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Variability in the number of tail vertebrae in four species of field mice (Rodentia: Muridae: *Apodemus*)

Variabilita v početnosti ocasních obratlů u čtyř druhů myšic (Rodentia: Muridae: *Apodemus*)

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Abstract. Variability in the number of tail vertebrae (TV) was investigated in 647 specimens of four *Apodemus* species (*A. flavicollis*, *A. sylvaticus*, *A. uralensis* and *A. witherbyi*) from the Czech Republic, Slovakia and Anatolia (Turkey). These species significantly differed in number of TV, but considerable overlapping did not enable reliable species identification. The number of TV increased in the order *A. uralensis*, *A. sylvaticus*, *A. witherbyi*, *A. flavicollis*, which is consistent with their supposed level of arboreality. In *A. uralensis*, significant differences were found among Bohemian, Pannonian and Anatolian samples. In contrast, there was no variation between Bohemian and Anatolian *A. flavicollis* or between two Bohemian samples of *A. sylvaticus*. There was no significant difference between *A. witherbyi* inhabiting forest and open habitats. Character displacement in *A. sylvaticus* occurring sympatrically with a stronger (*A. flavicollis*) or the weaker (*A. uralensis*) competitor was not demonstrated.

Key words. *Apodemus*, *Sylvaemus*, tail vertebrae, character displacement, Czech Republic, Anatolia.

INTRODUCTION

The mammalian tail possesses various functions, including mechanical, behavioural and physiological (see Bopp 1954 and Hickman 1979 for a review). In muroid rodents it has been well demonstrated that the tail is important balancing organ and that reducing its length considerably complicates certain movements, e.g. along above-ground narrow branches in *Mus musculus* Linnaeus, 1758 (Buck et al. 1925). The importance of a long tail has also been stressed in *Micromys minutus* (Pallas, 1771), a scansorial mouse inhabiting tall reeds and rushes of the north Palearctic (Piechocki 1958). Similarly, in the North American muroids *Peromyscus boylii* (Baird, 1855) and *P. truei* (Shufeldt, 1885), Smartt & Lemen (1980) found that the more arboreal individuals possess longer tails than less arboreal ones. Tail length has even been used as predictor of the degree of arboreality in individual populations of *P. leucopus* (Rafinesque, 1818) (Kaufman & Kaufman 1992). Also, petricolic rodents climbing in rocky fissures possess longer tails than their non-petricolic relatives. For example, the rock dwelling *A. mystacinus* uses its long tail not only as support but also as tactile organ (Mirić 1966). Similarly, the rock dwelling voles (genus *Chionomys*) have both absolutely and relatively longer tails (Gromov & Poljakov 1977).

There are also other factors affecting tail length, with ambient temperature being the most well known. According to Allen's rule, tails elongate with increased temperature, which has been documented both in laboratory mice and rats (e. g., Przibram 1925, Harrison et al. 1959) and in the wild (see Panteleev 1990 for a review).

Although tail length is one of the standard measurements recorded in the routine elaboration of captured mammal specimens, information on the number and variation of TV are rather scarce. This is surprising, because the number of TV is a simple meristic character which is stabile throughout the life of an individual, and in contrast to tail length it is not affected by measurement error.

In the genus *Apodemus* Kaup, 1829, relative tail length (expressed as the ratio: head plus body versus tail length) was previously commonly used for species identification (Heinrich 1951, Niethammer 1978a, b). However, this ratio is often strongly biased by various circumstances (e. g., *rigor mortis*, damage caused by snap traps, etc.). This is why some zoologists tried to express tail length by means of another meristic character – the number of the skin rings covering the tail surface (Wedemeyer 1936, Heinrich 1951). Later, it was found that due to large intraspecific variation, this character is inapplicable for reliable species identification. Only minimal attention has been focused on the number of tail vertebrae. The only information on their number in the literature was published by Niethammer (1978a, b) for a small number of *A. flavicollis* and *A. sylvaticus* from the vicinity of Bonn, Germany.

