

A Revised Classification of the Japanese Red-backed Voles

By

Mitsuru AIMI

Primate Research Institute, Kyoto University, Inuyama, Aichi 484

(Received June 18, 1979)

CONTENTS

Introduction	35
History of the Classification of the Japanese Red-backed Voles	36
Material and Methods	38
Secondary Sexual Difference	45
Systematic Accounts	47
Key to the species of the Japanese red-backed voles	47
Genus <i>Eothenomys</i>	48
<i>Eothenomys andersoni</i>	48
<i>Eothenomys smithi</i>	56
Genus <i>Clethrionomys</i>	62
<i>Clethrionomys rufocanus bedfordiae</i>	62
<i>Clethrionomys rutilus mikado</i>	69
Cranial comparison among species of <i>Clethrionomys</i>	71
Cranial comparison among the Japanese red-backed voles	72
Phylogenetic Relationship of <i>Eothenomys andersoni</i>	74
Dental morphology	75
Bacular morphology	76
Ectoparasites	76
Comparative karyology	78
Fossil evidence	78
General conclusion	79
Summary	80
Acknowledgments	80
References	81

Introduction

Red-backed voles are microtine rodents with a bony palate terminating in a simple shelf. In Japan, they are distributed in Hokkaido, Honshu, Shikoku, Kyushu,

and adjacent islands. In 1905 Thomas gave the first description of the Japanese red-backed voles *Evotomys* (= *Clethrionomys*) *smithii*, *E. bedfordiae*, *E. andersoni*, and *E. mikado*.

Recently there has been much debate not only on the specific division but also on the generic allocation of the Japanese red-backed voles, consequently there are many rival classifications for this group. For the voles of Hokkaido and its adjacent islands there are three different suggestions as to the specific division; that they should be divided into two species (Ota, 1956; Abe, 1968), into three species (Abe, 1973a, b) or into four species (Imaizumi, 1972). For the voles of Honshu, Shikoku, and Kyushu, it has been held that they should be divided into two species (Tokuda, 1941) or into five species (Jameson, 1961). Furthermore, there are three different opinions as to the generic allocation of *andersoni*, one placing it in the genus *Clethrionomys* (Tokuda, 1941), another in the genus *Aschizomys* (Imaizumi, 1965), and a third in the subgenus *Aschizomys* under the genus *Clethrionomys* (Jameson, 1961).

The wide diversity of classifications presented by these authors is based at least in part on an equally wide diversity of opinions about the geographic variation and phyletic relationships of the Japanese red-backed voles. Therefore, it is clear that a detailed study of the geographic variation of these voles is needed to elucidate the evolutionary relationships among them. The purpose of the present study was to propose a new classification of the Japanese red-backed voles and to elucidate their evolutionary relationships.

A large number of specimens from various localities were examined to elucidate the geographic variation statistically. Geographic variation was analysed on the basis of craniometry and comparison of occlusal patterns of the molars, both being important characters for the classification of mammals. Cranial dimensions were compared allometrically among the collections.

A difference will be found between the mean values of almost any two populations if the samples are sufficiently large. In other words, no two natural populations are identical. Therefore, the presence of such a difference in itself is of little value in terms of taxonomy, but if the means vary clinally from population to population then this variation may possibly throw light on the recognition of the species.

Phylogenetic relationships of the Japanese red-backed voles will be discussed on the basis of dental morphology, bacular morphology, ectoparasites, comparative karyology, and fossil evidence.

History of the Classification of the Japanese Red-backed Voles

Thomas (1905a) described *Evotomys* (= *Clethrionomys*) *smithii* and subsequently he (1905b) added another three species, *E. bedfordiae*, *E. andersoni*, and *E. mikado*,

to the genus. Anderson (1909) added one species, *Craseomys*(=*Clethrionomys*) *niigatae*, to it.

