Intraspecific morphological tooth variability and geographical distribution: Application to the Savi’s vole, Microtus (Terricola) savii (Rodentia, Arvicolinae)

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Abstract
The Italian peninsula exhibits a very interesting and contrasted geographical pattern offering a good opportunity to study the relationship between morphological variability and environment. Savi’s vole, Microtus (Terricola) savii, occupies the main part of the Italian peninsula from Ticino in the north southwards to Sicilia. The material studied comprises 55 local populations distributed over the whole Italian peninsula and characterising different types of environments and different types of conditions, e.g. natural or anthropic. Morphological variability is analysed using the first lower molar by taking 27 measures on the occlusal surface. The analysis has shown a clear morphological differentiation between north–central and south populations. Morphological tooth variability highlights two geographical scales. At a regional scale, morphological variability is clearly in relation to geography and consequently to the climate and environment. On the contrary, at a local scale, morphological variability can be due to the fragmentation of some particular areas leading to isolation of small populations characterised by different morphotypes.

Keywords: Biogeography, Italy, Microtus (Terricola) savii, morphology, voles

Introduction
Savi’s vole Microtus (Terricola) savii (de Sélys Longchamps, 1838) occurs in the Italian peninsula including Ticino in Switzerland, Sicilia and marginally the county of Nice in France on the western border of Liguria (Contoli 1999). The Tagliamento river seems to be the northeastern boundary between Veneto and Friuli Venezia Giulia, beyond which M. (T.) liechtenteini (Wettstein, 1927) replaces M. (T.) savii (Bon 1995; Lapini et al. 1995). Therefore, the presence of this species in Friuli Venezia Giulia reported by different authors (Dal Piaz 1929; Gerdol and Perco 1977; Gerdol et al. 1982) seems to be an error (Lapini et al. 1995). The only specimen found on Elba island (Toscana), reported by Vesmanis and Hutterer (1980), is very probably due to an accidental introduction, because previous
studies (Kahmann and Niethammer 1971; Contoli et al. 1988) have not confirmed its presence. In central and south Italy M. (T.) savii and Apodemus species constitute the principal prey of the tawny owl (Strix aluco Linnaeus, 1758) and the barn owl (Tyto alba (Scopoli, 1769)). Therefore, the absence of M. (T.) savii in a significant number of pellets must correspond to a true absence of this species in the hunting range of the owl (Contoli 1986). In the light of this hypothesis, M. (T.) savii seems to be absent from different localities of Italy: in Liguria (Sigillo 1982; Rosi 2000), north Toscana (Santini and Farina 1978), the coastal parts of the province of Grosseto in Toscana (Uttendörfer 1952; Contoli 1980; Contoli and Sammuri 1981; Sforzi 1991), San Marco di Castellabate, province of Salerno, Campania (Nappi 1998/99) and in Baia di Manacore, province of Foggia, Puglia (Bux et al. 2000). The main explanation seems to be rocky ground, unsuitable for this burrowing species. This species was found up to 2800 m in the National Park of Grand Paradis, in Valle d’Aosta (Santini 1983).

Four subspecies are recognised for M. (T) savii: the nominative subspecies M. (T.) savii savii (de Sélys Longchamps, 1838) described from near Pisa (Toscana), M. (T.) s. nebrodensis (Minà Palumbo, 1968) from Sicilia (Amori et al. 1999), and two recently described: M. (T.) s. tolfetanus from Monti della Tolfa, province of Roma in Lazio and M. (T.) s. niethammericus from headland of Gargano, province of Foggia in Puglia (Contoli 2003). Microtus (Terricola) brachycercus (von Lehmann, 1961) from Calabria, first described as a subspecies of M. (T.) savii, was recently considered, on a cytogenetic basis, as a distinct species (Galleni et al. 1992, 1994, 1998; Galleni 1995).

Previous studies of the first lower molar (M1) morphometry in ground vole species of the subgenus Terricola (Brunet-Lecomte 1988, 1990; Brunet-Lecomte and Chaline 1991; Brunet-Lecomte et al. 1993) have shown that the M. (T.) savii group constitutes an interesting model for the study of microevolution in micromammals. The aim of this study, based on the analysis of 55 local populations of M. (T.) savii from all areas of Italy, is to analyse and explain the variations of M1 morphometry in M. (T.) savii according to climatic and geographical factors.

