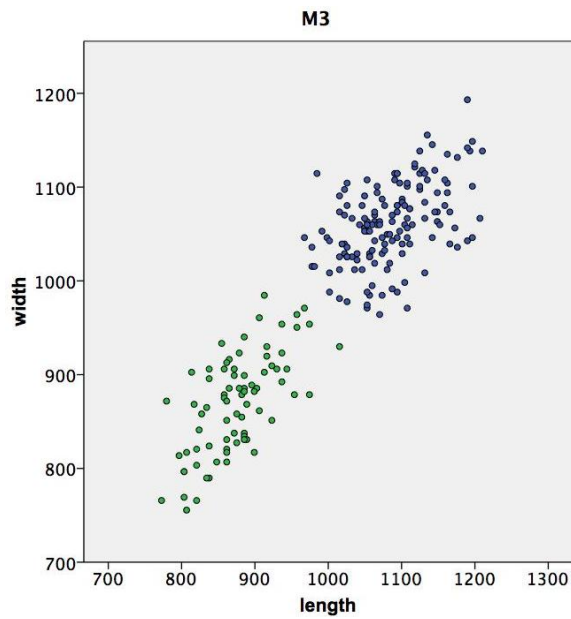
Fig. 17
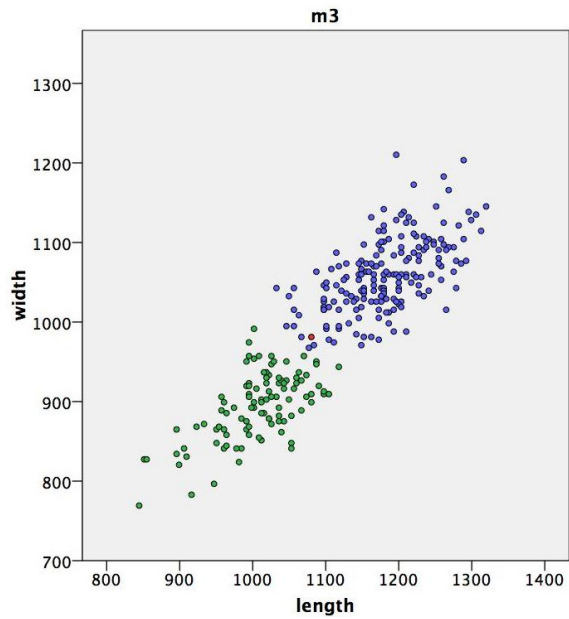
Fig. 18

Figs. 13-18: Scatterplots of size distributions of *Progonomys woelferi* (blue circles) and *Apodemus lugdunensis* (green circles) and *Progonomys hispanicus* (red circles); x- and y-axis scales in μm;

4. *Progonomys woelferi* BACHMAYER & ZAPFE, 1970

4.1 Description

M¹

Finding point		Length					Width				
	N	Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	81	2024	2390	2192	9	83	1227	1504	1378	5	43
Ko II	30	1983	2325	2154	16	88	1316	1538	1387	8	44
Ko III	17	2123	2362	2248	17	69	1313	1463	1374	9	38
Ko III oben	0	-	-	-	-	-	-	-	-	-	-
Ko III unten	74	2041	2359	2188	9	77	1289	1504	1382	5	33
o.A.	65	2085	2349	2207	8	62	1272	1545	1387	5	43
CM	41	2055	2465	2198	11	71	1313	1446	1378	5	32
Total	308	1983	2465	2194	4	77	1227	1545	1382	2	41

Table 3

M²

Finding point	N	Length					Width				
		Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	89	1371	1682	1538	7	70	1268	1463	1371	4	40
Ko II	10	1409	1672	1546	29	92	1299	1436	1385	15	46
Ko III	4	1497	1641	1559	34	69	1296	1422	1365	28	56
Ko III oben	0	-	-	-	-	-	-	-	-	-	-
Ko III unten	38	1395	1709	1564	12	74	1272	1422	1381	5	33
o.A.	24	1385	1747	1545	19	93	1320	1484	1400	8	39
CM	44	1409	1713	1545	11	74	1255	1415	1354	6	39
Total	209	1371	1747	1546	5	75	1255	1484	1373	3	41

Table 4

M³

Finding point	N	Length					Width				
		Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	20	978	1210	1071	15	68	988	1138	1064	9	40
Ko II	1	-	-	-	-	-	-	-	-	-	-
Ko III	3	1053	1207	1105	51	-	1029	1067	1050	11	-
Ko III oben	0	-	-	-	-	-	-	-	-	-	-
Ko III unten	59	981	1197	1104	7	53	964	1156	1067	6	44
o.A.	0	-	-	-	-	-	-	-	-	-	-
CM	65	968	1197	1073	6	47	971	1193	1057	6	45
Total	148	968	1210	1085	5	55	964	1193	1062	4	44

Table 5

m₁

Finding point	N	Length					Width				
		Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	83	1812	2154	1963	6	57	1077	1262	1172	4	34
Ko II	27	1826	2092	1954	14	73	1094	1251	1180	8	43
Ko III	16	1853	2099	1955	18	72	1056	1279	1165	16	62
Ko III oben	79	1826	2126	1968	8	67	1063	1241	1147	5	44
Ko III unten	64	1750	2126	1960	9	75	1094	1251	1167	5	39
o.A.	83	1832	2092	1971	7	62	1074	1258	1180	4	40
CM	64	1815	2092	1959	8	66	1067	1248	1166	5	43
Total	416	1750	2154	1964	3	66	1056	1279	1167	2	43

Table 6

m₂

Finding point		Length						Width			
	N	Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	86	1357	1716	1529	8	74	1152	1497	1304	7	64
Ko II	18	1439	1638	1507	14	61	1217	1398	1280	12	49
Ko III	6	1354	1573	1452	29	-	1176	1326	1254	25	-
Ko III oben	33	1364	1607	1471	10	57	1159	1330	1241	7	43
Ko III unten	44	1368	1624	1475	9	62	1173	1391	1260	8	50
o.A.	86	1344	1634	1486	7	62	1193	1429	1274	5	49
CM	54	1405	1597	1494	6	41	1179	1337	1259	5	39
Total	327	1344	1716	1496	4	65	1152	1497	1274	3	55

Table 7

m₃

Finding point		Length						Width			
	N	Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	25	1032	1320	1203	16	81	995	1210	1095	9	47
Ko II	4	1101	1244	1166	30	-	1029	1060	1041	7	-
Ko III	1	-	-	-	-	-	-	-	-	-	-
Ko III oben	19	1077	1248	1172	12	50	968	1101	1035	9	39
Ko III unten	47	1111	1289	1191	6	43	981	1145	1064	6	41
o.A.	39	1063	1299	1184	11	68	971	1203	1066	10	60
CM	51	1046	1279	1165	8	58	974	1108	1043	4	32
Total	186	1032	1320	1181	4	60	968	1210	1059	3	47

Table 8

Tables 3-8: Width an Length distributions in μm for M¹, M², M³, m₁, m₂ and m₃ of *Progonomys woelferi* from the different finding points within the locality of Kohfidisch; N= number of individuals, SE= standard error of mean, Stdev= Standard deviation;
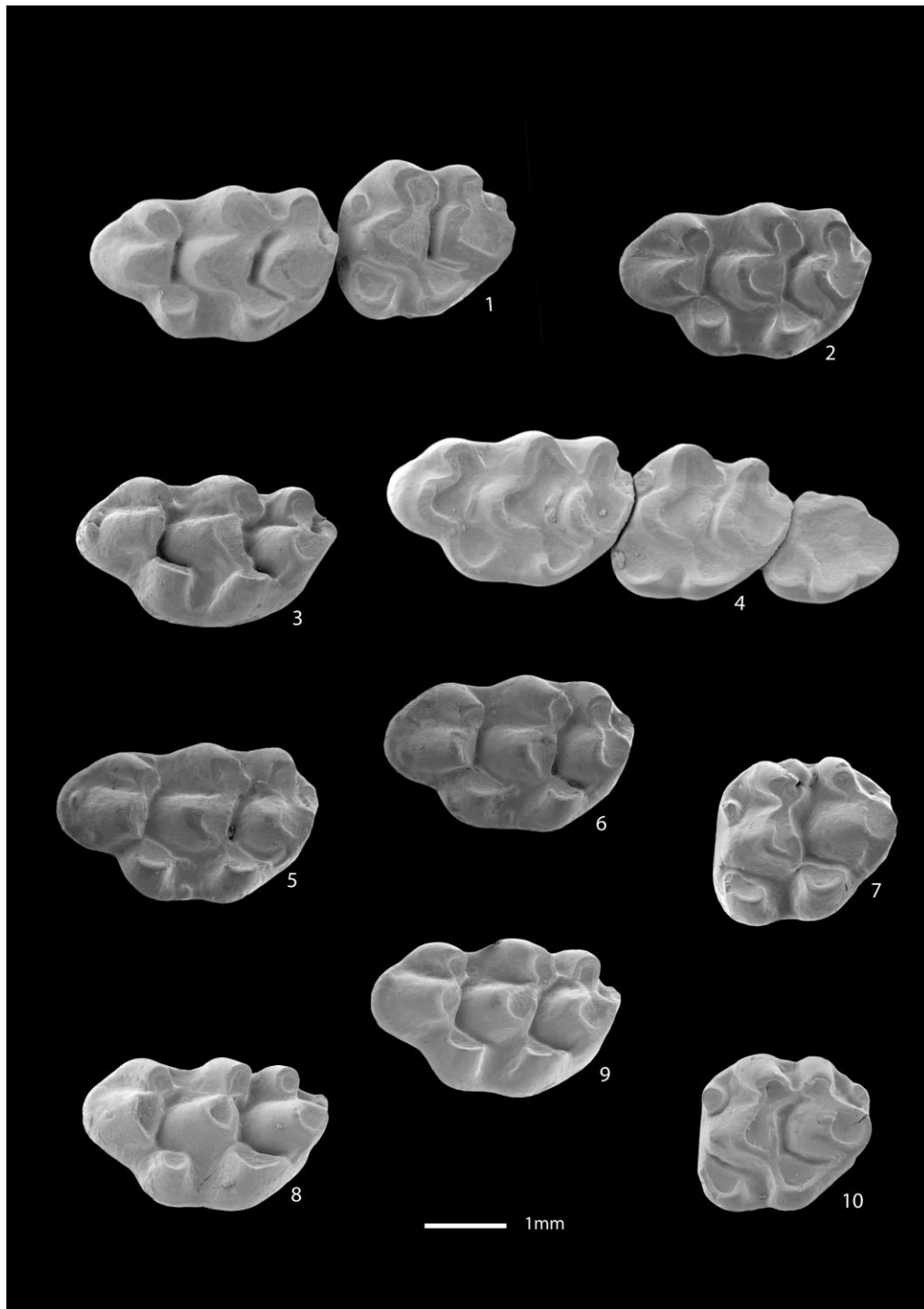
Plate 1: *Progonomys woelferi* Kohfidisch:

1) NHMW2011/0104/25: M^1-M^2 sin.
2) NHMW2011/0104/26: M^1 dex.
3) NHMW2011/0104/27: M^1 sin.
4) NHMW2011/0104/28: M^1-M^3 sin.
5) NHMW2011/0104/29: M^1 dex.
6) NHMW2011/0104/30: M^1 dex.
7) NHMW2011/0104/31: M^2 sin.
8) NHMW2011/0104/32: M^1 sin.
9) NHMW2011/0104/33: M^1 sin.
10) NHMW2011/0104/34: M^2 dex.
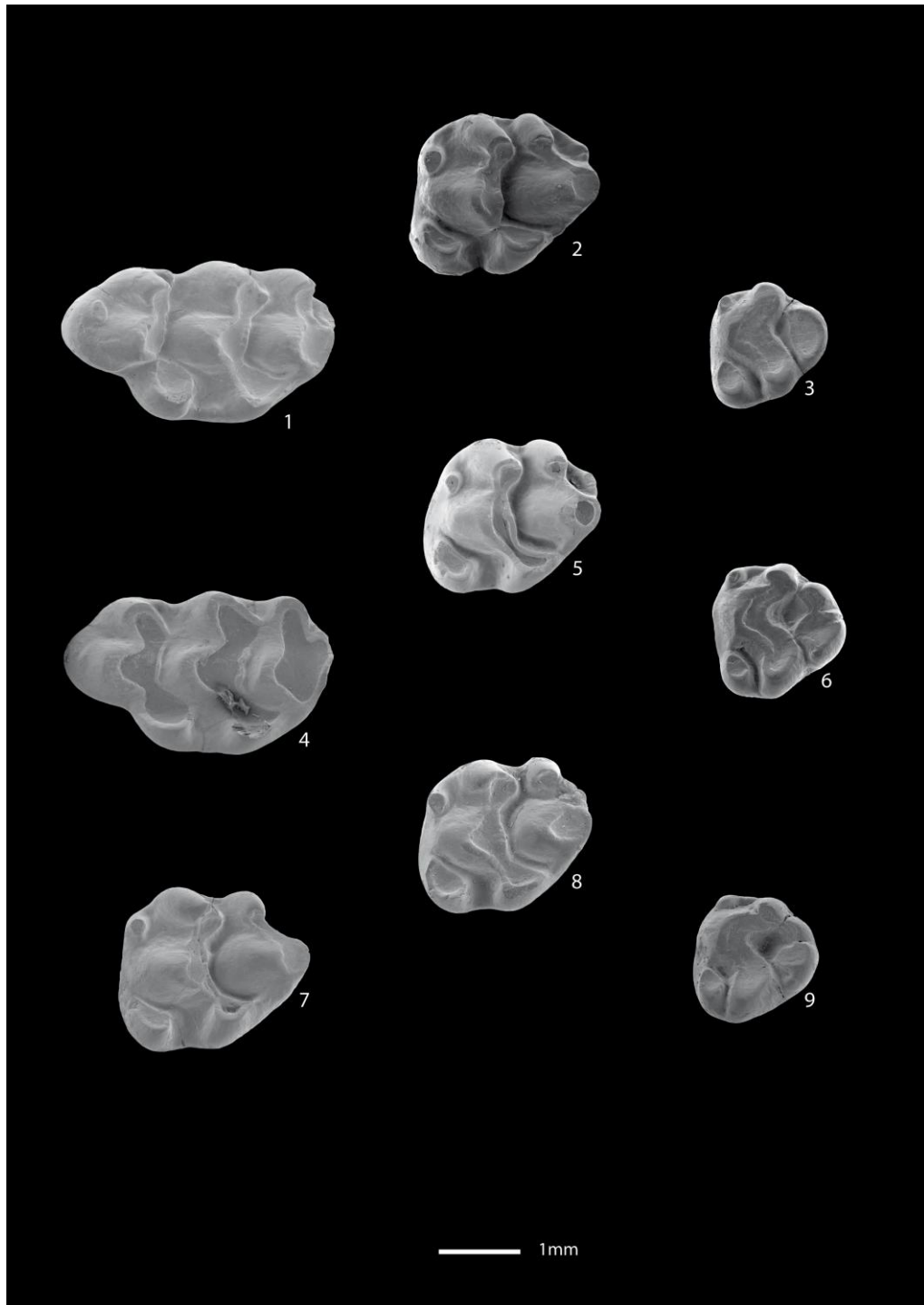
Plate 2: *Progonomys woelferi* Kohfidisch:

