

## Comparative morphometry and cytogenetics of *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) of the western French Alps

By P. BRUNET-LECOMTE and V. VOLOBOUEV

Centre des Sciences de la Terre, Université de Bourgogne, Dijon, France and Institut Curie,  
Paris, France

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### Abstract

The western French Alpine populations of *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) occupy the marginal distributional area of the species. Analysis of the characters of the Relative Length of the Anterior Part (RLAP) and of the Pitymyan Rhombus (PR) of the first lower molar ( $M_1$ ) of these populations and subsequent comparison with other populations from the Central Alps of France and Switzerland permits to distinguish the populations of the western French Alpine area (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) from the populations of the Central Alps belonging to the subspecies *multiplex*, *fatioi* and *druentius*. Karyological analysis of the population from Saint-Martin-de-la-Cluze confirms the cytogenetic differentiation of populations from the western French Alpine area which are characterized by a subtelocentric X chromosome and a metacentric Y chromosome. The synthesis of these results leads to the proposal of a new subspecies for the populations from the western French Alpine area, *Microtus (Terricola) multiplex niethammeri* nov. ssp.

### Introduction

European ground-voles of the subgenus *Terricola* constitute an advantageous group for study of speciation because of their geographic chromosomal variation (MEYLAN 1970, 1972; WINKING 1976; STORCH and WINKING 1977; GRAF and MEYLAN 1980) and their discontinuous distribution (NIETHAMMER and KRAPP 1982). The Alpine ground-vole *M. (T.) multiplex* (FATIO 1905), a species of the Middle European phyletic group (BRUNET-LECOMTE 1990) is characterized by chromosomal polymorphism of  $2n = 46$  to 48 and  $NF = 52$  to 54 (NIETHAMMER and KRAPP 1982). Since the species was first described by FATIO in 1905, six subspecies have been identified: *multiplex* (FATIO 1905) from Lugano (Ticino, Switzerland), *fatioi* (MOTTAZ 1990) from Zermatt (Wallis, Switzerland), *druentius* (in MILLER 1912) from Terres-Plaines near Barcelonnette (Alpes-de-Haute-Provence, France), *orientalis* (DAL PIAZ 1924) from Madonna di Campiglio (Trentino, Italy), *liechtensteini* (WETTSTEIN-WESTERSHEIM 1927) from the top of Mali Rainac mountain near Krasno (Croatia, Yugoslavia), *petrovi* (KRYSTUFEK 1983) from Socerga near Koper (Slovenia, Yugoslavia). In France the species occurs in the southern Central Alps (Mercantour, Ubaye, Briançonnais), northern Central Alps (Vanoise), western Pre-Alps (Vercors, Chartreuse) and perhaps further west as far as the Rhone Valley and eastern Massif Central (HEIM DE BALSAC and BEAUFORT 1966; BROSSET and HEIM DE BALSAC 1967; NIETHAMMER and KRAPP 1982; FAYARD 1984). Cytogenetic and electrophoretic studies of the western and Central Alpine subspecies *multiplex*, *fatioi* and *druentius* (GRAF and MEYLAN 1980) underline the differentiation of the population of La-Chapelle-en-Vercors from the western Pre-Alps of Vercors (Tab. 1). This population is characterized by a subtelocentric X chromosome (GRAF and MEYLAN 1980) and a high genetic distance of Nei in comparison with the other studied populations (between 0.09 and 0.18) (GRAF and MEYLAN 1980),

Table 1. Chromosome data of *Microtus (Terricola) multiplex*

Locality	2n	FN	Karyotype Autosomes	X	Y	References
1 Gudo (E), Meride (F), Varenzo (H), Zermatt (I)	48	50	2 IST + 2 mM + 42 A	SM	A	GRAF and MEYLAN (1980)
2 La Cayolle (J) Le Lautaret (C)	48	50	2 IST + 2 mM + 42 A	SM	M*	GRAF and MEYLAN (1980)
3 La-Chapelle-en- en-Vercors (B)	48	50	2 IST + 2 mM + 42 A	ST	A	GRAF and MEYLAN (1980)
4 Saint-Martin de la-Cluze (A)	48	50	2 IST + 2 mM + 42 A	ST	M	present study
5 Fivizzano (L)	46	48	2 IST + 2 mM + 40 A	SM	A	GRAF and MEYLAN (1980)
6 Arsié (M)	46	46	2 IA + 2 mM + 40 A	ISM	IA	STORCH and WINKING (1977)
7 Calliano (N)	46	46	2 IA + 2 mM + 40 A	ISM	ISM	STORCH and WINKING (1977)