The aims of the present study were: (1) to evaluate interspecific differences in the number of TV in four *Apodemus* species and try to use them for species identification; (2) to ascertain the extent of intraspecific variation and to identify influencing factors; and (3) to demonstrate the existence of character displacement in cases of sympatric occurrence with other species.

MATERIAL AND METHODS

The number of tail vertebrae (TV) was studied in four species of field mice, *Apodemus*, subgenus *Sylvaemus* Ognev, 1924. In total, we evaluated 647 specimens of the follwing mice originating from the Czech Republic, Slovakia and Anatolia, Turkey. *A. flavicollis* (Melchior, 1834): AF NH – 73 spec. from the Novohradské Mts., S Bohemia, Czech Rep., altitude ca. 750 m, beech-spruce forest – for more information on the locality see Vohralík et al. (1972); AF AN – 56 spec. from Anatolia, alt. 100–2,300 m, localities: Adana, Yukarı Karafakılı, 8 km NW of Yenice, Abant Gölü, Kabaca, 4 km SE of Güzyurdu – for more information on localities see Kryštufek & Vohralík (2007). *A. uralensis cimrmani* Vohralík, 2002: AU BO – 40 spec. from the vicinity of Žatec, NW Bohemia, Czech Rep., alt. 270–300 m, a solely agricultural landscape, mice collected in the fields and their margins – for more information see Vohralík (2002). *A. uralensis microps* Kratochvíl et Rosický, 1952: AU MS – 23 spec. from the locality Dyjákovičky, distr. Znojmo, S Moravia, Czech Rep., alt. 220 m, banks of an irrigation canal between fields, and 21 spec. from the localities Buzica, distr. Košice-okolie, alt. 200 m, and Hraň, distr. Trebišov, SE Slovakia, alt. 100 m; in both localities mice were collected in strips of ruderal vegetation along field margins. *A. uralensis* ssp.: AU AN – 59 spec. from Anatolia, mice were collected in the forest habitats of the Black Sea Mts., alt. 400–2,250 m, localities: Uludağ, Hanyatak, Abant Gölü, 2 km E of Seyfe, Sumela, Cankurtaran Geçidı, Damar, Kabaca – for more information see Kryštufek & Vohralík (2007). *A. sylvaticus:* AS PR – 191 spec. from the City of Prague, Czech Rep., alt. 180–310 m – for more information see Frynta et al. 1994; AS BO – 93 spec. from the vicinity of Žatec, NW Bohemia, Czech Rep., altitude 270–300 m, solely agricultural landscape, mice collected in field margins. *A. witherbyi* (Thomas, 1902): AW AN – 91 spec. from Anatolia, a) forest habitats, alt. 500–2,400 m, 30 spec.: Yazlık, Feke, 3 km S of Sarıkamış, Tanır, 10 km SE of Çırpılar, Uludağ, Abant Gölü, 5 km N of Safranbolu, Kabaca, 10 km SW Aydoğlu; b) open habitats, alt. 120–2,600 m, 61 spec. (i.e., steppes, shrubs, rocks): Balkusan, Adana, Ballı, Doğanköy, 10 km NE of Bardakçı, Karabulut, 4 km SE Güzyurdu, 3 km W of Handere, 3 km N of Sirbasan, 2 km NE Derebük, 1 km N of Erence – for more information on localities see Kryštufek & Vohralík (2007).

In the Czech Republic, mice were collected between 1971 and 2000, in Slovakia in 2000, in Anatolia between 1993 and 1995. They were collected by snap-traps and processed by standard mammalogical methods (sexed, weighted, measured and later prepared as study skins and skulls). All the material is deposited in the collections of the Department of Zoology, Charles University.