1) NHMW2011/0104/35: M^1 sin.
2) NHMW2011/0104/36: M^2 sin.
3) NHMW2011/0104/37: M^3 sin.
4) NHMW2011/0104/38: M^1 dex.
5) NHMW2011/0104/39: M^2 sin.
6) NHMW2011/0104/40: M^3 dex.
7) NHMW2011/0104/41: M^2 sin.
8) NHMW2011/0104/42: M^2 dex.
9) NHMW2011/0104/43: M^3 dex.
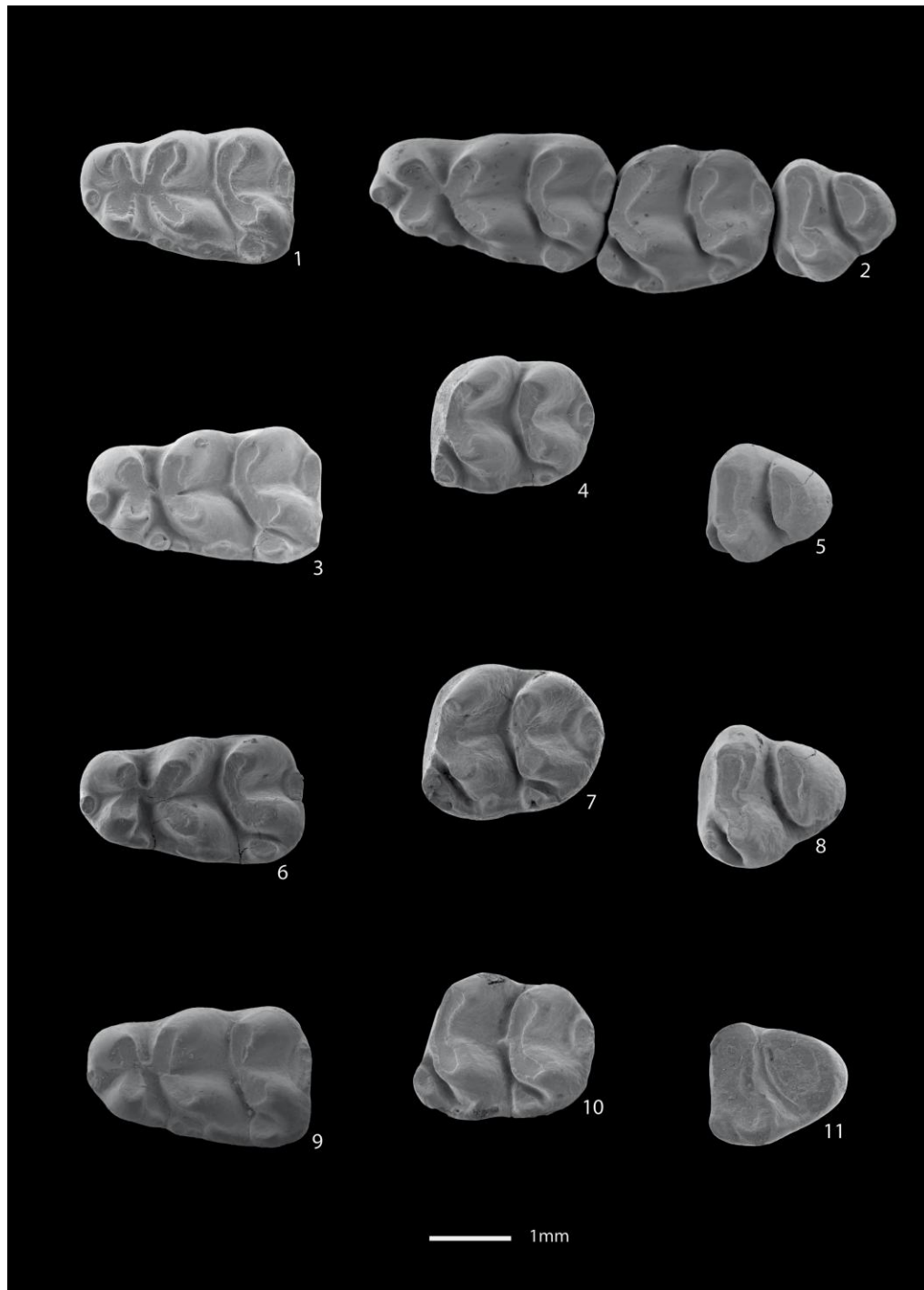
Plate 3: *Progonomys woelferi* Kohfidisch:
1) NHMW2011/0104/44: m_1 sin. 7) NHMW2011/0104/50: m_2 sin.
2) NHMW2011/0104/45: m_1-m_3 dex. 8) NHMW2011/0104/51: m_3 dex.
3) NHMW2011/0104/46: m_1 sin. 9) NHMW2011/0104/52: m_1 sin.
4) NHMW2011/0104/47: m_2 sin. 10) NHMW2011/0104/53: m_2 sin.
5) NHMW2011/0104/48: m_3 dex. 11) NHMW2011/0104/54: m_3 sin.
6) NHMW2011/0104/49: m_1 sin.
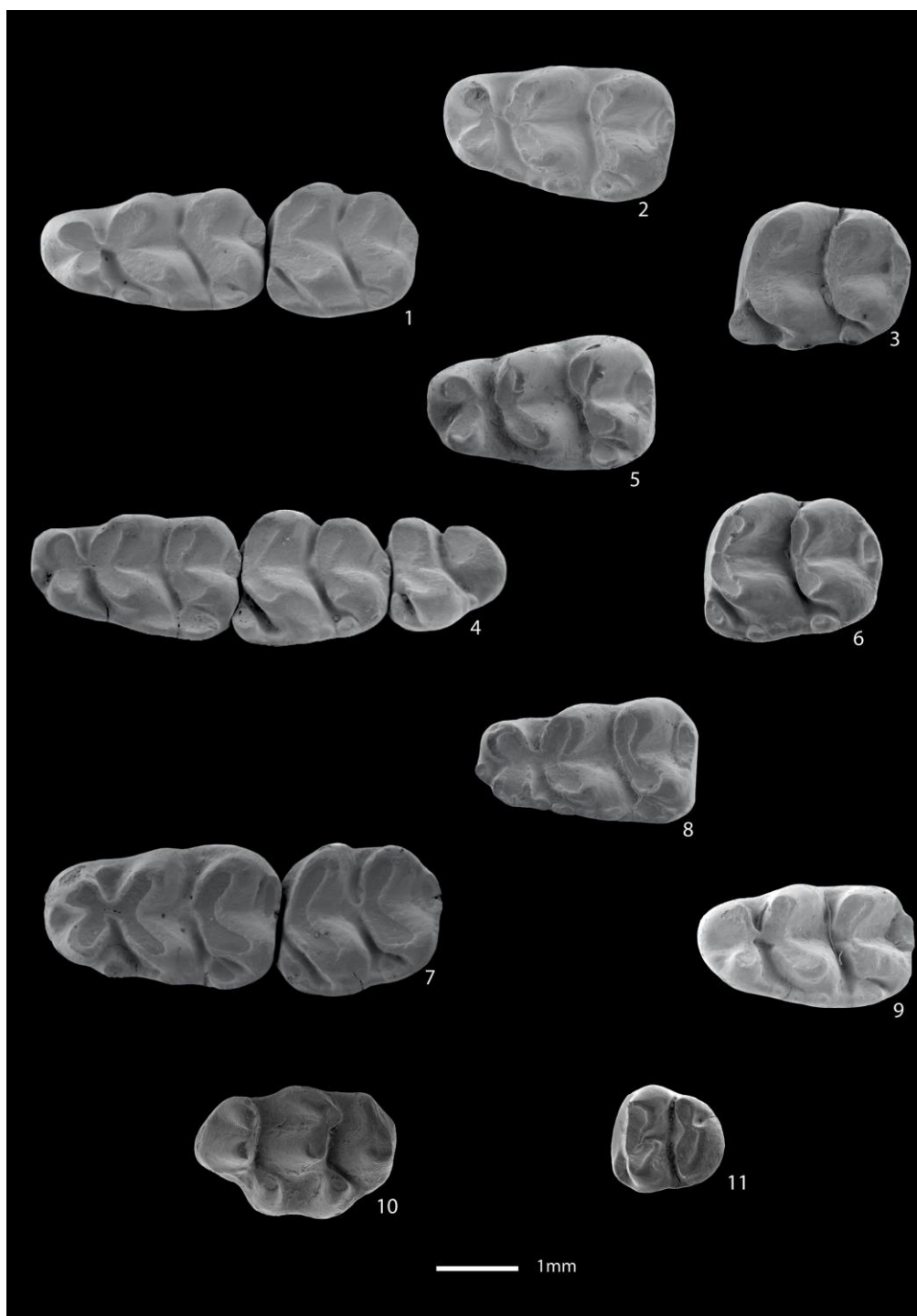
Plate 4: *Progonomys woelferi* Kohfidisch:

1) NHMW2011/0104/55: m_1-m_2 dex.
2) NHMW2011/0104/56: m_1 sin.
3) NHMW2011/0104/57: m_2 dex.
4) NHMW2011/0104/58: m_1-m_3 sin.
5) NHMW2011/0104/59: m_1 dex..
6) NHMW2011/0104/60: m_2 sin.
7) NHMW2011/0104/61: m_1-m_2 dex.
8) NHMW2011/0104/62: m_1 dex.
9) NHMW2011/0104/63: m_1 sin.

Progonomys cf. *hispanicus* Kohfidisch:

10) NHMW2011/0104/64: m_1 sin.
11) NHMW2011/0104/65: m_3 dex

M¹: (137 specimens)

The t1-t2-connection is definitely always existent, but weaker (more slender) compared to the t2-t3-connection in 59% (67/137). In two teeth the t1 was found to be divided! Generally the t1 is not very elongated and only slightly, but always in a posterior position. In 2 teeth it showed a well-developed spur, pointing in the direction of the t4-t5 connection. About 26%(35/137) of the specimens show what one may call a weak spur on the t3 (it could also be seen as a vertical edge on the side of the cusp), always pointing in the direction of the t5-t6-connection. The t4-t5-connection is usually well developed, but not quite as wide as the t5-t6-connection and was in two specimens even found to be missing. The t4-t8-connection is missing in 4%(6/137) and moderately to well developed in the Rest of the specimen. The t6-t9-connection is not present in 53%(73/137), moderately developed in 28%(38/137) and strong in 19%(26/137). The t9 is always connected to the t8 and never isolated. Its Position is transverse to slightly proverse. A t7 is clearly the exception and was present in only two specimens. The t12 is always present and comma-shaped or reduced to a slender ridge.

There can be an accessorial cuspule in the sinus between the t1 and t4 (18%, 25/137). In rare cases 4%(5/137) the "cingulum" around the t2 and t3 can show accessorial cuspules. In one tooth there was an accessorial cuspule attached to the posterior wall of the t3.

In *Progonomys* the t6 is always bigger than the t9, while in *Apodemus lugdunensis* they are the same size. The t3 is reduced and usually even smaller than the t9. Compared to *Apodemus lugdunensis* the teeth of *Progonomys woelferi* seem "cloddy" although the ridges are more slender compared to the cusps, except for t2-t3 and t5-t6 connections, which are always very wide. In *Progonomys woelferi*, the t6 is connected rather to the t8-t9 connection than to the t9 itself. The M1 of *Progonomys woelferi* is three-rooted. 73% of the teeth show a fourth, small, accessorial root. The lingual root is never separated.

M²: (122 specimen)

The M² in *Progonomys woelferi* is a very uniform tooth. The t1 is always larger than the t3. A t1bis is present in at least 8% (10/122) of the specimen. In some of the individuals its presence is impossible to detect because of the degree of wear. The t3 is very reduced, but can have an accessorial cuspule anterior or posterior in 2%(4/122). In 2 teeth a t2bis could be seen, although the t2 is always missing. Only one observed tooth showed an accessorial cusp between the t1 and t4. The t4-t5, and t4-t8 connections are always present. The t7 was found in 4/122 teeth (3%). There is a very low t6-t9 connection present in only a few cases (7%, 9/122) and a well developed one in even fewer (2%, 3/122). In about 24/122 cases (20%) the t 6can show a short spur. The t12 is usually comma-shaped and only in

very few cases reduced to a slender ridge. The M^2 has three roots. There are no accessorial roots.

M^3: (98 specimens)

Progonomys woelferi teeth are less variable than the M^3 of *Apodemus lugdunensis*.

The $t1$ is usually well developed (72/98, 73%). The $t3$ is very reduced but always present. A $t1bis$ was never observed. There is usually a very shallow ridge, connecting $t1$ and $t3$, or both of them with the $t5$ (55%, 54/98). A $t9$ was developed in only 14/98 specimens. There is never a $t7$. A $t6$-$t8$ connection is nearly always present, although it is very shallow in about 24% of the cases. A $t4$-$t8$-connection was observed in 40% (39/98) of the cases and missing in the remaining 60%. In very rare cases there can be a lingual connection between the $t1$ and the $t4$. There are no accessorial roots.

m_1: (150 specimens)

34/150 (23%) specimens show a well-developed anterocentral cusp, 92/150 (61%) a very reduced one, and only very rare specimens show no anterocentral cusp at all, or only a small cingulum between the anteroconid cusps. The anteroconid complex is either symmetrical, or the anterobuccal cusp is slightly bigger. The connection of the anterolingual and anterobuccal cusps is next to always very strong. In comparison the connection between the meta- and the protoconid is thinner and only well developed in 83% of the specimen (125/150). The connection between the anteroconid complex and the protoconid-metaconid-complex is thinner than the former two and is central or shifted a little to the lingual side. Only 2 of 150 cases show strong longitudinal spur. There is usually at least one accessorial cusp next to the posterior side of the anterobuccal cu*sp*. In 70%(105/150) there is a second accessorial cusp on the buccal cingulum next to or in slightly posterior position of the protoconid. There is nearly always a posterior accessorial cusp, which can be slightly reduced (33/150; 22%). The shape of the terminal heel is very variable and varies from round to elliptical to only a slender ridge.

In rare cases an extra accessorial cuspid could be observed the on the lingual side, next to the posterior wall of the anterolingual cu*sp*. All lower molars have two roots, but 47% of the m_1 show a small accessorial root.

m_2: (144 specimens)

The general shape (78%) of the m_2 in *Progonomys woelferi* is like a trapeze, the anterior side being wider than the posterior one. The anterolabial cusp is always present and well developed. The protoconid-metaconid connection is always wide and higher than the

hypoconid-entoconid one. The connection of the entoconid to the hypoconid is always well developed. The hypoconid and entoconid are usually the same size. There is hardly ever a longitudinal spur (114/144), but it can occur. In 74% (106/114) there are one or two accessorial cusps right next to the protoconid and hypoconid, where the one next to (or slightly posterior of) the hypoconid is always developed better. In the remaining 26% no actual cusps are visible on the cingulum, although next to the protoconid it is very wide. The posterior accessory cusp is well developed in 42% of the cases. It is far better developed than in *Apodemus lugdunensis*, which is fairly surprising, as in the m_1 the labial cingulum is generally better developed in *Apodemus lugdunensis*.

m_3: (118 specimens)

Here the anterobuccal cusp is usually reduced (87%; 103/118). The protoconid and metaconid are either the same size, or the metaconid is larger, in all specimens except for one where the protoconid is stronger. In general the shape of the protoconid-metaconid complex is very variable (It may not show an oval cusp form, but have squiggly outlines). A posterior accessory cusp is present in 45% (53/118). Once again the size and shape of the posterior lobe is very variable.

4.2   Discussion

4.2.1   Comparison of the findings of this study concerning *Progonomys woelferi* with the original descriptions:

In comparison, the results of this study and the findings of Bachmayer & Wilson (1970: 576-578; Bachmayer & Wilson, 1980: 378-383) correspond surprisingly well in morphology and measurements, given the different population samples and measuring techniques. The biggest difference to the original description seems to be the frequency of the anterocentral cusp in the m_1, which is clearly far more often well developed, than originally described in the past. The author also noticed that there seem to be two "morphotypes" of lower molars in *Progonomys woelferi* that do not differ in the abundance of character states at all. While most of the teeth are very angular and have rather steep cusps there are also teeth with a more elliptical outline that appear somewhat inflated. This difference could not be used to discriminate two groups since there are transition forms that cannot be assigned to either group with the naked eye.

4.2.2   Comparisons of *Progonomys woelferi* to other murine species

Comparison of *Progonomys woelferi* with *Huerzelerimys vireti* (SCHAUB, 1938) MEIN et al. 1993

Type locality: Mollon, Ain, France,

Otherlocalities: Lombrieu, Vaucluse, Provence-Alpes-Côte d'Azur, France (Mein & Truc, 1966); Cervillente 1, 2 and 3 (de Bruijn et al., 1975); Tortajada A, Valdecebro (van de Weerd, 1976); Aguanaces and Vivero de Pinos (Adrover, 1986); Fosso de la Fittaia (Engesser, 1989); Puente Minero (Alcalá et al., 1991; van Dam 1997)

Huerzelerimys vireti, Cervillente 2 and 4B (Suárez & Freudenthal, 1993)

Unfortunately the genus description:

> "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 week crest. M^1 and M^2 with a well-developed t9, and with t6 and t9 united in more than 50% of the specimens. M^3 without t9. M^1 with a reduced tma, and with a connection between the two anterior pairs of tubercles; three roots; cingula margin moderately developed. Tendency towards a strong size increase in the course of time."

in Mein et al. (1993: 49, 52), as well as the differential diagnosis concerning *Progonomys* in the same article:

> "Differs from *Progonomys* by having a connection between the two anterior pairs of tubercles in the m_1;"

are put in a form too general to differentiate *Huerzelerimys* from *Progonomys*. The author agrees with van Dam (1997: 52) that:

> "The general absence of the anteroconid-metaconid connection in m_1 should not be used as a character, because the connection is generally present in the type species *P. cathalai*"

and furthermore with Qiu et al (2004: 69) that:

> "The connection is generally present not only in the type species *Progonomys cathalai*, but also in the reference taxa selected by Mein et al. (1993), such as *P. cathalai* from Peralejos (van de Weerd, 1976) and *P. woelferi* from Siwalik deposits of Pakistan (Jacobs, 1978)."