Hinton (1926) critically reviewed the former classification. He concluded that *Evotomys smithii*, *E. "bedfordiae,"* *E. "andersoni,"* and *E. "niigatae"* belong to one form. His discussion was as follows: "*E. (Phaulomys) smithii* was based upon a young male. Later on Mr. Anderson collected thirteen in Hokkaido. The majority of these are adult, some even old; in size, skull form, and tooth pattern they are strikingly different from the material referred by Thomas to *E. smithii*. These were therefore described as a new species, *E. (Craseomys) bedfordiae*. In the same paper *E. (C.) andersoni* was described, from two specimens obtained in North Hondo, as 'very like *bedfordiae* externally, but with longer tail, and much less powerful teeth.' Both specimens, however, are merely large adolescents, intermediate in age between the adult material upon which *E. bedfordiae* was established and the immature material referred to *E. smithii* — hence the less powerful teeth as compared with *E. bedfordiae*. Lastly, Anderson's *E. niigatae* also has been founded upon an adolescent animal, its tail, though long averaging about 61 mm in a series of seven, can be matched quite well in the series referred to '*bedfordiae*' and '*smithii*,' and no other character can be found to give it the slightest support. On laying out all the skulls from Japan, whether labelled as '*smithii*,' '*bedfordiae*,' '*andersoni*,' or '*niigatae*,' in order of age, we find that the whole series forms an exact parallel to the series formed by the skulls of *E. r. rufocanus*, *E. r. shanseius*, and *E. r. regulus* when similarly arranged."

This classification has been followed by Ellerman (1941), Ognev (1950), Ellerman and Morrison-Scott (1951), and Rensch (1959). Kuroda (1931) examined Hinton's classification on the basis of a new specimen from Mt. Yarigatake, central Honshu. His conclusion was that at least *niigatae* was distinct from *bedfordiae* by its longer tail, more rounded occlusal pattern of molars, and range of distribution. He placed *niigatae* as a subspecies of *rufocanus* called *Evotomys rufocanus niigatae*. Hanaoka (1937) collected twelve new specimens from Mt. Yatsugatake, central Honshu and concluded that *niigatae* was a synonym of *andersoni*, classifying it as *Clethrionomys rufocanus andersoni*. Moreover, he made a comparison among *andersoni*, *bedfordiae*, and *smithii*, and claimed that they were distinct from one another by their structure of skull, tooth pattern, tail length, and range of distribution. He classified them as *Clethrionomys rufocanus andersoni*, *C. r. bedfordiae*, and *C. r. smithii*, respectively. Tokuda (1941) agreed with Hanaoka (1937) in general, except in the case of *andersoni* which he raised to a distinct species, *Clethrionomys andersoni*.

Imaizumi (1960) recognized *niigatae* as a species distinct from *andersoni* by its tail length, skull structure and molar pattern, but he placed them in *Aschizomys* not in *Clethrionomys* because of their rootless molars and dental pattern. Jameson (1961) agreed with Imaizumi (1960) that *andersoni* and *niigatae* were two distinct species.

He placed them together with *bedfordiae* and *imaizumii*, a new species, in *Aschizomys* which he regarded as a subgenus under the genus *Clethrionomys*. He wrote: "If I am correct in presuming that very old specimens of *Aschizomys lemminus* will tend to develop roots on the molars, then *Aschizomys* is more appropriately placed with *Clethrionomys*. Inasmuch as a few old individuals of *rufocanus* and *niigatae* have partly rooted molars, it seems best to place *Aschizomys* as a subgenus under *Clethrionomys*." Aimi (1967) examined two new specimens from Kii Peninsula, Honshu, and concluded that *imaizumii* should be placed as a subspecies of *andersoni*, i. e. *Clethrionomys andersoni imaizumii*, by reason of its possessing few distinct characteristics other than its isolated distribution.

Imaizumi (1957) described a new species of the genus *Eothenomys*, *E. kageus*, on the basis of the peculiarity in the number of mammae. In *kageus* there are two pairs of mammae, while in *smithi* three pairs. However, Miyao et al. (1964) disagreed with Imaizumi (1957) in this respect and regarded *kageus* as a synonym of *smithi* from the fact that two kinds of specimens were found from the same locality of Mt. Yatsugatake: one had two pairs of mammae and the other three pairs. Miyao (1967) stated an opinion opposite to that of Imaizumi (1957), "Number in mammae varies from two to four pairs in this form. ... *smithi* shows the tendency to decrease the number of mammae from four to two, and it is in the extreme in the central part of Honshu. ... It is clear that Imaizumi's (1957) division of this form into two, based on the difference in the number of mammae, is invalid." Tanaka (1971) examined the morphological variation of this group collected around Mt. Tsurugi, Shikoku. He concluded that *kageus* was a synonym of *smithi*, and placed it in *Phaulomys*, originally established by Thomas (1905a) for *smithi*, as *P. smithi*.

