Acta Theriologica 45 (4): 471–483, 2000.
PL ISSN 0001-7051

Comparative morphometrics of the first lower molar in *Microtus (Terricola)* cf. *liechtensteini* of the Eastern Alps

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Spitzenberger F., Brunet-Lecomte P., Nadachowski A. and Bauer K. 2000. Comparative morphometrics of the first lower molar in *Microtus (Terricola)* cf. *liechtensteini* of the Eastern Alps. Acta Theriologica 45: 471–483.

The M_1-morphology of seven isolated populations of voles displaying a pitymyan rhombus from the Eastern Alps (including the probably extinct *Microtus bavaricus*) was compared with that of *M. multiplex*, *M. liechtensteini*, and *M. tatricus* as well as among each other, by using discriminant and canonical discriminant analyses. The general morphometry of the M_1 and the analysis of the M_1 parameters show these populations to be related to *M. liechtensteini* and *multiplex*, more closely to *liechtensteini* but not in complete accordance with comparative *liechtensteini*-material from Slovenia and Croatia. The seven samples show a remarkable variation between each other that cannot be associated with their respective geographic provenance. They can be classified into three groups, one consisting of *M. bavaricus* only, one of true *liechtensteini* (Carinthia and Eastern Tyrol) and a third represented by a sample of the upper Enns valley in Styria, characterized by a very aberrant M_1 morphology.

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Key words: *Microtus bavaricus*, *M. liechtensteini*, *M. multiplex*, *M. tatricus*, Eastern Alps, postglacial colonization

Introduction

The systematics of *Microtus* forms displaying a pitymyan rhombus on the M_1 were confused until studies of karyotypic and protein variation, alongside paleontological investigations based on dental morphology, revealed three main phylogenetic traits of this arvicolid subgroup: (1) Polyphyletic origin of this character in nearctic and palaearctic forms (Chaline *et al.* 1988), and possible polyphyly within the palaearctic representatives (Zagorodnyuk and Zima 1992, Kryštufek *et al.* 1996), leading to the use of the subgeneric name *Terricola* for the *multiplex-subterraneus* group (Brunet-Lecomte 1990) (extended in this paper to the taxa *liechtensteini* and *bavaricus* because of their near relationship with *multiplex*). (2) Recognition of specific rank of the following 10 extant European species: *duodecimcostatus*, *felteni*, *liechtensteini*, *lusitanicus*, *multiplex*, *pyrenaicus*, *subterraneus*, *savii*, *tatricus*, and *thomasi*; *bavaricus* considered *incertae sedis*, becaue of the lack of karyological studies. (3) High degree of cytogenetical polytypy and polymorphism (eg *liechtensteini-multiplex*: Petrov and Živković 1971, Storch and Winking 1977, Graf and Meylan 1980, Brunet-Lecomte and Volobouev 1994; *savii*: Galleni *et al.* 1998; *subterraneus*: Sablina *et al.* 1989: *thomasi*: Giagia-Athanasopoulou and Stamatopoulos 1997), sometimes accompanied by remarkable morphological variation.

Although in many parts of Europe voles of the subgenus *Terricola* have been intensively studied, very little is known of these voles from the Eastern Alps. From the Alps east of a line connecting Lake Constance and Lago di Como, the following *Terricola* taxa have so far been reported: *bavaricus*, *liechtensteini*, *multiplex*, cf. *multiplex*, and *subterraneus*.

While *M. subterraneus* is widespread in the Eastern Alps, the two closely related taxa, *multiplex* and *liechtensteini*, have been reported to be confined to the south-facing slopes, where according to Storch and Winking (1977) the Adige valley forms the boundary between the western *multiplex* and the eastern *liechtensteini*. *Microtus liechtensteini*'s taxonomic position as a separate species, parapatric semispecies, or subspecies of *M. multiplex* has been changed several times. Described by Wettstein (1927) from the Velebit mountains in Croatia as a species, the examination of its karyotype (Petrov and Živković 1971, Král *et al.* 1978) initially corroborated its specific status. After finding a natural hybrid in the zone of contact, this was rejected by Storch and Winking (1977), Graf and Meylan (1980), Chaline (1987), Brunet-Lecomte (1990), and Brunet-Lecomte and Kryštufek (1993) who considered *multiplex* and *liechtensteini* to be a parapatric biospecies of a superspecies. Musser and Carleton (1993) and Kryštufek (1999) consequently included *liechtensteini* into the synonymy of *multiplex*, although Brunet-Lecomte and Volobouev (1994) had considered the karyotypic differentiation between the 2n = 46 *liechtensteini* and 2n = 48 *multiplex* (at Fivizzano/Tuscany locally 2n = 46) great enough to revert to species status.

