

The status and use of *Terricola* FATIO, 1867 in the taxonomy of Palaearctic "pine voles" (*Pitymys*) (Rodentia, Arvicolinae)

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Abstract

The authors appraise the taxonomic validity of the arvicolid genus *Terricola*. From an examination of specimens from representative species of *Terricola*, and from a review of the literature, we conclude that the name *Terricola*, although both available and valid, should not be applied to European pine voles and, as is presently used, refers not to a monophyletic group, but only to a morphological assemblage of no systematic validity. **Key words:** Palaearctic - *Terricola* - *Pitymys* - voles - phylogeny - taxonomy.

Résumé

Les auteurs évaluent la validité taxonomique du genre arvicolide *Terricola*. Après examen des spécimens d'espèces représentatives de *Terricola* et après consultation des données de la littérature, nous concluons que le nom *Terricola*, bien que disponible et valable, ne doit pas s'appliquer aux campagnols souterrains européens et que, dans son acception actuelle, il se réfère non pas à un groupe monophylétique, mais seulement à un assemblage morphologique sans validité systématique. **Mots clés:** Paléarctique, *Terricola*, *Pitymys*, campagnols souterrains, phylogénie, taxonomie.

Introduction

Despite being well-known components of the Holarctic fauna, the taxonomy of the so-called "pine voles" (often ascribed to genus *Pitymys* MCMURTRIE, 1831) that inhabit the Western Palaearctic represents a long-standing source of conflict and confusion. Overt dissatisfaction with the lower-rank systematics of the Arvicolinae dates back at least to the first quarter of the Twentieth Century, when MILLER (1912) remarked that "the most conspicuous instance of discontinuous distribution in the sub-family" was that seen in *Pitymys*, a genus present in south-eastern North America, the Himalayan Sub-region, and in Western Eurasia.

The type species of *Pitymys* is *Pitymys pinetorum* (LE CONTE, 1830) from the eastern United States. Even there, however, opinions differ with regard to the status of *Pitymys*, which may be considered as a distinct genus (ZAKRZEWSKI, 1985) or as a congener of *Microtus*

SCHRANK, 1798 (ANDERSON, 1985). *Pitymys* itself is readily distinguished from *Microtus* by the so-called "pitymoid" structure of the first lower molar: *i.e.* the 4th and 5th molar triangles are widely confluent (Fig. 1). Outside North America, a "pitymoid" first lower molar can also be found in a number of vole species from Europe and adjacent parts of Asia, and these too have been placed in *Pitymys*, the name being used as either a genus (ELLERMAN & MORRISON-SCOTT, 1966; CORBET, 1978) or a subgenus (NIETHAMMER & KRAPP, 1982). However, BRUNET-LECOMTE & CHALINE (1992) and CHALINE *et al.* (1988) suggest that Nearctic and Palaearctic members of *Pitymys* do not share a common ancestor, and further suggest the use of the name *Terricola* FATIO, 1867 (as a subgenus of *Microtus*) to encompass species from the Western Palaearctic. This viewpoint has become widely accepted (e.g. BRUNET-LECOMTE, 1990; MUSSER & CHARLETON, 1993) although both MILLER (1912) and OGNEV (1964) had previously noted that *Terricola* had been used by FLEMING (1827) for a molluscan genus, with OGNEV (*op. cit.*) explicitly stating that *Terricola* FATIO, 1867 is a preoccupied name.

Availability of *Terricola*

The name *Terricola* was introduced by FLEMING (1827), but he gives it no formal taxonomic rank, nor does he provide diagnostic characters to define it. More specifically, on page 225 of his monograph, Fleming divides the gastropod molluscan subgroup Pulmonifera into two series: *Terricola* and *Aquatica*. Neither of the two are proposed as a genus (nor as any other formal ranking), nor was *Terricola* used as such in the author's later volume for the Encyclopaedia Britannica, "Molluscous animals" (FLEMING, 1842). *Terricola* FATIO, 1867 is thus both valid, and available. When considering *Terricola* FATIO, 1867 to be a junior synonym of *Terricola* FLEMING, 1828, both MILLER (1912) and OGNEV (1950, 1964) seem to have relied upon the opinion of AGASSIZ (1848), even though Fleming's name fails to appear in later indexes of zoological nomenclature (e.g. MARSCHALL, 1873; SCHULZE *et al.*, 1938; NEAVE, 1939).