The number of TV was counted in each skinned mice body under a stereomicroscope. The first tail vertebra was identified by the following method. The cranial end of the *os coxae* was established according to the thick white cartilage; we then identified the four vertebrae forming the *os coxae* (Niethammer 1978a, b), and the next vertebra was considered as the first one of the tail. Tail vertebrae were counted from the base to the tip; specimens possessing a visibly damaged or incomplete tail tip were not evaluated.

In *A. sylvaticus* from Prague, age of mice was assessed according the degree of tooth abrasion (method by Steiner 1968). Statistical analyses were run in Statistica 6.0.

RESULTS

Sex, age and altitudinal variability

Sexual dimorphism and age variability in the number of TV were studied in the set of *A. sylvaticus* from Prague. Values in males varied between 28 and 34, mean=31.35±SE 0.10 (n=99), in females between 27 and 33, mean=31.24±SE 0.11 (n=92); the differences were statistically non-significant (F=0.6, p=0.44).

For an evaluation of age variability, every specimen was placed into one of six age categories (1 – the youngest, 6 – the oldest). We compared three age groups: age categories 2 and 3, and the pooled categories 4, 5 and 6. Mean values in the number of TV were 31.26±SE 0.11 (n=82), 31.42±SE 0.21 (n=33) and 31.27±SE 0.18 (n=26), respectively. These differences were also statistically non-significant (F=0.3, p=0.73). Therefore, sexual dimorphism and age variability in the number of TV were not considered for any sample.

Altitudinal variability was analysed in Anatolian samples of *A. uralensis* and *A. witherbyi*. In both species, however, the number of TV was not correlated with altitude (*A. uralensis*: n=59, r=0.16, p=0.24; *A. witherbyi*: n=82, r=0.15, p=0.17).

Interspecific differences

The distribution of TV numbers in individual samples is given in Table 1 and Fig. 1, with the lowest number of TV in *A. uralensis* and increasing in the order *A. sylvaticus*, *A. witherbyi*, *A. flavicollis*. These relations apply both to the range variation and means (Table 1). The statistical evaluation of all eight samples showed highly significant differences (F=120.1, p<0.001), and similar results were obtained when samples of identical species were pooled and the four *Apodemus* species were compared (F=225.2, p<0.001). Although there were clear interspecific differences in TV number, the considerable overlap in ranges did not allow this character to be used in species identification.

Intraspecific variation

The comparison of individual samples (Table 1) revealed that in *A. sylvaticus* and *A.flavicollis*, there were no differences between geographically distant populations (F=0.1, p=0.78 and F=0.3, p=0.56, respectively). However, in the case of *A. uralensis* both means number and ranges of

TV differed considerably among the three evaluated samples (F=59.5, p<0.001). Values were highest in mice from Anatolia, medium in the pooled sample from Moravia and Slovakia, and lowest in the mice from Bohemia; means of TV were 30.85±SE 0.13, 29.89±SE 0.13, 28.93±SE 0.10, respectively, i.e. the differences were of nearly identical magnitude. It is also of interest that the two Central European samples differ considerably (F=32.3, p<0.001).

To test the influence of habitat, we divided Anatolian *A. witherbyi* into two samples according to the habitat in which they were collected (forest versus open habitat). Surprisingly, mice from open habitats possessed a slightly higher mean number of TV (31.90±SE 0.14) than mice from the forest (31.67±SE 0.21); however this difference was statistically non-significant (F=0.9, p=0.34).