The northwestern boundary of *M. liechtensteini* is situated in the Austrian Alps. First recorded from the Karawanken by Bauer (1962) under the name *multiplex* (which he took as polytypic species including *liechtensteini*), similar voles were subsequently found further west in the Karnische Alpen (also part of the Southern Alps) and in the Defereggen mountains (a southern part of the Central Alps) by Král *et al.* (1978). The karyotypes of the two latter populations were examined by these authors and found to be identical with *liechtensteini*-chromosomes from the Julian Alps in Slovenia (Živković *et al.* 1975).

Under the name *Microtus* (*T.*) cf. *multiplex*, Reiner (1995) described a late glacial (^{14}C dated 12.430 ± 95 years BP) sample of *Terricola* voles from Badlhöhle in the Mur valley, Styria.

As a great surprise, another isolated vole population related to *Terricola* was found at the northern edge of the Eastern Alps in Garmisch Partenkirchen, Bayerische Alpen, Germany, and described by König (1962) as a new species – *Pitymys bavaricus*. A skull from an owl pellet found in Biberwier, Northern Tyrol, Austria was also identified as *bavaricus* (König 1982). König (1962) and Bauer (1962) emphasized the near relationship between *bavaricus* and *multiplex* (s.l.). In a morphological revision Kratochvíl (1970) placed these two forms together with *tatricus* in his alpine-carpathic group, later, after a karyological revision (Kratochvíl and Král 1971), *tatricus* was considered a separate phylogenetic lineage. Zagorodnyuk and Zima (1992) even suggested that *tatricus* might be a representative of *Microtus s.l.*, the pitymyan rhombus having evolved in a parallel or convergent way to voles belonging to the subgenera *Pitymys* and *Terricola*. Chaline *et al.* (1988) placed *bavaricus*, *multiplex*, and *tatricus* together with *subterraneus* and *majori* into their *subterraneus*-group.

In the 1990s several efforts were made to catch *M. bavaricus* at the terra typica in order to investigate it karyologically, but the all failed (R. Kraft, pers. comm.). It seems very probable, that this vole is extinct in the terra typica and its near vicinity. Brunet-Lecomte and Nadachowski (1998), comparing the morphology of the first lower molar of *M. bavaricus* (using 3 teeth only) with that of *multiplex* and *tatricus*, positioned *bavaricus* as an intermediate of the two taxa, but closer to *tatricus*.

Between 1976 and 1997 voles morphologically resembling *M. liechtensteini* were caught in the Eastern Alps north of the main chain, namely in Northern Tyrol (not far from Garmisch-Partenkirchen) as well as in Styria and Salzburg. During the present authors' survey of the Austrian mammal fauna more than 1000 *M. subterraneus* were found, but only 40 voles with a pitymyan rhombus but not belonging to *subterraneus* were collected. These Austrian populations were therefore considered to be isolated and small.

The purpose of this work was to study the taxonomic status of the Eastern Alpine voles displaying a pitymyan rhombus and not belonging to *subterraneus* by the morphological comparison of their lower first molars.

Material and methods

The authors examined the teeth of one population from Bavaria (*M. bavaricus*) and six populations from Austria (*M. liechtensteini* and cf. *liechtensteini*; Table 1).

Comparative material: Nineteen samples of *M. multiplex* (denoted M): Col du Lautaret (Hautes--Alpes, France), 48 teeth; Col du Montgenèvre (Hautes-Alpes, France), 17 teeth; Les Vigneaux (Hautes-Alpes, France), 10 teeth; Chabeuil (Drôme, France), 20 teeth; Marsaz (Drôme, France), 3 teeth; Hauterives (Drôme, France), 2 teeth; La-Chapelle-en-Vercors (Drôme, France), 12 teeth; Saint-Martin-de-la-Cluze (Isère, France) 10 teeth; Saint Romans (Isère, France), 24 teeth; Chantesse (Isère, France), 14 teeth; Zermatt (Wallis, Switzerland), 12 teeth; Gudo (Ticino, Switzerland), 12 teeth; Bedano (Ticino, Switzerland), 4 teeth; Isone (Ticino, Switzerland), 4 teeth; Meride (Ticino, Switzerland), 16 teeth; Bioggio (Ticino, Switzerland), 16 teeth; Varenzo (Ticino, Switzerland), 11 teeth; Mazzola (Tuscany, Italy), 48 teeth; Fivizzano (Tuscany, Italy), 12 teeth.