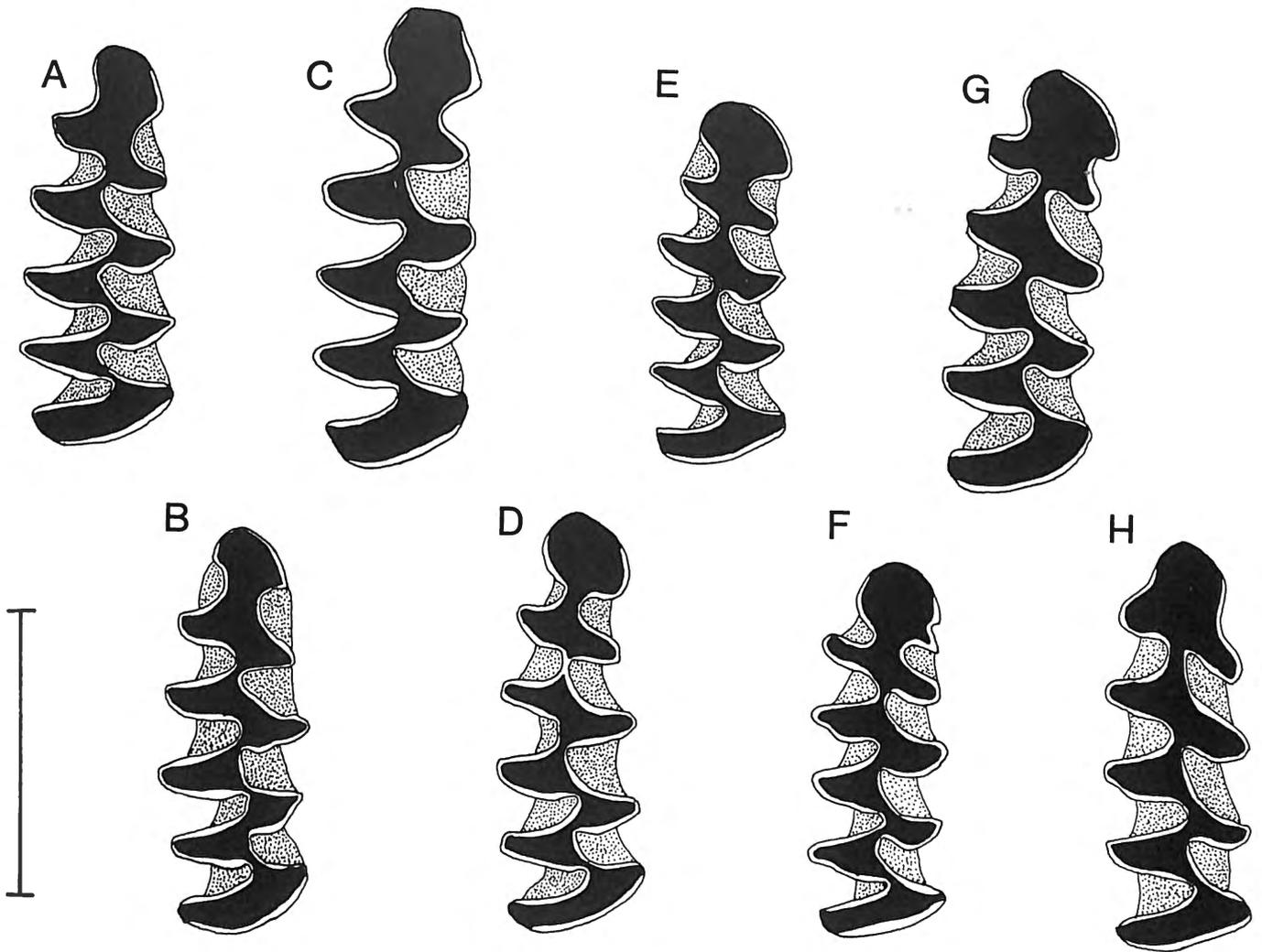


Fig. 1. – Variability in the enamel morphology of the right first lower molar of selected representative species of *Microtus* from the Western Palearctic (scale bar = 2 mm). (a) *Microtus arvalis*, Federal Republic of Yugoslavia, Montenegro, Žabljak (Durmitor Mts.), (b) *Microtus arvalis* (pitymoid morphotype), Croatia, spring of the Cetina River, (c) *Microtus guentheri*, Turkey, Cenik (near Burdur), (d) *Microtus tatricus*, Slovakia, Velika Fatra Mts., (e) *Microtus subterraneus*, Bosnia and Herzegovina, Mt. Bjelašnica above Sarajevo, (f) *Microtus savii*, Italy, Maiella Mts. (Caramanico), (g) *Microtus thomasi*, Federal Republic of Yugoslavia, Montenegro, Grahovo, (h) *Microtus duodecimcostatus*, France, Eyragues.