Recently Imaizumi (1971) described a new species which was collected on the Rishiri Island, off the northwestern coast of Hokkaido, and named it *Clethrionomys rex*. In addition to this, Imaizumi (1972) described another new species, *Clethrionomys montanus*, collected from Mt. Poroshiri, Hokkaido, and in the same paper he raised *bedfordiae* to a distinct species and classified it as *C. bedfordiae*.

Material and Methods

The material observed in the present study was collected from the field with the aid of snap-traps. Sites of collection and other data are shown in Figure 1 and Table 1 respectively.

Locations of specimens are abbreviated as follows:

- HA, Hisashi Abe, private collection
- MA, Mitsuru Aimi, private collection
- MK, Masaomi Kanamori, private collection

TM, Takeo Miyao, private collection
 YF, Yuzo Fujimaki, private collection
 YIO, Yamashina Institute of Ornithology

Measurements, in millimeters to the nearest 0.1 mm, were made by means of dial calipers on the following eight dimensions in all skulls (Fig. 2):

1. Nasal length — greatest length of nasals along median suture.
2. Rostral width — width across lateral surfaces of rostrum on roots of incisors.

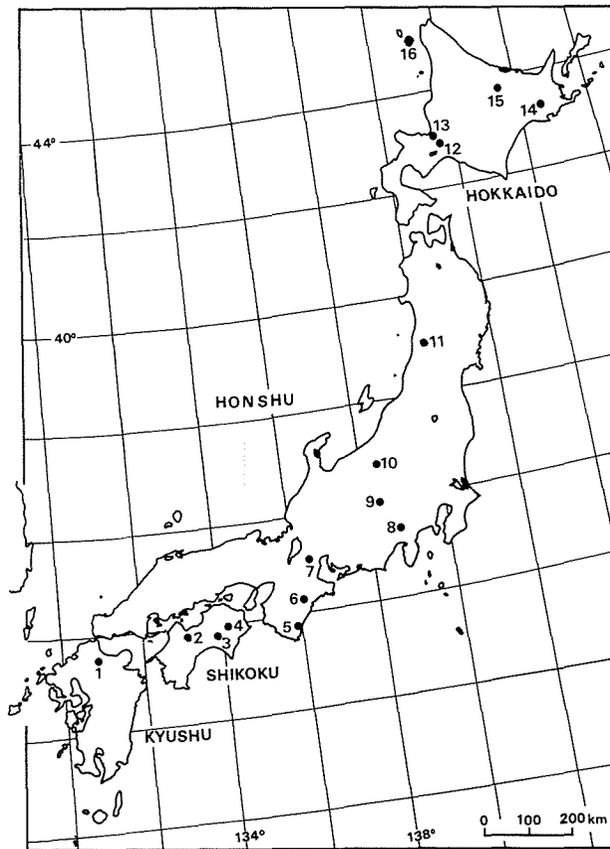


Figure 1. Location map of the collection sites in Japan.

1: Mt. Hiko; 2: Mt. Kamegamori; 3: Ohtaki; 4: Mt. Tsurugi;
 5: Nachi; 6: Mt. Ohdaigahara; 7: Mt. Gozaisho; 8: Mt. Fuji;
 9: Mt. Yatsugatake; 10: Shiga Heights; 11: Mt. Chokai; 12:
 Nopporo; 13: Ishikarifutomi; 14: Shibeche; 15: Oketo; 16:
 Rishiri Is.

Table 1. List of material examined.

a) *Eothenomys andersoni*

Locality	Date	Sex			Location of specimens*
		Male	Female	Unknown	
Nachi	'65. Dec.	0	1	0	MA
	'66. Apr.	0	1	0	MA
Mt. Ohdaigahara	'69. Aug.	1	0	0	MA
Mt. Yatsugatake	'62. Apr.-Dec.	75	60	0	TM
	'63. Jan.-Oct.	125	89	0	TM
	'67. Jun.	9	12	0	MA
Shiga Heights	'67. Oct.-'72. Sep.	11	10	0	MK
Mt. Chokai	'66. Sep.	3	6	0	MA
	'73. Nov.	4	2	7	MA

* For explanation see the text.