Ten samples of *M. liechtensteini* (denoted L) as described in Brunet-Lecomte and Kryštufek (1993): 163 teeth of *M. liechtensteini* from 28 samples from Slovenia and Croatia (1 – Planica Valley, 2 teeth;

Table 1. Number of teeth examined (*n*) of seven samples of *Microtus* (*Terricola*) cf. *liechtensteini* from the Eastern Alps.

Sample	Taxon	Province	Locality	*n*
1	*Microtus* (*T.*) *bavaricus*	Bavaria, Germany	Garmisch-Partenkirchen	27
2	*Microtus* (*T.*) sp. (karyotype unknown)	Carinthia, Austria	Karawanken	27
3	*M.* (*T.*) *liechtensteini* (karyotyped)	Carinthia, Austria	Karnische Alpen	18
4	*M.* (*T.*) *liechtensteini* (karyotyped)	Eastern Tyrol, Austria	Defereggen Gebirge	16
5	*Microtus* (*T.*) sp. (karyotype unknown)	Northern Tyrol, Austria	Rofan Gebirge	24
6	*Microtus* (*T.*) sp. (karyotype unknown)	Salzburg, Austria	Tweng, upper Mur valley	2
7	*Microtus* (*T.*) sp. (karyotype unknown)	Styria, Austria	Tauplitz and Bad Mitterndorf, upper Enns valley	4

2 – Kobarid, 3 teeth; 3 – Mt. Pokljuka, 1 tooth; 4 – Mt. Jelovica, 4 teeth; 5 – Jezersko, 1 tooth; 6 – Kamniška Bistrica, 1 tooth; 7 – Vojsko, 2 teeth; 8 – Ajdovščina, 2 teeth; 9 – Nova Gorica, Vogrsko, 4 teeth; 10 – Ljubljana, Ig, 3 teeth; 11 – Mt. Travna gora, 4 teeth; 12 – Sevnica, 1 tooth; 13 – Mokro polje, 1 tooth; 14 – Mt. Snežnik, 8 teeth; 15 – Klivnik, 2 teeth; 16 – Mt. Risnjak, 12 teeth; 17 – Kubed, 20 teeth; 18 – Sočerga, 1 tooth; 19 – Stena, 2 teeth; 20 – Mirna 1, 30 teeth; 21 – Mirna 2, 30 teeth; 22 – Mirna 3, 11 teeth; 23 – Mt. Učka, 11 teeth; 24 – Štirovača, Alan, 1 tooth; 25 – Zavižan, 2 teeth; 26 – Baske Ostarije, 1 tooth; 27 – Plitvice, 2 teeth; 28 – Mt. Makljen, 1 tooth). The specimens of *M. liechtensteini* were assigned to 10 geographical samples: sample A = samples 17 and 18; sample B = samples 14, 15, and 16; sample C = samples 1, 2, 3, and 4; sample D = sample 23; sample E = samples 7, 8, and 9; sample F = samples 24, 25, 26, and 27; sample G = samples 10 and 11; sample H = sample 20; sample I = sample 21; sample J = sample 22. The samples 5, 6, 12, 13, 19, and 28 were removed from the analysis because of the small sample size.

Three samples of *M. tatricus* (denoted T): Liptovske Hole (Tatra Mountains, Slovakia), 27 teeth; Hala Gąsienicowa (Tatra Mountains, Poland), 25 teeth; Babia Góra (Beskidy Mountains, Poland), 7 teeth.

Statistical analyses

Twenty-three measurements, denoted v1 to v23, were taken on the occlusal surface of first lower molars M_1 (Brunet-Lecomte 1988). Left and right M_1 of the same individual were treated as independent specimens. The general morphometry is expressed by 21 of these measurements (v1 to v13 and v15 to v22). Several derived variables were calculated in order to quantify particular morphotypes: the development of the anterior part of M_1 [AP = (v6 – v3)/v6], the tilt of the pitymyan rhombus (PR = v4 – v3), and the closure of the anterior loop (AL = v20 – v18).

