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Eomyids (Rodentia, Mammalia) in the St-Gérand-le-Puy Area (Allier, France; MN2a)

by

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Abstract

Previous and new data dealing with the eomyid rodents yielded by the St-Gérand-le-Puy area quarries are studied and make it possible to evidence in these quarries an evolution of the family which, however, remains within the limits of the MN 2 mammal level. The genera *Pseudotheridomys*, *Rhodanomys* and *Ritteneria* occur in these localities. *Pseudotheridomys parvulus* indicates a MN2a level. The morphological variations within the genus *Rhodanomys* indicate that it certainly gives rise to *Ritteneria*, but, as *Ritteneria* seems to be found together with *Rhodanomys*, we conclude that certainly several species of *Rhodanomys* evolved independantly and not simultaneously, so that *Ritteneria* of different sizes are to be found. Correlations between the localities of the St-Gérand area and with other European MN1 and MN2 localities are discussed.

Keywords: Eomyidae (Rodentia), evolution, Early Miocene, MN 2, St.-Gérand-le-Puy, France

Zusammenfassung

Alte und neue Daten von Eomyiden aus den Steinbrüchen in der Umgebung von St-Gérand-le-Puy wurden ausgewertet. Diese ermöglichen es nun, die Evolution der Eomyiden im Bereich des MN2 nachzuzeichnen. Die folgenden Genera sind in diesen Fundstellen anzutreffen: *Pseudotheridomys*, *Rhodanomys* und *Ritteneria*.*Pseudotheridomys parvulus* zeigt MN2a-Level an. Die morphologische Variation innerhalb der Gattung *Rhodanomys* läßt den Schluß zu, daß sich aus ihr die Gattung *Ritteneria* entwickelt hat. Da aber *Rhodanomys* und *Ritteneria* offensichtlich zeitgleich vorkommen, schließen wir daraus, daß sich einige Arten der Gattung *Rhodanomys* auch zeitlich unabhängig voneinander entwickelt haben. Deshalb findet man auch Vertreter des Genus *Ritteneria* in unterschiedlichen Größen. Korrelationen zwischen den Fundstellen der Gegend um St-Gérand sowie anderen europäischen Fundstellen aus den Stufen MN1 und MN2 werden diskutiert.

1. Introduction

1.1. Geographical situation and geological setting

St-Gérand-le-Puy (Allier) is a world-wide known locality for mammals and birds. It was first published in 1833 as a vertebrate locality, when Geoffroy-St-Hilaire described the first new mammals from there. It is situated in the French Massif Central, in the Limagne Bourbonnaise (Fig. 1), at the northern part of the 180 km long Limagne rift basin, which extends from Moulins (to the North), to Brioude (to the South). Related to the uplifting of the Alpine chain, a series of lakes of various extension developed in the rift and were filled by detritic sediments from the Eocene to the Early Miocene and then filled up. During the Early Miocene, this rift lake was restricted to about seventy kilometers in length, roughly from Moulins (Allier) to Clermont-Ferrand (La Roche Blanche/Gergovie, Puy-de-Dôme; Hugueney et al., 1999); St-Gérand-le-Puy stood at the margin of this lake, but, due to important subsidence and rifting movements, temporary small islands could develop (Wattinne et al., 2003).

In this fluvial/lacustrine environment, generally not far from the shore, the deposits are not regular layers, but stromatolitic limestones; various algae and numerous Trichoptera larvae produce stromatolitic bioconstructions of different forms: balls and columns are frequent so that these limestones are known as "calcaires en chou-fleur,

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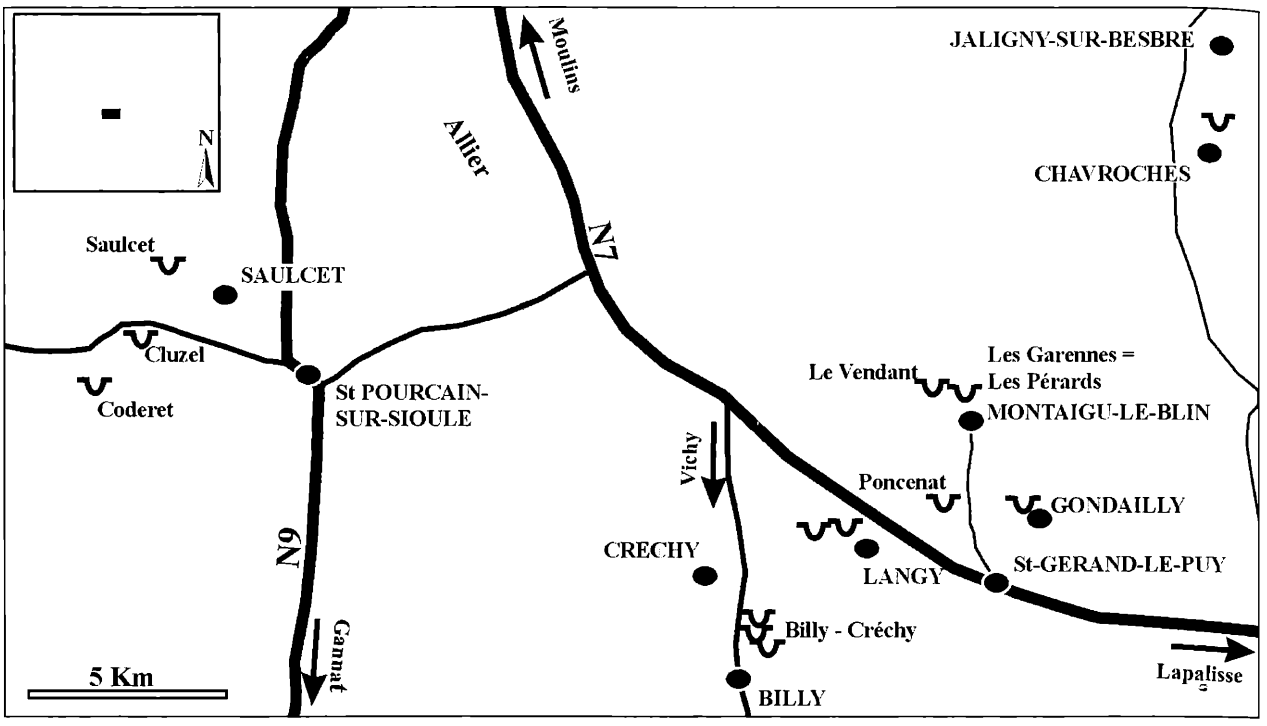

Figure 1: Map of the St-Gérand-le-Puy area indicating the quarries cited in the text.

calcaires à indusies, calcaires à phryganes". Contemporary marly sediments fill the gaps between these stromatolites either as more or less regular layers (Fig. 2), or often as fissure or pocket fillings (WATTINNE et al., 2003:fig. 3D). Some of them yield either terrestrial faunal assemblages or a mixture of terrestrial vertebrates and aquatic birds; mud-flows and rapid fluctuations of hydrological palaeoregime in this fluvio-lacustrine environment explain these formations (BÜCHER et al., 1985). All these deposits coalesced to form large limestone reefs which now appear as hills called "tureau(x)" (Fig. 3) and can reach twenty meters high.

The first excavations were situated on the main road from Paris to the Mediterranean Sea (now N7) near St-Gérand and Langy (Fig. 1), but later on the old quarries were abandoned and often filled up and new ones were exploited for lime, yielding also fossils. Thus the faunal list is a composite one and it is now impossible to know from which of these localities the material came. For more than fifty years, excavations no longer took place in the district of St-Gérand, but were pursued some kilometers eastwards, and particularly in the neighbourhood of the locality Montaigu-le-Blin, which has been chosen as reference locality of the Agenian mammal level MN 2 (Aquitanian, Early Miocene; DE BRUIJN et al., 1992; HUGUENEY, 1997). At least a dozen of quarries were fossiliferous, but they were certainly not excavated in the same level: perhaps, the fossils are not exactly of the same age. Moreover, on the restricted area of St-Gérand (10 km^2), the climatic conditions were certainly homogeneous, but local variations could exist, in relationship with the proximity of water or temporary isolation.