The following abbreviations have been used: AN, A. Nappi; CDSL, Dipartimento di Coltivazione e Difesa delle Specie Legnose, Sezione di Entomologia Agraria, Università degli Studi di Pisa; CMTLC, Collezione Microteriologica Longino Contoli, Roma; CREA, Centro Ricerche Ecologia Applicata, Coazze (TO); DBA, Dipartimento di Biologia Animale, Università degli Studi di Modena e Reggio Emilia; DBAP, Dipartimento di Biologia Animale, Università degli Studi di Palermo; DG, Dipartimento di Scienze Geologiche, Università degli Studi di Roma III; INFS, Istituto Nazionale Fauna Selvatica, Ozzano Emilia (BO); MCSNC, Museo Civico di Storia Naturale, Carmagnola (TO); MCSNG, Museo Civico di Storia Naturale, Genova; MCSNVE, Museo Civico di Storia Naturale, Venezia; MCSNVR, Museo Civico di Storia Naturale, Verona; MESN Museo di Ecologia e Storia Naturale, Marano sul Panaro (MO); MTSN, Museo Tridentino di Scienze Naturali, Trento; MZUF Museo Zoologico “La Specola”, Firenze.

**Material**

The material studied comprises 1351 M1 belonging to 55 local populations of M. (T.) savii from the following regions of Italy (Figure 1), and specimens are stored in various Italian institutions.
Piemonte

Ten populations. Population 1: (Province Alessandria) Frugarolo—Brignano (MTSN, MCSNG) \((n=5)\). Population 2: (Provinces Vercelli/Alessandria) Formigliana—Odalengo Grande (AN/CREA) \((n=29)\). Population 3: (Province Torino) Monte Lera, Rivoletto—Piossasco—Vaie—Rosta (CREA) \((n=8)\). Population 4: (Province Vercelli) Lame del Sesia
(CREA) \( n=7 \). Population 5: (Province Novara) Parco del Ticino—Borgolavezzaro—Cerano (CREA/MCSNC) \( n=43 \). Population 6: (Province Torino) Chieri (CREA) \( n=36 \). Population 7 (Province Cuneo) Val Pesio—Demonte (CREA/R. Toffoli) \( n=11 \). Population 8: (Province Novara Gozzano)—Casalbeltrame (MCSNG/MCSNC) \( n=13 \). Population 9: (Province Torino) Carmagnola (MCSNC) \( n=9 \). Population 10: (Province Cuneo) Benevolo—Piasco—Morozzo (CREA/R. Toffoli) \( n=20 \).

**Lombardia**

Two populations. Population 1: (Province Cremona) Soncino (F. Aceto) \( n=46 \). Population 2: (Province Bergamo) Caravaggio—Trezzo—Zanica (M. Mastrorilli) \( n=29 \).

**Veneto**

Four populations. Population 1: (Province Rovigo) Valle Bonello (AN) \( n=49 \). Population 2: (Province Venezia) Zelarino (MCSNVE) \( n=57 \). Population 3: (Province Venezia) Valle Millecampi (MCSNVE) \( n=49 \). Population 4: (Province Verona) Lotrago di Romagnano—Vajo della Gallina—Molina (MCSNVR) \( n=6 \).

**Emilia Romagna**

Nine populations. Population 1: (Province Bologna) Bologna—Monte Scalvato (INFS) \( n=4 \). Population 2: (Province Modena) Denzano di Marano—Vignola—Nirano, Fiorano—Festà di Marano (DBA/MESN) \( n=10 \). Population 3: (Provinces Bologna/Ravenna) Imola—Romitorio (INFS) \( n=10 \). Population 4: (Province Reggio Emilia) Salde Gatta (F. Aceto) \( n=53 \). Population 5: (Province Modena) Nonantola (DBA) \( n=10 \). Population 6: (Province Modena) Sestola (DBA) \( n=5 \). Population 7: (Province Modena) Mirandola (DBA) \( n=5 \). Population 8: (Province Modena) Riolunato (DBA) \( n=7 \). Population 9: (Provinces Reggio Emilia/Modena) Gattatico—Novi Punta Pietra—Carpi (DBA) \( n=15 \).