Univariate (one-way analyses of variance) and multivariate statistics (discriminant analyses) were used to assess similarities among Eastern Alpine samples and with reference material of *M. liechtensteini*, *M. multiplex*, and *M. tatricus*. Discriminant analyses were based on raw linear measurements of v1 to v13 and v15 to v22. Statistical analyses were performed with SAS Institute software.

Results

The variation in morphology of the first lower molar of the samples from the Eastern Alps is presented in Fig. 1. A discriminant analysis (DA) (Table 2) of the three reference species placed correctly 454 specimens out of 510. All *M. tatricus* were allocated to the appropriate group. The majority of the mis-classified specimens of *M. multiplex* was predicted to be *M. liechtensteini* and only 1.0% was placed in *M. tatricus*. Similarly, all mis-classified specimens of *M. liechtensteini*, with the exception of a single molar, were grouped with *M. multiplex*. The above results suggested a close morphological similarity between *multiplex* and *liechtensteini* and a fairly distinct position of *tatricus*.

Discriminant analysis was further used to test the morphological affinities of the seven samples from the Eastern Alps with the three reference species. As suggested by the results obtained when using a priori identified material, the emerging pattern (Table 2) indicated an enormous dispersion of specimens among the three reference species. In no single sample were all the specimens classified

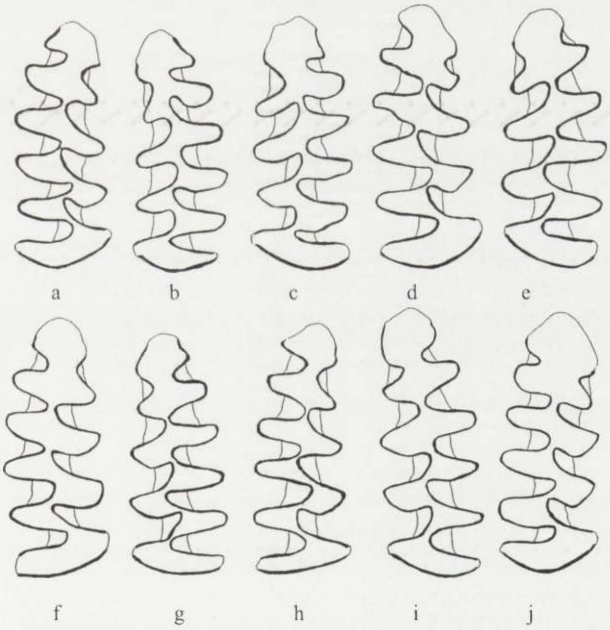

Fig. 1. Variation in morphology of first lower molar of *Microtus* (*Terricola*) from seven samples from the Eastern Alps. Characteristics of teeth (collection number / side of mandible / length of molar in mm) and sample attachment: a – SMF 19895 / right / 2.690 and b – SMF 19896 / left / 2.738 from sample 1, c – NMW 7904 / left / 2.579 and d – NMW 17316 / right / 2.685 from sample 2, e – NMW 33222 / left / 2.666 from sample 3, f – NMW 25033/ right / 2.568 from sample 4, g – NMW 24320 / left / 2.591 and h – NMW 24321 / right / 2.604 from sample 5, i – NMW 56158 / left / 2.761 from sample 6, j – NMW 34814 / right / 2.695 from sample 7. See Table 1 for the sample numbers.

Table 2. Classification of M_1-specimens by the cross-validation method of discriminant analysis. Frequency (percentage) of classification. MTM – *Microtus multiplex*, MTL – *M. liechtensteini* and MTT – *M. tatricus*.