At the beginning, workers or scientists picked up the material (maxillaries, teeth, bones) directly on the outcrops. These last forty years, however, regular visits to the accessible quarries conduced to numerous samplings which were screen-washed and sorted and made it possible to obtain faunal assemblages instead of isolated material of unknown origin. Thus assemblages were obtained from Chavroches, Gondailly, Poncenat and especially from large quarries North of Montaigu-le-Blin -Les Garennes=Les Pérards, Le Vendant -, and further westward from two quarries, Cluzel and Saulcet, which also yielded Aquitanian material. In two quarries (Gondailly and Cluzel) fossils were found in two superposed levels (Fig. 2) and gave the opportunity to test a possible evolutionary difference.

Unfortunately, except for glirids, which are not very useful for accurate biostratigraphy, the rodent material is generally very poor, but some of these quarries yielded eomyid teeth. This group is now recognised as a rapidly evolving family, and gives valuable results for biozonation (ALVAREZ-SIERRA, 1987; ENGESSER, 1990). The study of the recently discovered eomyid material was undertaken as a basis for comparison between the different quarries (and between the different levels of each quarry when necessary) and for correlation with the other localities attributed to the MN 2 level.

1.2. Eomyid localities

Birds, bats, carnivores, artiodactyles, and beavers from St-Gérand are numerous in many European collections, but small rodents, and especially eomyids, are rare. Only *Rhodanomys schlosseri* and *Pseudotheridomys parvulus* were cited in the faunal list of Montaigu-le-Blin (DE BRUIJN et al., 1992).

Figure 2: Cluzel quarry showing high *Trichoptera* columns embedded in marly layers. The first fossils came from the base of a column layer (= Cluzel 1); later, a higher level also yielded some teeth (= Cluzel 2).

Figure 3: Le Vendant tureau seen from Les Pérards quarry; on the left, the old quarry is seen at the top of the hill which no longer exists.

Old collections:

• in the Paris Museum, LAVOCAT (1952) briefly described a skull of St-Gérand-le-Puy as *Ritteneria*. This skull has been previously figured by FILHOL (1879) as *Myoxus murinus*; the same skull was compared by COMTE & VIANEY-LIAUD (1989) to *Eomys* skulls from Quercy.

• in the Basel Museum, ENGESSER (1990) figured from "Montaigu" a left maxillary of *Ritteneria manca* with M1 and M2 and two isolated upper teeth of a larger form attributed to *Ritteneria* nov. sp.

Recent collections:

The following localities yielded members of the *Rhodanomys* and *Pseudotheridomys* groups; the two groups can co-exist in the localities, but this is not always the case.

• **Chavroches**: *Pseudotheridomys parvulus* (40 teeth), *Rhodanomys schlosseri* (341 teeth, mandible and maxillary fragments) and ?*Ritteneria molinae* (three teeth).

• **Gondailly**, two superposed levels:

Gondailly 1: *Pseudotheridomys parvulus* (nine teeth), *Rhodanomys* aff. *schlosseri* (164 teeth, mandible and maxillary fragments), *Ritteneria molinae* (six teeth, maxillary and mandible fragments).

Gondailly 2, at the top: *Pseudotheridomys parvulus* (one tooth) and *Ritteneria* aff. *molinae* (eight teeth).

• **Montaigu**:

Les Garennes / Les Pérards: this large quarry encloses little quarries previously known as Les Garennes or Les Pérards; as it is now the only quarry still worked it is often simply designated as Montaigu. Some teeth of Eomyidae come from different pockets or fissures all situated in stromatolitic levels and before the major fluviatile event of WATTINNE et al. (2003). *Pseudotheridomys* (one tooth); *Ritteneria* aff. *molinae* (two teeth and two other damaged teeth)

Le Vendant: this was a small tureau, situated on the road from Montaigu to Boucé, in front of the Montaigu quarry (Fig. 3). It was worked and razed. It yielded only two *Ritteneria* teeth.

We have to notice that, in these quarries, pockets or fissures yielded almost exclusively a single species, for example the castorid pocket (HUGUENEY & ESCUILLIÉ, 1995). The Le Vendant eomyids come from two neighbouring pockets in a stromatolitic level, one with almost exclusively bats

		N	mean	range			N	mean	range
D4	L	4	87	84-90	d4	L	2	100	100-101
	W	4	89	83-92		W	2	73	72-74
P4	L	3	89	86-91	p4	L	4	95	90-98
	W	3	97	93-102		W	4	86	79-94
M1	L	7	94	89-99	m1	L	4	99	95-106
	W	7	108	101-115		W	4	93	87-100
M2	L	9	87	83-90	m2	L	1	96	—
	W	9	108	104-111		W	1	84	—
M3	L	3	67	65-68	m3	L	3	87	84-89
	W	3	91	89-93		W	3	80	77-89

Table 1: Measurements of *Pseudotheridomys parvulus* from Chavroches.

and the other with a dominance of soricids.

• **Poncenat** (Moulin or Rochers de): *Pseudotheridomys parvulus* (two teeth); *Ritteneria* aff. *molinae* (nine teeth).

• **Cluzel**: this locality is not in the St-Gérand area sensu stricto; as Saulcet, it is situated on the opposite side of the Limagne basin but it evidences the same formations and seems to pertain to the same lake. It was mentioned by Hugueney (1974), Hugueney & Ringeade (1990) and Hugueney et al. (1992) but not studied in detail. It yielded two superposed levels (Fig. 2)

Cluzel 1 (corresponding to the earlier mentioned Cluzel, with additional samplings): *Pseudotheridomys parvulus* (two teeth); *Rhodanomys* aff. *schlosseri* (86 teeth);

Cluzel 2, a later discovered and higher level: ?*Ritteneria* aff. *molinae* (18 teeth).

The material from Chavroches and Gondailly is stored in the Centre de Conservation et d'Etude des Collections, Museum d'Histoire naturelle de Lyon, MHNL; the material from the other localities is stored in the collections of the University Claude-Bernard, Lyon 1, FSL.

1.3. Methods

All the measurements are given in millimeters / 100 as L (length) x W (width). All the teeth are illustrated in occlusal view, except when otherwise indicated. When right teeth are illustrated, they are generally reversed and mentioned as: (r.r.) = right reversed); all the other figured teeth are left ones.

2. Systematic Palaeontology

Ordo Rodentia Bowdich 1821

Familia Eomyidae Winge 1887

Genus *Pseudotheridomys* Schlosser 1926

***Pseudotheridomys parvulus* (Schlosser 1884)**

(Plate 1, figs. 14-23)

Material and measurements:

• Chavroches (Tab. 1)

• Cluzel 1: d4 (102 x 76); m3 (87 x 86).

• Gondailly 1: P4 (89 x 95); M1 (87 x 96); M2 (84 x 104); M3 (70 x 85, 70 x 89); d4 (98 x 66); p4 (94 x 83); m1 (90 x 95); m3 (90 x 95).

• Gondailly 2: M3 (77 x 93).

• Montaigu-Les Pérards: m1 (113 x 104).

• Poncenat : P4 (95 x 100); M3 (76 x 91).

Discussion: Only Chavroches yielded a small population of this genus. No appreciable difference in size exists between the teeth of the different localities. Their size corresponds also to *Pseudotheridomys parvulus* from Ulm-Westtangente (Werner, 1994) and from Saulcet (Allier; Hugueney, 1974). These teeth seem to be a little larger than *P. bernensis*.

As in Ulm-Westtangente, the molars show lophodont crests; the longitudinal crest in the upper as well as in the lower molars is almost always interrupted; an additional crest between metalophid and mesolophid appears in only one of the five m1-2 from Chavroches; in Ulm-Westtangente it appears only in 9% of the teeth; a minute additional crest appears on the three m3 from Chavroches and on the m3 and d4 of Gondailly. Generally, no reduction of the mesoloph is seen in the upper molars, but in one P4 and one M2 it is interrupted in its middle.

So the material of these localities can be attributed to *Pseudotheridomys parvulus*. Consequently the localities should be assigned to the MN2 level, MN1 being characterized by the smaller and more complicated *P. bernensis*.

