

Bergmann's rule for *Neomys fodiens* in the middle of the distribution range

Research Article

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Abstract: The body size of Palearctic *Sorex* shrews decreases at higher latitudes, and as such the Bergmann's rule does not work. However, no analysis has ever been done for water shrew (*Neomys fodiens*) in the middle of distribution range. Analysis of available literature data showed that some body and skull measurements of *N. fodiens* are negatively correlated to latitude. Measurements of 158 water shrews from Estonia and Lithuania were also analyzed with respect to the short scale latitudinal pattern. We found that populations are separated (Wilk's lambda = 0.363, $p < 0.0001$). Differences are related to PC1 (skull size), explaining 49.80% of the variance and PC2 (body size), explaining 10.06% of the variance. Estonian shrews are smaller in their body and skull (most differences significant) and their skulls are relatively shorter and wider in the area of the brain case. Thus, the negative correlation of body and skull size to latitude in *N. fodiens* is applicable even over quite short latitudinal distances. Further analysis of diagnostic characters between *N. fodiens* and *N. anomalus* is required.

Keywords: Water Shrew • Latitude Dependent • Craniometrical Analysis • Lithuania • Estonia

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1. Introduction

The water shrew (*Neomys fodiens*) is a widely distributed species, inhabiting most of Europe and extending eastwards to reach Lake Baikal and NW Mongolia. The latitudinal distribution of the species in Europe covers an area from 40° N in Greece and 42° N in Spain to 70° N in Norway. Native to the Baltic countries of Lithuania, Latvia and Estonia [1], *N. fodiens* was the only species of the genus *Neomys* recorded in these countries until three *N. anomalus* individuals were identified in west Lithuania in 2009 [2].

In Lithuania and Estonia *N. fodiens* is quite widespread, but not common. It inhabits the shores of water bodies overgrown with trees, shrubs and dense weeds. It is sometimes trapped in reedbeds, meadows

and moist forests near water bodies, but is rarely trapped any great distance from the nearest water. In Estonia *N. fodiens* is also widespread on offshore islands.

It has recently been shown that Bergmann's rule (the body sizes of animals of warm-blooded species are larger in cold climates than in animals of the same species in warmer climates) does not work in the smallest of mammals, for example the body size of Palearctic shrews decreases at higher latitudes. This has been investigated in several species of g. *Sorex* [3,4]. For *N. fodiens*, no significant latitudinal size trend was found between 44° N and 53° N [5]. At higher latitudes however, no such analysis has ever been conducted for *N. fodiens*, despite the availability of data on body and skull measurements over quite a large geographic range in published sources.

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We tested the latitudinal pattern of body and skull parameters of *N. fodiens* to discover whether it conforms to Bergman's rule over the larger geographic area, using published material from the south to north of the range of the species, and also if it also works over shorter distances. Testing over the shorter distance was done using body and cranium measurements of *N. fodiens* from Lithuania and Estonia, countries that are in the middle of the latitudinal distribution range.

2. Experimental procedures

2.1 Material

For analysis of the relation of *N. fodiens* size to latitude, literature sources were analysed and data on mean, minimum and maximum values extracted [6–12]. Schematic representation of the locations for large scale analysis is given in Figure 1. Linear regression was employed for significantly correlated characters.

For the small scale analysis, 158 *N. fodiens* were used, collected between 1975–2013 in Lithuania, 54–56° N, (n = 105) and between 1980–2002 in Estonia, 57.5–59.5° N, (n = 53) (Figure 1). In the individuals where sex was determined, 49 were females (33 from Lithuania, 16 from Estonia) and 62 males (35 and 26 respectively). 38 individuals were adult shrews (19 and 19 respectively).