Locality: letters in brackets denote the labels of populations from figure 1. Karyotype: A = acrocentric, ST = subtelocentric, SM = submetacentric, M = metacentric, m = medium, l = large.  
\*: although the authors suggest that the unpaired medium-sized metacentric may be the Y chromosome, definitive interpretation is made by us.

corresponding to an inter-species distance, whereas the genetic distances calculated between the populations from Ticino (subspecies *multiplex*), Zermatt (subspecies *fatiosi*) and Briançonnais (subspecies *druentius*) are smaller (between 0.02 and 0.06).

The aim of this study is to present the karyotype of a population of *M. (T.) multiplex* from Saint-Martin-de-la-Cluze, in the Drac Valley, which lies near, although outside, the Pre-Alps of the Vercors; to compare the karyotype and the first lower molar morphology of this population with those of the other populations of the Alps and to clarify the systematics of the populations from the western French Alpine area.

## Material and methods

Nine populations were studied, each presented by 10 teeth ( $M_1$ ). The populations were from: A: Saint-Martin-de-la-Cluze (Isère, France); B: La-Chapelle-en-Vercors (Drôme, France); C: Col du Lautaret (Hautes-Alpes, France); D: Les Vigneaux (Hautes-Alpes, France); E: Gudo (Ticino, Switzerland); F: Meride (Ticino, Switzerland); G: Bioggio (Ticino, Switzerland); H: Varenzo (Ticino, Switzerland); I: Zermatt (Wallis, Switzerland).

Localities are mapped in figure 1.

## Morphology of the first lower molar ( $M_1$ )

The analysis of the characters Relative Length of the Anterior Part (RLAP) and Pytymyan Rhombus (PR) was based on the comparison of means between the populations according to the analysis of variance method completed by Scheffé's method.

## Chromosomal study

Chromosome preparations were obtained from primary fibroblast cultures from tail biopsies of four specimens (2♂♂ and 2♀♀) all from Saint-Martin-de-la-Cluze (Isère, France). Explants and a portion of the cells of studied specimens are routinely kept in liquid nitrogen in the cell and tissue collection of the Laboratoire de Structure et Mutagenèse Chromosomiques (Institut Curie, Paris, France).

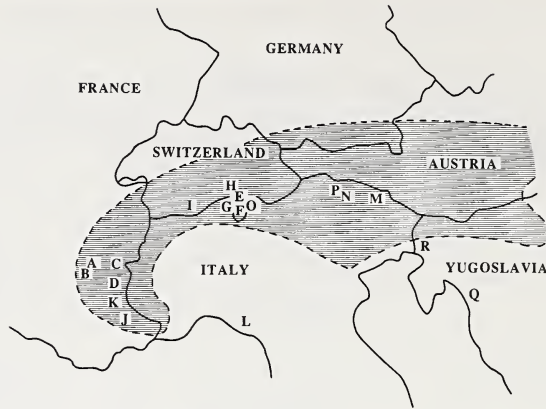


Fig. 1. Localities of the populations studied. Morphological study. A: Saint-Martin-de-la-Cluze (Isère, France); B: La-Chapelle-en-Vercors (Drôme, France); C: Col du Lautaret (Hautes-Alpes, France); D: Les Vigneaux (Hautes-Alpes, France); E: Gudo (Ticino, Switzerland); F: Meride (Ticino, Switzerland); G: Bioggio (Ticino, Switzerland); H: Varenzo (Ticino, Switzerland); I: Zermatt (Wallis, Switzerland). Karyological study. A; B; C; E; F; H; I; J: Col de la Cayolle (Alpes-de-Haute-Provence, France); L: Fivizzano (Toscana, Italy); M: Arsie (Italy); N: Calliano (Italy).