Genus *Rhodanomys* Depéret & Douxami 1902

***Rhodanomys schlosseri* Depéret & Douxami 1902**

(Plate 1, figs. 1-8; fig. 11)

Material and measurements:

• Chavroches (Tab. 2, fig. 4)

Discussion: The size of the material from Chavroches generally corresponds to that of *Rhodanomys schlosseri* from Fornant 11, a locality situated near the type-locality of Pyrimont (Ain). However, overall the teeth are a bit smaller, with some teeth, particularly among the M1 and m1, falling outside the ranges of variation found in Fornant 11. The smaller size is indicative for a more progressive level (Engesser, 1990). Morphologically, the teeth correspond well to the main characteristics of *R. schlosseri* from Fornant 11: a majority of teeth show a complete longitudinal crest

Table 2: Measurements of *Rhodanomys* from Chavroches, Gondailly 1 and Cluzel 1.

	Locality		N	mean	range		Locality		N	mean	range
	Cluzel 1	L	13	85	78-93		Cluzel 1	L	7	96	84-101
		W	13	85	81-91			W	7	65	60-70
D4	Gondailly 1	L	16	87	79-94	d4	Gondailly 1	L	5	104	94-110
		W	16	88	81-96			W	5	69	64-70
	Chavroches	L	26	89	78-99		Chavroches	L	12	102	95-110
		W	26	89	81-96			W	12	70	62-75
	Cluzel 1	L	7	84	86-93		Cluzel 1	L	4	80	74-96
		W	7	89	80-100			W	4	76	74-78
P4	Gondailly 1	L	21	87	79-94	p4	Gondailly 1	L	15	82	72-88
		W	21	92	82-100			W	15	76	69-80
	Chavroches	L	30	88	80-98		Chavroches	L	42	86	79-96
		W	30	91	83-102			W	42	81	74-91
	Cluzel 1	L	6	92	89-95		Cluzel 1	L	10	93	88-98
		W	6	98	93-104			W	10	92	87-97
M1	Gondailly 1	L	23	96	86-103	m1	Gondailly 1	L	20	94	85-100
		W	23	106	95-112			W	20	96	87-106
	Chavroches	L	47	97	87-109		Chavroches	L	54	97	85-107
		W	47	110	96-127			W	54	97	82-107
	Cluzel 1	L	9	84	73-91		Cluzel 1	L	9	83	77-87
		W	9	97	86-107			W	9	90	78-97
M2	Gondailly 1	L	19	85	78-93	m2	Gondailly 1	L	24	85	76-92
		W	19	103	92-109			W	24	90	83-98
	Chavroches	L	46	89	79-98		Chavroches	L	38	93	80-102
		W	46	107	94-119			W	38	95	84-105
	Cluzel 1	L	4	65	64-68		Cluzel 1	L	17	75	70-94
		W	4	77	75-79			W	17	76	66-86
M3	Gondailly 1	L	17	67	58-74	m3	Gondailly 1	L	10	77	70-85
		W	17	80	70-86			W	10	80	75-85
	Chavroches	L	20	71	63-85		Chavroches	L	29	81	71-93
		W	20	87	78-97			W	29	84	74-92

on P4, a long mesoloph on M1 and a longitudinal crest on M2 and predominantly longitudinal crests on lower molars (Tab. 3).

The form from Chavroches clearly pertains to *Rhodanomys* and differs from *Ritteneria*, in which the mesoloph of M1-2 is generally absent and reaches the labial border only as an exception. The progressive evolution acts first on the posterior molars and more advance features are seen in the M2, m2 and particularly in the M3.

We have to notice that some teeth (for example the maxillary with P4-M1: P4 = 98 x 102, M1 = 97 x 127; Pl. 1, fig. 1) present more or less outliers within the Chavroches distribution (Fig. 4). As they show no other particular morphological characteristics and as they are within the limits of *R. schlosseri* from Fornant 11 (ENGESSER, 1990), they are attributed to *R. schlosseri*. The situation is, however, unclear because still larger teeth from Montaigu, showing a pattern intermediate between *Rhodanomys* and *Ritteneria*, were figured as *Ritteneria* nov. sp. by ENGESSER (1990; ?P4/M1 = 118 x 132; M2 = 106 x 119). Moreover, one large m2 (102 x 112; Pl. 1, fig. 9) shows a lophodont pattern and its longitudinal crest is rather deeply interrupted as in *Ritteneria molinae*, but other teeth, not especially large (for example, maxillary with P4-M1: P4 = 89 x 90, M1 = 96 x 105; Pl. 1, fig. 10), show a *Ritteneria molinae* pattern; it is difficult to decide if they pertain to *R. molinae* or to the variability of *R. schlosseri*; they are figured as *?Ritteneria molinae*.

Rhodanomys schlosseri was cited from Saulcet (Allier; HUGUENEY, 1974). As later this form was considered characteristic for MN 1, Saulcet was attributed to MN 1/2 (HUGUENEY, 1997). The teeth of Saulcet are just a little larger than those of Chavroches and, because *R. schlosseri* is now demonstrated to continue into MN 2, Saulcet could also pertain to MN 2.

As noticed by ENGESSER (1990:72), *Rhodanomys schlosseri* lacks the longitudinal rib characteristic of the eomyid lower incisor; its lower incisor is smooth.

Rhodanomys aff. *schlosseri* DEPÉRET & DOUXAMI, 1902

(Plate 1, fig. 12; Plate 2, figs. 8-12; Plate 3, figs. 19-36)

Material and measurements:

- Gondailly 1: (Tab. 2, Fig. 4)
- Cluzel 1: (Tab. 2, Fig. 4)

Discussion: The teeth of Gondailly 1 and Cluzel 1 are generally a little smaller than those of Chavroches. That