**Toscana**

Three populations. Population 1: (Province Arezzo) Bracciolini Terranuova (MZUF) \( n=38 \). Population 2: (Province Firenze) Brozzi (MCSNG) \( n=2 \). Population 3: (Province Pisa) San Rossore (CDSL) \( n=50 \).

**Umbria**

Two populations. Population 1: (Province Perugia) Pietralunga—Bevagna (A. Gaggi, A. Paci/MCSNG) \( n=10 \). Population 2: (Province Perugia) Scalocchio (A. Gaggi, A. Paci) \( n=53 \).

**Abruzzo**

Two populations. Population 1: (Province L’Aquila) Pescasseroli—Gioia Vecchio (CMTLC/INFS) \( n=10 \). Population 2: (Province L’Aquila) Parco Nazionale d’Abruzzo (INFS) \( n=10 \).
**Lazio**

Five populations. Population 1: (Province Roma) Subiaco (MCSNG) \((n=7)\). Population 2: (Province Roma) Genzano (CMTLC) \((n=49)\). Population 3: (Province Roma) Riparo Salvini, Epigravettien (DG) \((n=22)\). Population 4: (Province Roma) Genazzano (A. Gaggi, A. Paci) \((n=49)\). Population 5: (Province Roma) Monti della Tolfa (CMTLC) \((n=36)\).

**Campania**

Eight populations. Population 1: (Province Caserta) Maiano (CMTLC) \((n=9)\). Population 2: (Province Caserta) Frazione Sala, Caserta (AN) \((n=51)\). Population 3: (Province Salerno) Capo d’Orso, Maiori (AN) \((n=6)\). Population 4: (Province Salerno) Auletta (AN) \((n=19)\). Population 5: (Province Benevento) San Giorgio del Sannio (AN) \((n=60)\). Population 6: (Province Napoli) Torre del Greco (AN) \((n=52)\). Population 7: (Province Avellino) Conza della Campania (AN) \((n=26)\). Population 8: (Province Napoli) Ottaviano (AN) \((n=55)\).

**Puglia**

Five populations. Population 1: (Province Taranto) Palombara, Monteparano (CMTLC) \((n=15)\). Population 2: (Province Lecce) Masseria Colonia, Melissano (CMTLC) \((n=23)\). Population 3: (Province Foggia) Alberona (CMTLC) \((n=42)\). Population 4: (Province Foggia) Nord Tavoliere delle Puglie (INFS) \((n=20)\). Population 5: (Province Brindisi) Ostuni, Pléistocène Supérieur (DG) \((n=30)\).

**Basilicata**

One population. Population 1: (Province Matera) Oasi WWF San Giuliano (F. Cecere, M. Visceglia) \((n=43)\).

**Sicilia**

Four populations. Population 1: (Province Messina) Tortorici (DBAP) \((n=7)\). Population 2: (Province Trapani) Fontasala (DBAP) \((n=8)\). Population 3: (Province Palermo) Roccapalumba (DBAP) \((n=5)\). Population 4: (Province Palermo) Piana degli Albanesi—Monreale (CMTLC/DBAP) \((n=8)\).

**Methods**

Twenty-seven linear-distance measurements, noted 1 to 27, were taken on the occlusal surface of M1 (Figure 2) according to Brunet-Lecomte (1988) and Laplana et al. (2000). The six first variables describe the global morphology of the tooth, and the other variables focus on the anterior part which is the most variable region. Measurements were taken with a Nikon Measuring Microscope MM-60 (precision=1 μm).
General morphometry

The general morphometry of the M₁ is studied by canonical discriminant analysis based on 27 measures taken on the occlusal surface of the tooth. Statistics are performed using Statistica version 6.1 (Statsoft, Tulsa, OK, USA).

Analysis of dental criteria

Five dental criteria were calculated (V is for variable):

1. Relative length of the anterior part of the M₁: \( LRPA = \frac{V6 - V3}{V6} \times 100 \).
2. Tilt of the pithymyian rhombus: \( RP = V4 - V3 \).
3. Closure of the anterior loop: \( BA = \frac{V20 - V18}{V21} \times 100 \).
4. Ratio of length to width: \( V621 = \frac{V6}{V21} \).
5. Ratio of relative width of pithymyian rhombus: \( V2521 = \frac{V25}{V21} \).
The total length of the M₁ (LT) and the five dental criteria were compared between groups of populations using analysis of variance, completed by a Bonferroni test or test of contrasts when necessary.