Type localities: O: Lugano (Ticino, Switzerland) = *multiplex*; I = *fatioi*; K: Terres-Plaines near Barcelonnette (Alpes-de-Haute-Provence, France) = *druentius*; P: Madonna di Campiglio (Trentino, Italy) = *orientalis*; Q: Top of Mali Rainac mountain near Krasno (Croatia, Yugoslavia) = *liechtensteini*; R: Socerga near Koper (Slovenia, Yugoslavia) = *petrovi*.

Hatching: the Alps

Mitotic chromosomes were studied with RHG R-banding and CBG C-banding (HARDEN and KLINGER 1985) after, CARPENTIER et al. (1972) and SUMMER (1972) respectively. Replication banding (RBG) was studied using the method of VIEGAS-PÉQUIGNOT and DUTRILLAUX (1978). At least 20 metaphase plates were analysed for each specimen.

## Results

### Morphological analysis of $M_1$ characters

- RLAP: The mean and the standard deviation of the RLAP of each population are given in table 2. The distribution of means of each population is given in figure 2. The RLAP is significantly less developed in the populations A and B (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) than in the populations C and D (Briançonnais) and E to H (Ticino); population I (Zermatt) having an intermediate RLAP between those of these populations.
- PR: The mean and the standard deviation of the PR of each population are given in table 3. The distribution of means of each population is given in figure 3. The PR is significantly greater (less inclined) in the populations C and D (Briançonnais) than in the other populations.

### Chromosomal study

Karyotypes of all four specimens from Saint-Martin-de-la-Cluze are similar and characterized by  $2n = 48$  and  $FN = 54$ . All pairs of autosomes and both sex chromosomes were precisely identified by high resolution R-banding (Fig. 4). Among autosomes two pairs are biarmed, one of them, the largest in the karyotype, is subtelocentric, while the other N° 6 is a medium sized metacentric. The X chromosome is subtelocentric and similar in size to

Table 2. Mean and standard deviation (SD) of the Relative Length of the Anterior Part (RLAP) of the  $M_1$  (no units)

Analysis of variance and Scheffé's test. Populations (Pop.) A–I as shown in figure 1

Pop.	N	Mean	SD	Group	N	Mean	SD	Scheffé's test*
A	10	0.507	0.019					
B	10	0.503	0.025	A and B	20	0.505	0.021	1
C	10	0.518	0.025					
D	10	0.528	0.014	C and D	20	0.523	0.020	2
E	10	0.525	0.011					
F	10	0.521	0.013					
G	10	0.521	0.012	E to H	40	0.523	0.012	2
H	10	0.525	0.012					
I	10	0.513	0.015	I	10	0.513	0.015	1
							Analysis of variance	p = 0.0007

\* Means with the same number are not significantly different.

Table 3. Mean and standard deviation (SD) of the Pitymyan Rhombus (PR) of the  $M_1$

Analysis of variance and Scheffé's test. Populations (Pop.) A–I as shown in figure 1 (unit  $10^{-2}$  mm)

Pop.	N	Mean	SD	Group	N	Mean	SD	Scheffé's test*
A	10	1.40	3.47					
B	10	-0.30	2.58	A and B	20	0.55	3.10	1
C	10	10.40	3.57					
D	10	4.80	5.27	C and D	20	7.60	5.24	2
E	10	2.90	2.38					
F	10	0.70	2.98					
G	10	4.80	3.29	E to H	40	3.55	3.33	1
H	10	5.80	2.39					
I	10	2.10	3.31	I	10	2.10	3.31	1
							Analysis of variance	p < 0.0001

\* Means with the same number are not significantly different.

the largest acrocentric pair, the Y chromosome is metacentric and similar in size to 14–15th pairs of autosomes. C-banding analysis (Fig. 5) revealed that all the autosomes possess a small centromeric block of C-heterochromatin. The Y chromosome is almost entirely C-positive. The short arms of the X chromosomes are late replicating and thus heterochromatic (Fig. 4) although C-heterochromatin was detected in their proximal parts (Fig. 5). No obvious variation of C-heterochromatin was noticed either among the cells or among the animals studied.