Also in the type species of *Progonomys woelferi*, a connection between the anteroconid and metaconid/protoconid is nearly always developed and missing only in less than 5%.

Huerzelerimys vireti is generally bigger than *Progonomys woelferi*, but size overlap occurs. This is especially true for the m_2 of the lower jaw, and for very small populations of *H. vireti* such as the one from Puente Minero (van Dam, 1997: 57-59). The teeth of *H. vireti* are not so much longer, as they are wider than those of *P. woelferi*, resulting in a larger width/length ratio.

The comparison with the type species from Mollon on the basis of the original description (Schaub 1938: 25-26) proves to be difficult, since the author does not give the number of specimens used for the description, with the exception of the M^1 of which only 2 were available at the time. Van de Weerd (1976: 89) however states that *Valerymys* (=*Huerzelerimys*) *vireti* from Valdecebro 4, Alfambra and Tortajada A are identical in morphology and size to those of *V. vireti* from its type locality Mollon.

In the m_1 the anterocentral cusp in *H. vireti* from these localities is less frequent than in *P. woelferi*. Morphologically the m_2 of both species do not seem to differ. The labial cingulum is equally probably developed than in both species. In the m_3 the posterior accessory cusp is never present in *H. vireti*, while in *P. woelferi* it is present in 45%. In the first upper molar the t6-t9 connection is more frequent in *H. vireti* and even more so in the second upper molar, in which this connection in *P. woelferi* is far less developed than in the M^1. The t4-t8 connection on the other hand is better developed in *P. woelferi*. Again in the M^3 there are no morphological differences.

Comparison of *Progonomys woelferi* with *Huerzelerimys minor* MEIN et. al, 1993
Type locality: Ambérieu 2C, Ain, France (Farjanel & Mein, 1984; Mein, Suárez & Agustí, 1993)
Other references: *Parapodemus sp.* Peralejos B, C &D, Teruel, Spain (van de Weerd, 1976: 84); *Progonomys* cf. *cathalai* La Roma II, Teruel, Spain (Adrover et al., 1982)
Apodemus sp. Cortijo de la Piedra, Granada, Spain (Sesé, 1989)

As van Dam (1997: 64) states: "*Huerzelerimys* and *Progonomys* are rather similar in their general habitus." This is especially true for *Huerzelerimys minor*, since it is the only species of *Huerzelerimys* that falls into the size range of *Progonomys*. It is slightly bigger than *Progonomys cathalai*, but size overlap exists.

The size ranges of *H. minor* and *P. woelferi* especially from their respective type localities largely overlap. The biggest size differences between the two populations lie in the M^1 and m_2, which are wider in *H. minor*.

Morphologically the M^1 of *Huerzelerimys* has a higher frequency of a t6-t9 connection than *P. woelferi*, but the statement of Mein et al. (1993: 58) that this connection is always missing in *P. woelferi* is not true. In *H. minor* the t12 is stouter and more tubercular. The t4-t8 connection in the M^1 is equally developed in both species. Interestingly this connection in the M^2 seems to be slightly more frequent in *P. woelferi*. The t6-t9 connection in this tooth however is present much more often in *H. minor* (64%) than in *P. woelferi* (9%). The third upper molars of both species probably do not differ much. The m_1 of *H. minor* differs in that the frequency of the anterocentral cusp in *H. minor* is slightly higher. It can be connected to the labial anteroconid by a small crest, which is never the case in *P. woelferi*. The hypoconid-entoconid complex is bigger and somewhat more symmetrical in *P. woelferi*. The labial cingulum is larger in *H. minor*.

Comparison of *Progonomys woelferi* with the genus type species *Progonomys cathalai* SCHAUB, 1938

Type locality: Montredon sup. and dep., Aude, Languedoc- Roussillon, France (Schaub 1938, Michaux 1971, Aguilar 1982;)

Other localities: Ravin de la Pluie (de Bonis & Melentis, 1975); Masía del Barbo B, Peralejos 4, Peralejos A (van de Weerd, 1976); Biodrak (de Bruijn 1976); Freiria do Rio Mayor (Antunes & Mein, 1979); Bayratktepe 2 (Ünay, 1981); Soblay, Ambérieu (Farjanel & Mein, 1984);

The original description of *Progonomys cathalai*, given by Schaub (1938: 19-21), lacks the width measurements and information about sample size. In 1971 Michaux (1971: 10-13) publishes more (and probably more accurate) measurements form later excavations at the type locality. The following comparative study focuses on these later descriptions.

Progonomys woelferi is slightly bigger than *P. cathalai* from its type locality but size overlap occurs. In the upper molars the connection of the t4 to the t8 in *P. cathalai* is not as well developed as in *P. woelferi* from Kohfidisch, which is also true for the t6-t9 connection. While Aguilar delineates that in *P. cathalai* there is no correlation between size and degree of stephanodonty, in P *woelferi* it is clearly notable that smaller specimen have a higher probability of a t6-t8 connection than bigger ones. Judging from the pictures of Michaux alone the t1 in *P. cathalai* is not placed backwards very much, but further than

in *P. woelferi.* In the M^2 of *P. woelferi* the t4-t8 connection is even stronger than in the M^1. For *P. cathalai* this is not the case according to Michaux (1971: 11). While there are different "shape-morphotypes" in P *woelferi*, the angular one being more frequent, all of the *P. cathalai* specimens seem to be of the type with a more round outline. Schaub describes a bigger frequency of a developed anterocentral cusps in the upper one of the two fossiliferous strata, but does not give actual numbers or percentages for any of the two layers. Neither do Michaux or Aguilar, but since all three state that the tma is almost never well developed, it can be inferred that the frequency of a well-developed tma is much higher in *P. woelferi*. While there is never as much as a hint of a longitudinal crest in *P. cathalai*, there occasionally is a very small trace of it in *P. woelferi*. The most striking difference between the two species however is the morphology of the m$_3$! This tooth is far more reduced in *P. woelferi* than in *P. cathalai*. While in *P. cathalai* there exist teeth that still show a differentiation into hypoconid and entoconid, this is never the case in *P. woelferi*.

In the material of Kohfidisch there could only be found one very aberrant tooth (plate 4, fig. 11), which is not clearly assignable to one of the two known species. Size-wise it could fall into the m$_2$ cluster of *Parapodemus lugdunensis* or the m$_3$ cluster of *Progonomys woelferi*. Its root structure is the one of an m$_3$, but its occlusal morphology looks more like the one of a very reduced m$_2$. It has to be noted, that it looks very much like the m$_3$ of *Progonomys cathalai* depicted by Michaux.

Mein et al. (1993) exclude *Progonomys cathalai* from Kastellios K3 (de Bruijn et al., 1971; de Bruijn & Zachariasse, 1981) from this species because of 4 reasons. The first of these is the absence of a t4-t8 connection. This absence was never described in any of the two works and is merely existent in one M^1 depicted in de Bruijn & Zachariasse (1981: 221, fig. 3). The other upper teeth (1 M^1, 2 M^2) depicted in the work of 1971 do show very clearly that a t4-t8 connection is present. Also the second reason for the exclusion of this population, namely the absence of a t12 is never mentioned in the description and cannot be seen in any of the depicted teeth of the prior work. Again this character is only present in one M^1 depicted in the later work about the small mammals of Kastellios hill. The third reason, the greater development of the labial cingulum is not comprehensible comparing the published pictures. The forth and last reason, namely the lack of a third root in the M^1 of Kastellios hill cannot be verified, because it is never mentioned in prior descriptions. Considering the original description and pictures of *P. cathalai* from Kastellios hill in de Briujn (1971) it might be a little precipitant to exclude this population from the species.

If the population of Kastellios hill is indeed appurtenant to *P. cathalai*, diverse theories that *P. woelferi* could be a descendant of *P. cathalai* would proof to be very unlikely.

Comparison of *Progonomys woelferi* with *Progonomys hispanicus* MICHAUX, 1971

Type locality: Masía del Barbo A and B, Teruel basin, Zaragoza, Aragon, Spain (Freudenthal, 1966; Michaux, 1971; van de Weerd, 1976; van Dam, 1997)
Other localities: Peralejos A, B, C, D and 4(van de Weerd, 1976; van Dam, 1997); Masía de la Roma 4, 5, 7, 8, 9 and 11, La Salle, Puente Minero 2, La Roma 1 and 2, Los Aguanaces 5, La Gloria 11 (van Dam, 1997); Castelnou 1B (Aguilar, 1991);

Mein et al. (1993) like others before them argue that in the name of vertical classification *Progonomys hispanicus* should be transferred to the genus Occitanomys in order to make *Progonomys* a monophyletic genus. Van Dam (1997: 51,52) argues against this transfer and gives several good reasons supporting his contradiction, in my view most important of which is the fact that *P. hispanicus* is simply morphologically much closer to *P. cathalai* than to *O. brailloni*. I agree with all of his arguments and do not believe the generic attribution of *P. hispanicus* should be changed.

P. hispanicus from all its currently known finding sites is smaller, and without the range of *Progonomys woelferi*. In the M^1 of *P. hispanicus* the t1 is placed further backwards than in *P. woelferi*. It is in the former case only connected to the t2 via a very long, high and slender ridge, which can be missing altogether. In *Progonomys woelferi* this is never the case. In teeth of this species, where the t1 is placed backwards a little further and not so close to the t2, the ridge is always rather stout and shallow. As a rule of thumb one might say: the further back the t1, the shallower the ridge connecting it to the t2. Furthermore in *P. hispanicus* the connection of the t1 to the t2 can be thickened (which is interpreted as a precursor to a t1bis) or even show a developed t1bis. The t2 and t3 are close together in both species. Van Dam (1997: 48), as the only author gives percentages for some morphological characters of *P. hispanicus* from its type locality. Unfortunately he does so only for the fist molars in the upper and lower jaw. A developed t6-t9 connection is described to be present in only 9%. This is far less than in *P. woelferi* from Kohfidisch. Also the t4-t5 connection is present much more frequent in *P. woelferi* in both the M^1 and M^2. While in *Progonomys woelferi* the t9 can be straight or have a more anterior position, it is always in a straight angle to the longitudinal axis in *P. hispanicus* (van Dam, 1997:

52). In the M^1 the anterocentral cusp is better developed in *P. woelferi*, than in *P. hispanicus*, although informations of the varying authors, concerning this character are contradictory. The conules on the labial cingulum are better developed in *P. woelferi*. A longitudinal spur might be somewhat better developed in *P. hispanicus*. The third lower molars of the two species are morphologically practically indistinguishable, when ignoring the size difference.

Comparison of *Progonomys woelferi* with *Progonomys sinensis* QUI et al., 2004

Type locality: Bahe Formation at Lantian, Shaanxi Province, China (Qui, Zheng, & Zhang, 2004)

P. sinensis is so far probably the closest species to *P. woelferi*.

The first upper two molars of *P. sinensis* from its type locality lie well within the size range of *P. woelferi* but within the lower end of the range. Only the M^3 is shorter and without the length ratio of *P. woelferi*. The distributions of width of the M^3 however, overlap. The size distributions of the lower molars largely overlap, although on average *P. woelferi* seems to be slightly bigger. Considering the much smaller sample sizes for *P. sinensis* published by Qui, Zheng & Zhang, 2004, the possibility must be considered that the two species have in fact the same size.

In the first upper molar of *P. sinensis* the t1 is placed backwards much further than in *P. woelferi*. The t3 is reduced in size in both species but more so in *P. sinensis*. Since no absolute or relative frequencies have been published for the t4-t8 connection it is hard to compare the two species with respect to this character. The t6-t9 connection however is present more often, and better-developed in *P. woelferi* in the M_1 as well as in the M^2. The two species also seem to be similar concerning the tendency to build accessorial cuspules anterior to the t3 or t2 in the first upper molars. The lower molars are also very close in development of the tma, although in *P. woelferi* it is never connected to the anteroconid complex. Both the anteroconid- and the protoconid-metaconid-complex are more symmetrical in P. *woelferi* than in *P. sinensis*. The labial cingulum is far better developed in P. *woelferi*.
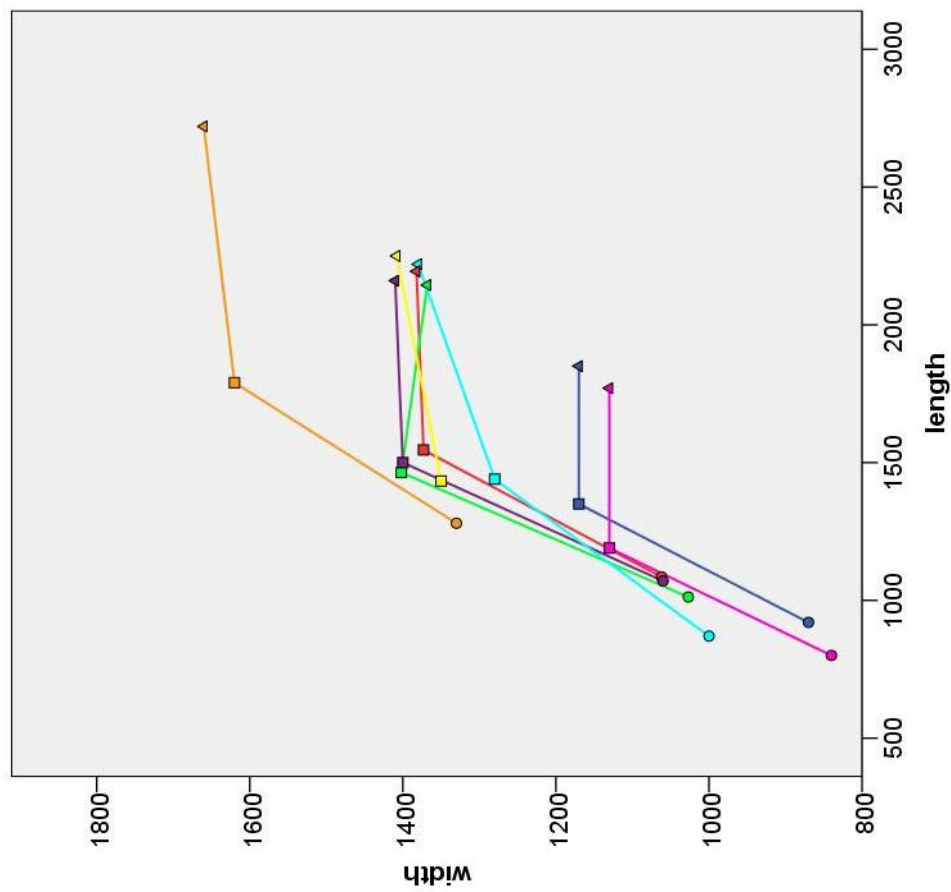
Fig. 19
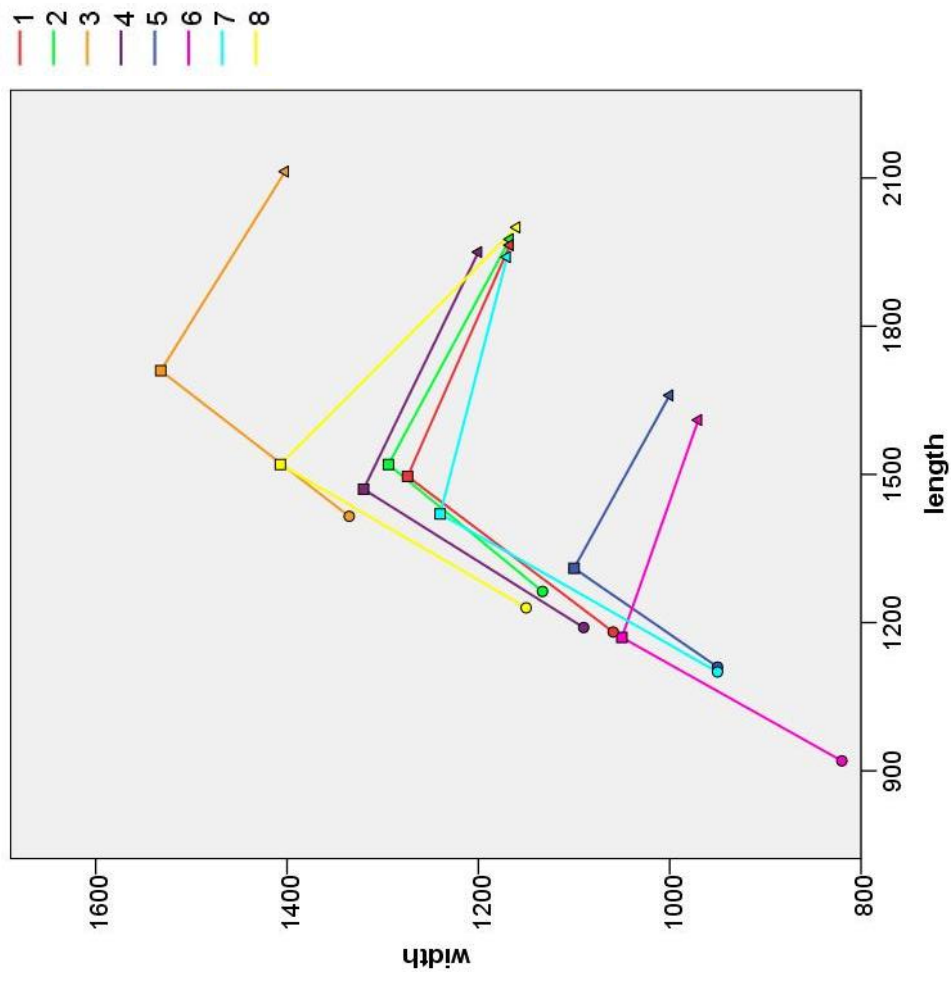
Fig. 20