Species/sample	*n*	MTM		MTL		MTT	
		n	%	*n*	%	*n*	%
MTM	295	262	88.8	30	10.2	3	1.0
MTL	156	22	14.1	133	85.3	1	0.6
MTT	59	0	0	0	0	59	100
1	27	8	29.6	13	48.2	6	22.2
2	18	5	27.8	11	61.1	2	11.1
3	16	5	31.3	8	50.0	3	18.7
4	14	6	42.9	7	50.0	1	7.1
5	24	15	62.5	8	33.3	1	4.2
6	2	1	50.0	1	50.0	0	0
7	4	1	25.0	2	50.0	1	25.0

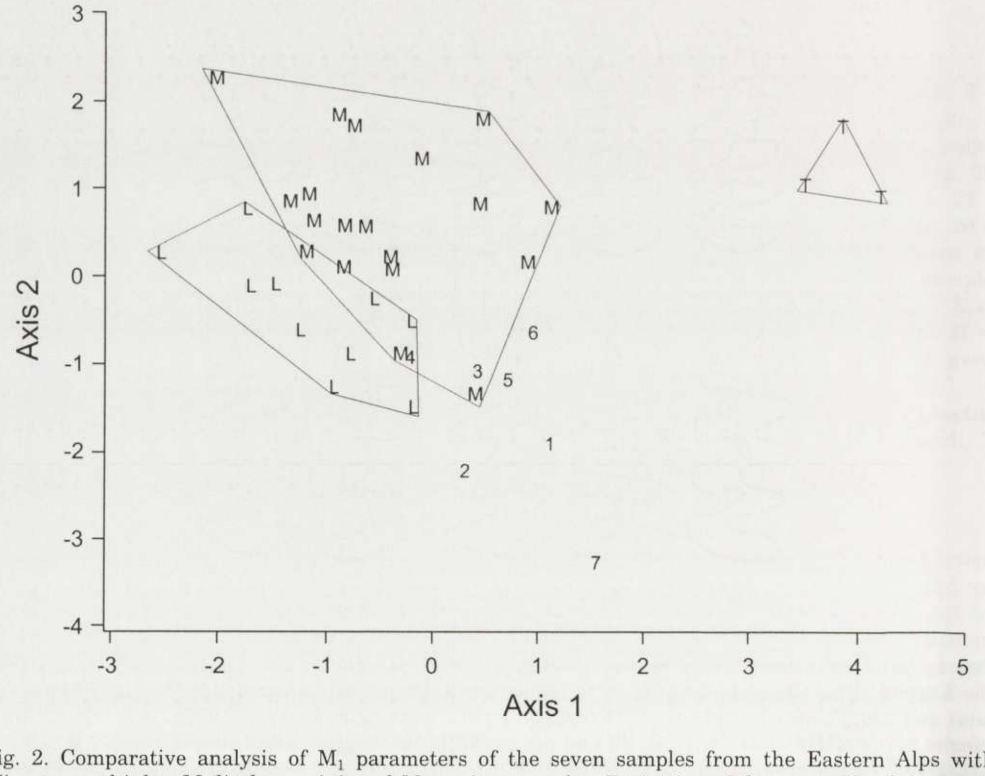

Fig. 2. Comparative analysis of M_1 parameters of the seven samples from the Eastern Alps with *Microtus multiplex*, *M. liechtensteini*, and *M. tatricus* samples. Projection of the centroids of the seven *Terricola* samples from the Eastern Alps (denoted 1–7) and distinct geographic samples of *M. multiplex* (M), *M. liechtensteini* (L), and *M. tatricus* (T) onto the first two canonical discriminant axes.