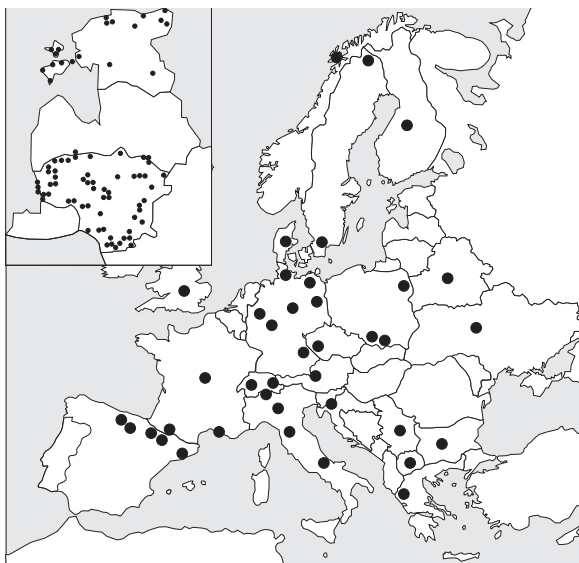


Figure 1. Location of data samples for large scale and small scale analysis. Data for large scale analysis from [5–11].

2.2 Methods

Five body and 18 skull, mandible and dental measurements were used. Body mass was measured with a Pesola or electronic balances to an accuracy of 0.1 g. Body, tail, hind foot and ear lengths were obtained using a vernier caliper to an accuracy of 0.1 mm. Eighteen craniometric measurements (Figure 2) were taken under a binocular microscope with an micrometric eyepiece or digital caliper, both graduated to 0.1 mm.

To minimize dispersion related to collection month, we did not use braincase depth measurement as it varies depending on the season [3]. While body weight

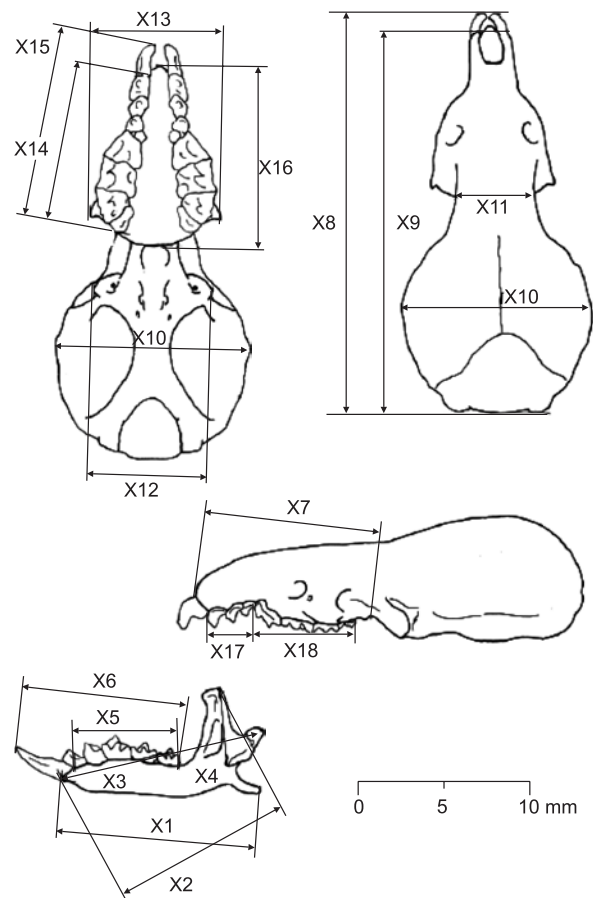


Figure 2. Skull measurements used for *N. fodiens* (according Peman 1983, Balčiauskas and Balčiauskienė 2012) Measurements: X1 – angular length of mandibula, X2 – coronoid length of mandibula, X3 – length of mandibula, X4 – height of coronoid process, X5 – length of mandibular tooth row, X6 – length of mandibular tooth row with incisive, X7 – rostral length, X8 – condyloincisive length, X9 – condylobasal length, X10 – cranial width, X11 – interorbital breadth, X12 – post-glenoidal width, X13 – zygomatic width, X14 – length of maxillary tooth row, X15 – length of maxillary tooth row with incisive, X16 – palatal length, X17 – length of the unicuspid tooth row and X18 – length of the molariform tooth row.

and lengths of the body, tail, hind foot and ear were measured by several collectors, all skull measurements were taken by a single person, thus minimizing potential error.