b) *Eothenomys smithi*

Locality	Date	Sex			Location of specimens
		Male	Female	Unknown	
Mt. Hiko	'65. Mar.	5	5	0	TM
Shikoku					
Mt. Kamegamori	'65. Mar.	11	16	0	TM
Ohtaki	'66. Nov.	10	4	0	MA
Mt. Tsurugi	'65. Jul.	3	7	16	MA
Mt. Gozaisho	'66. Jan.	8	19	0	TM
Mt. Fuji	'68. Nov.	5	10	0	TM
Mt. Yatsugatake	'61. Aug.	1	2	0	TM
	'63. Jul.-Aug.	10	14	0	TM

c) *Clethrionomys rufocanus*

Locality	Date	Sex			Location of specimens
		Male	Female	Unknown	
Nopporo	'63. Mar.-Nov.	75	60	0	MA
	'64. Mar.-Jun.	58	49	0	MA
Ishikarifutomi	'66. Jul.	9	20	0	HA
Shibecha	'66. Aug.	4	5	0	MA
	'68. Aug.-Oct.	11	10	0	MA
Rishiri Is.	'65. Jul.	5	8	0	TM
	'68. Aug.	8	4	0	MA
Continent					
Korea	'29. Jun.	1	0	0	YIO
	'30. Mar.	0	1	0	YIO
Northeastern part of China	'37. Jun.	7	1	0	YIO
Khabarovsk	'67. Jul.	2	1	0	MA

Table 1. (Continued)

d) *Clethrionomys rutilus*

Locality	Date	Sex			Location of specimens
		Male	Female	Unknown	
Ishikarifutomi	'66. Jul.	10	9	0	HA
Oketo	'62. Oct.	1	7	0	YF
	'64. Mar.-Nov.	32	17	0	YF
	'65. Aug.	3	4	0	YF
Continent					
Khabarovsk	'67. Jul.	1	1	0	MA
Irkutsk	'67. Aug.	5	1	0	MA

e) *Clethrionomys glareolus*

Locality	Date	Sex			Location of specimens
		Male	Female	Unknown	
Moskow	'66. Sep.	1	3	0	MA
France	'66. Oct.	1	4	1	MA

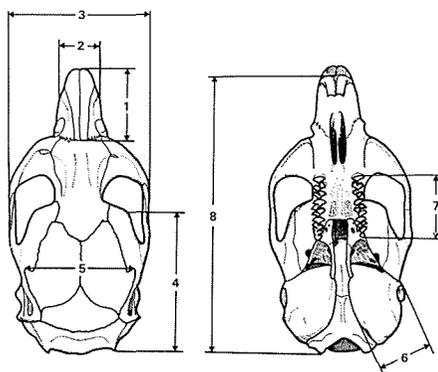


Figure 2. Cranial dimensions measured.

1: nasal length; 2: rostral width; 3: zygomatic width; 4: braincase length; 5: parietal width; 6: auditory bulla width; 7: length of upper molar row; 8: condylobasal length.

3. Zygomatic width — greatest width across the zygomatic arches.
4. Braincase length — distance from postorbital projection of squamosal to lambdoidal crest along median line of cranium.
5. Parietal width — greatest transverse width measured from the lateralmost projections of parietal bones.

6. Auditory bulla width — greatest width measured from lateral projection of external auditory meatus to innermost margin of the bulla.
7. Length of upper molar row — alveolar length of the tooth row.
8. Condylbasal length — condyles to the foremost points of the premaxillae, between the incisors.

Cranial measurements were studied allometrically in their proportion to the overall length of the skull, i.e. condylbasal length. Regression lines have been calculated on logarithmic scale and have been compared statistically after the method by Reeve (1940). Among the above dimensions, parietal width shows virtually no increase in absolute size within the range of material available so that in this case mean values can be compared directly. The criterion of significance used in *F*- and *t*-test was $P < .05$.

Dental characters

The principal characters distinguishing the Japanese red-backed voles from one another are root formation, occlusal enamel pattern and tooth size. The dental terminology adopted in this work, a modification of that by Hershkovitz (1962), is shown in Figure 3.

Non-metrical observations were carried out on the crown pattern of the molars of each species in order to study its geographic variation. Each molar was examined with respect to characters which were classified as follows:

First upper molar:

- a. Shape of the anterior wall
T: trilobed, B: bilobed, S: single-lobed.
- b. Comparison of the sizes of the anterolabial conule (7) and the anterolingual conule (8).
- c. Second minor fold (NF2)
D: developed, M: moderate, U: undeveloped.
- d. Second secondary fold (SF2)
D: developed, M: moderate, U: undeveloped.

Second upper molar:

- a. Shape of the anterior wall
B: bilobed, S: single-lobed.
- b. Second minor fold (NF2)
D: developed, M: moderate, U: undeveloped.
- c. Second secondary fold (SF2)
D: developed, M: moderate, U: undeveloped.