Application of *Terricola*

In the opinion of MILLER (1912), European *Pitymys* (as understood by him) was "... the genus of European voles which presents the greatest diversity of cranial and dental characters". In fact, the only character known to be shared by all members of the group is the "pitymoid" molar (Table 1), although this may also be expressed as a rare morphotype in species such as *M. arvalis* (PALLAS, 1778) (JANOSSY & SCHMIDT, 1960; KRYŠTUFEK, 1986). Other characters also said to be common to *Terricola* voles include the possession of five plantar tubercles, and reduction of the number of teats to two abdominal pairs. Unfortunately, examination of our own specimens (held in the collections of the Slovene Museum of Natural History, Ljubljana, and the Department of Systematic Zoology of Charles University, Prague) and consultation

with various published sources, reveal that these last two character states are unreliable (Table 1). Although possession of five plantar tubercles is common in *Terricola* spp., five tubercles is also common in *Microtus* (*Sumeriomys*) *socialis* (PALLAS, 1773) and its sister species (OGNEV, 1950), whilst six tubercles is the norm in *Microtus* (*T.*) *tatricus* (KRATOCHVÍL, 1952). Furthermore, reduction in the number of teats is unstable in *M. savii* and *M. subterraneus*, both of which may possess either two or three pairs (although two is more common) (see KRAPP, 1982; KRYŠTUFEK *et al.*, 1994), whilst at least one member of *Terricola* (*Microtus majori* THOMAS, 1906) normally carries an additional (third) pair of pectoral teats (NIETHAMMER, 1972).

The phenotypic diversity seen in *Terricola* suggests that it is unlikely that it is monophyletic, and recent studies provide further evidence for this. Palaeontological and

Table I: Expression of different diagnostic characters in European voles ascribed to *Terricola* FATIO, 1867

Species	Pitymoid lower M ₁	Pairs of teats (n)	Plantar pads (n)
<i>bavaricus</i> KÖNIG, 1962	+	2	5
<i>duodecimcostatus</i> DE SELYS-LONGCHAMPS, 1839	+	2	5
<i>felteni</i> MALEC & STORCH, 1963	+	2	5
<i>gerbei</i> GERBE, 1879	+	2	5
<i>liechtensteini</i> WETTSTEIN, 1927	+	2	5
<i>lusitanicus</i> GERBE, 1879	+	2	5
<i>majori</i> THOMAS, 1906	+	3	5
<i>multiplex</i> DE FATIO, 1905	+	2	5
<i>savii</i> DE SELYS-LONGCHAMPS, 1838	+	2/3	5
<i>subterraneus</i> DE SELYS-LONGCHAMPS, 1836	+	2/3	5
<i>tatricus</i> KRATOCHVÍL, 1952	+	2	6
<i>thomasi</i> BARRET-HAMILTON, 1903	+	2	5

electrophoretic data presented by CHALINE & GRAF (1988) and BRUNET-LECOMTE & CHALINE (1992) suggest either paraphyly or polyphyly, and karyological data led ZAGORODNYUK & ZIMA (1992) to state that the phenetic characters by which *M. tatricus* resembles other European members of *Terricola* could be the result of convergence. Furthermore, BRUNET-LECOMTE & NADACHOWSKI (in press) report that the structure of the first lower molar of *Microtus thomasi* BARRET-HAMILTON, 1903 differs significantly from that seen in other Mediterranean *Terricola*, including *Microtus duodecimcostatus* (DE SELYS-LONGCHAMPS, 1839), with which it had previously been considered to be either closely-related or conspecific (ELLERMAN & MORRISON-SCOTT, 1966). As a result, BRUNET-LECOMTE & NADACHOWSKI (*op. cit.*) suggest that *M. thomasi* BARRET-HAMILTON, 1903 probably represents an independent lineage within *Terricola*.

Conclusions

New evidence (e.g. BRUNET-LECOMTE & CHALINE, 1992) strongly suggest evolutionary convergence amongst voles displaying the "pitymoid" character, therefore these species cannot form a compact taxonomic group. Nevertheless, a stable, "pitymoid" first lower molar does

have some practical advantages: for example, its presence is of considerable assistance in the determination of taphonomically-altered material, such as specimens from Quaternary fossil assemblages and raptor pellets. Therefore the use of a term to accommodate those species exhibiting this character does have a certain logic, even though such "collective names" have no validity under the terms of the ICZN. Despite this, even though the name *Terricola* FATIO, 1867 is available, we believe that it is not proper to apply it to delineate all Western Palearctic voles with a pitymoid first lower molar. At present it probably does not represent a natural, monophyletic group, and its boundaries (and hence membership) cannot be readily defined (although it may eventually be shown to have some value in infrageneric systematics). The use of the term "pitymoid" should be similarly avoided, except perhaps as a technical term used in morphological studies, but, even then, only when used without any taxonomic implication.

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