## Discussion

The analysis of the characters RLAP and PR shows that populations A and B (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) can be clearly distinguished, on the one hand, from populations C and D (Briançonnais) of the inner French Alps by their more steeply inclined PR and by their less developed RLAP, and on the other hand, from populations E to H of Ticino by their less developed RLAP. This same analysis of characters shows that populations A and B are close to population I of Zermatt (Wallis) despite the geographical isolation of this latter population (GRAF and MEYLAN 1980). In comparison with other existant European species, *Microtus (Terricola) multiplex* is charac-

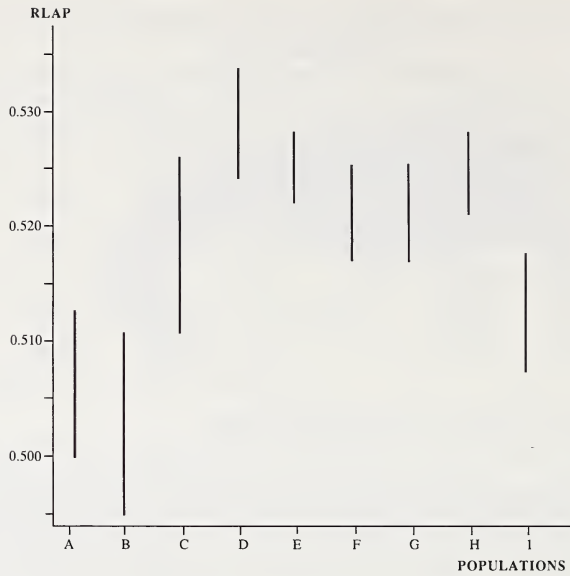


Fig. 2. Distribution of the mean  $\pm$  standard error of the mean of the Relative Length of the Anterior Part (RLAP) of the  $M_1$ . For populations' A-I distribution see figure 1 (no units)

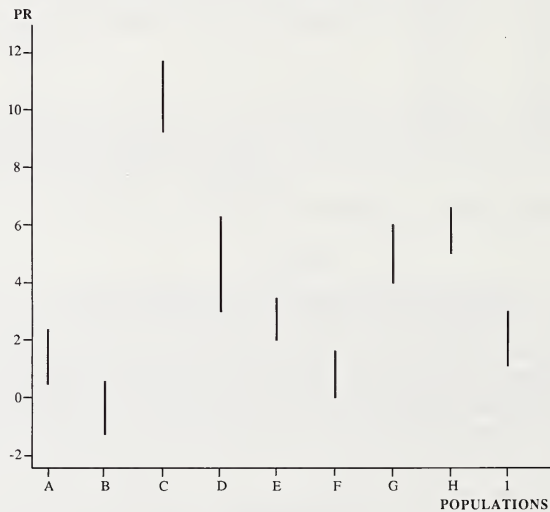


Fig. 3. Distribution of the mean  $\pm$  standard error of the mean of the Pitymyan Rhombus (PR) of the  $M_1$ . For populations' A-I distribution see figure 1 (unit  $10^{-2}$  mm)

terized by a poorly inclined PR (BRUNET-LECOMTE 1990). Therefore the inclined PR of populations A and B leads us to believe that the populations from the western French Alps are derived from a Central Alpine subspecies (*druentius* or *multiplex*).

*Microtus (Terricola) multiplex* has been relatively well studied karyologically: to date, at least 25 populations have been studied over most of its distributional area (see ZIMA and KRAL 1984; ZAGORODNYUK 1990). The published data show that all cases of chromosomal