Fig. 19-20: Comparison of mean lengths and widths of upper (fig.19) and lower (fig.20) molars; x- and y-axis scales in µm; circles indicate third, squares second and triangles first molars;

1) *Progonomys woelferi* (Kohfidisch)   2) *Karnimata darwini* (Siwalik 182 A)   3) *Huerzelerimys vireti* (Tortajada A)
4) *Huerzelerimys minor* (Amberieu 2C)   5) *Progonomys cathalai* (Montredon)   6) *Progonomys hispanicus* (Masia del Barbo B)
7) *Progonomys sinensis* (Bahe Formation)   8) *Parapodemus sp.* (Siwalik 182 A)

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4.2.3 *Progonomys woelferi* with populations from other localities attributed to the same species

Karnimata darwini JACOBS, 1978 and *Parapodemus sp.*, Siwalik Deposits 182A, Pakistan

All of the 14 specimens of *Parapodemus sp.* described by Jacobs (1978: 46-51) fall into the range of variation of *Progonomys woelferi* from Kohfidisch. In the species from 182A the M1 never shows a t7 and both connections between t6-t9 and t4-t8 are present, but thin. There is also an accessory cuspule between the t1 and the t4 in 2 out of 4 teeth, just as in some specimens from Kohfidisch. A real pericingulum, as described by Jacobs (1978: 48) could not be observed in *P. woelferi* from Kohfidisch, although some teeth showed accessory cuspules anterior to the t2. A twinning or bifurcation of the lingual root, as described for one tooth from 182A, could not be observed in a single tooth M^1 from *P. woelferi*. Jacobs (1978: 48) suggests from the outline of a broken root, that the M^2 could have been 4 rooted, which is never the case in *P. woelferi*.

In one of two first lower molars in *Parapodemus sp.* An accessorial cusp was described between the anterolingual cusp and the metaconid, which in rare cases can also be seen in *P. woelferi*. Mein et al. (1993: 46-47) assign *Parapodemus sp.* from 182A to *Progonomys woelferi*. Since the only valid distinction between this species and *Progonomys* mentioned by Jacobs (1978: 49) is the fairly well developed t6-t9connection, a character also seen in 47% of the M^1 this point of view seems plausible. The convergence of the t6 and t9 in M^2 however, is a character that could not be seen in *P. woelferi* very often. Although the posterior accessory cusp in the m_1 of *Parapodemus sp.* is described to be well developed (Jacobs, 1978: 49) in the text, the single picture included in the analyses shows an M^1 with posterior accessorial cusp far less developed than in *P. woelferi*. More material from 182A and relative abundances of character states would be needed to be able to really assess the affiliation of *Parapodemus sp.* from 182A to *Progonomys woelferi*.

Mein et al. (1993: 46, 47) also attribute *Karnimata darwini* from 182A to *Progonomys woelferi*, but grant that in the former the tma is more frequent than in the latter. Since prior estimations of the tma frequencies of *P. woelferi* were too low, this difference is in reality not existent. The M^f of *Karnimata darwini* have the approximately the same size range and mean as *P. woelferi*, the range for the M^2 is slightly smaller but overlaps with the range of *P. woelferi*, the M^3 are smaller and even further out of range than the M^2 but still overlap with the range of *P. woelferi*. The same relation, but in an inverse sense, is

true for the lower teeth. While the m_1 of *Karnimata darwini* and *Progonomys woelferi* have the same measurements, the m_2 is only slightly bigger than the one of *Progonomys woelferi* and the m_3 even more so. The width distributions of the two species do not differ. Jacobs describes the t3 to be slightly larger than the t1(a remark that is not supported by the included drawings), which is usually not the case in *P. woelferi*. While the abundance of the t3spur are the same in *K. darwini* and *P. woelferi*, in *P. woelferi* a t1spur could never be investigated. The t12 in the M^2 of *Karnimata* is described as very reduced to a slender ridge, which is not the case in *P. woelferi*. Also in this tooth a t1spur is reported to be present in 3/37 specimens, a character never observed in *P. woelferi*.

Karnimata darwini has no t7 in the M^1 and also in *P. woelferi* this character is extremely rare and if developed very little. In both, *Karnimata darwini* and *Progonomys woelferi* in the M^2 a t7 is seldom, but can occur. The labial cingulum is far less developed in *Karnimata darwini*.

I agree with Mein et al. as far as the assignation of *Karnimata darwini* to *Progonomys*. *Karnimata* shows a combination of derived (reduction of t 12, t1- and t3-spur) and primitive features (t6-t9 separated, reduced labial cingulum in lower molars). It is therefore difficult to decide which one of the two species is the more primitive.

Progonomys woelferi from Kastellios hill, Greece (de Bruijn et al., 1971; de Bruijn & Zachariasse 1981)

As de Bruijn and Zachariasse (1981) already describe *Progonomys woelferi* from Kastellios Hill on average is larger than *P. woelferi* from Kohfidisch. They also already state that while a t6-t9 connection is never present in either M^1 or all but one M^2 of the Population from Kastellios hill, this apomorphism is far better developed in the Kohfidisch population (see also table 15 and 16). Judging from the pictures of the publications alone, it also seems that the posterior accessorial cusp in both M^1 and M^2 is somewhat better developed in Kohfidisch than in Kastellios hill. All in all *P. woelferi* from Kastellios seems more primitive which is in accordance with the higher age attributed to this fauna.

***Progonomys* aff. *cathalai* from Torrent de Febulines, Trinxtera Sur Autopista 2, Trinxtera Nord Autopista 2, Can Perellada (Augustí, 1981; Augustí & Gilbert, 1982)**

Mein et al. (1993: 46) assign *P.* aff. *cathalai* from the previously mentioned localities to *P. woelferi.*

The material so far described in publications and appurtenant to this group is very scarce. Overall the sizes of the very view single teeth described mostly fall into the size range of *P. woelferi*, with the exception of one M^1, one M^2 and one M^3 that are all only slightly shorter than the minimum length measured from the type locality.

In the material from Torrent de Febulines the M^1 is described to have a t1 spur connecting it to the t5, a trait that could also be seen, although only in 2out of 137 teeth from Kohfidisch. A t6-t9 connection was not described in any of the specimen from TF. This might be due to the really small sample of 3 first upper molars, but on the other hand could also mean that this trait is simply not as common as in *P. woelferi* fro Kohfidisch. In the M^1 the posterior accessory cusp is well developed in both species. The M^1 from TF also show a minute tma, which is also very frequent in Kohfidisch. However this character is missing in all the other localities from the Vallés-Penedés basin. Because of the rather short descriptions, the small sample size and the lack of adequate pictures in the publications, it is not possible to assign the material to either *P. cathalai* or *P. woelferi* without further investigation. If it is indeed appurtenant to *P. woelferi*, it is surely a form much more primitive form than the one found at Kohfidisch.

***Progonomys* cf. *woelferi* from Racor, Rambla de Cordoba section, Huércal-Overa basin, Andalusia, Spain (Guerra-Merchán et al., 2001)**

Two M^1 and one m_1 from Racor are slightly shorter than the range of *P. woelferi*. The rest of the teeth fall into the lower range. So contradictory to Guerra-Merchán (2001: 88) the Racor population is not the not the largest population appurtenant to the genus *Progonomys*, but *P. woelferi* from Kohfidisch. In the M^1 from Racor the t4 and t8 are connected by a weak crest just like in *P. woelferi*. The weak connection of the t6 to the t9 is present in all of the Racor specimens, which could mean that this species is already slightly more evolved than *P. woelferi* from Kohfidisch. Also the fact that the t12 is slightly more developed than in the type species could be an indicator for the progressive state in evolution of the Racor species.

In the m_1 in Racor the anterocentral cusp is always large, while in the Kohfidisch population it is mostly only moderately developed. The labial cingulum is probably better developed in the Racor species, although it is hard to tell since the described sample is very small and there is only one picture of an m_1 of desiderate quality.

As a conclusion the derived morphology of the Racor population, compared to *P. woelferi* from Kohfidisch is somewhat contradictory to its smaller size, considering that the genus generally underwent an increase in size in the course of its evolution during the late Miocene.

Progonomys cf. *woelferi* from Lo Fournas 6 (Aguilar et al., 1986)

Progonomys cf. *woelferi* previously described from Lo Fournas 6 (Languedoc-Roussillon Region, France) described by Aguilar et al. in 1986, is also listed in the populations attributed to the species *Progonomys woelferi* by Mein et al. (1993) in their revision of the genus *Progonomys*. However, this population in later publications is rather assigned to *Huerzelerimys vireti* (Aguilar & Michaux, 1996).

4.2.4   Spatial and temporal distribution of *Progonomys woelferi*

In total *P. woelferi* so far is known from at least 8 sites, taking into account *Parapodemus sp.* from 184 Siwalik. Since its first description (Bachmayer & Wilson, 1970) *P. woelferi* has been put into several evolutionary lineages. Either as a descendent of *P. cathalai* (Mein et al., 1993) or as the Miocene starting point of a lineage giving rise to *Huerzelerimys vireti* (Aguilar, 1982). Depending on whether or not the Population from Kastellios hill is really *P. cathalai* or not, the first scenario is more or less likely. If *P. cathalai* from the Kastellios hill is really present in only the second of the two strata, but not in the first, this would mean that *P. woelferi* was first to immigrate into this region. This would in turn make the decent of *P. woelferi* from *P. cathalai* very unlikely, although not completely impossible.
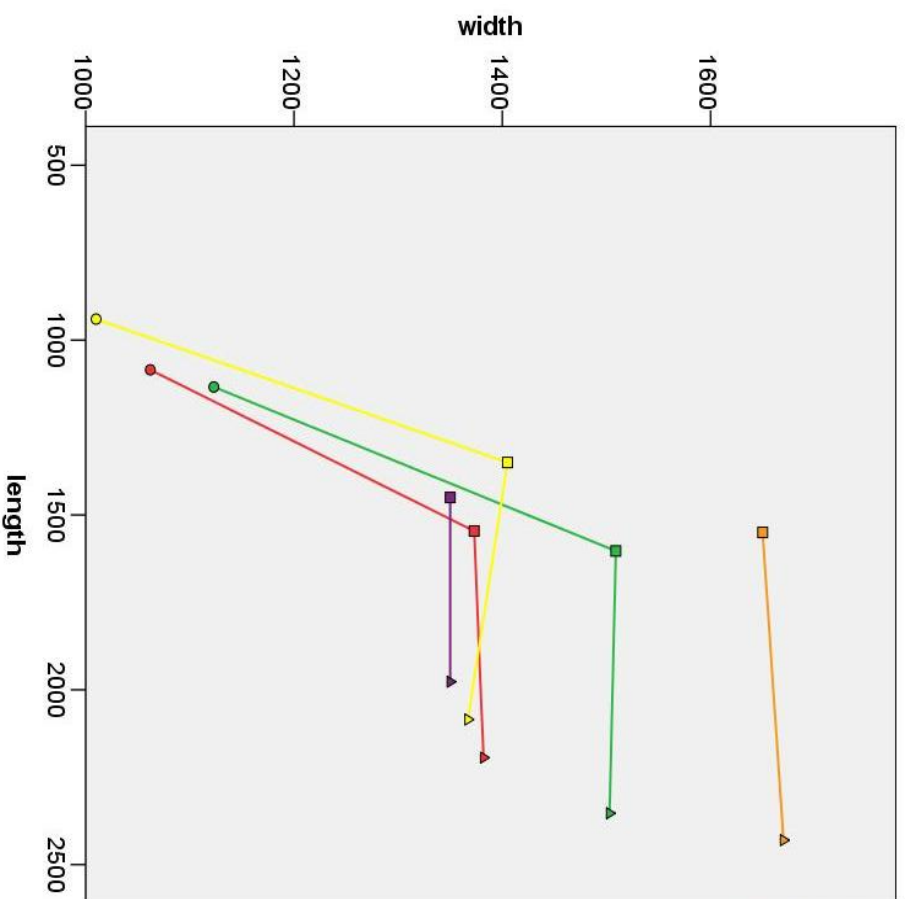
Fig. 21
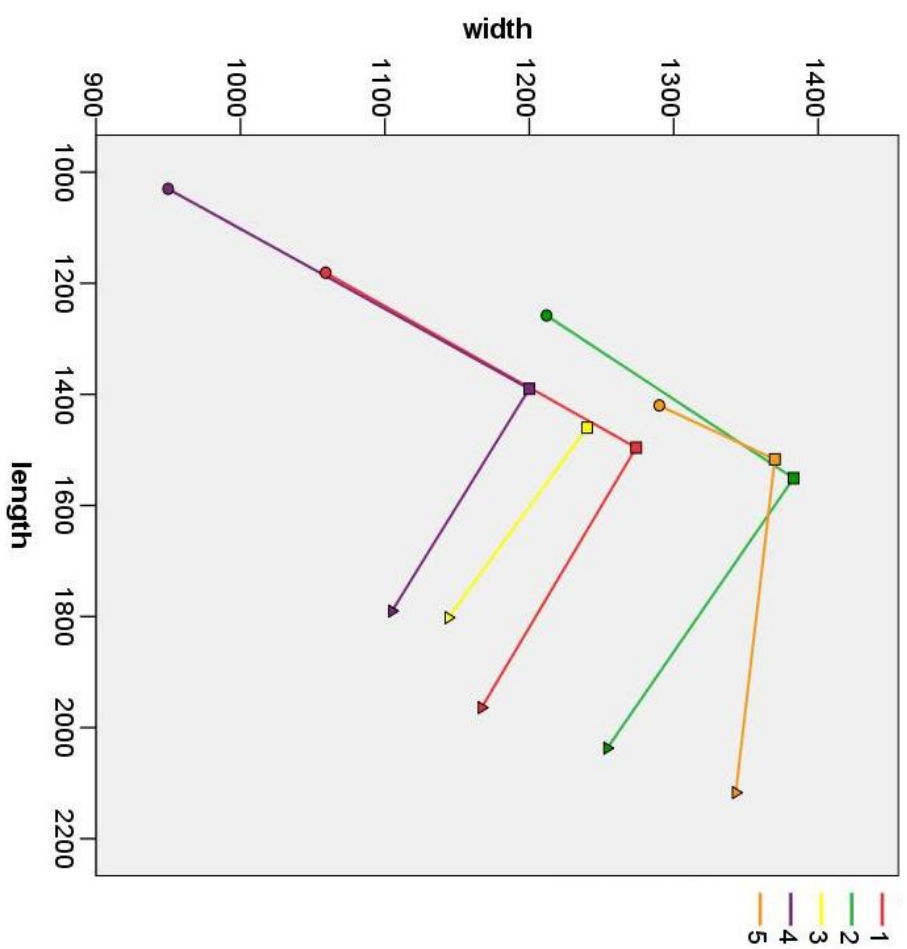
Fig. 22

Fig. 21-22: Comparison of mean lengths and widths of upper (fig.21) and lower (fig.22) molars of populations assigned to *Progonomys woelferi*; circles indicate third, squares second and triangles first molars; x-and y-axis scales in µm; 1)*Progonomys woelferi* (Kohfidisch)
2) *Progonomys woelferi* (Kastellios hill)   3) *Progonomys aff. cathalai* (Torrent de Febulines)
4) *Huerzelerimys vireti* (*Progonomys vireti*, Racor)   5) *Progonomys* cf. *woelferi* (Lo Fournas)

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4.2.5   Discussions on Taxonomy of the genus *Progonomys*

Mein et al. revised the genus *Progonomys* in 1993. They propose an amended diagnosis and exclude several species in order to construct a monophyletic genus. Allthough *P. woelferi* is one of the two species left inside the genus *Progonomys*, it is worth mentioning that many authors do not agree with their view on murine systematics. Van Dam (1997: 52) argues that, firstly "The absence of the anteroconid-metaconid connection in m_1 should not be used as a character, because the connection is generally absent in the type species *P. cathalai,* secondly the genus (sensu Mein et al.) is still paraphyletic, because it does not include the proposed descendants *Huerzelerimys* and *Anthracomys* included in the phylogenetic tree constructed by these authors. Thirdly Van Dam also argues in favour of evolutionary taxonomy as opposed to a cladistic approach.
The controversy of horizontal vs. vertical classification is not a new one and flares up regularly among Taxonomists.