Character displacement

Character displacement was studied in three samples of *A. sylvaticus* from the Czech Republic: 1. Prague: allopatric population, 2. Prague: sympatric with *A. flavicollis* and 3. Žatec: sympatric with *A. uralensis*. There were no statistically significant differences in number of TV (F=0.6, p=0.56) among populations living in either the absence (mean 31.24±SE 0.10) or presence

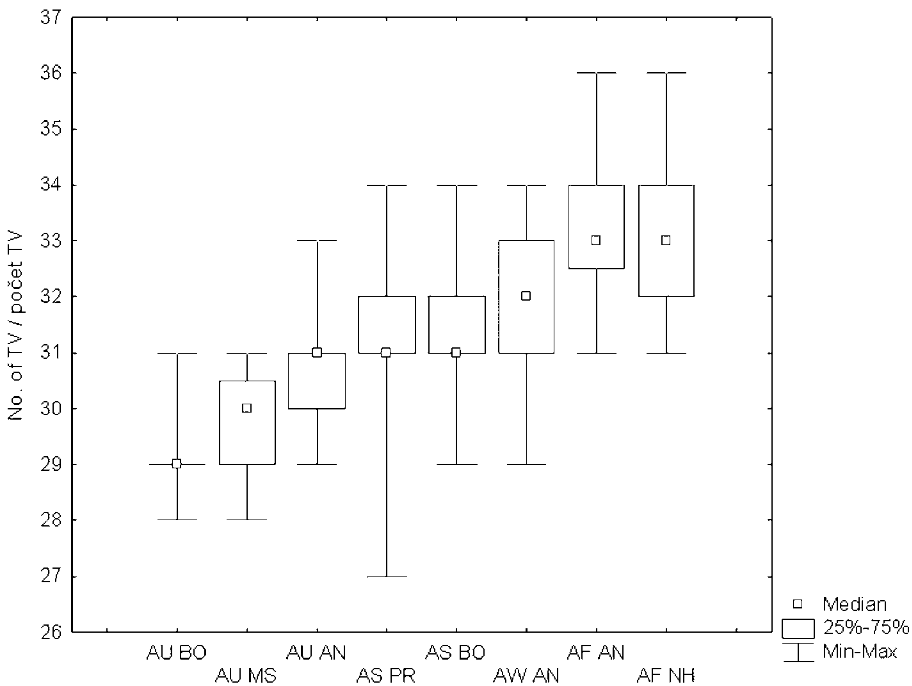

Fig. 1. Box plots of individual samples arranged according to increasing number of TV (for sample abbreviations see Material and methods).
Obr. 1. Jednotlivé vzorky seřazené podle vzrůstajícího počtu TV (zkratky vzorků uvedeny v kap. Material and methods).

Table 1. Variability in number of TV in the evaluated samples (for sample abbreviations see Material and methods)
Tab. 1. Variabilita v počtu TV u jednotlivých vzorků (zkratky vzorků uvedeny kap. Material and methods)

species / druh	no. of TV / počet TV 27	28	29	30	31	32	33	34	35	36	n	mean / průměr
AU BO	–	8	28	3	1	–	–	–	–	–	40	28.93
AU MS	–	4	8	21	11	–	–	–	–	–	44	29.89
AU AN	–	–	3	20	23	9	4	–	–	–	59	30.85
AS PR	1	1	3	32	71	65	17	1	–	–	191	31.30
AS BO	–	–	1	17	35	31	8	1	–	–	93	31.33
AW AN	–	–	2	7	25	34	17	6	–	–	91	31.82
AF AN	–	–	–	–	2	12	17	15	8	2	56	33.38
AF NH	–	–	–	–	3	16	19	17	12	6	73	33.51

of a stronger (*A. flavicollis*, mean 31.39±SE 0.11) or weaker competitor (*A. uralensis*, mean 31.33±SE 0.10).

DISCUSSION

The only published data on TV number in our studied species is from the vicinity of Bonn, Germany: *A. flavicollis* 33–36 (n=18), *A. sylvaticus* 31–34, mean=32.6 (n=20) (Niethammer 1978a, b). Ranges found in our samples were rather wider; however this may be due to the larger sample sizes. Means in both our samples of *A. sylvaticus* are lower (31.30 and 31.33) than those reported from Germany.