Results

General morphometry of the first lower molar

A first canonical discriminant analysis was carried out between the 55 local populations of *M. (T.) savii* in order to verify the relationship between the geographical origin of populations and the distribution of centroids of these populations in the canonical plan 1-2. Plan 1-2 explains 34% of the variance, 21% and 13% for axes 1 and 2, respectively. The distribution of centroids in plan 1-2 (Figure 3) confirms this relation except for four populations:

1. One population from Emilia Romagna (population 8) is located on the negative sides of both axes whereas the other Emilia Romagna populations are located on the positive side of axis 1 and the negative side of axis 2.
2. One population from Lazio (population 5) is very positively situated on axis 2.
3. One population from Piemonte (population 9) is negatively situated on the two axes in contrast to the other nine populations which are all located close to the centre of plan 1-2.

Figure 3. Canonical discriminant analysis with the distribution of the centroids on the two first axes of 55 populations from the different regions of Italy.
4. One population from Sicilia (population 1) is located on the positive side of axis 2 whereas the other three are on the negative side.

All the other populations can be clustered in 11 homogeneous geographical groups: group 1 (denoted AB) composed of all seven populations from Abruzzo, Toscana, and Umbria; group 2 (denoted C1) with four populations from Campania (populations 1, 3, 6, and 8); group 3 (denoted C2) with the four other populations from Campania (populations 2, 4, 5, and 7); group 4 (denoted ER), with five populations from Emilia Romagna (populations 1, 2, 5, 7, and 9); group 5 (denoted LA), all populations from Lazio except population 5; group 6 (denoted PI), all populations from Piemonte except population 9; group 7 (denoted LO), populations from Lombardia; group 8 (denoted VE), all populations from Veneto and three populations from Emilia Romagna (populations 3, 4, and 6); group 9 (denoted P1) with three populations from Puglia (populations 1, 2, and 3) and the population from Basilicata; group 10 (denoted P2) with the other two populations from Puglia (populations 4 and 5); and group 11 (denoted SI), all populations from Sicilia except population 1.

The second canonical discriminant analysis was carried out between the 11 groups defined above. All Mahalanobis distances between groups are significant ($P<0.0001$ in all cases). Plan 1-2 explains 58% of the variance, 40% and 18% for axes 1 and 2, respectively. The distribution of centroids of the groups in plan 1-2 is given in Figure 4. Axis 1 separates the five groups of south Italy (Mezzogiorno) located on the positive side, and corresponding to Campania 1 (C1) and 2 (C2), Puglia 1 (P1) and 2 (P2), Sicilia (SI), from the six groups of north–central Italy located on the negative side and corresponding to Veneto (VE), Emilia Romagna (ER), Lazio (LA), Piemonte (PI), Lombardia (LO), and Abruzzo–Toscana–Umbria (AB). The second axis separates, on the one hand, with respect to north–central Italy, the group of Emilia Romagna (ER), on the negative side, from the groups of Veneto (VE), Lazio (LA), Piemonte (PI), Lombardia (LO), and Abruzzo–Toscana–Umbria (AB) on the positive side and, on the other hand, with respect to the Mezzogiorno,
the groups of Campania 2 (C2), Puglia 1 (P1), and Sicilia (SI), on the negative side, from
the groups of Campania 1 (C1) and Puglia 2 (P2), on the positive side. The groups on the
negative side of axis 2 are characterised by a total length of M1 smaller than the groups on
the positive side.

**Analysis of the first lower molar criteria**

The description and the comparison of the M1 criteria are given in Table I. All criteria are
significantly different between the 11 geographical groups. The main interesting results can
be summarised as follows.