2.3 Statistical analysis

Differences between shrew samples for the small scale analysis were tested using ANOVA and Fisher's F statistics. Kolmogorov-Smirnov test was used to test the normality of character values. For analysis of variance, the difference of variation coefficient between countries was tested using Levene test for homogeneity of variance and One-way ANOVA to test if differences in the characters were associated with a geographic dependence of the sample. To test correctness of separation of individuals between countries of origin, we used discriminant analysis based on characters which were not sex-dependent. Skull measurement correction with respect to condylobasal length was also used. Small scale analysis was done using PCA, extraction of factors was based on eigenvalue >1 [13], and the two factors having the highest impact on between-country difference in *N. fodiens* were defined according to [14]. PCA combined different body, skull and dental

characters according to [5]. Prior to PCA, data were log₁₀ transformed to minimize variance [5]. All statistics were done in Statistica ver. 6.

3. Results

3.1 Latitude effect on *Neomys fodiens* size

After tabulating literature data on *N. fodiens* measurements across a wide latitudinal range to check if there was a relationship between measurements and latitude, we found several significant negative correlations (Table 1). From data representing latitudes between 40–42° N (Greece, Spain, Macedonia) and 65–69° N (Finland, Norway, N. Scandinavia), it could be concluded that the length of the tail was not related to latitude. Minimum hind foot length, minimum and mean of body length, minimum, average and maximum values of both condylobasal length and height of coronoid process were all negatively correlated to latitude, the dependence weak however (Table 1, Figure 3a,b).

The results of the small scale analysis show that the relationship between measurements and latitude is much stronger in the latitudes between 54–59° N (Lithuania

Table 1. Correlations (Pearson's *r*) of *Neomys fodiens* measurements with latitude (large scale analysis). Minimum, mean and maximum body and cranial measurements (sample size *n* = 28–44) obtained from literature sources [5–11].

	Minimum value	Mean value	Maximum value
Body length	-0.41; <i>p</i> = 0.011	-0.35; <i>p</i> = 0.053	-0.04; NS
Tail length	-0.04; NS	0.05; NS	0.19; NS
Hind foot length	-0.38; <i>p</i> = 0.022	-0.19; NS	0.23; NS
Condylobasal length	-0.34; <i>p</i> = 0.031	-0.31; <i>p</i> = 0.054	-0.40; <i>p</i> = 0.025
Height of coronoid process	-0.44; <i>p</i> = 0.019	-0.36; <i>p</i> = 0.018	-0.34; <i>p</i> = 0.073

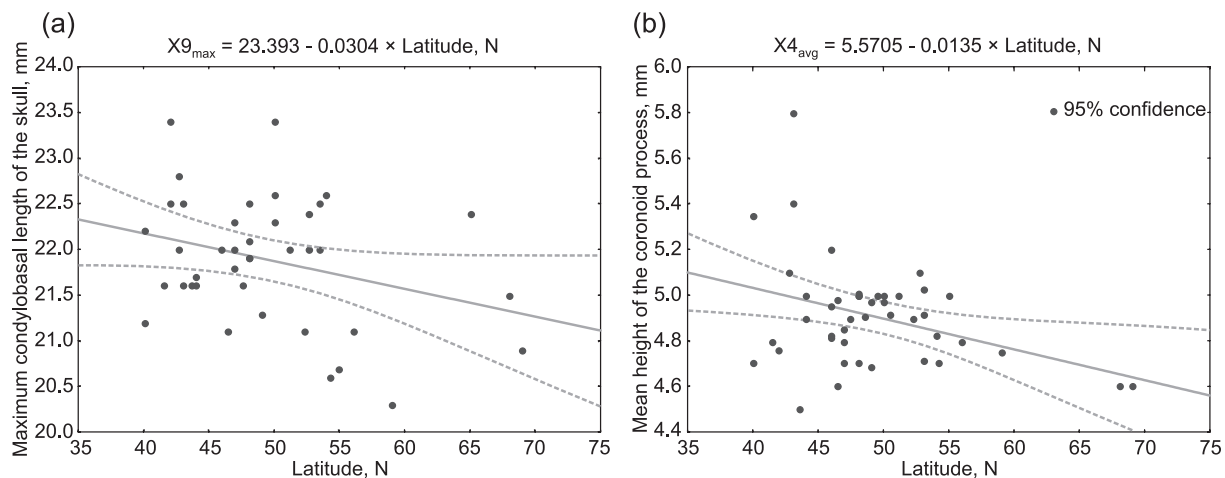


Figure 3. Dependence of *Neomys fodiens* body and skull measurements on latitude from large scale analysis. Maximum condylobasal length of the skull, mm (a), Mean height of the coronoid process, mm (b).

and Estonia). While correlations with body weight, tail and ear length were significant but weak (Table 2), all cranial and dental characters, with exception of palatal length, were significantly negatively correlated with latitude (Table 2, Figure 4a-d). It is important that one

of the diagnostic characters between *N. fodiens* and *N. anomalus*, the height of the coronoid process, is over 4 mm (Figure 4a) in the northern part of the investigated species range, as opposed to less than 4 mm in *N. anomalus*.