According to the literature, sexual dimorphism in *A. sylvaticus*, *A. flavicollis* and *A. uralensis* is negligible, with males being just a bit bigger (Amtmann & Amtmann 1965, Niethammer 1978a, b, Steiner 1978). The only exception was reported by Steiner (1978), who found body length and tail length slightly but significantly bigger in females in a sample of *A. uralensis* from Moravia. No sexual dimorphism was found with number of TV in our *A. sylvaticus* from Prague.

In the Alps, the mean number of TV increased with altitude in the bank vole (*Clethrionomys glareolus* (Schreber, 1780)) and the common shrew (*Sorex araneus* Linnaeus, 1758); populations from an altitude of 1,100 m had 1.0 (5.4%) and 1.2 (7.6%) higher numbers of TV than those from 620 m, respectively (Claude 1968). Our results of *A. uralensis* and *A. witherbyi* from Anatolia suggest a similar but very weak trend.

Interspecific differences in number of TV found in our samples are in good agreement with other differing morphological characters (body weight, body and skull measurements, brightness of the back coloration, etc.) commonly used in the species identification within the subgenus *Sylvaemus*, i.e., means and ranges increase in the order *A. uralensis* – *A. sylvaticus* – *A. witherbyi* – *A. flavicollis*. However, the considerable overlap in TV number prevents reliable species identification (cf. Steiner 1968, Niethammer 1969, Filippucci et al. 1996).

The link between length of tail and climbing ability has been demonstrated in North American muroids of the genus *Peromyscus* Gloger, 1841 (Smartt & Lemen 1980, Kaufman & Kaufman 1992). Similarly, interspecific differences in the number of TV found in our samples can be explained by the different degree of arboreality in these studied species. *A. flavicollis* and *A.*

sylvaticus are considered as relatively arboreal species (Kratochvíl 1968), with this behaviour being more pronounced in the former (Holišová 1969, Hoffmeyer 1973, Montgomery 1980). On the contrary, based on morphological characters, i.e. smaller eyes, shorter ears, shorter and less numerous *vibrissae mystaciales* (Kratochvíl 1968), and food composition (Holišová et al. 1962), *A. uralensis* seems to be more terrestrial. However, concerning ecological preferences, there is considerable discrepancy in descriptions of its favoured habitat. While in Central Europe and Ukraine it mainly occupies open habitats both in the lowland and above the forest belt of the mountains (Kratochvíl 1962, Mošanský 1962, Petrov 1979), in Russia and Turkey it is a typically woodland species (Gromov & Erbajeva 1995, Kryštufek & Vohralík 2007).

In *A. whiterbyi*, information on ecological requirements is scarce because the species was only recently recognized as a separate species (Filippucci et al. 1989, 1996, Kryštufek 2002). In Anatolia it has been collected in a wide spectrum of habitats, from the steppe, shrubs and isolated poplar stands, to extensive forests (Kryštufek & Vohralík 2007). Data on its climbing ability are completely lacking. According to our results (Fig. 1), it seems to be more praeadapted to climbing than the other studied species, with the exception of *A. flavicollis*.

From the species we evaluated, clear intraspecific differences were found only in *A. uralensis*. These differences could be caused by three basic possibilities (a) geographical distance, (b) the very different habitats in which mice were collected (i.e. forest vs. field) or (c) taxonomic differences among evaluated populations. Although the minimum geographical distance between two the Central European sample regions (ca. 190 km) is much lower than are those between the Central European and Anatolian ones (ca. 1,000 km), mutual differences in number of TV in all three samples are of similar rank. In contrast, mean numbers and ranges of TV in *A. flavicollis* from the Czech Rep. and Anatolia are nearly identical (means 33.43 and 33.38, respectively). Both of these facts cast doubt on the geographical hypothesis. Similarly, considerable differences in TV values of the two Central European field populations of *A. uralensis* do not support the habitat hypothesis. Also, the absence of a significant difference in the number of TV between *A. witherbyi* originating from forest versus open habitats does not support habitat as an explanatory factor. Concerning the taxonomic relations among the studied geographical samples of *A. uralenis*, considerable morphological differences in the skull and tooth characters found between the west Bohemian population and *A. u. microps* inhabiting the Pannonian lowland (including south Moravia and south Slovakia) has resulted in the former being described as a separate taxon – *A. u. cimrmani* (Vohralík 2002). Currently, there is no available information about taxonomic relationships between Anatolian and Central European *A. uralensis*. However, according to distributional maps (Mezhzherin 1997) it is evident that Anatolian populations originated from the Caucasus region, which suggests taxonomic and consequently also morphological distinctness from Central European ones.