Between north–central and south Italy, two criteria, closure of the anterior loop (test of
contrasts, $P<0.0001$) and ratio $V_{25}/V_{21}$ (test of contrasts, $P<0.0001$), distinguish the five
Mezzogiorno groups (Campania C1 and C2, Puglia P1 and P2, and Sicilia SI) from the
north–central Italian groups. The closure of the anterior loop is more open in the
Mezzogiorno groups (Sicilia: $35.7\pm 10.8\%$; Puglia 2: $29.6\pm 7.3\%$; Puglia 1: $28.2\pm 8.1\%
; Campania 2: $26.9\pm 7.3\%$; Campania 1: $26.1\pm 9.4\%$) than in the central and northern
groups (Veneto: $25.5\pm 7.9\%$; Lombardia: $25.3\pm 7.4\%$; Piemonte: $25.0\pm 7.0\%$; Abruzzo:
$23.7\pm 6.7\%$; Lazio: $23.2\pm 7.0\%$) except for the Emilia Romagna group ($27.5\pm 10.8\%$).
The ratio $V_{25}/V_{21}$ is higher in the Mezzogiorno groups (Sicilia: $0.175\pm 0.037$; Campania
2: $0.174\pm 0.038$; Puglia 1: $0.173\pm 0.032$; Puglia 2: $0.172\pm 0.039$; Campania 1:
$0.166\pm 0.032$) than in central and northern groups (Lombardia: $0.164\pm 0.028$; Lazio:
$0.163\pm 0.030$; Abruzzo: $0.154\pm 0.030$; Emilia Romagna: $0.152\pm 0.026$; Veneto:
$0.151\pm 0.027$; Piemonte: $0.146\pm 0.028$).

Within the north–central Italian populations, two criteria distinguish the Veneto
group (including three populations of Emilia Romagna) from the Emilia Romagna
group: the total length of the M1 is greater in the Veneto group ($2.580\pm 0.127$ mm)
than in the Emilia Romagna group ($2.443\pm 0.151$), and the ratio $V_{621}$ is greater in
the Emilia Romagna group ($2.70\pm 0.15$ mm) than in the Veneto group ($2.57\pm 0.09$).
One criterion, the closure of the anterior loop, distinguishes the Veneto and Emilia
Romagna groups from the Abruzzo, Piemonte, Lombardia, and Lazio groups, (test of
contrasts, $P=0.0014$). The anterior loop is more open in the Emilia Romagna
($27.7\pm 10.8\%$) and Veneto groups ($25.5\pm 7.9\%$) than in the Lombardia ($25.3\pm
7.4\%$), Piemonte ($25.0\pm 7.0\%$), Abruzzo ($23.7\pm 6.7\%$), and Lazio ($23.2\pm 7.0\%$
) groups.

Within south Italian populations, one criterion distinguishes the Campania 1 group from
the Campania 2 group: the total length of the M1 is greater in the Campania 1 group
($2.654\pm 0.171$ mm) than in the Campania 2 ($2.484\pm 0.134$). One criterion distinguishes
the Puglia 1 group from the Puglia 2 group: the total length of the M1 is greater in the
Puglia 2 group ($2.616\pm 0.119$ mm) than in the Puglia 1 ($2.510\pm 0.117$). Four criteria
characterise the Sicilia group, a very open anterior loop ($35.71\pm 0.8\%$), a reduced anterior
part of the M1 ($50.0\pm 1.6\%$), a pitymyan rhombus poorly tilted ($-0.0045\pm 0.041$ mm)
and a great ratio $V_{25}/V_{21}$ ($0.175\pm 0.037$).

Moreover, population 5 from Lazio is characterised by a greater total length of the M1
($t$-test, $P<0.0001$) ($2.728\pm 0.175$ mm) in comparison to the other Lazio groups
($2.592\pm 0.123$ mm). The sample size of three other excluded populations (population 8
of Emilia Romagna, population 9 of Piemonte, and population 1 of Sicilia) from the
analyses of groups is too small ($n<10$) to express conclusions.
Table I. Description and analysis of variance (ANOVA) of the first lower molar criteria completed by Bonferroni’s test of geographical groups of populations of Microtus (Terricola) savii.