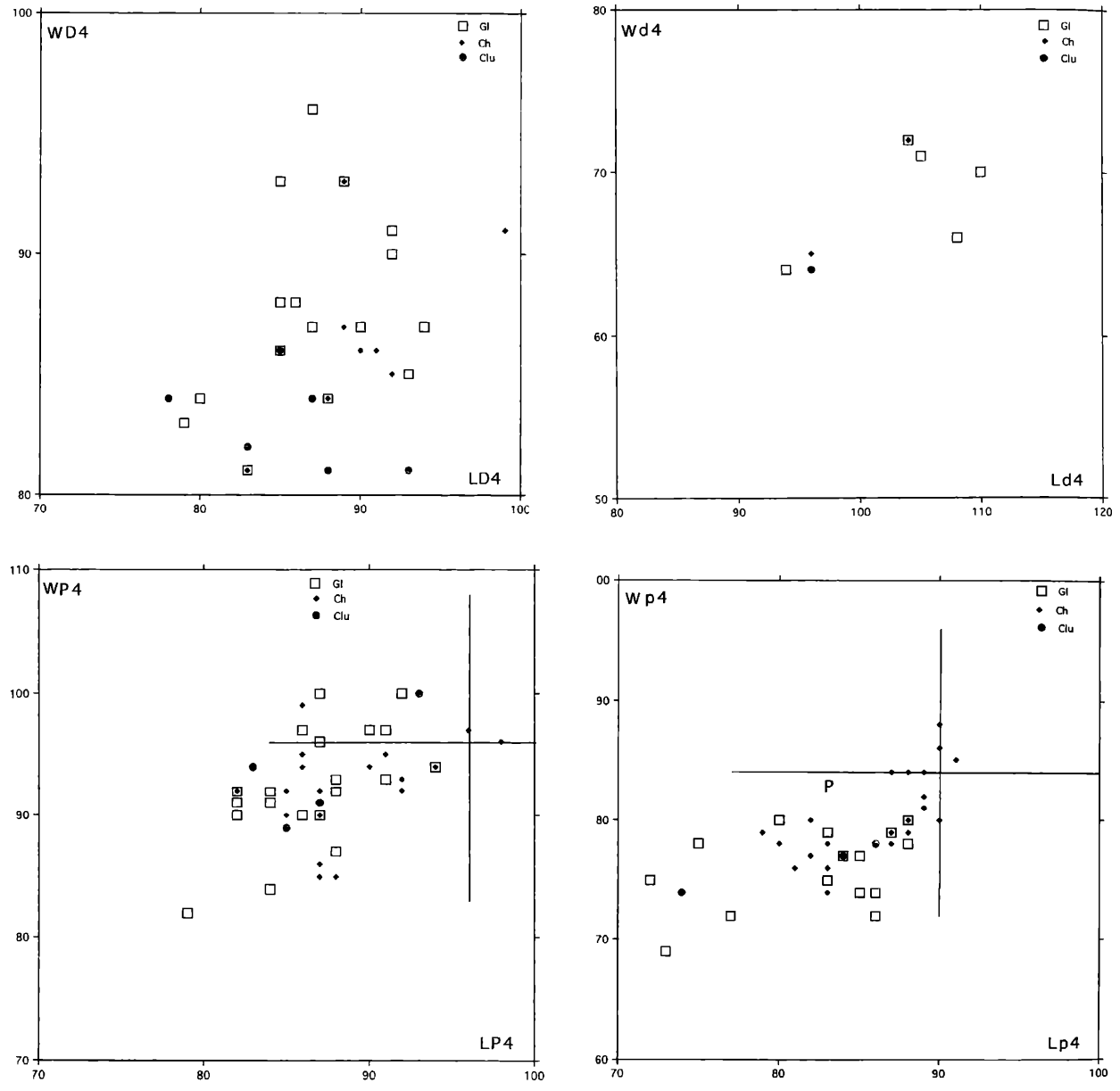

Figure 4a: Length (L) – Width (W) diagrams of *Rhodanomys* from Chavroches, Gondailly 1 and Cluzel 1: upper and lower lacteal teeth and premolars. Cross lines correspond to the dimensions of *R. schlosseri* in Fornant 11 (after ENGESSER, 1990) and P represent the values of the teeth of Pyrimont. Arrows indicate especially large teeth that are cited in the text.

implies all the permanent teeth except P4 and m1. Some teeth of Cluzel 1 are even smaller than those of Gondailly 1. The morphology of the teeth is more frequently evolved in the direction of *Ritteneria* (Tab. 3), but the major characteristics of *Rhodanomys* (longitudinal crest on P4 and M2 and long mesoloph on M1 and M2) show predominant percentages and the longitudinal crests of the lower molars are scarcely or not interrupted.

Genus *Ritteneria* STEHLIN & SCHAUB 1951

Ritteneria molinae ALVAREZ-SIERRA 1987

(Plate 1, figs. 9-10, 13; Plate 2, figs. 13-15)

Material and measurements:

• Gondailly 1: maxillary with P4-M3 (P4 = 91 x 97, M1 = 96 x 110, M2 = 85 x 108, M3 = 67 x 90); mandible with m1 (m1 = 97 x 186).

• Chavroches: maxillary with P4-M1 (P4 = 89 x 90, M1 = 96 x 105); m2 = 102 x 112.

Discussion: In the material from Gondailly 1, a complete maxillary directly stands out because its morphology is typical of *R. molinae*: P4 and M3 without mesoloph, M1 and M2 with short mesoloph and nearly or completely interrupted longitudinal crest. This morphology exists on some teeth of advance *R. schlosseri*, but because all the teeth show this pattern here, we can hypothesize the presence of *R. molinae* concurrently with *R.* aff. *schlosseri*. The sizes of the teeth correspond to *R. schlosseri* as well as to *R. molinae*. In the lower teeth, a mandibular fragment shows a large m1, particularly in width; the mandible itself is much larger than the mandibles of *R.* aff. *schlosseri* of

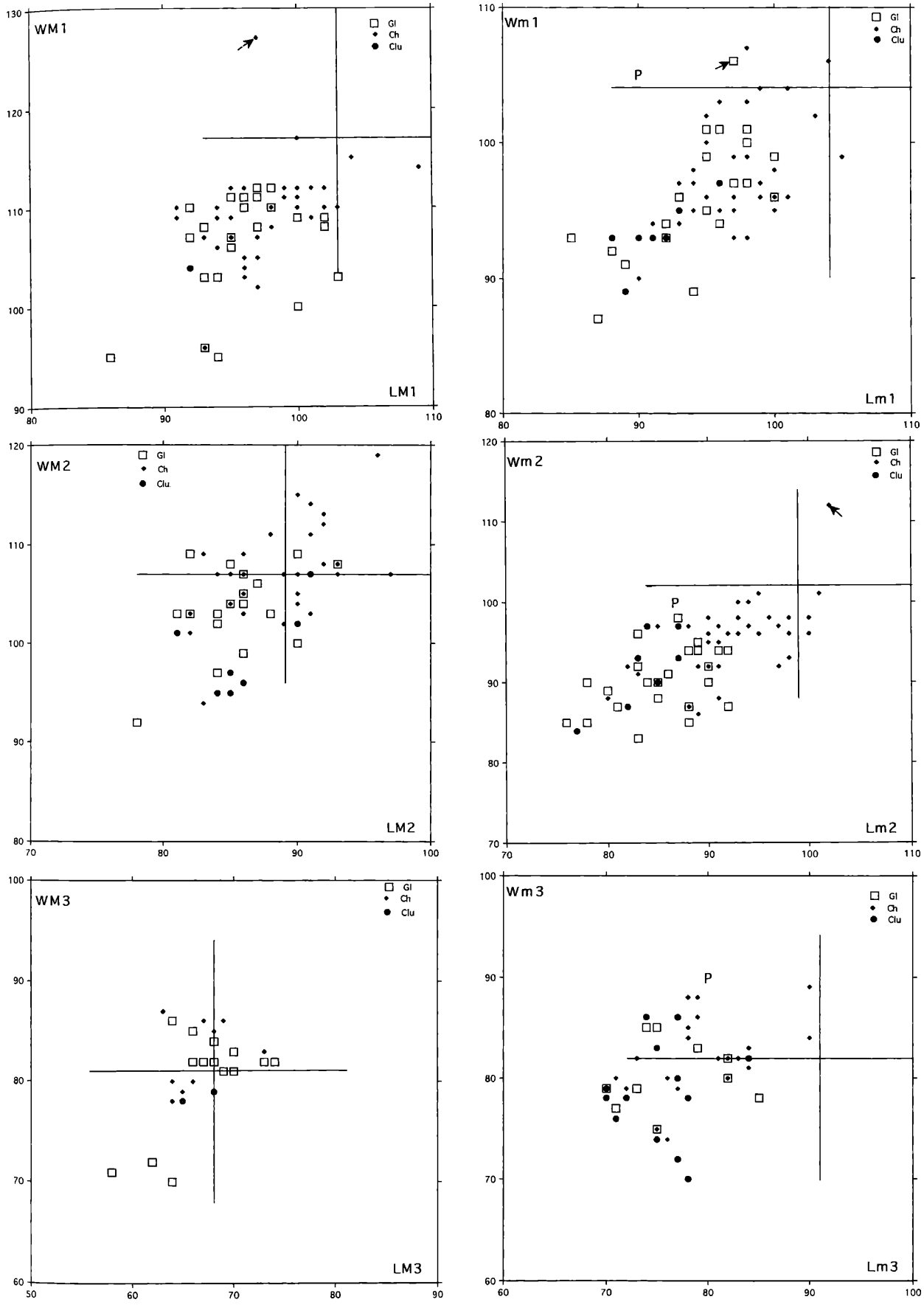

Figure 4b: Length (L) – Width (W) diagrams of *Rhodanomys* from Chavroches, Gondailly 1 and Cluzel 1: upper and lower molars. Cross lines correspond to the dimensions of *R. schlosseri* in Fornant 11 (after ENGESSER 1990) and P represent the values of the teeth of Pyrimont. Arrows indicate especially large teeth that are cited in the text.