Table 2. Correlations (Pearson's *r*) of *Neomys fodiens* measurements with latitude (small scale analysis).

Character	Q	L	C	P	A	X1	X2	X3
<i>r</i>	-0.21	0.10	-0.18	-0.16	-0.28	-0.40	-0.42	-0.48
N	128	133	125	125	60	124	149	151
<i>p</i>	0.017	NS	0.047	0.080	0.033	<0.0001	>0.0001	<0.0001
Character	X4	X5	X6	X7	X8	X9	X10	X11
<i>r</i>	-0.70	-0.55	-0.45	-0.51	-0.55	-0.51	-0.51	-0.30
N	152	152	152	134	106	106	107	137
<i>p</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0004
Character	X12	X13	X14	X15	X16	X17	X18	
<i>r</i>	-0.48	-0.48	-0.50	-0.40	0.09	-0.30	-0.51	
N	132	130	149	144	101	152	150	
<i>p</i>	<0.0001	<0.0001	<0.0001	<0.0001	NS	0.0002	<0.0001	

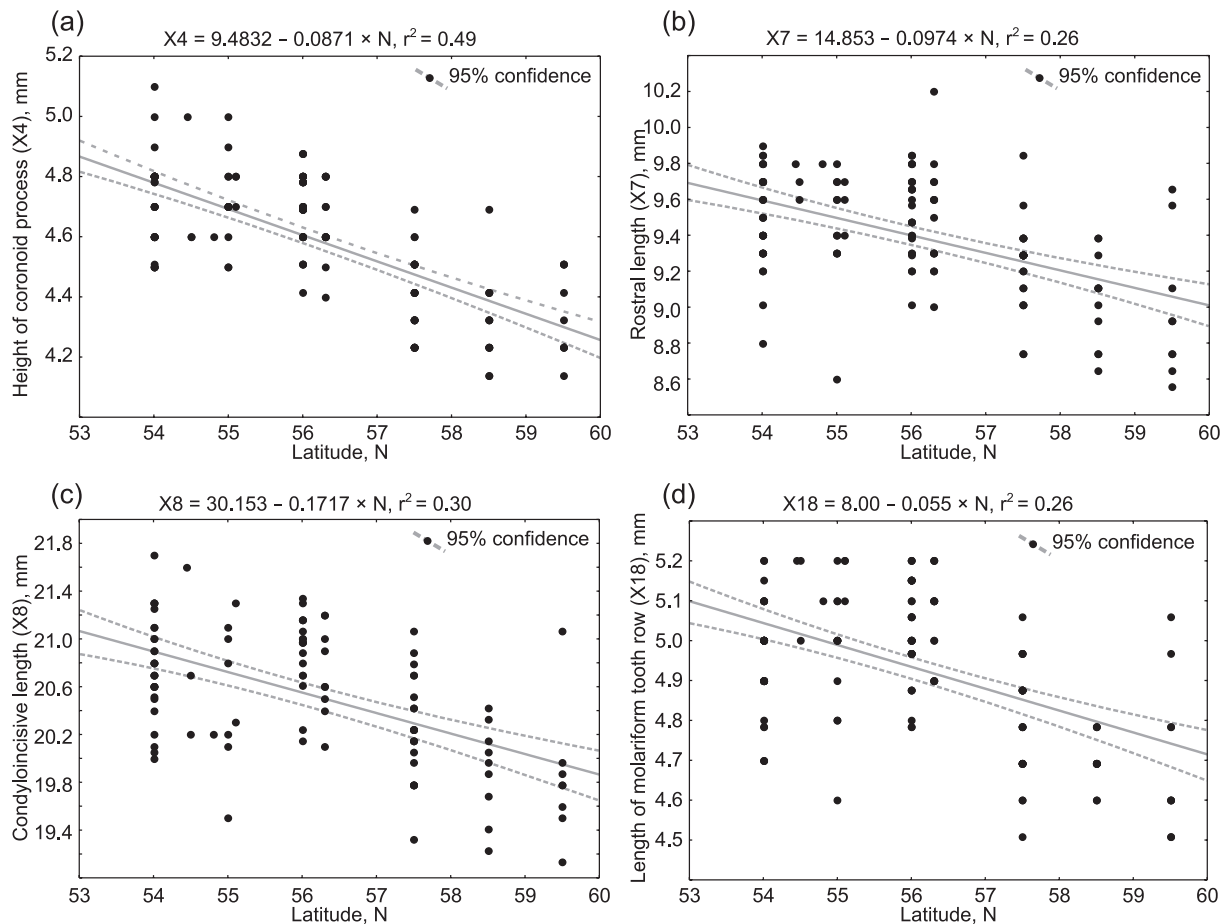


Figure 4. Dependence of *Neomys fodiens* body and skull measurements on latitude from small scale analysis.

3.2 Variability of body and skull size in *Neomys fodiens*

Most of the body and skull parameters in *N. fodiens* did not differ between males and females significantly, with the exception of the length of the mandibular tooth row ($t = 3.37$, $df = 108$, $p = 0.001$), the length of the mandibular tooth row with incisors ($t = 3.18$, $df = 108$, $p = 0.002$), the length of the maxillary tooth row ($t = 2.65$, $df = 108$, $p = 0.009$), palatal length ($t = 2.37$, $df = 73$, $p = 0.02$) and the length of the molariform tooth row ($t = 2.29$, $df = 108$, $p = 0.024$). In the further analysis, both groups (except the sex-dependent parameters) were treated as a single sample, thus increasing the sample size.

As already mentioned, measurements of body parameters were taken by several collectors, hence a high variation in the parameters was found. The variation coefficient (CV) of body length was 6.1% in Lithuania and 7.5% in Estonia, of tail length 7.1% and 7.6%, of hind foot length 4.2% and 