| Population<sup>a</sup> | N<sup>b</sup> | Mean   | SD     | Minimum | Maximum | Bonferroni’s test<sup>c</sup> |
|------------------------|--------------|--------|--------|---------|---------|--------------------------------|
| Total length of the first lower molar (LT) |             |        |        |         |         |                                |
| AB                     | 173          | 2.590  | 0.121  | 2.220   | 2.948   | BAC                            |
| ER                     | 44           | 2.443  | 0.151  | 2.065   | 2.641   | F                              |
| P1                     | 123          | 2.510  | 0.117  | 2.179   | 2.724   | EDF                            |
| P2                     | 50           | 2.616  | 0.119  | 2.349   | 2.898   | BA                             |
| LA                     | 127          | 2.592  | 0.123  | 2.323   | 2.840   | BAC                            |
| C1                     | 122          | 2.654  | 0.171  | 2.16   | 3.172   | A                              |
| C2                     | 156          | 2.484  | 0.134  | 2.176   | 2.802   | EF                             |
| VE                     | 229          | 2.580  | 0.127  | 2.141   | 2.857   | BDC                            |
| LO                     | 75           | 2.523  | 0.133  | 2.221   | 2.897   | EDC                            |
| PI                     | 172          | 2.602  | 0.142  | 2.210   | 2.923   | BA                             |
| SI                     | 21           | 2.526  | 0.106  | 2.303   | 2.764   | EDC                            |
| Relative length of the anterior part of M<sub>1</sub> (LRPA) |             |        |        |         |         |                                |
| AB                     | 173          | 51.617 | 1.421  | 48.311  | 54.971  | A                              |
| ER                     | 44           | 51.118 | 1.853  | 42.637  | 53.821  | BAC                            |
| P1                     | 123          | 50.456 | 1.629  | 45.580  | 54.857  | DC                             |
| P2                     | 50           | 50.363 | 1.559  | 47.150  | 53.451  | BDC                            |
| LA                     | 127          | 51.113 | 1.460  | 45.409  | 54.187  | BAC                            |
| C1                     | 122          | 51.173 | 1.464  | 46.505  | 55.129  | BAC                            |
| C2                     | 156          | 50.882 | 1.397  | 48.126  | 54.844  | BAC                            |
| VE                     | 229          | 51.394 | 1.431  | 42.252  | 54.881  | BA                             |
| LO                     | 75           | 50.782 | 1.197  | 48.368  | 53.511  | BDC                            |
| PI                     | 172          | 51.277 | 1.375  | 45.815  | 54.745  | BA                             |
| SI                     | 21           | 50.029 | 1.587  | 46.982  | 52.721  | D                              |
| Tilt of the pitymyan rhombus (RP) |             |        |        |         |         |                                |
| AB                     | 173          | −0.029 | 0.045  | −0.219  | 0.071   | BC                             |
| ER                     | 44           | −0.038 | 0.034  | −0.113  | 0.022   | C                              |
| P1                     | 123          | −0.010 | 0.039  | −0.097  | 0.081   | BA                             |
| P2                     | 50           | −0.021 | 0.036  | −0.087  | 0.045   | BAC                            |
| LA                     | 127          | −0.020 | 0.035  | −0.130  | 0.079   | BAC                            |
| C1                     | 122          | −0.010 | 0.048  | −0.122  | 0.187   | BA                             |
| C2                     | 156          | −0.004 | 0.039  | −0.099  | 0.123   | A                              |
| VE                     | 229          | −0.022 | 0.034  | −0.099  | 0.098   | BAC                            |
| LO                     | 75           | −0.028 | 0.033  | −0.114  | 0.047   | BC                             |
| PI                     | 172          | −0.023 | 0.040  | −0.155  | 0.114   | BAC                            |
| SI                     | 21           | −0.004 | 0.041  | −0.073  | 0.091   | A                              |
| Closure of the anterior loop (BA) |             |        |        |         |         |                                |
| AB                     | 173          | 23.655 | 6.709  | 8.566   | 47.725  | ED                             |
| ER                     | 44           | 27.689 | 10.819 | 10.251  | 57.684  | CBD                            |
| P1                     | 123          | 28.173 | 8.104  | 5.682   | 55.771  | CB                             |
| P2                     | 50           | 29.616 | 7.316  | 14.606  | 48.889  | B                              |
| LA                     | 127          | 23.175 | 7.006  | 10.168  | 47.059  | E                              |
| C1                     | 122          | 26.086 | 9.363  | 4.264   | 54.118  | CEBD                           |
| C2                     | 156          | 26.929 | 7.294  | 3.646   | 56.419  | CEBD                           |
| VE                     | 229          | 25.549 | 7.932  | 6.641   | 51.176  | CEBD                           |
| LO                     | 75           | 25.309 | 7.373  | 10.023  | 43.220  | CED                            |
| PI                     | 172          | 24.968 | 6.957  | 4.248   | 55.118  | CED                            |
| SI                     | 21           | 35.740 | 10.797 | 13.379  | 52.513  | A                              |
| Ratio of length to width (V621) |             |        |        |         |         |                                |
| AB                     | 173          | 2.574  | 0.121  | 2.321   | 2.904   | BCD                            |
| ER                     | 44           | 2.697  | 0.146  | 2.412   | 3.039   | A                              |
| P1                     | 123          | 2.630  | 0.133  | 2.358   | 3.003   | BC                             |
| P2                     | 50           | 2.615  | 0.112  | 2.388   | 2.881   | BCD                            |
Discussion and conclusion