Characteristics of the teeth	For. 11-La Chaux	Chavroches	Gondailly 1	Cluzel 1
4th syncline on P4	95%-20%	95% (18)	54% (15)	50% (4)
complete longitudinal crest on P4	66%-0%	100% (17)	76% (17)	60% (5)
long mesoloph on M1	100%-0%	97% (39)	93% (27)	50% (6)
longitudinal crest present on M2	100%-43%	100% (35)	100% (19)	100% (8)
long mesoloph on M2	95%-0%	50% (37)	71% (21)	78% (9)
long mesoloph on M3	55%-0%	0% (15)	0% (18)	0% (4)
complete longitudinal crest on m1	97%-0%	89% (45)	100% (22)	60% (10)
short mesolophid on m1	78%-0%	64% (42)	44% (23)	50% (10)
complete longitudinal crest on m2	89%-0%	90% (48)	96% (24)	90% (9)
short mesolophid on m2	88%-0%	50% (48)	53% (19)	45% (5)
complete longitudinal crest on m3	86%-0%	50% (28)	91% (11)	60% (14)

Table 3: Percentages of morphological characteristics on the teeth of the *Rhodanomys* / *Ritteneria* lineage (in brackets = number of teeth). The data of Fornant 11 (*Rhodanomys schlosseri*) and La Chaux (*Ritteneria manca*) are from ENGESSER (1990).

the same locality and its morphology seems to be different. In Chavroches, an isolated m2 , especially wide and with interrupted longitudinal crest, and a maxillary fragment which shows similarities with that of Gondailly 1 could also correspond to *R. molinae*; their size is not different of that of *R. schlosseri.*

Ritteneria aff. *molinae* ALVAREZ-SIERRA 1987

(Plate 2, figs. 1-7; Plate 3, figs. 3-9)

Material and measurements:

- Montaigu-Les Pérards (recent collection): P4 (92 x 96); M1-2 (91 x 114)
- Gondailly 2 (upper level): D4 (92 x 89); M1 (83 x 88); M1-2 (83 x 111); M2 (80 x 101); d4 (99 x 67); m1 (90 x 95); m2 (80 x 95); m3 (76 x 73).
- Poncenat: 3 P4 (81 x 89, 83 x 87, 94 x 95); d4 (94 x 68); 2 p4 (78 x 75, 76 x 76); m1 (91 x 101); 2 m2 (92 x 99, 93 x 104).

Discussion: The two teeth of Montaigu correspond in their dimensions to the material of *R. manca* from La Chaux (MN 2), but also to that of *R. molinae* from Cetina de Aragon (MN 2). The P4 show two major transverse crests separated by a deep furrow, with just an indication of the longitudinal crest; remnants of the first and a longer fourth syncline are present. As in the Basel maxillary (ENGESSER, 1990: fig. 49c), the moderately worn M1-2 shows a faint trace of the first syncline, but the oblique longitudinal crest, with a short indication of the mesoloph, is better developed and joins the two transverse crests. The two crests show a tendency to join on the lingual and on the labial borders, especially on the labial one. This tooth shows a lesser degree of evolution than the teeth of La Chaux and fits better with the morphology of *R. molinae.*

In Gondailly 2 and Poncenat the teeth are small and fall in the lower part of the variation of *R. molinae* / *R. manca*, or even smaller. In the lacteal teeth of the two localities mesoloph or mesolophid are lacking and they correspond well to those of *Ritteneria.* The upper teeth of Gondailly 2 and Poncenat lack a mesoloph and show a partly interrupted longitudinal crest, which indicates an evolution in the direction of *Ritteneria.* In the lower teeth, however, the longitudinal crest is scarcely interrupted. In the unworn ?M1 from Gondailly 2, the anterior cingulum is situated distinctly below the upper surface of the tooth.

These teeth show a more primitive pattern than *R. manca* from Le Vendant and correspond better to the pattern of *Ritteneria molinae*, but their size is smaller. They correspond well to the material of Lautern 2 (late MN 1), attributed to this species by ZIEGLER & WERNER (1994) despite its small size, which is in contradiction with the hitherto observed evolution of the genera *Rhodanomys* and *Ritteneria.*

?*Ritteneria* aff. *molinae* ALVAREZ-SIERRA 1987

(Plate 3, figs. 10-18)

Material and measurements:

- Cluzel 2: 2 D4 (84 x 81, 85 x 81); P4 (77 x 75); M2 (78 x 84); 4 M3 (64 x 79, 65 x 80, 67 x 78, 68 x 83); d4 (105 x 71); 2 p4 (78 x 75, 86 x 78); 2 m1 (82 x 93, 89 x 92); m2? (83 x 81); 3 m3 (74 x 75, 77 x 81, 79 x 75).

Discussion: These teeth correspond to the smaller teeth of *R. manca* or may be even smaller and are a little smaller than those of the St-Gérand area. They show smaller M1-2 and m1-2 than *Ritteneria* aff. *molinae* from Lautern 2 (MN1; ZIEGLER & WERNER, 1994). The D4 shows a mesoloph, which is also indicated on M1-2; on P4 and M3, however, mesolophs are lacking. The d4 is long but the other lower teeth are short. The longitudinal crest is complete on p4 and m1-2, but interrupted on m3; the lower molars show a well-developed anterolophid. They differ from *Ritteneria* and particularly *R. manca* by the presence of a long mesoloph on D4 and M2 and by their almost complete longitudinal crest on the lower molars. These primitive characteristics remind of *Rhodanomys* but the total lack of mesoloph (or mesolophid) on P4, M3 and d4, the relatively high crown indicate a more progressive level closer to *Ritteneria* aff. *molinae* from Lautern 2, even if some teeth are a little smaller. It is difficult to assign these teeth with certainty to a described taxon.

Ritteneria manca STEHLIN & SCHAUB 1951
(Plate 3, figs. 1-2)

Material and measurements:
• Old collections: Basel Museum left maxillary with M1-2 (Ph. 4956): M1 = 96 x 115; M2 = 84 x 109;
• Recent collections: Le Vendant quarry: left m1 = 106 x 98; left m3 = 78 x 80.
Discussion: The maxillary with M1-2 from Montaigu (ENGESSER, 1990:fig. 49c) corresponds by its small size and its two transverse crests without longitudinal crest to the material of *R. manca* from La Chaux (Suisse).
The size of the two lower molars from Le Vendant corresponds well to *R. manca*; the crown is separated in two distinct parts by a deep furrow; crests are reduced to an anterior and a posterior one with just faint remnants of the longitudinal crest situated very low, so that the tubercular part of the crown is high. On these unworn teeth, the trigonid is distinctly higher than the talonid. Their high simplification degree indicates a proximity with the level of La Chaux and correspond to the minute *Ritteneria* of the old collections.

3. Conclusions

In the St-Gérand-le-Puy area, eomyids are various but rare and, consequently, their evolution is difficult to follow. However, when two levels are superposed in a quarry, differences are seen in their evolutionary degree, indicating a long duration for the deposits. The analysis of the eomyid taxa of the St-Gérand-le-Puy area sites makes it possible, despite their scarcity, to draw the following results:

3.1. Evolutionary results

• The lineage of *Pseudotheridomys* is representated by the species *P. parvulus*; its size and morphology correspond well to the material of Ulm-Westtangente, near the type-locality of this species, which is characteristic of MN 2 (WERNER, 1994).
• The genus *Rhodanomys* exists in this area with the species *R. schlosseri* in Chavroches. *Rhodanomys* aff. *schlosseri* from Gondailly 1 and Cluzel 1 is smaller and a bit more evolved in the direction of *Ritteneria*. The general evolutionary tendencies are the same as in other regions (reduction of size, tendency to simplification of the occlusal surface by reduction to two parallel crests with progressive disappearing of the longitudinal crest) but here the timing seems to be different. *R. schlosseri* was actually considered to disappear at the end of MN 1 and to be replaced by *Ritteneria* in MN 2 (ALVAREZ-SIERRA, 1987; ENGESSER, 1990 - with doubt, however) but it seems to continue its evolution in the St-Gérand-le-Puy area longer than in other regions. In the MN 2 levels, *Rhodanomys schlosseri* diminishes in size but maintains its typical morphology (mesoloph of the upper teeth and longitudinal crest in the lower ones).
ZIEGLER &WERNER (1994) described a real minute *Ritteneria* in a late MN 1 German locality demonstrating that there is not an unique *Rhodanomys* - *Ritteneria* lineage as previously supposed, but that different *Ritteneria* species could either derive locally from different *Rhodanomys* species or migrate from other regions at different levels. *Ritteneria* aff. *molinae* described by ZIEGLER & WERNER (1994) does not fit with the *R. molinae* - *R. manca* model of evolution as it is smaller than the later populations of *R. molinae* and *R. manca*.
• In Chavroches and Gondailly 1, some teeth seem exceptionally large; still larger teeth from Montaigu were figured as *Ritteneria* nov. sp. by ENGESSER (1990). The morphology and size of these teeth are not very different from *R. schlosseri* and they are so rare that it is difficult to decide whether they pertain to a really different species or are only extreme variants of *Rhodanomys*. As a maxillary and a mandible show a typical *Ritteneria* pattern, we hypothesize that *Ritteneria molinae* could coexist with *Rhodanomys schlosseri* and could derive from a larger *Rhodanomys* (*R. oscensis* or *R. latens*; see WERNER, 1994).
• The genus *Ritteneria* exists also in the St-Gérand area and characterises the upper levels:
Ritteneria manca is present in Le Vendant. *Ritteneria* aff. *molinae* in the upper level of Gondailly (Gondailly 2), in Poncenat and Montaigu-Les Pérards and perhaps a smaller form in Cluzel 2.