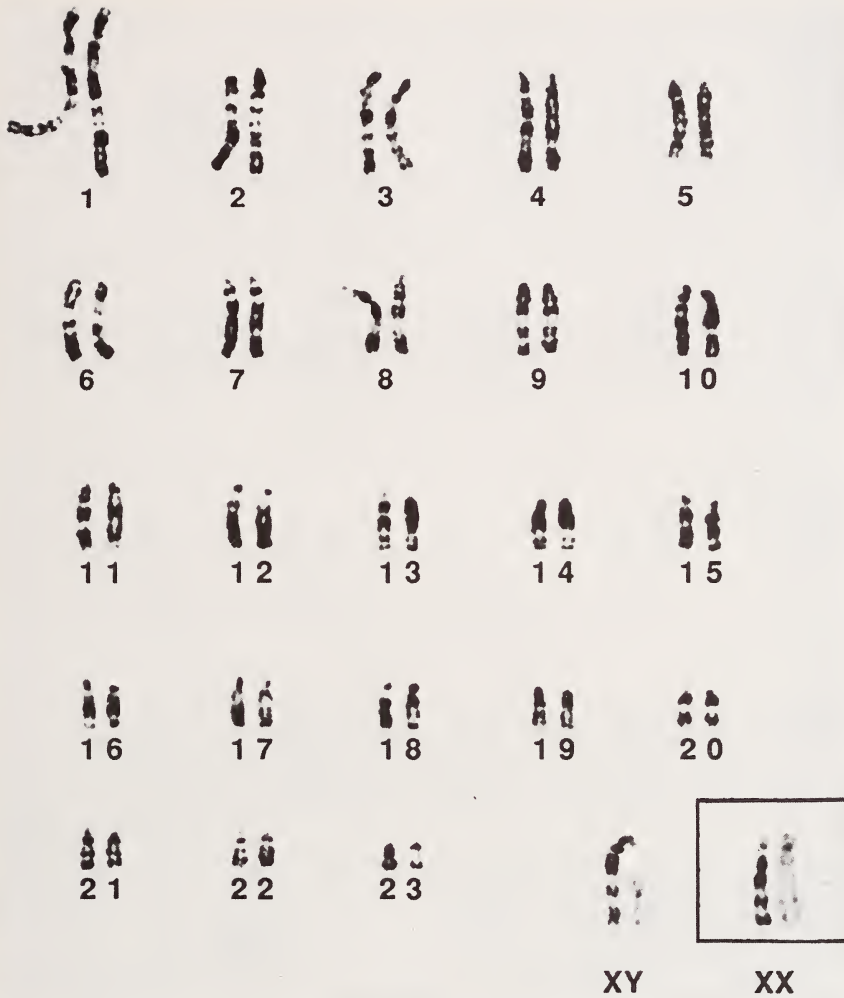


Fig. 4. R-banded (RBG) chromosomes of *Microtus (Terricola) multiplex*. Female sex chromosomes are given in the insert. One of the X chromosomes and both short arms are late replicating

variation but one (see below) have been observed between populations, thus, pointing to chromosomal polytypy and not chromosomal polymorphism. All known chromosome forms including the new one from Saint-Martin-de-la-Cluze are presented in table 1. As can be seen from these data, there are two types of karyotypes among these forms, with 46 and 48 chromosomes. The Italian karyotypic forms with  $2n = 46$  are different from each other. The form from Fivizzano (GRAF and MEYLAN 1980) differs from the 48 chromosome forms by the loss of a pair of acrocentric autosomes, while the sex chromosomes are similar to those in form 1 (Tab. 1). The next two forms with  $2n = 46$  (differing from each other by morphology of the Y chromosome) both belong to subspecies *liechtensteini* and are different from all 48 chromosome forms, as well as that with  $2n = 46$  from Fivizzano. These differences consist in a translocation of both sex chromosomes into a pair of large