4.2% and of ear length 18.4% and 13.1% respectively (none of differences significant). Between the countries, the CV differed for body weight (the CV for Lithuania 14.9%, for Estonia 26.6%, Levene test for homogeneity of variance, $F_{1,129} = 12.42$, $p = 0.0006$). Two other significant differences were interorbital breadth (3.7% and 2.6 respectively, $F_{1,141} = 4.81$, $p = 0.03$) and the length of the unicuspid tooth row (4.1% and 3.3% respectively, $F_{1,156} = 5.14$, $p = 0.024$). Variation of the skull parameters, other than already mentioned, in both countries was in the range of 3–4%, and the differences were not significant.

PCA analysis of variability of *N. fodiens* measurements revealed two factors with eigenvalue >1 , explaining 59.86% of the total variance, both related to animal size (Table 3). The first one is interpreted as skull size and includes cranial (rostral length, condyloincisive length, condylobasal length) as well as mandibular (coronoid length of mandibula, length of mandibula, height of coronoid process) characters, the second one is body size. All character-factor correlations are above 0.70 and highly significant.

3.3 Small scale differences

Most of the measured parameters had normal distribution. Difference from normal distribution was significant at 0.05 level for X7, X13, X17 and X18, at 0.01 for hind foot length, X4, X5 and X11 (Kolmogorov-Smirnov test). Means of all measurements and their statistics for both countries are given in Table 4. In all parameters, Estonian *N. fodiens* were smaller, and most

Table 3. Factor loadings, eigenvalues and explained variance for *Neomys fodiens*, small scale analysis. Sex-dependent characters not analysed, significant scores in bold. Characters as in Figure 2, those with factor loadings <0.70 are omitted.