The general dental morphology of arvicoline can be considered as adaptative in relation to their diet compared to other groups of rodents such as murines or cricetines. Indeed, this particular outline with alternated triangles combined with the hypsodonty of the teeth is well adapted to a diet with high content of silica which is a very abrasive. Within the arvicoline sub-family, tooth outline is extremely variable. Two main hypotheses can be made to explain this morphological variability. Firstly, morphological variability can result from selection pressure of climatic conditions. Secondly, this variation can be due to some isolation phenomena leading to very small populations which may be more sensitive to a bottleneck effect. This last hypothesis has been previously noted within the Microtus (Terricola) complex in relation to fragmentation of habitat (Contoli et al. 1992). Moreover, some authors have observed morphological variation between different generations (Krapp and Winking 1976).

In our study, canonical discriminant analyses highlight a clear separation of the general morphology of $M_1$ between populations from south Italy and populations from central and north Italy. The analysis of $M_1$ criteria confirms this fact, in particular for the criterion of the closure of the anterior loop, which is more open in southern populations than in central and northern populations. A similar effect was previously observed, at the specific level, in the western Mediterranean species $M. (T.)$ duodecimcostatus de Sélys-Longchamps, 1839, in comparison to other species of Terricola such as $M. (T.)$ subterraneus (de Sélys-Longchamps, 1836) or $M. (T.)$ multiplex (Fatio, 1905) (Brunet-Lecomte 1988, 1990). A similar observation can be noted for the relative length of the anterior part of $M_1$, which is less developed in southern species, such as $M. (T.)$ duodecimcostatus, or southern populations of $M. (T.)$ savii.

### Table I. (Continued.)

| Population | $N$ | Mean | SD  | Minimum | Maximum | Bonferroni’s test |
|------------|-----|------|-----|---------|---------|-------------------|
| LA         | 127 | 2.562| 0.117| 2.183   | 2.803   | D                 |
| C1         | 122 | 2.560| 0.133| 2.275   | 2.943   | D                 |
| C2         | 156 | 2.583| 0.128| 2.299   | 3.074   | BCD               |
| VE         | 229 | 2.572| 0.094| 2.309   | 2.945   | BCD               |
| LO         | 75  | 2.566| 0.116| 2.274   | 2.820   | CD                |
| PI         | 172 | 2.557| 0.102| 2.320   | 2.872   | D                 |
| SI         | 21  | 2.634| 0.129| 2.366   | 2.837   | BA                |

Ratio of relative width of pitymyan rhombus (V2521)

| $N_1$ | $V_1$ | $V_2$ | $V_3$ | $V_4$ | $V_5$ | $V_6$ | $V_7$ |
|-------|-------|-------|-------|-------|-------|-------|-------|
| 173   | 0.154 | 0.030 | 0.079 | 0.225 | BC    |
| 44    | 0.152 | 0.026 | 0.100 | 0.205 | BC    |
| 123   | 0.173 | 0.032 | 0.092 | 0.246 | A     |
| 50    | 0.172 | 0.039 | 0.093 | 0.250 | A     |
| 127   | 0.163 | 0.030 | 0.077 | 0.252 | BAC   |
| 122   | 0.166 | 0.032 | 0.061 | 0.240 | BA    |
| 156   | 0.174 | 0.038 | 0.083 | 0.312 | A     |
| 229   | 0.151 | 0.027 | 0.080 | 0.230 | BC    |
| 75    | 0.164 | 0.028 | 0.107 | 0.225 | BA    |
| 172   | 0.146 | 0.028 | 0.053 | 0.200 | C     |
| 21    | 0.175 | 0.037 | 0.133 | 0.261 | A     |

Analysis of variance for each criterion: $P<0.0001$.