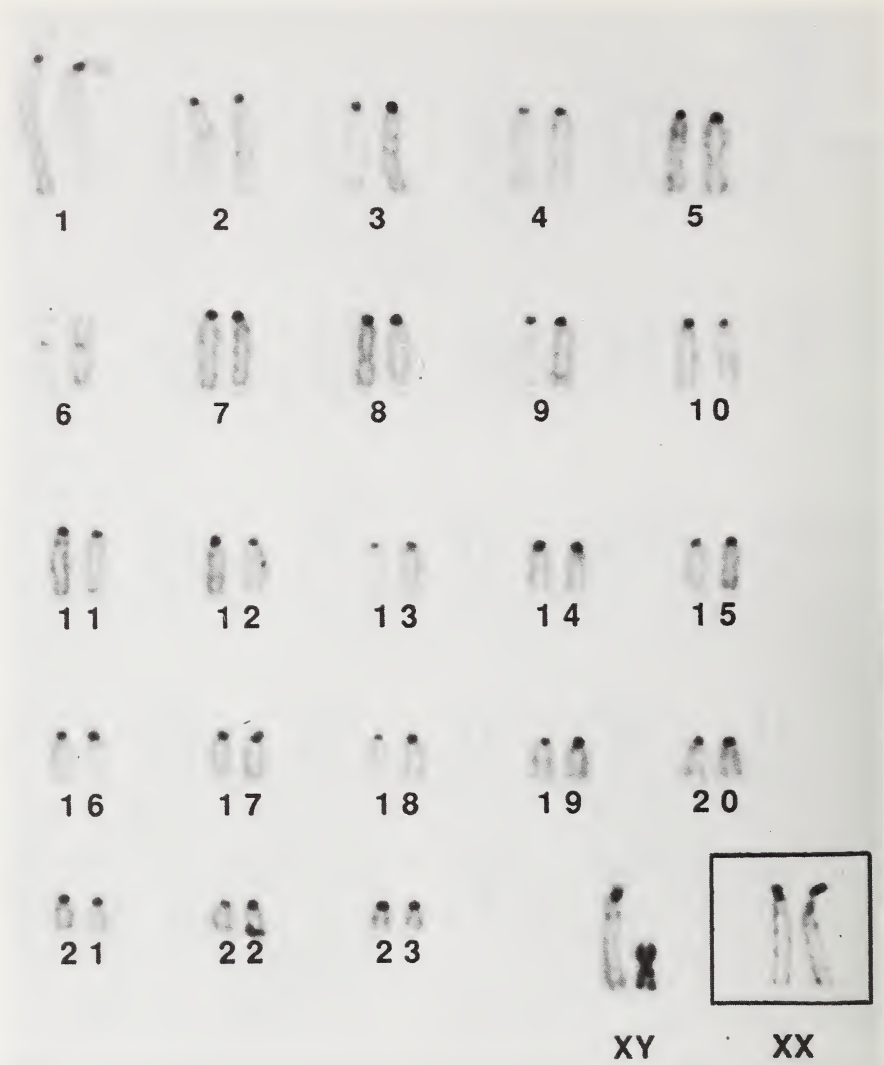


Fig. 5. C-banded chromosomes of *Microtus (Terricola) multiplex*. The sex chromosomes of a female are given in the insert

acrocentric autosomes, and an acrocentric state of the largest pair of autosomes in comparison with a submetacentric state in all other forms and the presence of an additional subtelocentric pair of autosomes. In our opinion these rearrangements are sufficient to ensure cytogenetic isolation of this form, and we subscribe to PETROV and ŽIVKOVIC's (1971) conclusion that *liechtensteini* is a distinct species although this was queried in subsequent studies (STORCH and WINKING 1977; GRAF and MEYLAN 1980; ZAGORODNYUK 1990). The differences between karyotypic forms with  $2n = 48$  are caused by different morphology of the sex chromosomes. Therefore, the X chromosome may be submetacentric or subtelocentric and the Y chromosome acrocentric or metacentric. All four possible combinations of different variants of the X and the Y chromosomes are found in nature,

always in different populations. The only exception is a female heterozygous specimen featuring submetacentric and subtelocentric variants of the X chromosome. It was collected in a population of Briançonnais not far from the population of La-Chapelle-en-Vercors (Tab. 1) and was probably of hybrid origin (GRAF and MEYLAN 1980).

The karyological differences between 48 chromosome forms are hardly capable of providing cytogenetic isolation by themselves but they might serve as indications as to the level of differentiation and origin of the chromosome forms. Therefore, the occurrence of the same variant of the X chromosome in two neighbouring populations of *M. (T.) multiplex* (Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors) not found elsewhere undoubtedly means they have a common origin. The close relationships between these populations also follow from morphological analysis of  $M_1$ . On the other hand, the population of La-Chapelle-en-Vercors is genetically more distant from all the other studied populations (GRAF and MEYLAN 1980). These observations are in agreement with paleontological data on the isolation of western Alpine populations of *M. (T.) multiplex* during the Upper Pleistocene cited by GRAF and MEYLAN (1980).

Thus, the data provide new evidence concerning the particular taxonomic position of populations in the western French Alps.