While it is an estimable attempt to use vertical classification or base a system purely on cladistic taxonomy, the reality is that it may not always be easy to achieve and very often simply not practical. Especially when general evolutionary trends that occur across clades blur the picture or when the fossil record is scarce, all of which is true for the murines.

5.   Apodemus lugdunensis (SCHAUB, 1938) MARTÍN-SUÁREZ & MEIN, 1996

5.1   Description

M¹

Finding point		Length					Width				
	N	Min	Max	Mean	SE	Stdev	Min	Max	Mean	SE	Stdev.
Ko I	19	1624	1973	1821	21	91	1084	1183	1138	7	31
Ko II	9	1638	1856	1765	25	-	1087	1200	1149	13	-
Ko III	5	1747	1973	1863	47	-	1132	1238	1188	21	-
Ko IIIoben	0	-	-	-	-	-	-	-	-	-	-
Ko IIIunten	26	1621	1897	1784	15	77	1026	1262	1144	1621	55
o.A.	34	1579	1983	1790	16	93	1036	1255	1144	9	58
CM	20	1501	1983	1797	24	108	971	1234	1138	1501	67
Total	113	1501	1983	1796	9	92	971	1262	1144	5	53

Table 9

M²

Finding point		Length					Width				
	N	Min	Max	Mean	SE	Stdev	Min	Max	Mean	SE	Stdev.
Ko I	9	1162	1429	1321	24	-	1121	1227	1169	13	-
Ko II	2	1303	1333	1318	15	-	1162	1179	1171	9	-
Ko III	2	1275	1313	1294	19	-	1149	1156	1152	3	-
Ko III oben	0	-	-	-	-	-	-	-	-	-	-
Ko III unten	61	1186	1456	1310	8	65	1046	1251	1147	6	45
o.A.	0	-	-	-	-	-	-	-	-	-	-
CM	17	1193	1412	1292	14	57	1019	1207	1121	12	49
Total	91	1162	1456	1308	7	63	1019	1251	1145	5	46

Table 10

M³

Finding point		Length					Width				
	N	Min	Max	Mean	SE	Stdev	Min	Max	Mean	SE	Stdev.
Ko I	15	797	985	864	13	49	779	944	854	12	45
Ko II	0	-	-	-	-	-	-	-	-	-	-
Ko III	0	-	-	-	-	-	-	-	-	-	-
Ko III oben	0	-	-	-	-	-	-	-	-	-	-
Ko III unten	41	773	974	866	7	44	756	971	863	8	54
o.A.	0	-	-	-	-	-	-	-	-	-	-
CM	21	766	964	889	11	52	821	1015	910	11	49
Total	77	773	1015	876	6	50	756	985	870	6	53

Table 11

m₁

Finding point	Length						Width				
	N	Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	16	1535	1812	1673	19	77	913	1070	986	12	46
Ko II	9	1590	1692	1644	12	-	937	1060	996	12	-
Ko III	3	1590	1826	1675	75	-	944	1026	981	24	-
Ko III oben	19	1576	1795	1686	14	62	954	1074	1016	8	34
Ko III unten	34	1518	1798	1660	12	70	892	1094	985	8	45
o.A.	17	923	1087	1001	13	54	1556	1726	1658	12	50
CM	22	1467	1768	1634	18	85	862	1067	985	12	55
Total	121	1467	1826	1661	6	71	862	1094	994	4	47

Table 12

m₂

Finding point	Length						Width				
	N	Min	Max	Mean	SE	Stdev	Min	Max	Mean	SE	Stdev.
Ko I	13	1135	1398	1305	18	67	957	1156	1079	17	62
Ko II	3	1227	1296	1270	21	-	1015	1077	1056	21	-
Ko III	3	1200	1303	1262	31	-	1009	1121	1083	37	-
Ko III oben	12	1176	1337	1267	14	50	1002	1108	1068	10	34
Ko III unten	53	1169	1405	1273	7	50	961	1159	1063	6	47
o.A.	14	1166	1347	1285	13	50	1022	1148,7	1080	10	36
CM	14	1190	1398	1254	14	53	995	1183	1065	14	51
Total	112	1135	1405	1275	5	53	957	1183	1068	4	47

Table 13

m₃

Finding point	Length						Width				
	N	Min	Max	Mean	SE	Stdev.	Min	Max	Mean	SE	Stdev.
Ko I	21	851	1097	1020	14	64	797	981	898	10	44
Ko II	0	-	-	-	-	-	-	-	-	-	-
Ko III	4	985	1053	1021	17	-	841	950	883	25	-
Ko III oben	5	950	1067	1012	21	-	824	957	896	25	-
Ko III unten	49	855	1118	1000	8	55	821	991	897	6	40
o.A.	9	916	1087	1011	17	-	783	947	884	17	-
CM	15	844	1080	1009	16	61	769	957	896	12	47
Total	103	844	1118	1008	5	56	769	991	895	4	43

Table 14

Tables 9-14: Width and Length distributions for M^1, M^2, M^3, m_1, m_2 and m_3 of *Apodemus lugdunensis* from the different finding points within the locality of Kohfidisch; N= number of individuals, SE= standard error of mean, Stdev= Standard deviation;
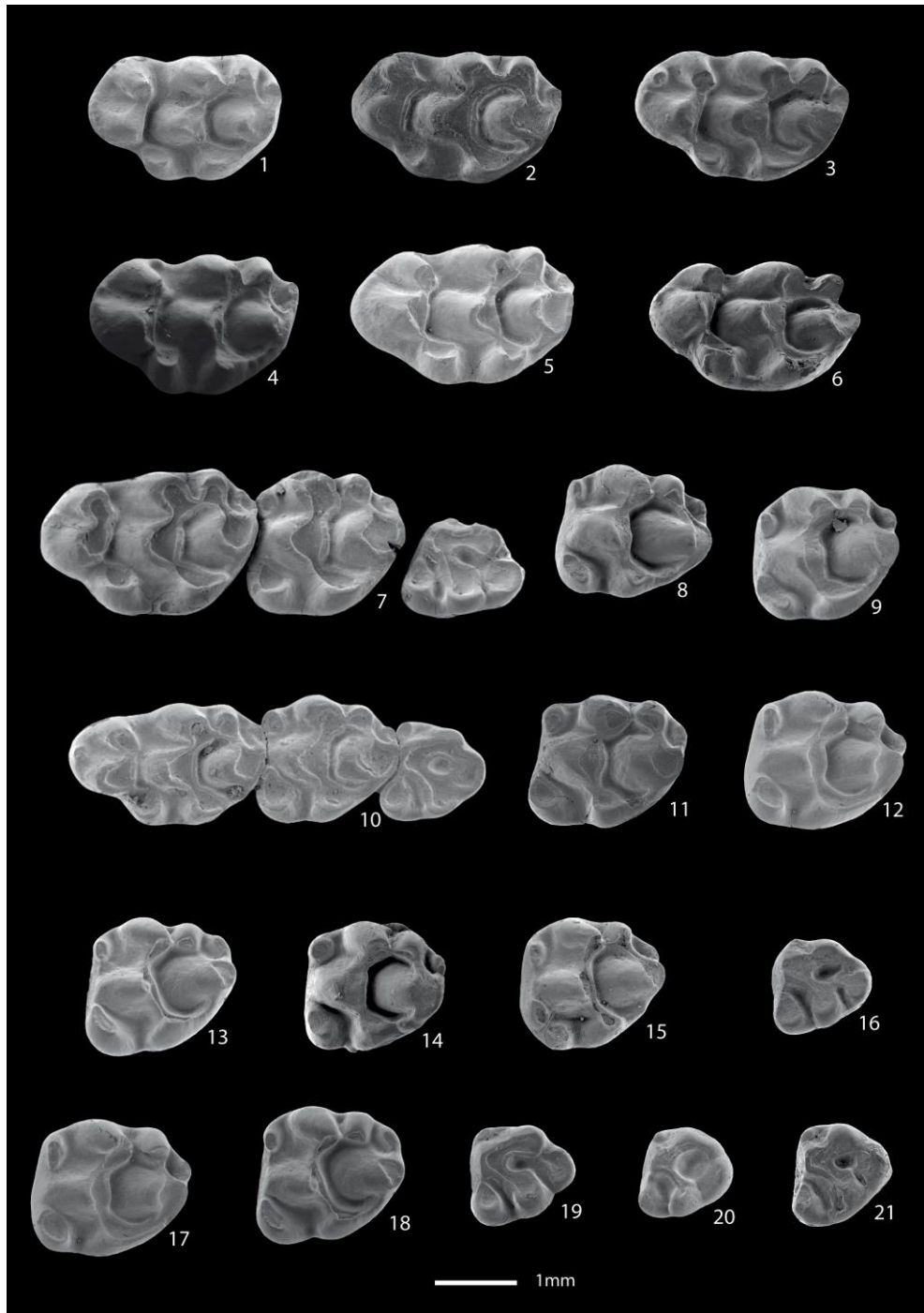
Plate 5: *Apodemus lugdunensis* Kohfidisch:

1) NHMW2011/0106/21: M^1 sin.
2) NHMW2011/0106/22: M^1 sin.
3) NHMW2011/0106/23: M^1 sin.
4) NHMW2011/0106/24: M^1 dex.
5) NHMW2011/0106/25: M^1 sin.
6) NHMW2011/0106/26: M^1 sin.
7) NHMW2011/0106/27: M^1-M^3 sin.
8) NHMW2011/0106/28: M^2 sin.
9) NHMW2011/0106/29: M^2 sin.
10) NHMW2011/0106/30: M^1-M^3 sin.
11) NHMW2011/0106/31: M^2 dex.
12) NHMW2011/0106/32: M^2 sin.
13) NHMW2011/0106/33: M^2 sin.
14) NHMW2011/0106/34: M^2 sin.
15) NHMW2011/0106/35: M^2 sin.
16) NHMW2011/0106/36: M^3 dex.
17) NHMW2011/0106/37: M^2 sin.
18) NHMW2011/0106/38: M^2 sin.
19) NHMW2011/0106/39: M^3 sin.
20) NHMW2011/0106/40: M^3 dex.
21) NHMW2011/0106/41: M^3 sin.
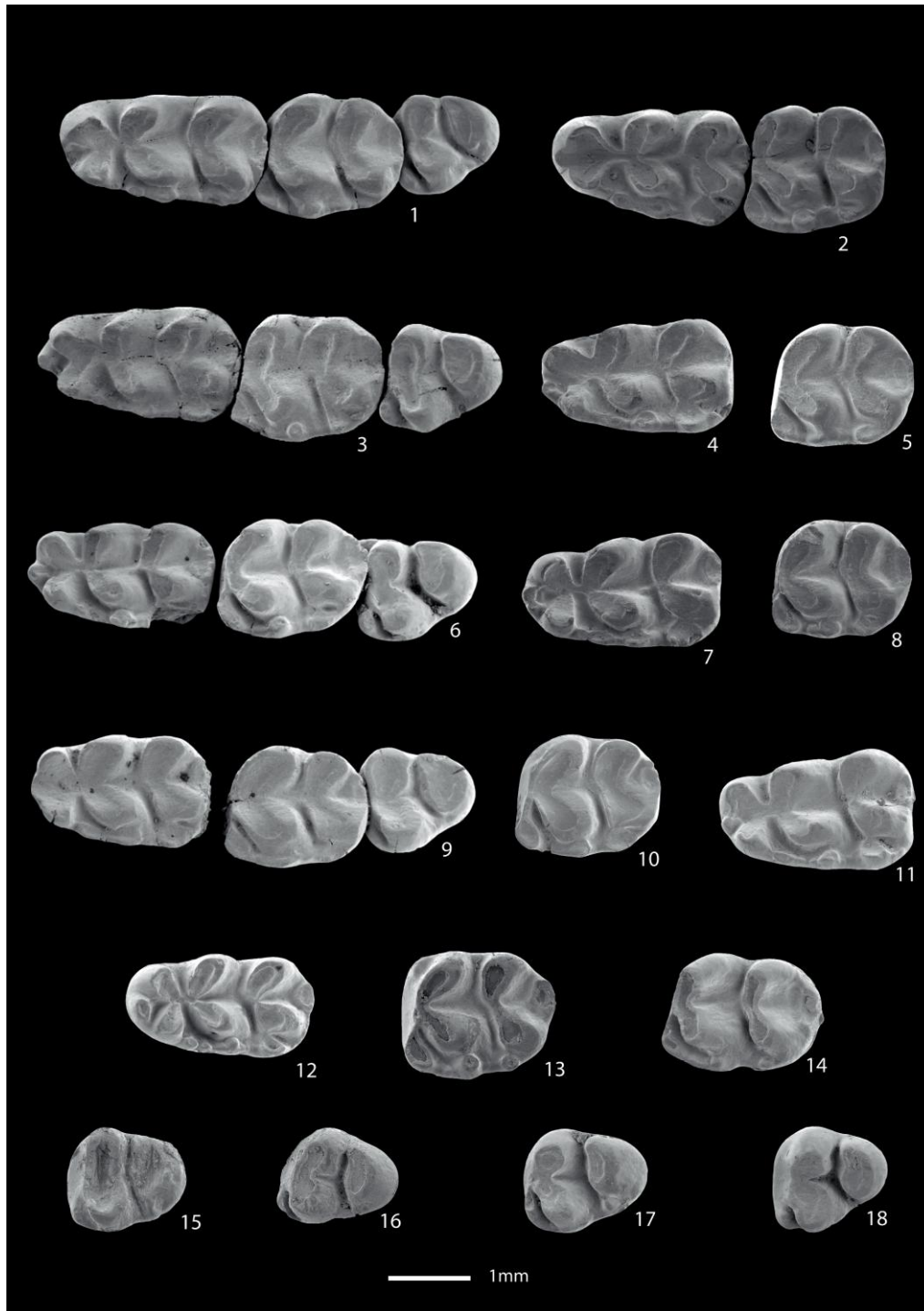
Plate 6: *Apodemus lugdunensis* Kohfidisch

1) NHMW2011/0104/42: m_1-m_3 dex.
2) NHMW2011/0104/43: m_1-m_2 dex.
3) NHMW2011/0104/44: m_1-m_3 dex.
4) NHMW2011/0104/45: m_1 dex.
5) NHMW2011/0104/46: m_2 sin.
6) NHMW2011/0104/47: m_1-m_3 sin.
7) NHMW2011/0104/48: m_1 dex.
8) NHMW2011/0104/49: m_2 dex.
9) NHMW2011/0104/50: m_1-m_3 sin.
10) NHMW2011/0104/51: m_2 dex.
11) NHMW2011/0104/52: m_1 sin.
12) NHMW2011/0104/53: m_1 sin.
13) NHMW2011/0104/54: m_2 sin.
14) NHMW2011/0104/55: m_2 dex.
15) NHMW2011/0104/56: m_3 sin.
16) NHMW2011/0104/57: m_3 dex.
17) NHMW2011/0104/58: m_3 sin.
18) NHMW2011/0104/59: m_3 sin.

M¹: (51 specimens)

T1-t2-connection is usually high 76% (39/51) but always very slender. The t1 is always in a retroverse position, which is sometimes hard to see, because the t3 is also retroverse making the whole anterior complex symmetric and letting it appear transverse. (57%) of the specimens have shown a t3-spur, which can in rare cases be connected to the t5-t6-ridge. None of the specimens showed neither a t1- nor a t2-bis, but a high tendency to build accessorial cuspules anterolabial to the t3. The t4-t8-connection is always present and very strong, and compared to the other ridges rather wide. About 4% show a very reduced t7, being either a nodule in the t4-t7/8 connection, or a little, only somewhat separated bump at the edge of the t8. The t4 position is always very proverse. The t6-t9 connection is present in 98% of the cases but mostly not quite as strongly developed as the t4-t7/8-connection. The variation of the t12 is very big. It is nearly always well displaced from the t8 (although always connected through a slender ridge) and mostly comma shaped (80%), sometimes round (12%), but can in very rare cases (5%) also be reduced to a slender ridge. The M1 usually has three roots, although a small accessorial one is present in rare cases.