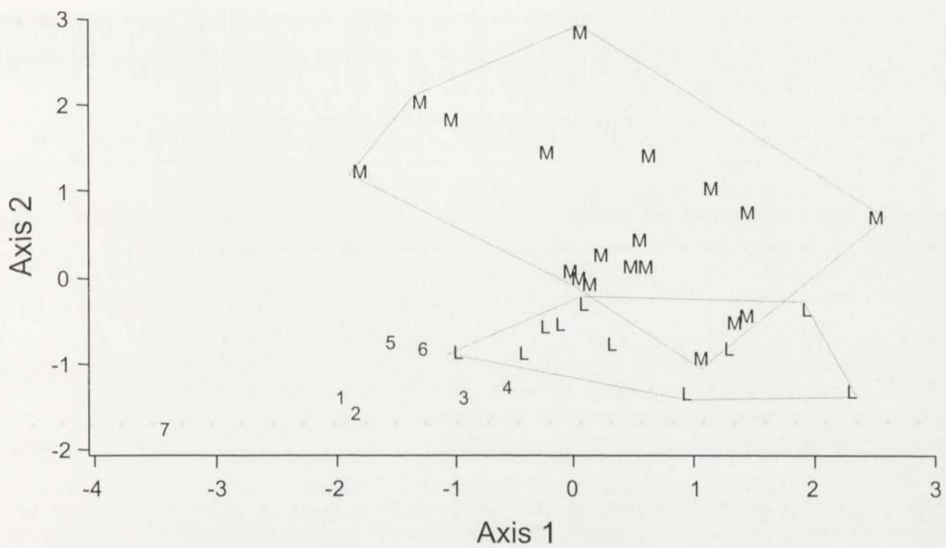

Fig. 3. Comparative analysis of M_1 parameters of the seven samples from the Eastern Alps with *Microtus multiplex* and *M. liechtensteini* samples. Projection of the centroids of the seven *Terricola* samples from the Eastern Alps (denoted 1–7) and distinct geographic samples of *M. multiplex* (M) and *M. liechtensteini* (L) onto the first two canonical discriminant axes.

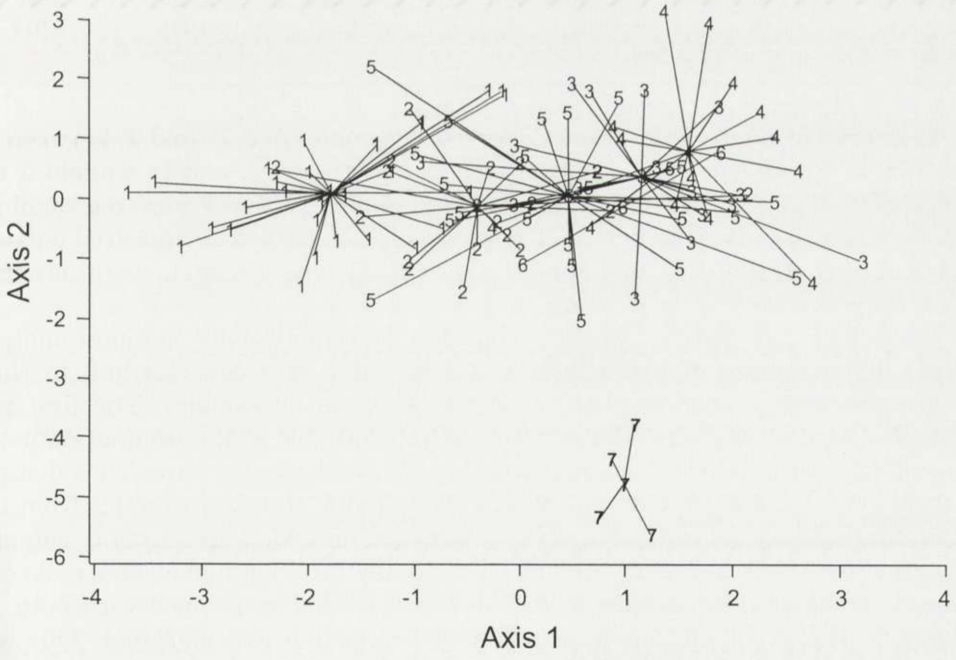

Fig. 4. Projection of scores for specimens from the Eastern Alpine samples (denoted 1–7) on the plot of first two axes resulting from the canonical discriminant analysis CDA 3. Each specimen is linked to the centroid of its sample.

Table 3. Canonical discriminant analysis based on seven samples from the Eastern Alps. First-row value: squared Mahalanobis distance, second-row value: *F*-statistics for squared distance (for 23 and 76 degrees of freedom), third-row value: probability level.

Samples	1	2	3	4	5	6
2	5.690					
	2.070					
	0.010					
3	9.660	7.540				
	3.270	2.150				
	< 0.001	0.007				
4	12.690	8.220	3.020			
	3.940	2.180	0.760			
	< 0.001	0.006	0.767			
5	7.510	4.290	5.160	6.040		
	3.220	1.490	1.670	1.800		
	< 0.001	0.099	0.051	0.030		
6	28.670	20.910	25.800	25.320	15.460	
	1.800	1.270	1.550	1.490	0.960	
	0.030	0.218	0.081	0.099	0.521	
7	31.790	27.540	27.230	31.430	26.990	45.550
	3.730	3.040	2.940	3.300	3.120	2.050
	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.011

into only one of the three reference species. In samples 1, 2, 3, and 4, between 48 and 61% of specimens were classified as *M. liechtensteini*, and in sample 5 the majority (62%) were placed with *M. multiplex*. Samples 6 and 7 were too small for any firm conclusions to be drawn. The position of *M. bavaricus* appeared particularly puzzling, as six teeth, including the ones of the type specimen, were classified as *M. tatricus*.