Third upper molar:

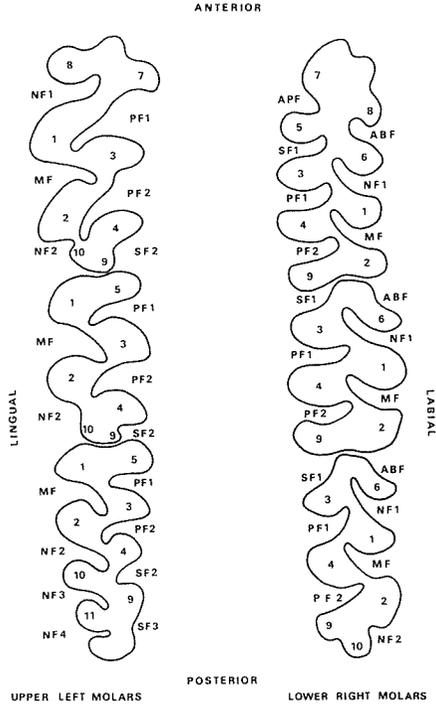


Figure 3. Diagram of the occlusal surface of molars showing all elements present in the enamel pattern of the Japanese red-backed voles.

Names of folds: MF, major fold; NF1, first minor fold; NF2, second minor fold; NF3, third minor fold; NF4, fourth minor fold; PF1, first primary fold; PF2, second primary fold; SF1, first secondary fold; SF2, second secondary fold; ABF, anterior labial fold; APF, anterior primary fold.

Names of cusps:

Upper molars: 1. Protocone, 2. Hypocone, 3. Paracone, 4. Metacone, 5. Anteroloph, 6. Anteroconule, 7. Anterolabial conule, 8. Anterolingual conule, 9. Posteroloph, 10. Anterior posteroconule, 11. Posterior posteroconule.

Lower molars: 1. Protoconid, 2. Hypoconid, 3. Metaconid, 4. Entoconid, 5. Anterolophid, 6. Anteroconulid, 7. Anterolingual conulid, 8. Anterolabial conulid, 9. Posterolophid, 10. Posteroconulid.

- a. Shape of the anterior wall
B: bilobed, S: single-lobed.
- b. Third minor fold (NF3)
D: developed, M: moderate, U: undeveloped.
- c. Fourth minor fold (NF4)
D: developed, M: moderate, U: undeveloped.
- d. Second secondary fold (SF2)
D: developed, M: moderate, U: undeveloped.
- e. Third secondary fold (SF3)
D: developed, M: moderate, U: undeveloped.
- f. Posteroloph (9)
D: developed, M: moderate, U: undeveloped.
- g. Posterior posteroconule (11)
D: developed, M: moderate, U: undeveloped.

First lower molar:

- a. Shape of the anterior wall
T: trilobed, B: bilobed, S: single-lobed.
- b. Comparison of the sizes of the anterolingual conulid (7) and the anterolabial conulid (8)
- c. Shape of the posterior wall
B: bilobed, S: single-lobed.

Second lower molar:

- a. First secondary fold (SF2)
D: developed, M: moderate, U: undeveloped.
- b. Anterior labial fold (ABF)
D: developed, M: moderate, U: undeveloped.
- c. Shape of the posterior wall
B: bilobed, S: single-lobed.

Third lower molar:

- a. First secondary fold (SF1)
D: developed, M: moderate, U: undeveloped.
- b. Second minor fold (NF2)
D: developed, M: moderate, U: undeveloped.
- c. Posteroconulid (10)
D: developed, M: moderate, U: undeveloped.

Cusps are connected with neighbouring cusps by isthmuses. In the present study, whether or not these isthmuses, shown in Figure 4 with numbers, were closed or not was observed. The criterion employed here to classify them as closed was that

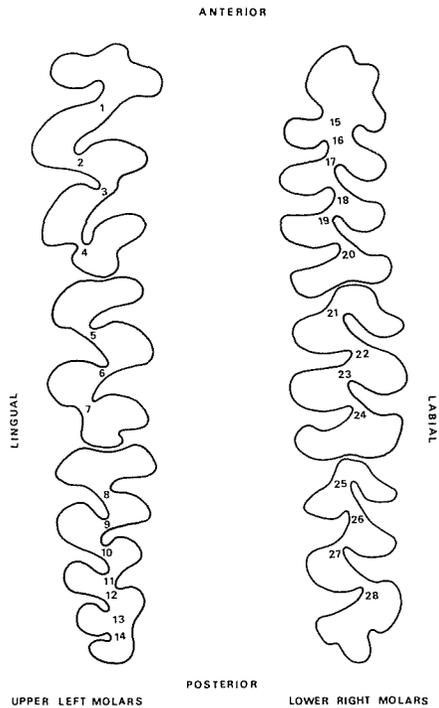


Figure 4. Diagram of the occlusal surface of molars showing locations of numbered isthmuses in the enamel pattern of the Japanese red-backed voles.