M²:(50 specimens)

The t1 is about 2-3times the size of the t3, which is extremely reduced. In rare cases (6%) a t1bis can be present which is not visible in teeth that are very worn down, because it fuses with the t1 at its base. The t4-t5 connection is always wide and high, just as the t4-t8. The t6-t9-connection is weak (24%)or sometimes even missing (14%) and strong in the remaining 62%. The t9 is usually extremely proverse. In 38% of the cases there is a minute t7, represented by a thickening in the t4-t8 connection. The t12 is also very reduced and only about half the size of the t3. The M² has 3 roots. In very rare cases the lower half of the lingual root was bifurcated.

M³: (72 specimens)

A t1 is always existent and always well developed. In very rare cases tiny a t1bis can be developed. A t3 is always developed although usually less than 1/3 the size of the t1. The t1 and t3 are connected by a very low ridge, which also connects them to the back of the t5. This ridge is considerably better developed than in *Progonomys woelferi*. 69% (50/72) show a tiny t9. The connection of the t6 to the t8/t9 is present in 93% (67/72) of teeth. In about 78% (47/72) of the specimens show a t4-t8-connection, which is nearly always weaker than the t6-t8/t9 connection. When present the t4-t8 connection is strong, it can be a double one in the sense that there can be a lingual and a buccal ridge connecting the

t4 and the t8, which is separated by a little valley. It could also be seen in a way, that the t4-t8 connection is a very wide one, which shows a little depression in the middle. This depression in turn is shallower that the sinus. The m_3 always has three roots, of which the lingual is the smallest one in diameter.

Problem 1: One of the problems in determining the "strength" of a ridge is that the more worn a tooth is, the broader the ridges get. Certain points also seem relatively higher as the tooth gets word down, because the contrast is stronger. If a tooth is not very worn down the very same point will appear a lot lower, because of the comparison to the (still existing) high cusps.
This was especially observed for the t4-t8-connection. Which was more likely to be described as nonexistent in high teeth.

Problem 2: a subdivision of a cusp is not very likely to be observed in very worn teeth, as the separating valley might have been above the level of wear; Probably very often the case for the subdivided t8

m_1 :(60 specimens)
In almost all specimens (77%) an anterocentral cusp (a) is present, which is in a central position (as opposed to shifted to the labial side as in *Progonomys woelferi*), giving the teeth a rather square outline. The anteroconid complex is usually symmetrical. The connection of the protoconid and metaconid is always relatively strong and high.
Compared to it the protoconid-metaconid-connection the hypoconid-entoconid-connection is thinner and not quite as well developed. This connection lies on the lingual side of the middle line of the teeth. The Metaconid is nearly always smaller than the protoconid or they are of equal size. In 50% (30/70) of cases there is a longitudinal spur, although in 25% of the remainder there is even (what could be concerned as the opposite of a longitudinal spur) a little concave mould. There are mostly 2 accessorial cusps, one slightly posterior of the protoconid and one in the middle of the outer margin of the sinusid between the anterolabial cusp and the protoconid.
The posterior accessory cusp is very well developed. The terminal heel varies in shape but is always in slightly lingual position. All lower molars are two-rooted. Only in very rare cases a minute accessorial root was present in the m1.

m₂: (57 specimens)

The overall shape of the m$_2$ in *Apodemus lugdunensis* is more rectangular or "rhomboid" especially compared to *Progonomys woelferi*, where it is more like a trapeze (the anterior side being a lot wider than the posterior one). This difference in shape is probably mainly related to some difference in position/shape and size of the accessory cusps. The Protoconid-Metaconid connection is strong and usually higher than the Hypoconid-Entoconid connection. There can be a very shallow longitudinal spur (32/57; 56%). The relation of the Hypoconid and entoconid is very variable, although most of the time they are of equal size. There is usually only one accessory cusp on the labial cingulum (excluding the posterior accessory cusp and the anterolabial one). Sometimes (20% of the cases) a second accessory cusp is present between the first and the anterolabial cu*sp*. The posterior accessorial cusp is not nearly as well developed as in *Progonomys woelferi*. The terminal heel is always well developed and shifted to the lingual side.

m₃: (79 specimen)

37% (29/79) of the specimens have a well-developed anterolabial cusp, 58% (46/79) a reduced one (sometimes to the point where only a thin ridge is left). The protoconid-metaconid connection is always strong. The protoconid and metaconid are either the same size or the protoconid is bigger. In *Apodemus lugdunensis* the posterior cusp is very variable in shape.

5.2 Discussion

5.2.1 Transfer form *Parapodemus* SCHAUB, 1938 to *Apodemus* KAUP, 1826

Suárez & Mein (1998) include the genus *Parapodemus* into the genus *Apodemus* with the exception of the type species *Parapodemus gaudryi* for which they believe the type specimens to be lost and wrongfully declare *Parapodemus gaudryi* as a nomen nudum. But in cases where the type material is lost or the name bearing type is indeterminate the species name should be referred to as nomen dubium.

However the type material was later rediscovered (Mein in Freudenthal & Martín-Suárez, 1999) and the discussion on the meaning and affiliation of *Progonomys gaudryi* is far from resolved. Suárez & Mein (1998) argue that the differences between *Apodemus* and

Parapodemus "were based upon the degree of development of different character states, which may present a problem in intermediate populations". The author agrees with this view, and consequently will follow the nomenclature presented in their paper.

5.2.2 Comparison of the findings of this study concerning *Apodemus lugdunensis* with the original descriptions:

As for *P. woelferi* also the measurements for *Apodemus lugdunensis* accord very well with previous results from Bachmayer & Wilson (1970, 1978,1980), although the congruence is not quite as large as for *P. woelferi*. The width and length ranges derived from measurements taken in the course of this study are larger and differ from previous measurements as much as 200 µm. The largest disagreement in the results for the mean was found in the length of M^2, where the result differs as much as 40 µm. These deviances are not considered significant, taken into account the vast differences in sample size, which in Bachmayer and Wilson (1980) never exceed an n of 15! Also the morphological descriptions of this study and previous ones agree very well, although some details referred to in this work are not mentioned earlier and can therefore not be compared.

5.2.3 Comparison of *Apodemus lugdunensis* from Kohfidisch with populations attributed to the same species

***Comparison with Apodemus lugdunensis* from its type locality Mollon (Schaub, 1938; Michaux 1971)**
Other localities: Los Mansuetos (Michaux, 1971); Vivero de Pinos (Adrover, 1986); Alfambra and Tortajada A (Van de Weerd, 1976); Eichkogel (Daxner-Höck, 1977); Dorn-Dürkheim (Franzen & Storch, 1975); Cervillente1,2,3 and 4B (Suárez & Freudenthal, 1993)

Mollon is a French locality currently assigned to the upper MN11. A detailed morphological comparison of the population from Kohfidisch with the population from its type locality Mollon is unfortunately not possible given that the material from Mollon is very scarce and there are only two teeth described by Schaub. Those are one M^1 and one m_2 both of which fall into the upper size range of the Kohfidisch population. Van de Weerd (1976: 76-78) publishes probably more exact measurements of the original teeth described by Schaub and some additional material from the type locality stored in Basel, which

however is also not very abundant. It comprises one m_1, 6 m_2 and 2 M^1 and according to the author is in perfect agreement with the material from Tortajada A and Alfambra.

Comparison with *Apodemus lugdunensis* from Los Aguanaces 3 and Puente Minero (van Dam, 1997)

The mean length and width measurements for *A. lugdunensis* from Kohfidisch and Los Aguanaces 3on average agree very well, just as the other the means of the other localities in the Teruel-Alfambra region which have yielded *Apodemus lugdunensis*. The values of minima and maxima of the dimensions of Kohfidisch on the other hand are always smaller and larger respectively. A pattern that one would expect when comparing a larger to a particularly small sample size, which is exactly what is the case in the Teruel-Alfambra region. It can therefore be said that the Kohfidisch sample is a better representative of the true range of variation of size for the species *Apodemus lugdunensis*.

As in the M^1 from Los Aguanaces 3 the t1 can be slightly elongated and is usually in a posterior position. A t3 spur is very common in both populations, but again the comparison of frequencies of character sates is tricky since the sample sizes described from Los Aguanaces 3 are so small. Frequencies and degree of development for both the t6-t9 and t4-t8 connection are similar in both populations. While there was never a t7 found in Los Aguanaces 3, 2 out of 51 M^1 showed a t 7 in Kohfidisch. The M^2 and m_1 and m_2 do not seem to show any differences whatsoever. Van Dam does not describe the third upper and lower molars because they cannot be distinguished from the ones of Occitanomys *sondaari*.

Ultimately it can be seen that the populations from Los Aguanaces 3 and Kohfidisch do probably not differ at all. This is not surprising since both localities are assigned to the lower part of MN11.

Comparison with *Apodemus lugdunensis* from Eichkogel, Austria (Daxner-Höck, 1977)

The dimensions of *Apodemus lugdunensis* from the Eichkogel published by Daxner-Höck (1977: 20-23), contrary to the measurements published in 1970 by the same author, agree very well with the measurements taken in the course of this study. Contrary to the material from the Eichkogel a t1 bis was never observed in the M^1 of *A. lugdunensis* from Kohfidisch. The t3 spur is about equally developed in both populations, as is the t4-t7/t8 connection. The t6-t9 connection in the M^1 is also equally well developed in both

populations, contrary to the M^2 where the same connection is slightly better developed in the population from the Eichkogel. Contrary to the Eichkogel population, the t3 in the M^3 is next to always present in Kohfidisch. While the t9 in the same tooth is reduced in the Eichkogel population and only present in 2/100 specimens, it is only missing in 22/72 specimens from Kohfidisch. Surprisingly the longitudinal spur in the first lower molars seems to be somewhat better developed in Kohfidisch. The accessorial cingulum in all lower molars is a lot better developed in the Eichkogel than in Kohfidisch. In some m$_3$ in Kohfidisch there is a little, very reduced, but clearly noticeable posterior accessorial cusp preserved which is never the case in the Eichkogel population.

Generally speaking the two *A. lugdunensis* populations from Kohfidisch and the Eichkogel are very similar, the biggest differences being the upper and lower third molars (which are clearly more reduced in the Eichkogel population), and the development of the labial cingulum in the lower molars (which is more advances in the Eichkogel population). Both factors indicate a clearly more advanced state in evolution of the Eichkogel population. This more advanced state of the Eichkogel population is in accordance with the younger age attributed to the site (Daxner-Höck, 1980; Daxner-Höck, 1996).

5.2.4 Comparison of *Apodemus lugdunensis* from Kohfidisch to other murine species

Comparison with *Apodemus barbarae* VAN DE WEERD, 1976

Type locality: from Los Mansuetos, Spain;

A. barbarae from its type locality is clearly larger than *Apodemus lugdunensis* from Koh, although there is a size overlap. This size overlap is smaller for the first molars than for the second ones both in the upper and lower jaw. The size overlap is also smaller for the width of all molars than for the respective lengths meaning that A. barbarae has a larger width/length ratio than *A. lugdunensis*. While the M^1 of *A. barbarae* never shows a t7, it can be present in rare cases of *A. lugdunensis*. After the comparison of the descriptions of the literature this seems to be the only difference. The M^2 of A *lugdunensis* opposed to *A. barbarae* in rare cases shows a t1bis. In contrast to A. barbarae where the t9 in the M^3 is sometimes even separated from the t8, in *A. lugdunensis* it is mostly not even well developed.

In the m_1 in *A. barbarae* the anterocentral cusp is always developed while it can be missing in rare cases in *A. lugdunensis*. The m_2 of both species can only be differentiated by size but not by morphology, the only difference being that the posterior accessory cusp is probably better developed in *A. lugdunensis*. Also the m_3 can only be distinguished by size.

Comparison with *Apodemus meini* (MARTÍN-SUÁREZ & FREUDENTHAL, 1993) MARTÍN-SUÁREZ & MEIN, 1998

Type locality: Crevillente 7, Spain

Apodemus meini from Crevillente 7 and *A. lugdunensis* from Kohfidisch are readily distinguishable by the bigger size of *A. meini*. A very minute size overlap occurs only for the M^3 and the length of the m_2.

There seem to be no noteworthy morphological differences between the first upper molars of the two species. Also the M^2 shows no significant differences in morphological variation, apart from the fact that the t12 is slightly more reduced in *A. meini*. While the t9 in the M^3 of *A. meini* is relatively well developed and always constricted from the t8, this is not usually the case in *A. lugdunensis*.

In the m_1 the tma of *A. meini* is usually bigger and more prominent than the one of *A. lugdunensis*. While there is no longitudinal spur in *A. meini*, it is present in about 50% of the m1 of *A. lugdunensis*.

In the m_2 of *A. meini* the anterolabial cusp is isolated contrary to *A. lugdunensis*, where it is connected to the hypoconid by a high but slender ridge. As in the m1 the labial cingulum in the m_2 is better developed in *A. meini*. In the m_3 both species show a very reduced or absent posterior accessorial cusp while in the anterolabial cusp is clearly more reduced in *A. meini* than in *A. lugdunensis*. Otherwise there seem to be no morphological differences.
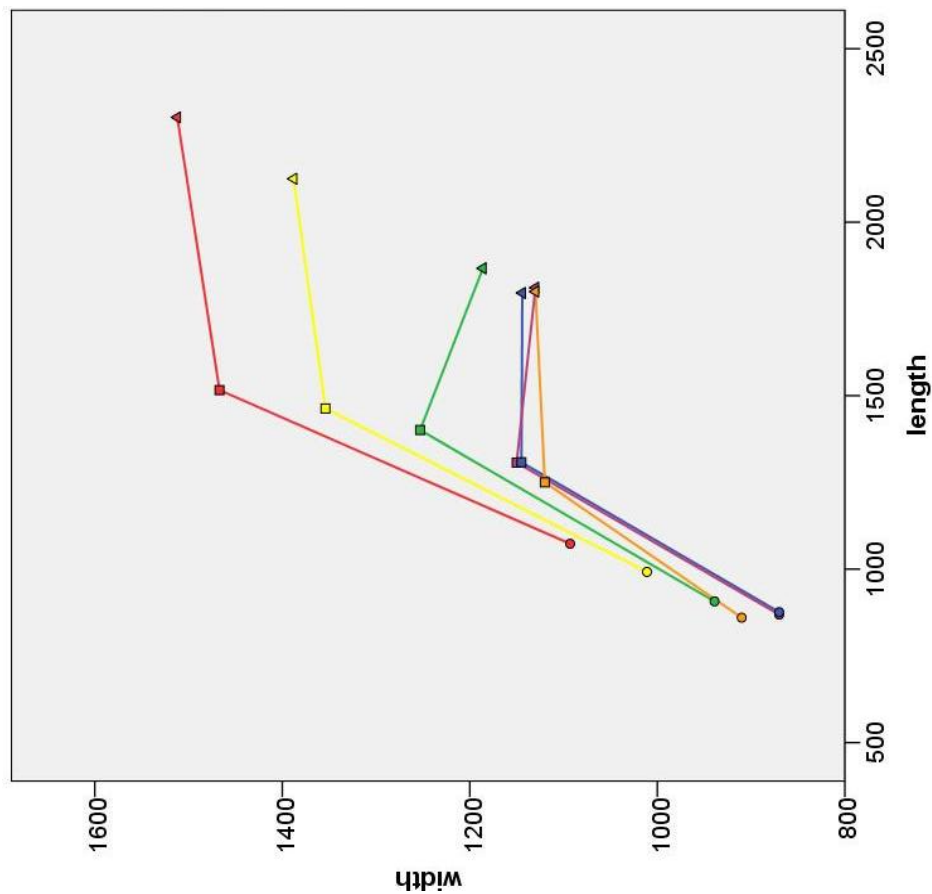
Fig. 23
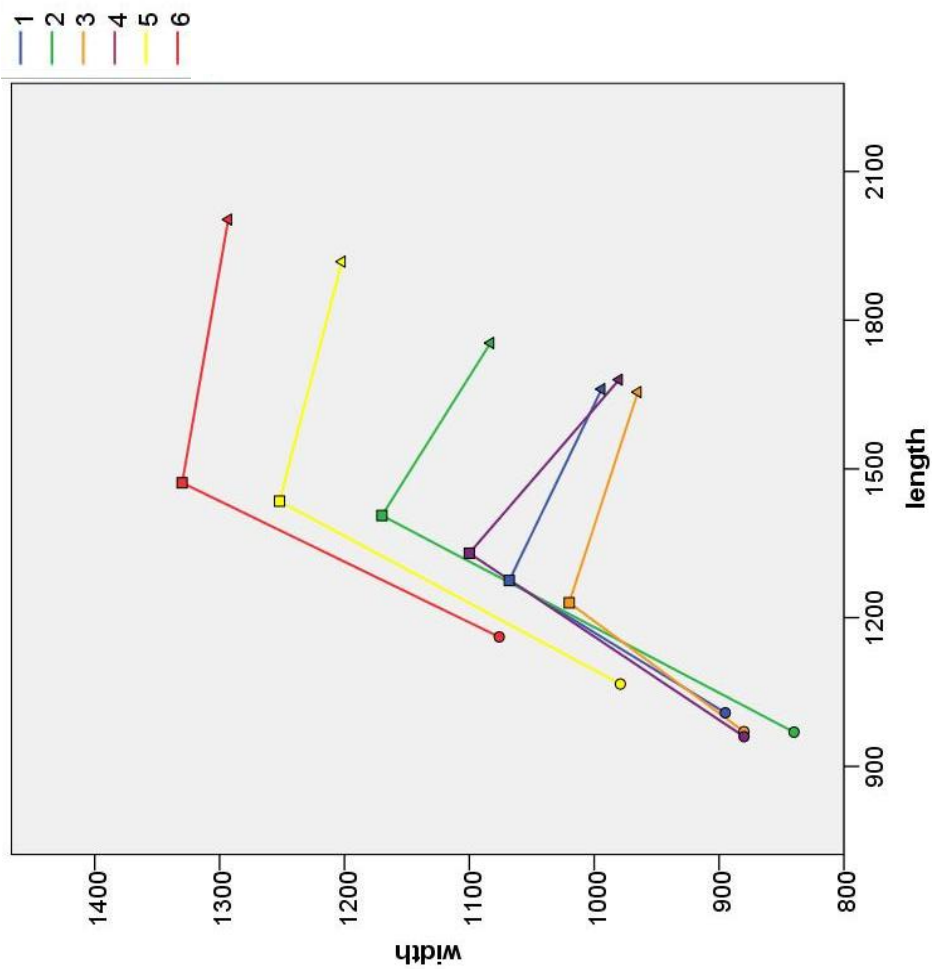
Fig. 24