The karyological, genetical and morphometrical analyses made by GRAF and MEYLAN (1980) and our research lead to the following conclusion: the populations from Saint-Martin-de-la-Cluze and La-Chapelle-en-Vercors are sufficiently differentiated to be classified as belonging to at least a new subspecies.

#### *Microtus (Terricola) multiplex niethammeri* nov. ssp.

**H o l o t y p e :** Adult male (skin and skull), Centre des Sciences de la Terre de l'Université de Bourgogne N° DIMMUL891001.

**T y p e l o c a l i t y :** Saint-Martin-de-la-Cluze, Isère, Rhône-Alpes, France.

**D i a g n o s i s :** Subspecies characterized by the following karyotype: Autosomes: 2 large subtelocentrics, 2 medium metacentrics, 42 acrocentrics; X chromosome: subtelocentric, Y chromosome: metacentric.

Morphological diagnosis of  $M_1$ : RLAP not very well-developed for the species *Microtus (Terricola) multiplex*: mean  $\pm$  standard error of the mean = 0.507  $\pm$  0.006 (no units). PR inclined for the species *Microtus (Terricola) multiplex*: mean  $\pm$  standard error of the mean = 1.40  $\pm$  1.1 (unit  $10^{-2}$  mm).

**D i s t r i b u t i o n :** Known from Saint-Martin-de-la-Cluze. The population from La-Chapelle-en-Vercors which differs by its Y acrocentric chromosome can be include in this subspecies.

**E t y m o l o g y :** In honour of Prof. Dr. Jochen NIETHAMMER, Bonn, for his work on European voles.

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## Résumé

### *Morphométrie et cytogénétique comparées de *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) des Alpes occidentales françaises*

Les populations de la partie occidentale des Alpes françaises de *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) occupent une position marginale dans l'aire de distribution de l'espèce. La comparaison des caractères longueur relative de la partie antérieure et rhombe pitymyen permet de séparer les populations de la partie occidentale des Alpes françaises des autres populations des Alpes internes. L'analyse cytogénétique de la population de Saint-Martin-de-la-Cluze (Isère, France) confirme la différenciation chromosomique des populations de la partie occidentale des Alpes françaises, lesquelles sont caractérisées par un chromosome X subtelocentrique et un chromosome Y métacentrique. La synthèse de ces résultats et de ceux de la littérature conduit à proposer une sous-espèce nouvelle pour les populations de la partie occidentale des Alpes françaises, *Microtus (Terricola) multiplex niethammeri* nov. ssp.

## Zusammenfassung

### *Morphometrie und Cytogenetik von *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) der westlichen französischen Alpen im Vergleich*

Die Populationen von *Microtus (Terricola) multiplex* (Arvicolidae, Rodentia) im westlichen Teil der französischen Alpen nehmen eine Randposition bei der räumlichen Verteilung der Art ein. Der Vergleich der Merkmale relative Länge des Vorderteils des M<sub>1</sub> und Pitymys-Rhombus am M<sub>1</sub> erlaubt eine Abtrennung der Populationen des westlichen Teils der französischen Alpen von den Populationen der inneren Alpen. Die Analyse der Chromosomensätze der Population von Saint-Martin-de-la-Cluze (Isère, France) bestätigt die chromosomale Differenzierung der Populationen des westlichen Teils der französischen Alpen, die gekennzeichnet sind durch ein subtelozentrisches X-Chromosom und ein metazentrisches Y-Chromosom. Diese Ergebnisse und die aus der Literatur führen zu dem Vorschlag einer neuen Unterart in den Populationen des westlichen Teils der französischen Alpen: *Microtus (Terricola) multiplex niethammeri* nov. ssp.

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*Authors' addresses:* PATRICK BRUNET-LECOMTE, Centre de paléontologie analytique et géologie sédimentaire, URA CNRS 157, Laboratoire de préhistoire et paléoécologie du Quaternaire de l'EPHE, Centre des sciences de la terre, 6 Bd Gabriel, F-21000 Dijon, France and VITALY VOLOBOUEV, Institut Curie, Structure et mutagenèse chromosomiques, URA CNRS 620, 26 rue d'Ulm, F-75321 Paris Cedex 05, France