the minimum width of an isthmus measured between the outer surfaces of both inner and outer enamels be less than 0.1 mm. The width of each isthmus was measured by using an Olympus UP 350 magnifier at a magnification of $\times 20$.

For the root formation of molars, direct observations were carried out on all skull specimens of *Eothenomys andersoni*.

Juvenile and senile individuals were excluded from the material used to compare the crown patterns, because in the former the third molars were not yet fully erupted and in the latter the enamel had been worn out.

Secondary Sexual Difference

Prior to the detailed study of geographic variation, males and females in each species were compared craniometrically to understand the extent of sexual differences. The collection of *Eothenomys andersoni* from Mt. Yatsugatake, the largest series of

Table 2. Equilibrium constants (a) and initial growth indices (b) for skull measurements of *andersoni* from Mt. Yatsugatake.

Dimension		Males (19.3–28.3)*		Females (20.7–28.5)	
			t _{.05} S.E.		t _{.05} S.E.
Nasal length	a	1.1311	0.1230	1.1803	0.1423
	b	-0.6989	0.1736	-0.7659	0.2003
Rostral width	a	0.7784	0.1125	0.9321	0.1312
	b	-0.5068	0.1587	-0.7236	0.1846
Zygomatic width	a	1.0631	0.0757	1.1628	0.0909
	b	-0.3424	0.1068	-0.4822	0.1279
Braincase length	a	0.6485	0.0654	0.6116	0.0794
	b	0.1963	0.0922	0.2467	0.1118
Auditory bulla width	a	0.8759	0.0724	0.8179	0.1144
	b	-0.4322	0.1020	-0.3532	0.1610
Length of upper molar row	a	0.8924	0.0817	0.9590	0.1370
	b	-0.4925	0.1152	-0.5847	0.1928

* Range of condylobasal length (in mm).

Table 3. *F*-values for slope and positional differences between males and females of *Eothenomys andersoni* at Mt. Yatsugatake.

Difference	NL N=361	RW N=375	ZW N=359	BL N=372	AW N=377	ML N=377
Slope differences	0.254	2.921	2.649	0.479	0.741	0.734
Positional differences	1.375	0.009	0.136	2.164	3.810	1.122

Table 4. Parietal width of the red-backed voles examined (in mm).

Species and locality	N	Mean	t _{.05} S.E.	Range	
<i>andersoni</i>					
Mt. Yatsugatake	Males	201	11.1174	0.0480	10.2–12.2
	Females	166	11.0422	0.0569	10.0–12.0
	Males & Females	367	11.0834	0.0369	10.0–12.2
Shiga Heights	20	10.91	0.1757	10.4–11.7	
Mt. Chokai	19	10.7632	0.2015	10.2–11.7	
<i>smithi</i>					
Mt. Hiko	9	10.4000	0.2241	9.9–10.7	
Shikoku	64	10.3892	0.0843	9.7–11.2	
Mt. Gozaisho	25	10.1280	0.1897	9.4–11.3	
Mt. Fuji	14	9.9000	0.1710	9.5–11.0	
Mt. Yatsugatake	27	9.7111	0.1673	8.8–10.8	
<i>rufocanus</i>					
Nopporo	240	11.0558	0.0415	10.2–12.0	
Ishikarifutomi	28	11.1607	0.1167	10.5–11.8	
Shibechea	30	11.0700	0.1189	10.2–11.8	
Rishiri Is.	24	11.4583	0.1397	10.9–11.9	
Continental form	13	10.8923	0.1770	10.3–11.2	
<i>rutilus</i>					
Ishikarifutomi	19	10.3474	0.1703	9.7–10.9	
Oketo	59	10.5475	0.0697	10.2–11.1	
Continental form	7	10.4000	0.2505	10.0–10.7	
<i>glareolus</i>					
Continental form	10	10.6700	0.2862	10.2–11.1	

one species obtained from one locality, was used as material for this purpose.