3.2. Biostratigraphical results

• Relative age of the MN 2 localities in the St-Gérand-le-Puy area: if we suppose a normal evolution of the Eomyidae, Chavroches is the older locality, then Gondailly 1, then Cluzel 1, with a progressive decrease in size of *Rhodanomys schlosseri*. Gondailly 2, Montaigu-Les Pérards, Poncenat could be equivalent in age and more recent than the former localities. Le Vendant seems to be a little younger. Cluzel 2 reaches also the *Ritteneria molinae* level, but with an exceptionally minute size; this locality, situated on the opposite border of the Limagne lake and now isolated by faults, could perhaps have been more completely isolated during the Early Miocene and have been subjected to a different evolution.
• Superposed levels evidence a conspicuous evolution of the Eomyidae, and demonstrate that the St-Gérand-le-Puy area deposits cover the whole MN 2a duration. As the total duration of MN 2 is estimated at two My (MEIN, 1999), the Aquitanian deposits in St-Gérand could correspond to, at least, one My.
• Comparison with other regions:
The timing of the evolution of *Rhodanomys* and *Ritteneria* in the St-Gérand area is not completely in accordance with what is known in other regions (Germany, Swiss or Spain) and makes it difficult to draw precise correlations with them. The best correlation is that of Le Vendant where *R. manca* seems to correspond well to the level of

La Chaux; Le Vendant seems to be the youngest level of the St-Gérand area.

So the study of the Eomyids in the St-Gérand area evidences a more complex evolution than previously thought. All the localities of this area are not exactly of the same age, although remaining within the limits of the MN 2a reference level; their age depends on their position in the filling of the lake which had a duration sufficiently long to make noticeable evolutionary changes possible.

4. Acknowledgements

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5. References

Alvarez-Sierra, M.A., 1987. Estudio sistematico y bioestratigrafico de los Eomyidae (Rodentia) del Oligoceno superior y Mioceno inferior espanol. — Scripta Geologica, **86**:1–207, Leiden.

Bruijn de, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P. & Morales, J., 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. — Newsletter on Stratigraphy, **26**:65–118, Berlin-Stuttgart.

Bücher, H., Ginsburg, L.& Cheneval, J., 1985. Nouvelles données et interprétations sur la formation des gisements de vertébrés aquitaniens de Saint-Gérand-le-Puy (Allier, France). — Geobios, **18**:823–832, Lyon.

Comte, B. & Vianey-Liaud, M., 1989. Eomyidae (Rodentia) de l'Oligocène d'Europe occidentale. — Palaeontographica, A, **209**:33–91, Stuttgart.

Engesser, B., 1990. Die Eomyidae (Rodentia, Mammalia) der Molasse der Schweiz und Savoyens. Systematik und Biostratigraphie. — Schweizerische Paläontologische Abhandlungen, **112**: 1–144, Basel.

Filhol, H., 1879. Etude des Mammifères fossiles de Saint-Gérand-le-Puy (Allier). — Annales des Sciences Géologiques, **10** (1re Part):1–253, Paris.

Geoffroy-Saint-Hilaire, I., 1833. Considération sur des ossemens fossiles la plupart inconnus, trouvés et observés dans les bassins de l'Auvergne. — Revue Encyclopédique, **59**:76–95, Paris.

Hugueney, M., 1974. Gisement de petits Mammifères dans la région de Saint-Gérand-le Puy (Allier): stratigraphie relative. — Revue Scientifique Bourbonnais: 52–68, Moulins.

Hugueney, M., 1997. Biochronologie mammalienne dans le Paléogène et le Miocène inférieur du centre de la France: synthèse réactualisée. — [in:] Aguilar, J-P., Legendre, S., Michaux, J. (eds.). Actes du Congrès BiochroM'97: Biochronologie mammalienne du Cénozoïque en Europe et domaines reliés, E.P.H.E. — Sci. Vie Terre, **21**:417–430, Montpellier.

Hugueney, M.& Escuillié, F., 1995. K-strategy and adaptative specialization in *Steneofiber* from Montaigu-le-Blin (dept. Allier, France; Lower Miocene, MN 2a, ± 23 Ma): first evidence of fossil life-history strategies in castorid rodents. — Paleogeography, Paleoclimatology, Paleoecology, **113**:217–225, Amsterdam.

Hugueney, M., Mein, P. & Ringeade, M., 1992. Nouvelle datation des gisements de mammifères du bassin de Digne (Lambert et Barles; Sud-Est de la France); extension probable de la transgression aquitanienne dans cette région. — Paleontologia i Evolucio, **24-25**:123–134, Barcelone.

Hugueney, M., Poidevin, J.L., Bodergat, A.M., Caron, J.B. & Guérin, C., 1999. Des Mammifères de l'Aquitanien inférieur à La Roche-Blanche-Gergovie (Puy-de-Dôme, France), révélateurs de l'activité post-oligocène du rift en Limagne de Clermont. — Comptes-Rendus de l'Académie des Sciences, Paléontologie, **328**:847–852, Paris.

Hugueney, M. & Ringeade, M., 1990. Synthesis on the "Aquitanian" lagomorph and rodent faunas of the Aquitaine basin (France). — [in:] Lindsay, E.H., Fahlbusch, V. & Mein, P. (eds.). European Neogene mammal chronology:139-156, (Plenum Press), New York.

Lavocat, R., 1952. Sur une portion de crâne appartenant au genre *Ritteneria* Stehlin et Schaub. — Eclogae Geologicae Helvetiae, **45** (**2**):337–338, Basel.

Mein, P., 1999. European Miocene Mammal Biochronology. — [in:] Rössner, G.E. & Heissig, K. (eds.). The Miocene Land Mammals of Europe:25-38, (F. Pfeil), München.

Wattinne, A., Vennin, E. & de Wever, P., 2003. Evolution d'un environnement carbonaté lacustre à stromatolithes, par l'approche paléo-écologique (carrière de Montaigu-le-Blin, bassin des Limagnes, Allier, France). — Bulletin de la Société géologique de France, **3**:243–260, Paris.

Werner, J., 1994. Beiträge zur Biostratigraphie der Unteren Süsswasser-Molasse Süddeuchtschland- Rodentia und Lagomorpha (Mammalia) aus den Fundstellen der Ulmer Gegend. — Stuttgarter Beiträge zur Naturkunde, B, **200**:1–263, Stuttgart.

Ziegler, R. & Werner, J., 1994. Die Kleinsäugerfauna von Lautern 2 bei Ulm. Ein Beitrag zur Biostratigraphie der Unteren Süsswasser-Molasse Süddeutschlands. — Stuttgarter Beiträge zur Naturkunde, Serie B, **207**:1–69, Stuttgart.

PLATE 1

***Rhodanomys schlosseri* Depéret & Douxami – Chavroches**

Fig. 1-8 1 - damaged max. + P4-M1 (MHNL-20-270 000): 1a - occlusal view, 1b- lingual view; 2 - M1 (MHNL-20-270 001); 3 - M2 (MHNL-20-270 002); 4 - M3 (r.r.) (MHNL-20-270 003); 5 - D4 (MHNL-20-270 004); 6 - D4 (MHNL-20-270 005); 7 - damaged mand.+ p4-m2 (r.r.) (MHNL-20-270 006): 7a - occlusal view, 7b - labial view; 8- m3 (MHNL-20-270 007).

***?Ritteneria molinae* Alvarez-Sierra – Chavroches**

Fig. 9-10 9 - m2 (r.r.) (MHNL-20-270 008): 9a - occlusal view, 9b-labial view; 10- damaged max. + P4-M1 (MHNL-20-270 009): 10a - occlusal view, 10b - lingual view.

***Rhodanomys schlosseri* Depéret & Douxami – Pyrimont (Ain), lectotype (FSL 213068)**

Fig. 11 mand.+ p4-m3 (r.r.): 11a - occlusal view, 11b - labial view.

***Rhodanomys* aff. *schlosseri* Depéret & Douxami – Gondailly 1**

Fig. 12 damaged mand. + p4-m2 (MHNL-20-270 288): labial view (see also Pl. 2, fig. 11).