Character	Factor1	Factor 2
Log ₁₀ Q	-0.4410	-0.7365
Log ₁₀ L	-0.1941	-0.7861
Log ₁₀ X2	-0.7971	-0.0203
Log ₁₀ X3	-0.8352	-0.0352
Log ₁₀ X4	-0.7958	0.0058
Log ₁₀ X7	-0.8079	0.1588
Log ₁₀ X8	-0.8382	0.2345
Log ₁₀ X9	-0.8300	0.2342
Log ₁₀ X10	-0.7311	-0.0432
Log ₁₀ X12	-0.7443	-0.1014
Log ₁₀ X13	-0.7612	-0.1552
Log ₁₀ X15	-0.7198	0.2614
Eigenvalue	7.470	1.508
% of total variance	49.80	10.06

of the differences are significant. Non significant were just differences in body length ($F_{1,133} = 1.41$, $p = 0.24$), ear length ($F_{1,59} = 0.00$, $p = 0.96$) and palatal length ($F_{1,103} = 2.77$, $p < 0.10$).

Distribution of the measurements and discriminant analysis show that *N. fodiens* populations are separated at the small scale (Wilk's lambda = 0.363, $F_{14,143} = 17.88$, $p < 0.0001$). The percentage of correctly classified shrews of Lithuanian origin is 94.3%, while of Estonian origin is 83.0%. Examples of separation based on body mass and cranium measurements at the small scale distance is shown in Figure 5.

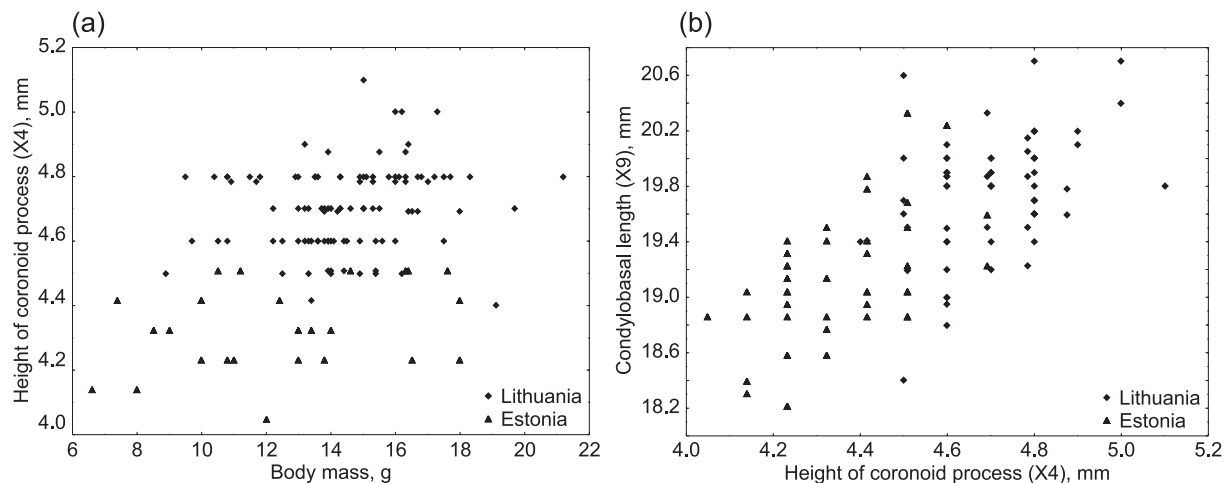
Correction of skull measurements, carried out by dividing the skull measurements by its condylobasal length, yielded a reduction in the number of significant differences between countries (Table 5). No differences in the corrected lengths were found mainly in characters defining skull width (X10–X13) and length of the rostral part of the skull (X15–X17). There were also no differences in the mandibular parameters X1 and X6. Generalizing, skulls of Estonian *N. fodiens* were relatively shorter and wider in the area of brain case.

4. Discussion

It is known that 67% of mammalian species display size trends which conform to Bergmann's rule [15], but those with a body weight between 4 and 500 g have a lower tendency to conform. Body mass responds to Bergmann's rule better than linear or dental measurements [16]. It has

Table 4. Body and skull measurements of *Neomys fodiens* from Lithuania and Estonia. Differences by ANOVA (Fisher's F). X1–X18 as in Figure 1