For nasal length, rostral width, zygomatic width, braincase length, auditory bulla width, and length of upper tooth row against condylobasal length, regression lines were calculated on a logarithmic scale (Table 2) and compared statistically. Examination of F -values of slope and positional differences for each regression line (Table 3), did not show a significant difference ($P > .05$) between any pair of lines.

Among the dimensions used in the present study, parietal width showed no increase in absolute size within the range of material available, and therefore, means can be compared directly between the sexes (Table 4, Fig. 5). This character showed no significant variation ($P > .05$).

All of the dimensions adopted here for the craniometry show no significant difference between males and females. Accordingly, specimens of each collection from various localities will be treated for further analyses of variation without separation of males and females.

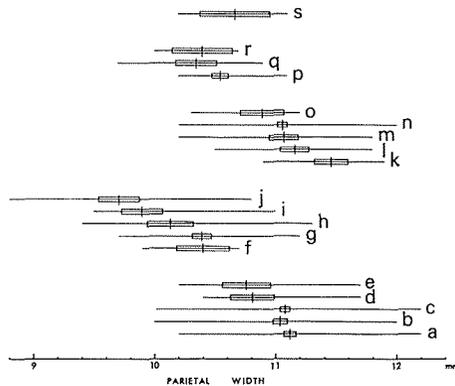


Figure 5. Parietal width of the red-backed voles examined. Vertical lines, horizontal lines, and rectangles indicate mean values, ranges and 95% confidence ranges, respectively. Alphabetical letters indicate localities of samples as shown below:

Eothenomys andersoni a: Mt. Yatsugatake, males; b: Mt. Yatsugatake, females; c: Mt. Yatsugatake, males and females combined; d: Shiga Heights; e: Mt. Chokai.

E. smithi f: Mt. Hiko; g: Shikoku; h: Mt. Gozaisho; i: Mt. Fuji; j: Mt. Yatsugatake.

Clethrionomys rufocanus k: Rishiri Is.; l: Ishikarifutomi; m: Shibechea; n: Noppero; o: Continent.

C. rutilus p: Oketo; q: Ishikarifutomi; r: Continent.

C. glareolus s: Continent.

Systematic Accounts

Key to the species of the Japanese red-backed voles

Lower incisors relatively short, extending backwards at least to base of condylar

process, lingual to M_1 and M_2 , labial to M_3 . The folds of the cheekteeth partly filled with cement. The skull is lightly built, with poorly developed squamosal crest; the supraorbital ridges weak and widely separated in the adult, not forming a median interorbital crest; the braincase broad. Bony palate ending posteriorly as a simple straight transverse shelf. Palatal foramina well developed, long. Bullae simple, lacking spongy tissue internally; stapedial artery naked. External form not much modified; palmar pads 5, plantar pads 6. Chromosomes, $2n=56$.

- | | | |
|----|--|---|
| 1 | Cheekteeth rooted in adult (<i>Clethrionomys</i>) | 2 |
| | Cheekteeth evergrowing (<i>Eothenomys</i>) | 3 |
| 2 | Tail densely haired, sharply bicolored; cheekteeth rooted at an early stage in life; skull gracile | <i>Clethrionomys rutilus mikado</i> |
| 2' | Tail sparsely haired, not clearly bicolored; cheekteeth rooted at a later stage in life; skull robust | <i>Clethrionomys rufocanus bedfordiae</i> |
| 3 | Mammae 2-2=8; tail long, more than half of head and body length; braincase rounded; bullae large and well inflated | <i>Eothenomys andersoni</i> |
| 3' | Mammae 0-2=4 or 1-2=6, rarely 2-2=8; tail short, less than half of head and body length; braincase flattened; bullae small | <i>Eothenomys smithi</i> |

Genus *Eothenomys*

Eothenomys andersoni (Thomas, 1905)

Evothomys andersoni Thomas, 1905, *Abstr. Proc. Zool. Soc. London*: 18. [type: Tsunagi, near Morioka, Iwate Prefecture, Honshu, Japan; British Mus. (Nat. Hist.)]

Evothomys (Craseomys) andersoni Thomas, 1905, *Proc. Zool. Soc. London*: 354.

Craseomys niigatae Anderson, 1909, *Ann. Mag. Nat. Hist.*, Ser. 8, 4: 317. [type: Akakura, Niigata Prefecture, Honshu, Japan; British Mus. (Nat. Hist.)]

Evothomys rufocanus smithii Hinton (in part), 1926, *Monogr. Voles & Lemmings*, 1: 257.