***Ritteneria molinae* Alvarez-Sierra – Gondailly 1**

Fig. 13 damaged mand. + m1 (MHNL-20-270 299): labial view (see also Pl. 2, fig. 15).

***Pseudotheridomys parvulus* Schlosser – Chavroches**

Fig. 14- 14 - D4 (MHNL-20-270 010); 15 P4 (r.r.) (MHNL-20-270 011); 16 - M1 (MHNL-20-270 012); 17 - M2 (MHNL-20-270 013); 18 - M3 (r.r.) (MHNL-20-270 014); 19 - d4 (MHNL-20-270 015); 20 - p4 (r.r.) (MHNL-20-270 016); 21 - m1 (MHNL-20-270 017); 22 - m2 (MHNL-20-270 018); 23 - m3 (MHNL-20-270 019).

Scale bars represent 1 mm; the shorter for fig. 12-13, the longer for fig. 1-11 and 14-23.

PLATE 1

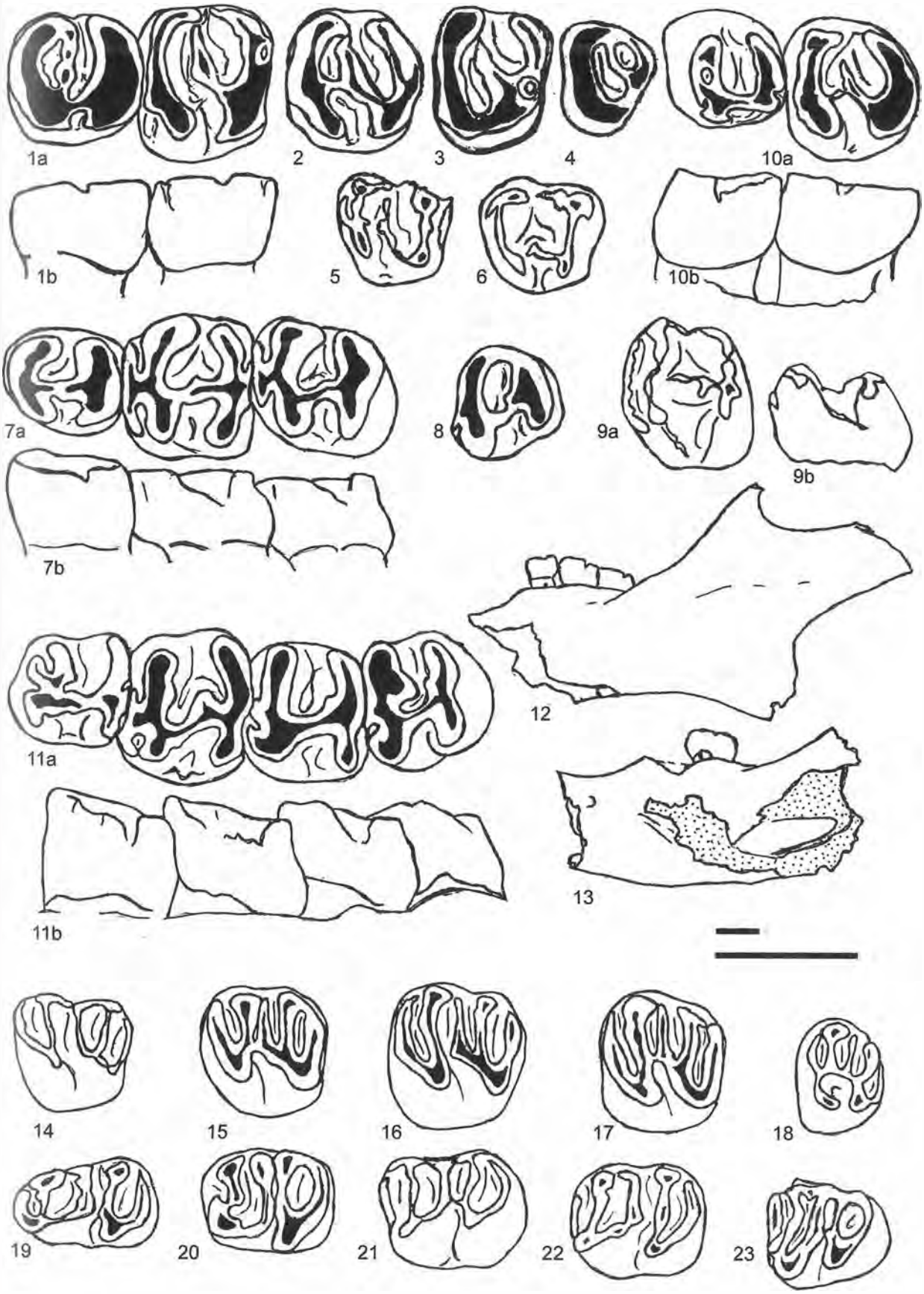
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PLATE 2

***Ritteneria* aff. *molinae* Alvarez-Sierra – Gondailly 2**

Fig. 1-7 1 - D4 (MHNL-20-270 290); 2 - ?M1 (r.r.) (MHNL-20-270 291): 2a - occlusal view, 2b - lingual view; 3 - M1-2 (MHNL-20-270 292): 3a - occlusal view, 3b - lingual view; 4 - d4 (r.r.) (MHNL-20-270 293); 5 - m1 (MHNL-20-270 294); 6 - m2 (r.r.) (MHNL-20-270 295): 6a - occlusal view, 6b - labial view; 7 - m3 (r.r.) (MHNL-20-270 296).

***Rhodanomys* aff. *schlosseri* Depéret & Douxami – Gondailly 1**

Fig. 8-12 8 - P4 (MHNL-20-270 285); 9- D4 (MHNL-20-270 286); 10 - damaged max. + M1-3 (MHNL-20-270 287): 10a - occlusal view, 10b - lingual view; 11- damaged mand. + p4-m2: (MHNL-20-270 288): 11a - occlusal view, 11b - labial view; 12 - d4 (r.r.) (MHNL-20-270 289).

***Ritteneria molinae* Alvarez-Sierra – Gondailly 1**

Fig. 13- 13 - max. + P4-M3 (r.) (MHNL-20-270 297): 13a - occlusal view, 13b - lingual view; 14 - D4 (MHNL-20-270 298); 15 - damaged mand.+ m1(MHNL-20-270 299): 15a - occlusal view, 15b - labial view of m1.

Scale bar represents 1 mm.