In general, factors influencing variability in the number of TV in the studied *Apodemus* species still remains unclear. Neither habitat type nor simple geographic distance seems to be responsible. However, considerable interspecific as well as intraspecific differences in *A. uralensis* suggest that these variations are not random. Most probably, there exist other, as yet undiscovered factors.

The absence of character displacement in the number of TV in *A. sylvaticus* from Prague is congruent with results by Mikulová & Frynta (2001), who studied body as well as cranial measurements in Prague populations of this species occurring sympatrically with *A. flavicollis*. Similarly, Barčiová & Macholán (2006) were not able to demonstrate this phenomenon with the use of traditional and geometric morphometrics in four Bohemian localities with the sympatric occurrence of these two species. In addition, the sympatric occurrence of a smaller (i.e., possibly weaker) competitor, *A. uralensis*, did not provoke any changes in tail vertebrae number in *A. sylvaticus*. It may be that the relationships among these three *Apodemus* species are more complex than can be described by simply character displacement (cf. Dayan & Simberloff 1998).

SOUHRN

Určování západopalearktických druhů myšic z podrodu *Sylvaemus* na základě morfologických znaků již dlouhou dobu patří k nejobtížnějším úkolům evropské mammaliologie (Steiner 1968, Niethammer 1969, 1978a, b, Kryštufek & Vohralík 2007). U naprosté většiny dosud užívaných znaků byl zjištěn značný překryv, který znemožňuje spolehlivou druhovou identifikaci. Minimální pozornost však byla zatím věnována meristickým znakům. Takovým znakem je např. počet ocasních obratlů. V předložené práci byl hodnocen počet ocasních obratlů (TV) u 647 exemplářů čtyř druhů myšic (*Apodemus flavicollis*, *A. sylvaticus*, *A. uralensis* a *A. witherbyi*) pocházejících z České republiky, Slovenska a turecké Anatolie. Studované druhy se v počtu TV výrazně lišily, avšak značný překryv hodnot neumožnil jejich spolehlivé určení. Byl zaznamenán zvyšující se počet TV v řadě *A. uralensis* – *A. sylvaticus* – *A. witherbyi* – *A. flavicollis*, což je v souladu s předpokládanou mírou jejich arboreality. U pražského vzorku myšice křovinné (*A. sylvaticus*) nebyl prokázán pohlavní dimorfismus ani věková variabilita. U anatolských populací myšice malooké (*A. uralensis*) a myšice stepní (*A. witherbyi*) bylo zjištěno slabé, avšak statisticky neprůkazné zvýšení počtu TV s rostoucí nadmořskou výškou. U myšice malooké byly zjištěny značné rozdíly mezi českým, pannonským (jižní Morava a jižní Slovensko) a anatolským vzorkem. Naopak u myšice lesní (*A. flavicollis*) z Čech a Anatolie ani u myšice křovinné z Prahy a Žatecka nebyly zjištěny vnitrodruhové rozdíly. U myšice stepní byly srovnávány populace obývající lesní a otevřené biotopy v Anatolii, aniž byl mezi nimi zjištěn statisticky významný rozdíl. Posun znaků (character displacement) byl studován u populací myšice křovinné žijících společně s větší myšicí lesní na území Prahy a u populace obývající na Žatecku polní biotopy společně s menší myšicí malookou. V obou případech nebyl posun znaků prokázán.

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