$^a$Abbreviations of geographical groups: AB, Abruzzo–Umbria–Toscana; ER, Emilia Romagna; P1, Puglia 1; P2, Puglia 2; LA, Lazio; C1, Campania 1; C2, Campania 2; VE, Veneto; LO, Lombardia; PI, Piemonte; SI, Sicilia.

$^bN_1$, number of $M_1$. $^c$Bonferroni’s test: means within each criterion with the same letter are not significantly different ($P>0.05$).
Another fact highlighted by canonical discriminant analyses is the isolated position of the populations from Veneto and Emilia Romagna, two regions of the Padana plain. Two hypotheses can be proposed to explain this morphometrical divergence: (1) the important change of this region due to human activity; (2) the complex hydrography of this plain. Concerning the first hypothesis, since the beginning of historic times, the extensive forest was progressively transformed into an agricultural plain. At the start of this deforestation, *M. (T.) savii* colonized a new and a dislocated area. Firstly, this dislocated area perhaps has lead to the emergence of small populations characterized by a different morphotype of the M1. Secondly, the development of agricultural activity in the Padana plain has permitted the colonisation of a great part of the Veneto and the Emilia Romagna by *M. (T.) savii* populations characterised by this new morphotype. Regarding the second hypothesis, the complex hydrography of the Padana plain can be a favourable factor in the process of the isolation of populations, by playing a barrier role. These two hypotheses also can act together.

Size variation is noted within three geographical groups, Veneto–Emilia Romagna, Campania, and Puglia. In the Veneto–Emilia Romagna groups, five populations from Emilia Romagna (Emilia Romagna group) are characterised by smaller size. The explanation can be probably found in a secondary role of the above factors. The fragmentation of habitat usually acts as a stress on individuals which are often smaller than in more optimal ecological conditions (Marchand et al. 2003). In the Campania groups, the small-size group (C2) is composed of four populations from inland localities characterised by cold winters (Grassi and Milone 1985), a climatic condition which can reduce the size development of specimens. On the contrary, the large-size group (C1) is composed of four populations from coastal localities with Mediterranean conditions. In the case of the Puglia groups, no climatic, hydrographic, or human activity factors seem to be able to explain the observed size variations. Moreover, the size difference is lesser within groups from Puglia (0.116 mm) than within groups from Campania (0.170 mm).

In our study, on a regional scale, morphological variability corresponds to the first hypothesis and therefore is related to geography, and consequently to climate and environment. A clear separation of the general morphology of M1 between populations from south Italy and populations from central and north Italy has been observed. The second hypothesis does not seem to act at the regional level.

On the contrary, on a local scale, the second hypothesis cannot be rejected. As observed in the Padana Plain, morphological variability can be due to the fragmentation of this particular area leading to the isolation of populations characterised by different morphotypes.

In conclusion, the same morphological pattern is observed at an intraspecific level, within *Microtus (Terricola) savii* between north–central and south populations in Italy, as at an interspecific level within the sub-genus *Microtus (Terricola)*, between northern and southern species in western Europe. Two morphological criteria, the anterior loop (BA) and the relative length of the anterior part (LRPA) of the first lower molar, distinguish species living in north-western Europe such as *M. (T.) subterraneus* (LRPA=52.8±1.3 and BA=14.7±4.9) from species living in Mediterranean areas, such as *M. (T.) duodecimcostatus* (LRPA=49.4±1.5 and BA=34.8±8.1) (Brunet-Lecomte 1990). In *M. (T.) subterraneus* and in northern populations of *M. (T.) savii*, the relative length is greater and the anterior loop is more closed than in the species *M. (T.) duodecimcostatus* or populations of *M. (T.) savii* living in the south. The morphological variability of these two criteria seems to be in relation to the geography at both intra- and inter-specific levels.
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