Fig. 23-24: Comparison of mean lengths and widths of upper (fig.23) and lower (fig.24) molars; x- and y-axis scales in μm; circles indicate third, squares second and triangles first molars; *mean widths and lengths of lower molars have not been published and had to be estimated by min.+max./2
1) *Apodemus lugdunensis* (Kohfidisch)   2) *Apodemus lugdunensis* (Tortajada A)   3) *Apodemus lugdunensis* (Los Aguanaces)
4) *Apodemus lugdunensis* (Eichkogel)*   5) *Apodemus barbarae* (Los Mansuetos)   6) *Apodemus meini* (Crevillente 7)

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6. Progonomys cf. *hispanicus*

6.1. Description and Discussion

In the course of this study two teeth (one M^1 and one m_3) could be found that were not assignable to either of the two known species. Their pictures are shown on plate 4, fig. 10 and 11.

The first upper molar falls into the size range of *Apodemus lugdunensis*, but is clearly assignable to the genus *Progonomys* because of its lack of any longitudinal connections. Its length and width are: 1839 and 1234 µm respectively. The m_3 also falls into the size range of *Apodemus lugdunensis* and has the measurements 1080 and 9812 µm.
Both teeth fall into the upper size ranges of *Progonomys hispanicus* and the middle size range of *Progonomys cathalai*, which is why it is preferred to assign the teeth to *P.* aff. *cathalai.*

In the M^1 both the t1 and t4 are shifted backwards quite a bit and set of a little, meaning that the t1-t2 connection and the t4-t5 connection are both a lot lower than the connections between the other cusps. The t2 and t3 are very close together and their posterior walls almost form a straight transverse line. The t3 has no spur. There are no connections, neither between the t4 and t8 nor between t6and t9. The t9 is reduced to a very slender form. There is neither a t7 nor a t12.

The m_3 is remarkable in that all four cusps: protoconid, metaconid, entoconid and hypoconid fully developed, although the entoconid is very small, compared to the hypoconid.

7. Conclusion

The comparison of the material from different finding points was able to show that there are indeed some subtle differences, which may lead to speculations about whether or not the fillings could indeed have slightly different ages. The strongest differences concerned the ratio of murine species. *Apodemus lugdunensis* generally has later range of occurrence than *P. woelferi* and Kohfidisch is one of very few (to my knowledge two) localities where the two species coexist. Whether the finding point III unten, where *A. lugdunensis* is over-proportionally abundant, is indeed slightly younger compared to the main cave (finding point I), whether the differences are due to ecological variations over time, or whether the results are the product of improbable chance can not be determined since none of the other small mammals showed significant size differences between the finding points (pers. Comm. Dr. Daxner-Höck, Seekirchen). In contrast the Morphology of the occurring species did not show any stringent differences. A multivariate analysis of the size distributions of the occurring species did indicate some significant differences, but which again did not deliver any distinctive pattern.

The aim of this study was the review of the murine fossils of the locality of Kohfidisch, of which only a small portion was described in former studies.

The findings of this study concerning the already known species agreed very well with the descriptions of the former studies of Friedrich Bachmayer and Robert Wilson. Especially the high degree of accordance of the measurements was surprising in the light of the very different measuring techniques used. However there have been various points that could be added to the morphological descriptions and various comparisons could be refined. The greater size ranges and morphological variations described in this study compared to former descriptions come as no surprise in the light of the bigger samples used. A third species, *Progonomys* cf. *hispanicus*, previously unknown from Kohfidisch could be detected. This species is however very rare at Kohfidisch and only represented in the form of very view single molars. Although the appearance at the locality is one of the latest occurrences of *P. hispanicus*, if the fossils are indeed attributable to this species, the population seems to be a very primitive one. It should be noted that there is still a small remainder of mostly upper molars that could not be assigned to *P. woelferi*, *A. lugdunensis* or *P.* cf. *hispanicus*. Whether these molars are simply very aberrant forms of one of the former two species or indeed belong to a forth one present still remains unclear and will be the subject of further investigations.

Although unfortunately not a primary research objective of this study, the comparisons of the murines of Kohfidisch with other populations of Upper Miocene fossil sites of Europe and Asia revealed general evolutionary trends that occur throughout different clades. The most obvious being a general increase in size of all molars as demonstrated for the length of the M^1 in figures 25. and 26. Other general trends are the increase in crown height (hypsodonty) and an increase in longitudinal connections (stephanodonty). A closer investigation of these evolutionary trends, which could also shed some light at certain taxonomical problems, would be a very interesting field for further studies.
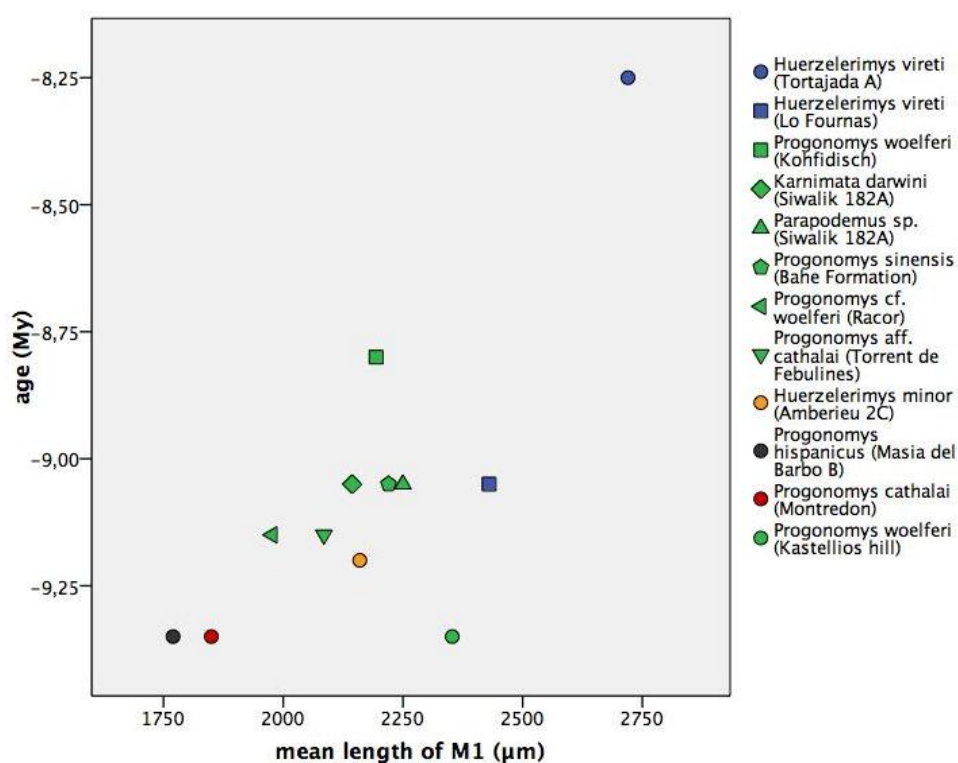
Fig. 25
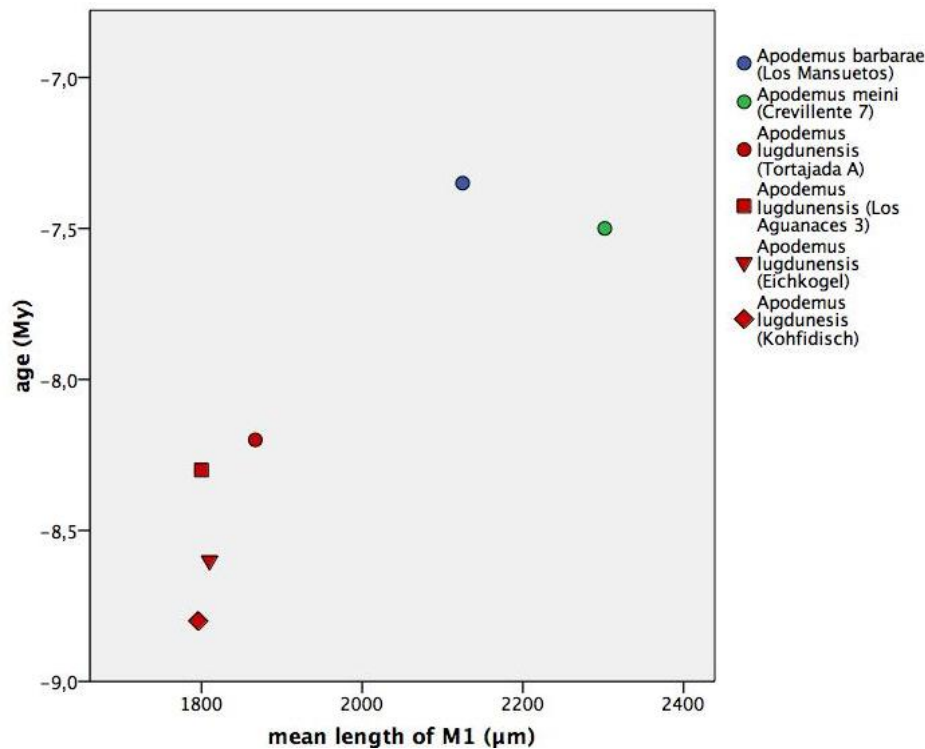
Fig. 26

Fig. 25-26: show an increase of mean lengths of the M¹ in the course of time. Aproximate ages of the localities were estimated according to specifications in the respective literature (for an overview of approximate relative stratigraphic positions of the localities see Appendix fig. 27).

8. Acknowledgements

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APPENDIX

Progonomys woelferi

M¹

Character	States of character	KoI n=50	%	KoIII n=50	%	CM n=37	%	total n=137	%
t1-2 connection	Absent	0	0	0	0	0	0	0	0
	Weak	23	46	27	54	17	46	67	49
	Strong	27	54	23	46	20	54	70	51
t1bis	Absent	50	100	50	100	36	97	136	99
	present	0	0	0	0	1	3	1	1
t1 position	Inline with t3	1	2	5	10	8	22	14	10
	Shifted backwards	49	98	45	90	29	78	123	90
t3 spur	Absent	37	74	36	72	28	76	101	74
	Small	11	22	13	26	7	19	31	23
	Well developed	2	4	1	2	2	5	4	3
t4-t5 connection	Absent	0	0	1	2	0	0	1	1
	Weak	2	4	6	12	3	8	11	8
	Strong	48	96	43	86	34	92	125	91
t4 position	Inline with t6	29	58	20	40	16	43	65	47
	Shifted backwards	21	42	30	60	21	57	72	53
t4-t7/t8 connection	Absent	1	2	5	10	0	0	6	4
	Weak	30	60	24	48	16	43	70	51
	Strong	19	38	21	42	21	57	61	45
t6-t9 connection	Absent	25	50	26	52	22	59	73	53
	Weak	24	48	12	24	2	5	38	28
	Strong	1	2	12	24	13	35	26	19
t7	Absent	49	98	50	100	37	100	136	99
	Present	1	2	0	0	0	0	1	1
t12	Absent	0	0	0	0	0	0	0	0
	Present	50	100	50	100	37	100	137	100
t12 shape	Round	0	0	5	10	3	8	8	6
	Commashaped	41	82	31	62	26	70	98	72
	Slender ridge	9	18	14	28	8	22	31	23
Acc. cusp betw. t1 and t4	Absent	46	92	44	88	24	65	114	83
	Present	4	8	6	12	13	35	23	17

Table 15

M²

Character	States of character	KoI n=48	%	KoIII n=38	%	CM n=36	%	total n=122	%
t1bis	Absent	43	90	33	87	36	100	112	92
	present	5	10	5	13	0	0	10	8
Acc. cusp labial of t3	Absent	48	100	34	89	36	100	118	97
	present	0	0	4	11	0	0	4	3
4-t5 connection	Weak	0	0	5	13	3	8	8	7
	Strong	48	100	33	87	33	92	114	93
	Absent	0	0	0	0	0	0	0	0
t4-t7/t8 connection	Weak	5	10	5	13	3	8	13	11
	Strong	43	90	33	87	33	92	109	89
	Absent	0	0	0	0	0	0	0	0
t6 spur	present	9	19	7	18	8	22	24	20
	Absent	39	81	31	82	28	78	98	80
t6-t9 connection	Weak	3	6	3	8	3	8	9	7
	Strong	1	2	0	0	2	6	3	2
	Absent	44	92	35	92	31	86	110	90
t7	Present	0	0	3	8	1	3	4	3
	Absent	48	100	35	92	35	97	118	97

Table 16

M³

Character	States of character	Ko I n=15	%	KoIII n=46	%	CM n=37	%	total n=98	%
t1 exist	Absent	0	0	26	57	0	0	26	27
	Present	15	100	20	43	37	100	72	73
t1-t3 connection	Absent	4	27	12	26	26	70	42	43
	Weak	10	67	32	70	7	19	49	50
	Strong	1	7	2	4	2	5	5	5
t9	Absent	10	67	44	96	30	81	84	86
	small	4	27	1	2	6	16	11	11
	Well developed	1	7	1	2	1	3	3	3
t4-t8 connection	Absent	6	40	26	57	29	78	61	62
	Weak	6	40	19	41	5	14	30	31
	Strong	3	20	1	2	3	8	7	7
	Double	2	13	0	0	0	0	2	2
T6-t8 connection	Absent	0	0	2	4	1	3	3	3
	Weak	5	33	17	37	2	5	24	24
	Strong	10	67	27	59	34	92	71	72

Table 17

m₁

Character	States of character	Kohfidisch I		KohIII		CM		total	
		n=50	%	n=50	%	n=50	%	n=150	%
a	Absent	16	32	2	4	6	12	24	16
	small	25	50	37	74	30	60	92	61
	Well developed	9	18	11	22	14	28	34	23
bc-de connection	Absent	5	10	0	0	3	6	8	5
	Weak	30	60	35	70	43	86	108	72
	Strong	15	30	15	30	4	8	34	23
d-e connection	Absent	0	0	0	0	0	0	0	0
	Weak	8	16	7	14	10	20	25	17
	Strong	42	84	43	86	40	80	125	83
i	Absent	45	90	45	90	37	74	127	85
	Weak	5	10	3	6	13	26	21	14
	Strong	0	0	2	4	0	0	2	1
Nr. of k	0	16	32	12	24	4	8	32	21
	1	20	40	13	26	14	28	47	31
	2	10	20	12	24	25	50	47	31
	3	4	8	11	22	5	10	20	13
	4	0	0	2	4	2	4	4	3
j	Absent	1	2	1	2	0	0	2	1
	small	13	26	14	28	6	12	33	22
	Well developed	36	72	35	70	44	88	115	77
Acc. cusp posterior of c	Absent	50	100	48	96	49	98	147	98
	Present	0	0	2	4	1	2	3	2