PLATE 2

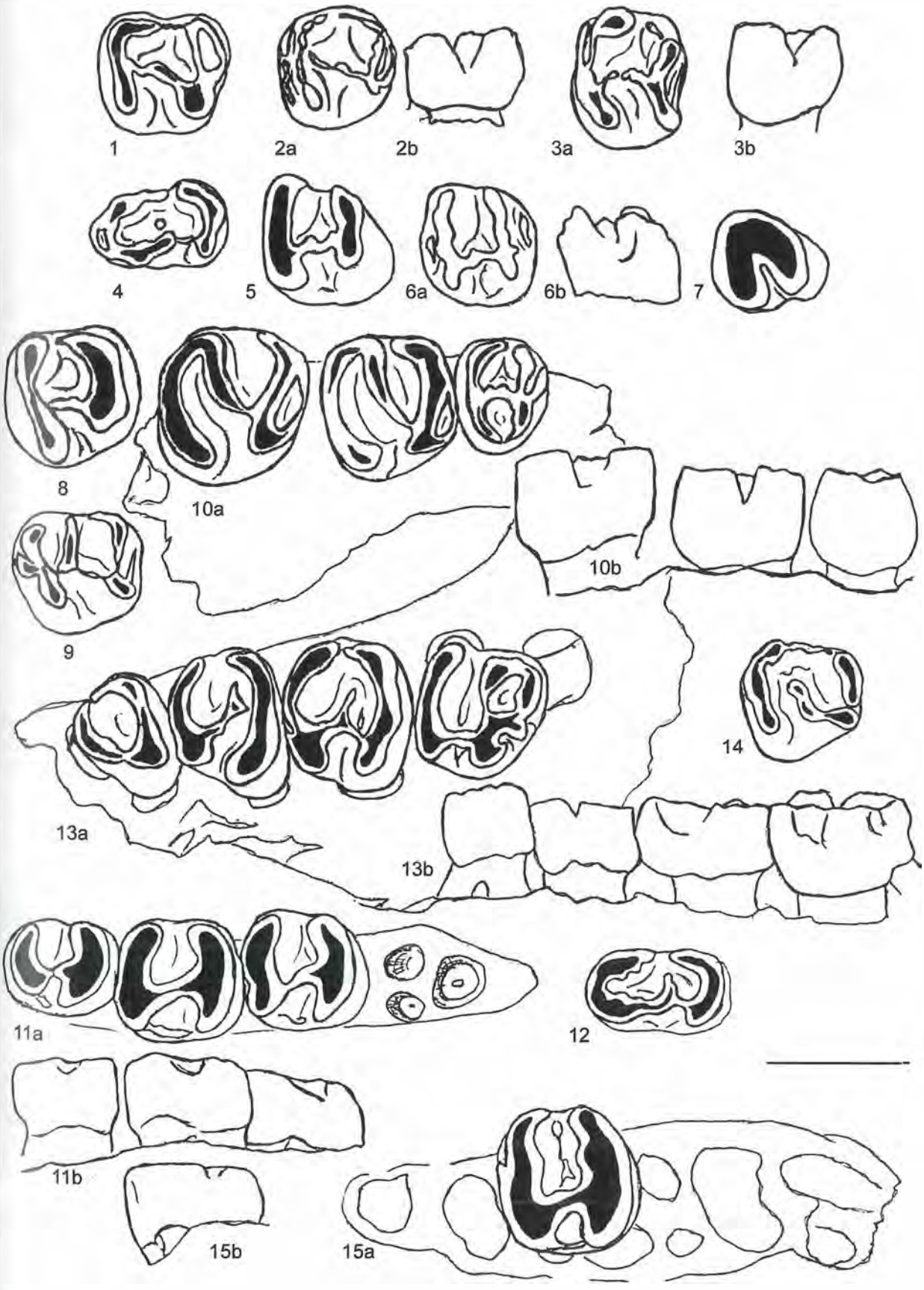


PLATE 3

***Ritteneria manca* Stehlin & Schaub – Le Vendant**

Fig. 1-2 1 - m1 (FSL 98100): 1a - occlusal view, 1b - labial view; 2 - m3 (FSL 98101): 2a - occlusal view, 2b - labial view.

***Ritteneria* aff. *molinae* Alvarez-Sierra – Montaigu-Les Pérards**

Fig. 3-4 3 - P4 (FSL 98102); 4 - M1-2 (FSL 98103).

***Ritteneria* aff. *molinae* Alvarez-Sierra – Poncenat**

Fig. 5-9 5 - P4 (FSL 98104); 6 - P4 (r.r.) (FSL 98105); 7 - d4 (r.r.) (FSL 98106); 8 - p4 (r.r.) (FSL 98107); 9 - m1 (FSL 98108): 9a - occlusal view, 9b - labial view.

? *Ritteneria* aff. *molinae* Alvarez-Sierra – Cluzel 2

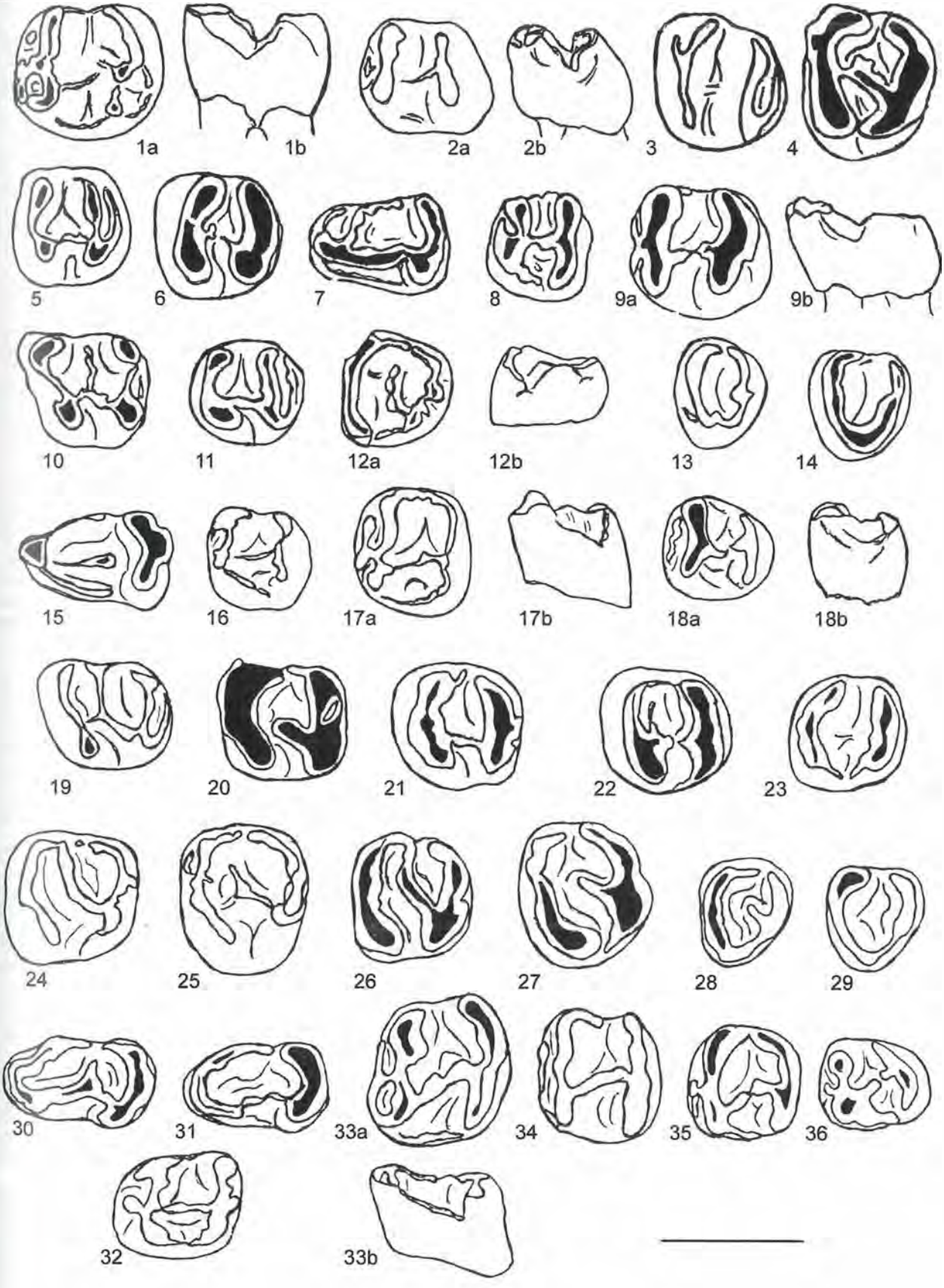
Fig. 10-1810 - D4 (r.r.) (FSL 98109); 11 - P4 (r.r.) (FSL 98110); 12 - M2 (FSL 98111): 12a - occlusal view, 12b - lingual view; 13 - M3 (r.r.) (FSL 98112); 14 - M3 (FSL 98113); 15 - d4 (r.r.) (FSL 98114); 16 - p4 (r.r.) (FSL 98115); 17 - m1 (r.r.) (FSL 98116): 17a - occlusal view, 17b - labial view; 18 - m3 (FSL 98117): 18a - occlusal view, 18b - labial view.

***Rhodanomys* aff. *schlosseri* Depéret & Douxami – Cluzel 1**

Fig. 19- 19 - D4 (r.r.) (FSL 98118); 20 - D4 (FSL 98119); 21-22 - P4 (r.r.) (FSL 98120, 98121); 23 - P4 (FSL 98122); 24-25 - M1 (r.r.) (FSL 98123, 98124); 26-27 - M2 (r.r.) (FSL 98125, 98126); 28-29 - M3 (FSL 98127, 98128); 30-31 - d4 (FSL 98129, 98130); 32 - p4 (r.r.) (FSL 98131); 33 - m1 (r.r.) (FSL 98132): 33a - occlusal view; 33b - labial view; 34 - m2 (FSL 98133); 35-36 - m3 (FSL 98134, 98135).

Scale bar represents 1 mm.

PLATE 3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