	Lithuania		Estonia		Difference
	mean±SE	Min–max	mean±SE	Min–max	
Q	14.51±0.21	8.90–21.20	12.38±0.65	6.6–18.0	$F_{1,128}=15.85, p<0.0001$
C	61.78±0.47	50.50–73.10	59.31±0.71	48.0–68.0	$F_{1,125}=8.35, p<0.005$
P	18.03±0.08	16.30–19.60	17.53±0.12	16.0–19.0	$F_{1,126}=12.30, p<0.001$
X1	10.17±0.04	9.00–11.00	9.75±0.06	8.8–10.7	$F_{1,126}=36.11, p<0.00001$
X2	9.08±0.03	8.30–10.10	8.66±0.05	7.9–9.7	$F_{1,152}=54.80, p<0.00001$
X3	10.66±0.03	9.50–11.80	10.20±0.04	9.3–10.8	$F_{1,154}=64.07, p<0.00001$
X4	4.71±0.01	4.40–5.10	4.34±0.02	4.0–4.7	$F_{1,155}=241.24, p<0.00001$
X5	6.15±0.01	5.60–6.53	5.87±0.02	5.4–6.3	$F_{1,155}=108.88, p<0.00001$
X6	9.09±0.02	8.40–9.70	8.74±0.04	8.1–9.4	$F_{1,155}=65.87, p<0.00001$
X7	9.51±0.03	8.60–10.20	9.12±0.04	8.6–9.8	$F_{1,137}=66.72, p<0.00001$
X8	20.76±0.05	19.50–21.70	20.04±0.07	19.1–21.1	$F_{1,109}=68.16, p<0.00001$
X9	19.75±0.05	18.40–20.70	19.14±0.07	18.2–20.3	$F_{1,109}=47.64, p<0.00001$
X10	10.56±0.03	10.03–11.13	10.14±0.05	9.4–10.9	$F_{1,110}=57.20, p<0.00001$
X11	4.29±0.02	3.86–4.70	4.20±0.02	3.9–4.4	$F_{1,140}=13.50, p<0.0005$
X12	6.10±0.02	5.80–6.40	5.90±0.02	5.6–6.3	$F_{1,135}=48.49, p<0.00001$
X13	6.56±0.02	6.07–7.00	6.26±0.03	5.8–6.5	$F_{1,132}=58.49, p<0.00001$
X14	8.22±0.03	7.50–8.65	7.86±0.03	7.5–8.5	$F_{1,152}=73.22, p<0.00001$
X15	9.60±0.03	8.90–10.20	9.26±0.04	8.7–9.9	$F_{1,147}=51.56, p<0.00001$
X17	3.06±0.01	2.80–3.40	2.96±0.01	2.7–3.1	$F_{1,155}=24.21, p<0.00001$
X18	5.00±0.01	4.60–5.20	4.75±0.02	4.5–5.1	$F_{1,153}=121.09, p<0.00001$

**Figure 5.** Divergence of *Neomys fodiens* body and skull measurements in small scale analysis. Height of coronoid process vs. body mass (a) and condylbasal length vs. height of coronoid process (b).

also been shown that food supply and availability at the different latitudes, temperature regimes in summer and winter and other factors (altitude, time of collection) may be involved [17–21]. In this paper we do not pretend to analyze factors other than geographical position on the south-north axis, *i.e.*, latitude. However, we concede that not all published data may be directly comparable,

as some authors used direct measurements such as body weight or condylbasal length of the skull, while others used residuals or corrected measurements (“controlled” according to [4]) or principal components [3,5,10,20–23].

Shrews, as the smallest terrestrial mammals, are good examples of an exception to Bergmann's rule. Five

Table 5. Skull measurements of *Neomys fodiens* from Lithuania and Estonia, corrected by condylobasal length of the skull. Differences by ANOVA (Fisher's F). X1–X18 as in Figure 1