Next, the entire material was introduced into a canonical discriminant analysis (CDA). The samples of the reference species were treated according to their geographic origin, meaning that CDA was based on 39 samples. The first two canonical variates explained 26 and 15% of the variance in the original data set, respectively. Projection of group centroids onto the two axes revealed a distinct pattern (Fig. 2). The first canonical axis separated *M. tatricus* samples from the remaining ones. The centroids of *M. multiplex* and *M. liechtensteini* samples broadly overlapped, although the former generally attained higher values for the second canonical axis. Samples from the Eastern Alps overlapped with both *M. multiplex* and *M. liechtensteini*, although their position was marginal. This was particularly evident for sample 7. Squared Mahalanobis distances among seven samples from the Eastern Alps and the reference species were significant at $p < 0.05$.

Table 4. Descriptive statistics, analysis of variance and Scheffé's test of the first lower molar in seven samples of the Eastern Alps. Scheffé's test: samples with the same letter are not significantly different ($p \geq 0.05$).

Sample	n	Mean	Standard deviation	Scheffé's test	Analysis of variance
		Total length (mm)			$p = 0.670$
1	27	2.66	0.10	A	
2	18	2.64	0.19	A	
3	16	2.72	0.19	A	
4	14	2.68	0.18	A	
5	24	2.66	0.12	A	
6	2	2.77	0.01	A	
7	4	2.69	0.04	A	
		Anterior part (without unit)			$p = 0.042$
1	27	0.534	0.017	A	
2	18	0.528	0.017	A	
3	16	0.523	0.017	A	
4	14	0.517	0.017	A	
5	24	0.520	0.023	A	
6	2	0.510	0.004	A	
7	4	0.529	0.008	A	
		Inclination of the pitymyian rhombus (mm)			$p = 0.004$
1	27	0.002	0.041	B	
2	18	−0.002	0.035	B	
3	16	0.017	0.058	A B	
4	14	0.019	0.036	A B	
5	24	0.026	0.035	A B	
6	2	0.045	0.007	A B	
7	4	0.085	0.031	A	
		Closure of the anterior loop (mm)			$p < 0.001$
1	27	0.153	0.046	B	
2	18	0.196	0.062	B	
3	16	0.258	0.110	A B	
4	14	0.208	0.113	B	
5	24	0.170	0.051	B	
6	2	0.200	0.014	B	
7	4	0.393	0.038	A	

Since the position of *M. tatricus* in a morphospace was so crearly unique, it was excluded from further analysis. CDA was repeated on the remaining 36 samples. The first two canonical axes explained 21 and 17% of the variance, respectively. All the samples overlapped broadly along the first canonical axis (Fig. 3). The second axis, however, to a certain degree separated the centroids of the samples of the two reference species. The position of the Eastern Alpine samples suggested closer affinities to *M. liechtensteini* than to *M. multiplex*.

A canonical discriminant analysis was also performed on the East Alpine samples alone. In total, 62% of the variance was explained by the first two canonical axes (38 and 24%, respectively). When scores for specimens were plotted (Fig. 4), the first axis separated *M. bavaricus* from the Austrian samples, although there was some overlap with the Austrian sample 2. The second axis separated sample 7 from the other samples. The percentage of specimens classified into the actual group ranged between 61% (sample 2) and 100%. Distance matrix and probabilities are given in Table 3.

A One Way ANOVA did not reveal a significant interlocality heterogenity (at $p < 0.01$) among the seven Eastern Alpine samples in the total length of M_1 and in the degree of development of its anterior part (Table 4). The means of the tilt of the pitymyan rhombus (PR) differed between samples ($p = 0.004$) and Scheffé's test showed that PR was less tilted in sample 7 than in samples 1 and 2. Samples differed significantly ($p < 0.001$) in the closure of the anterior loop, which was most opened in sample 7, followed by sample 3.