Table 18

m$_2$

Character	States of character	Kohfidisch I		KohIII		CM		total	
		n=50	%	n=45	%	n=49	%	n=144	%
Shape	Square	16	32	5	11	10	20	31	22
	Trapeze	34	68	40	89	39	80	113	78
i	Absent	48	96	40	89	42	86	130	90
	small	2	4	5	11	7	14	14	10
Nr. of k	0	25	50	11	24	2	4	38	26
	1	23	46	29	64	20	41	72	50
	2	2	4	5	11	20	41	27	19
	3	0	0	0	0	7	14	7	5
g-f connection	Weak	2	4	6	13	23	47	31	22
	Strong	48	96	39	87	26	53	113	78
j	Absent	4	8	3	7	3	6	10	7
	Small	22	44	17	38	36	73	75	52
	Strong	26	52	25	56	10	20	61	42

Table 19

m$_3$

Character	States of character	Kohfidisch I		KohIII		CM		total	
		n=24	%	n=48	%	n=46	%	n=118	%
b	Absent	0	0	1	2	0	0	1	1
	Small	21	88	40	83	42	91	103	87
	Present	3	13	7	15	4	9	14	12
d-e relation	e bigger	5	21	29	60	3	7	37	31
	Same size	17	71	17	35	43	93	77	65
	d bigger	2	8	2	4	0	0	4	3
j	Absent	11	46	31	65	23	50	65	55
	Present	13	54	17	35	23	50	53	45

Table 20

Apodemus lugdunensis

M¹

Character	States of character	Kohfidisch I		KohIII		CM		total	
		n=15	%	n=20	%	n=16	%	n=51	%
t1-2 connection	Absent	1	7	0	0	0	0	1	2
	Weak	1	7	3	15	7	44	11	22
	Strong	13	87	17	85	9	56	39	76
t1bis	Absent	15	100	20	100	16	100	51	100
	present	0	0	0	0	0	0	0	0
t1 position	Inline with t3	0	0	4	20	2	13	6	12
	Shifted backwards	15	100	16	80	14	88	45	88
t3 spur	Absent	7	47	11	55	5	31	23	45
	Small	6	40	8	40	11	69	25	49
	Well developed	2	13	2	10	0	0	4	8
t4-t5 connection	Absent	0	0	0	0	0	0	0	0
	Weak	1	7	0	0	1	6	2	4
	Strong	14	93	20	100	15	94	49	96
t4 position	In horizontal line with t6	13	87	14	70	9	56	36	71
	Shifted backwards	2	13	6	30	7	44	15	29
t4-t7/t8 connection	Absent	0	0	0	0	0	0	0	0
	Weak	0	0	0	0	0	0	0	0
	Strong	15	100	20	100	16	100	51	100
t6-t9 connection	Absent	0	0	0	0	0	0	0	0
	Weak	3	20	0	0	1	6	4	8
	Strong	12	80	20	100	15	94	47	92
t7	Absent	14	93	20	100	15	94	49	96
	Present	1	7	0	0	1	6	2	4
t12	Absent	0	0	0	0	0	0	0	0
	Present	15	100	20	100	16	100	51	100
t12 shape	Round	1	7	5	25	0	0	6	12
	Comma shaped	10	67	15	75	16	100	41	80
	Slender ridge	4	27	0	0	0	0	4	8

Table 21

M²

Character	States of character	KoI n=7	%	KoIII n=27	%	CM n=16	%	total 50	%
t1bis	Absent	7	100	25	93	15	94	47	94
	Present	0	0	2	7	1	6	3	6
t4-t5 connection	Absent	0	0	0	0	0	0	0	0
	Weak	0	0	1	4	0	0	1	2
	Strong	7	100	26	96	16	100	49	98
t4-t7/t8 connection	Absent	0	0	0	0	0	0	0	0
	Weak	0	0	0	0	0	0	0	0
	Strong	7	100	27	100	16	100	50	100
t6 spur	Absent	6	86	25	93	16	100	47	94
	Present	1	14	2	7	0	0	3	6
t6-t9 connection	Absent	2	29	5	19	0	0	7	14
	Weak	3	43	7	26	2	13	12	24
	Strong	2	29	15	56	14	88	31	62
t7	Absent	6	86	14	52	11	69	31	62
	Present	1	14	13	48	5	31	19	38

Table 22

M³

Character	States of character	Ko I n=11	%	KoIII n=44	%	CM n=17	%	total n=72	%
t1-t3 connection	Absent	2	18	2	5	4	24	8	11
	Weak	3	27	5	11	9	53	17	24
	Strong	7	64	37	84	4	24	48	67
t9	Absent	6	55	10	23	6	35	22	31
	Small	4	36	34	77	6	35	44	61
	Well developed	1	9	0	0	5	29	6	8
t4-t8 connection	Absent	1	0	6	14	9	53	16	22
	Weak	7	64	8	18	5	29	20	28
	Strong	3	18	30	68	3	18	36	50
	Double	3	27	0	0	0	0	3	4
T6-t8 connection	Absent	0	0	5	11	0	0	5	7
	Weak	2	18	9	20	1	6	12	17
	Strong	9	82	30	68	16	94	55	76

Table 23

m₁

Character	States of character	Koh I		KohIII		CM		total	
		n=12	%	n=29	%	n=19	%	n=60	%
a	Absent	2	17	2	7	3	16	7	12
	Small	0	0	9	31	6	32	15	25
	Well developed	10	83	11	38	10	53	31	52
bc-de connection	Absent	0	0	0	0	1	5	1	2
	Weak	1	8	16	55	11	58	28	47
	Strong	11	92	13	45	7	37	31	52
d-e connection	Absent	0	0	1	3	0	0	1	2
	Weak	0	0	8	28	4	21	12	20
	Strong	12	100	20	69	15	79	47	78
i	Absent	5	42	18	62	7	37	30	50
	Weak	5	42	7	24	6	32	18	30
	Strong	2	17	4	14	6	32	12	20
Nr. of k	0	1	8	1	3	1	5	3	5
	1	1	8	3	10	2	11	6	10
	2	2	17	15	52	10	53	27	45
	3	8	67	10	34	5	26	23	38
	4	0	0	0	0	1	5	1	2
j	Absent	0	0	0	0	0	0	0	0
	Small	1	8	11	38	2	11	14	23
	Well developed	11	92	18	62	17	89	46	77
Acc. cusp posterior of c	Absent	12	100	29	100	18	95	59	98
	Present	0	0	0	0	1	5	1	2

Table 24

m₂

Character	States of character	Koh I n=12	%	KohIII n=34	%	CM n=11	%	total n=57	%
Shape	Square	9	75	29	85	4	36	42	74
	Trapeze	3	25	5	15	7	64	15	26
i	Absent	2	17	18	53	4	36	24	42
	Small	10	83	13	38	4	36	27	47
	big	0	0	2	6	3	27	5	9
Nr. of k	0	2	17	2	6	1	9	5	9
	1	10	83	28	82	9	82	47	82
	2	0	0	4	12	1	9	5	9
g-f connection	Weak	8	67	16	47	10	91	34	60
	Strong	4	33	18	53	1	9	23	40
j	Absent	1	8	0	0	0	0	1	2
	Small	2	17	19	56	7	64	28	49
	Strong	9	75	15	44	4	36	28	49

Table 25

m₃

Character	States of character	Koh I n=20	%	KohIII n=45	%	CM n=14	%	total n=79	%
b	Absent	3	15	0	0	0	0	3	4
	Small	13	65	22	49	12	86	47	59
	Present	4	20	23	51	2	14	29	37
d-e relation	e bigger	1	5	3	7	0	0	4	5
	Same size	16	80	31	69	14	100	61	77
	d bigger	3	15	11	24	0	0	14	18
j	Absent	17	85	35	78	8	57	60	76
	Small	3	15	8	18	5	36	16	20
	Big	0	0	2	4	1	7	3	4

Table 26

Tables 15-26: Summary of abundances of character states within the single tooth positions for *Progonomys woelferi* and *Apodemus lugdunensis*.
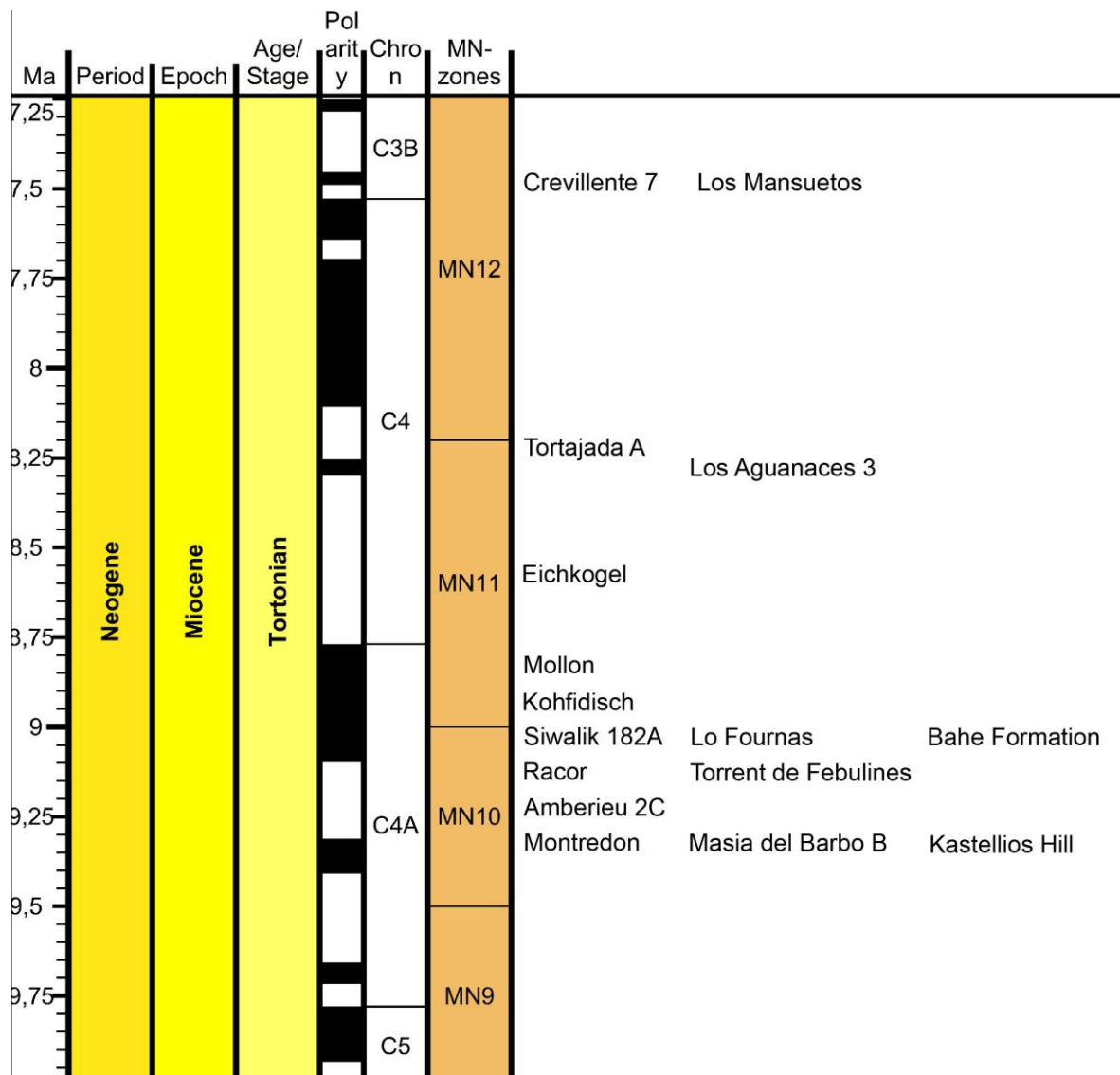
Fig. 27: Timetable showing the approximate ages and relative stratigraphig positions of the mentioned localities.

CURRICULUM VITAE

Born: 03.07.1983, Linz

Parents:	Veronika Bartl
	Gernot Hietler

Education:

1989/90- 1992/93	Primary school 25 Keplerstr.11 Linz, Harbach
1993/94- 2000/2001	Europagymnasium Auhof/ Linz International School Auhof Aubrunnerweg 4 Linz, Auhof
1996 (Michaelmas Trimester)	Student exchange Dover College Folkestone Road Dover, Great Britain
1997	Language course Exchange program Nice, France
2001	Austrian Matura (in English, German, Mathematics, Biology)
2001	International Baccalaureates (in English, German, Mathematics, Biology, Chemistry)
2001	Master study Biology Palaeontology at the University of Vienna.
2008- 2009	1 year of abroad studies of Geosciences with ERASMUS exchange programme at the Université Montpellier 2, Montpellier, France.

Scientific Career:

1999, 2003	Fieldwork, preparation and taxonomic identification of fossils at the Palaeolithic excavation site of the „Laboratoire Départemental de Pehistoire du Lazaret", Nice, France.
2003	Fieldwork, and fossil preparation for the Natural History Museum Vienna in the course of the excavation Atzelsdorf (Miocene).
2003	Preparation of rock and sediment samples from Ukrainian and Austrian Miocene for Prof. Dr. Martin Zuschin (Institute of Palaeontology, University of Vienna), and Priv.-Doz. Dr. Mathias Harzhauser (Natural History Museum Vienna).
2003	Construction of a replica of a dugongid skeleton (*Metaxitherium krahuletzi*) in cooperation with Mag. Martin Maslo for the „Atlantis Kindermuseum" in Duisburg under the guidance of Prof. Dr. Peter Pervesler (Institute of Palaeontology, University of Vienna).
2006	Project collaboration with Univ. Doz. Dr. Daxner-Höck Gudrun (Natural History Museum Vienna).
WS 2007/2008	Tutor for the practical course 300652 „Paläobiologie der Tiere" at the institute of palaeontology, University of Vienna.
WS 2010/2011 SS 2011	Tutor for the excursion 300698 „Paläontologische Arbeitsmethoden - Gelände" at the institute of palaeontology, University of Vienna.
2011	Taxonomic identification and digitalisation of vertebrate fossils of the palaeontological collection at the „Biologiezentrum Linz, OÖ Landesmuseen".

2011	Digitalisation of photo and video material from the field work dokumentation of the excavation of the cave and fissure system of Kohfidisch, and production of a short film for the Natural History Museum Vienna.
WS 2011/2012	Tutor for the practical course 300483 „Paläontologische Arbeitsmethoden - Lobor" at the institute of palaeontology, University of Vienna.

Job history:

1998	Assistant secretary – Jägerland Wildspezialitäten GmbH
2002-2005	Operator – IFES, Institut für empirische Sozialforschung
2007	Assistant secretary – Psychiatric clinic Wels, Upper Austria
2008	Service employee – Manpower Hospitaliy Austria
2009	Secretary – Adenbeck GmbH
2011	Sales assistant – M-design GmbH
Scince 2011	Service employee – Manpower Hospitaliy Austria

Congress participations:

2010	General Assembly of the Eropean Geosciences Union, Vienna
2011	General Assembly of the Eropean Geosciences Union, Vienna
2011	PALGES - 82. yearly convention of the „Paläontologische Gesellschaft

LINGUISTIC PROFICIENCY

German, mother tongue

English, like a second mother tongue (8 years of bilingual college, student exchange with Dover College, many holidays in England and America, many international friends)

French, good in spoken and written (6 years in college, vacations and internships, 1 year of study abroad)

Spanish (5 years in college, some holiday trips)

COMPUTER LITERACY AND ADDITIONAL QUALIFICATIONS

Common computer packages for Mac and Windows, Microsoft Office (with Access), Open Office, Adobe CS5, CorelDraw, Gimp, SPSS, PAST, MATLAB, R, ArcGIS, KISS-med, tps-programs, EVAN-toolbox, AMIRA;

Electron microscopic training, geometric morphometrics, multivariate statistics;

PUBLICATIONS

WÖGER J. (2011): The Murines (Rodentia, Mammalia) of Kohfidisch (Burgenland, Austria) at second glance – A comparative morphological study, Beiträge zur Paläontologie, 32: p.42;