	Lithuania		Estonia		Difference
	mean±SE	Min–max	mean±SE	Min–max	
X1 _c	0.510±0.009	0.00–0.56	0.506±0.002	0.47–0.53	F _{1,88} =0.05, NS
X2 _c	0.459±0.002	0.42–0.49	0.451±0.002	0.43–0.48	F _{1,108} =10.53, p<0.002
X3 _c	0.541±0.002	0.51–0.58	0.532±0.002	0.49–0.55	F _{1,108} =10.36, p<0.002
X4 _c	0.238±0.001	0.22–0.26	0.228±0.001	0.21–0.24	F _{1,109} =64.47, p<0.00001
X5 _c	0.312±0.001	0.29–0.33	0.306±0.001	0.29–0.32	F _{1,108} =21.72, p<0.00001
X6 _c	0.461±0.001	0.42–0.48	0.455±0.002	0.43–0.47	F _{1,108} =8.96, p<0.004
X7 _c	0.482±0.001	0.46–0.51	0.476±0.001	0.46–0.50	F _{1,104} =10.20, p<0.002
X8 _c	1.052±0.002	1.01–1.08	1.047±0.002	1.02–1.07	F _{1,108} =3.23, p<0.10
X10 _c	0.536±0.002	0.49–0.56	0.533±0.002	0.50–0.58	F _{1,100} =0.98, NS
X11 _c	0.217±0.001	0.20–0.23	0.219±0.001	0.21–0.23	F _{1,108} =2.55, NS
X12 _c	0.309±0.001	0.29–0.33	0.309±0.001	0.29–0.32	F _{1,105} =0.01, NS
X13 _c	0.330±0.002	0.20–0.35	0.328±0.002	0.30–0.34	F _{1,94} =0.39, NS
X14 _c	0.417±0.001	0.38–0.43	0.411±0.002	0.38–0.43	F _{1,109} =9.08, p<0.005
X15 _c	0.487±0.001	0.45–0.51	0.484±0.002	0.46–0.51	F _{1,105} =1.67, NS
X16 _c	0.474±0.003	0.43–0.51	0.483±0.002	0.46–0.50	F _{1,73} =6.08, p<0.02
X17 _c	0.155±0.001	0.14–0.17	0.155±0.001	0.14–0.17	F _{1,109} =0.01, NS
X18 _c	0.253±0.001	0.24–0.26	0.248±0.001	0.23–0.26	F _{1,109} =27.51, p<0.00001

out of six studied *Sorex* species, the common shrew (*S. araneus*), the pygmy shrew (*S. minutus*), the tundra shrew (*S. tundrensis*), the Laxmann's (masked) shrew (*S. caecutiens*) and the masked shrew (*S. cinnereus*) do exhibit size depression in higher latitudes, while the taiga shrew (*S. isodon*) does not [3,4].

Not conforming to Bergmann's rule, both *N. fodiens* and *N. anomalus* are larger in the southern parts of the range. For *N. anomalus*, this was shown by [5], and we found a negative correlation of body and skull size to latitude in *N. fodiens*. Even over quite short latitudinal distances, the sizes of both shrew species significantly differ. For *N. anomalus*, it has been shown in Turkey (Thrace and Anatolia, difference 3.5° N) that individuals from more southern populations exhibited larger body and skull measurements than individuals from more northern populations [24]. In Spain, comparing two populations in the most southern part of the distribution range (Catalonia and Navarre), the skulls of *N. fodiens* from the sample more to the north were larger in most characters, excluding three skull base characters [10]. On the other hand, no latitudinal size pattern was found in *N. fodiens* along a transect from Bosnia and Herzegovina to Poland [5].

According to [25], morphological differences should reflect differences in resource use, mainly relating to the

efficiency of food gathering and processing. The role of resources was also considered by [19]. Though resources and feeding of shrews were not investigated in Lithuania and Estonia, we may expect resources to diminish to the north. For example, the number of species of Tipuloidea (the larvae of water-living Diptera reported as food [26]) decreases to the north: in the case of the smaller Limoniidae, the number of species drops from 201 in Lithuania to 81 in Estonia, where in the bigger Tipulidae, the respective figures are 96 to 61 [27]. Along with a decrease in the mean annual temperature from 6.0°C in Lithuania to 5.1°C in Estonia [28], both factors may have an influence on morphological differences. However, this is a preliminary statement which needs additional investigation.

Concluding, we found that *N. fodiens* does not conform to Bergman's rule. In the full range of the species, the non-conformance is less expressed than over the shorter geographic distance between 54–53° N: Estonian shrews are significantly smaller than Lithuanian ones in body size and cranial measurements. Having in mind that *N. anomalus* was only recently discovered in Lithuania [2], the body size of the two *Neomys* species, both not conforming to Bergmann's rule, requires further analysis of the diagnostic characters of *N. fodiens* and *N. anomalus*, possibly using skull collections from Belarus and the western part of Russia.

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