The general morphometry of M_1 and the analysis of M_1 parameters showed that: (1) Samples 1, 2, 5, and 7 were similar to, though not identical with *M. liechtensteini* and *M. multiplex*; (2) Samples 1–4 and 6–7 were closer to *M. liechtensteini* than to *M. multiplex*; (3) There was no strict consistency between the geographical provenance of the samples and their morphometric link with *M. liechtensteini* (sample 2 being closer to sample 5 than to samples 3 and 4); (4) Sample 1, *M. bavaricus,* was close to *M. liechtensteini* but showed morphological similarities also to *M. tatricus* (22% of *bavaricus* were classified as *tatricus*); (5) Samples 3 and 4 were comparable with *M. liechtensteini*; (6) Sample 7, however, was morphologically very different from the other samples (open anterior loop, only slightly tilted pitymyan rhombus), however, because of its small size (only 4 teeth), conclusions are tentative.

Discussion

The comparative morphological study of the M_1 of the seven Eastern Alpine samples showed them to be related to *M. liechtensteini* and *multiplex*, being closer to *liechtensteini*. This result was not unexpected as the Carinthian and Eastern Tyrolian samples (2–4) are situated near the northwestern border of the known Illyrian range of this species in Slovenia. This specific status of two of these populations (3, 4) had already been confirmed by karyological investigation (Král *et al.* 1978). It was less expected that all the other alpine isolates (including *bavaricus*) also showed clear relationships with *liechtensteini*.

The fact that the Austrian and Bavarian populations are not identical with *liechtensteini* from the Balkan peninsula, as described by Brunet-Lecomte and Kryštufek (1993), agrees with the intense interpopulational geographic variability in the karyotype, body, skull, and dental morphology of this species within the territory of the former Yugoslavia (sex chromosomes: Živković *et al.* 1975, Tvrtkovic *et al.* 1979; body measurements: Petrov and Živković 1979; body and teeth measurements: Kryštufek 1983, Brunet-Lecomte and Kryštufek 1993).

Similar to peripheral *multiplex* populations (*fatioi, druentius, niethammeri* – Brunet-Lecomte and Volobouev 1994), the Eastern Alpine *liechtensteini*-populations could be expected to display a high degree of differentiation from the nominate form as well as from each other. In accordance with this the seven samples were classified into 3 groups. The first consisted of *bavaricus* (sample 1) only. Differences from the nearest other northern alpine sample (5) were unexpectedly great. The morphometric analysis thus confirmed the marginal position of *bavaricus* in relation to other alpine *Terricola* voles. The second group represented populations belonging to *liechtensteini sensu stricto* from southwestern Carinthia and Eastern Tyrol (samples 3 and 4). These populations had already been assigned to *liechtensteini* by their karyotype. Sample 7 from the upper Enns valley in Styria formed the third group. It was morphologically the most different (open anterior loop, only slightly tilted pitymyan rhombus) from all the other samples, and the question of its systematic position requires further study.

Samples 2, 5, and 6 are difficult to classify. The Karawanken sample (2) was expected to be associated with *liechtensteini* populations 3 and 4 owing its geographic location, however, it showed some similarities to the otherwise isolated *bavaricus*. The Rofan mountain sample (5) is morphometrically somewhat similar to *liechtensteini* and *multiplex*, but surprisingly different from the geographically near *bavaricus*. Sample 6 (upper Mur valley, Salzburg) is represented by one individual only and can therefore not be assigned to one of the groups.

Nevertheless, the overall pattern is quite clear. There seems to be little doubt that the recent distribution of populations 1–7 indicates an earlier more extensive range of *M. liechtensteini*. The high degree of interpopulational variation is a further indication of the distinct relict character of these large Eastern Alpine *Terricola*. Already Kratochvíl (1970) and Kratochvíl and Král (1974) had suggested that *bavaricus* might have survived one or more glacials at its rather sheltered type locality. It should be noted that not only the populations from the northern edge of the Alps (1 and 5) but also population 7 in Styria are living in or very near the areas that had already been recognised by Merxmüller (1952) as (Würm) glacial refugia for higher plants at the northern edge of the Alps. The locality of sample 6 is situated in an area glaciated during the last ice age, but the voles could have reached their present range in the upper reaches of the River Mur at Tweng by postglacial colonization via the river valley, which was covered by a glacier reaching only as far as Judenburg (some 80 km from Tweng).

Acknowledgements: The authors wish to thank C. Leidenroth and F. Dieterlen, Staatliches Museum für Naturkunde in Stuttgart, and G. Storch, Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt/M. for the loan of *Microtus bavaricus* specimens of the type series and B. Herzig for taking the photographs of the teeth.

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Received 10 May 1999, accepted 20 November 1999.