Evothomys rufocanus niigatae Kuroda, 1931, *Zool. Mag. (Jap.)*, 43: 661.

Clethrionomys rufocanus andersoni Hanaoka, 1937, *Zool. Mag. (Jap.)*, 49: 429.

Clethrionomys andersoni Tokuda, 1941, *Trans. Biogeogr. Soc. Jap.*, 4: 49.

Clethrionomys rufocanus smithii Ellerman (in part), 1941, *Fam. & Genera Living Rodents*, 2: 572.

Aschizomys andersoni Imaizumi, 1960, *Colored Illustrations Mamm. Jap.*: 134.

Aschizomys niigatae Imaizumi, 1960, *Colored Illustrations Mamm. Jap.*: 133.

Clethrionomys (Aschizomys) andersoni Jameson, 1961, *Pacific Sci.*, 15: 599.

Clethrionomys (Aschizomys) niigatae Jameson, 1961, *Pacific Sci.*, 15: 599.

Clethrionomys (Aschizomys) imaizumii Jameson, 1961, *Pacific Sci.*, 15: 599. [type: Nachi, Wakayama Prefecture, Honshu, Japan; E. W. Jameson, Jr.]
Clethrionomys andersoni imaizumii Aimi, 1967, *Zool. Mag. (Jap.)*, 76: 44.

Geographic variation was analysed from the skull dimensions and the dental characters of specimens from three localities: Mt. Yatsugatake, Shiga Heights, and Mt. Chokai.

For the skull dimensions regression lines were calculated on logarithmic scales (Table 5), and the data were compared statistically. *F*-values for slope and positional differences were examined (Table 6), with the result that no significant difference ($P > .05$) in slope was found between any pair of lines. Differences in position are of significance ($P < .01$) in rostral width, zygomatic width, braincase length, and auditory bulla width. Nasal length and length of upper molar row shows no significant difference in position ($P > .05$).

Table 5. Equilibrium constants (a) and initial growth indices (b) for skull measurements in samples of *Eothenomys andersoni*.

Dimension		Mt. Yatsugatake (19.3–28.5)*		Shiga Heights (20.5–27.1)*		Mt. Chokai (19.9–24.9)*	
		<i>t</i> _{.05}	S.E.	<i>t</i> _{.05}	S.E.	<i>t</i> _{.05}	S.E.
Nasal Length	a	1.1443	0.0924	1.1434	0.2693	1.0089	0.2875
	b	−0.7165	0.1303	−0.7090	0.3754	−0.5354	0.3955
Rostral width	a	0.8359	0.0850	0.8452	0.2333	0.9899	0.2871
	b	−0.5880	0.1198	−0.5821	0.3251	−0.7789	0.3948
Zygomatic width	a	1.0984	0.0579	1.0614	0.1554	1.0172	0.2740
	b	−0.3920	0.0815	−0.3351	0.2165	−0.2717	0.3767
Braincase length	a	0.6379	0.0502	0.5662	0.0999	0.5219	0.2055
	b	0.2106	0.0707	0.3062	0.1393	0.3571	0.2824
Auditory bulla width	a	0.8598	0.0630	0.9384	0.2088	0.7964	0.2264
	b	−0.4106	0.0887	−0.5350	0.2910	−0.3509	0.3113
Length of upper molar row	a	0.9134	0.0732	0.6659	0.3376	0.7277	0.2927
	b	−0.5214	0.1031	−0.1807	0.4704	−0.2710	0.4025

* Range of condylobasal length (in mm).

Table 6. *F*-values for slope and positional differences among samples of *Eothenomys andersoni* collected at Mt. Yatsugatake, Shiga Heights, and Mt. Chokai.

Difference	NL N=403	RW N=419	ZW N=402	BL N=414	AW N=421	ML N=421
Slope differences	0.380	0.539	0.370	1.148	0.474	2.658
Positional differences	2.031	23.777**	5.665**	15.864**	49.533**	2.029

** $P < .01$

The mean value of parietal width is smallest in Mt. Chokai specimens and greatest in Mt. Yatsugatake specimens, with that in Shiga Heights specimens intermediate between them (Table 4, Fig. 5). There is no significant difference in this dimension ($P > .05$) between any pair of the neighbouring localities.

The sample sizes of the collections from Nachi and Mt. Ohdaigahara were too small to be analysed statistically. The range of their skull dimensions is included within that of Mt. Yatsugatake specimens.

Dental characters

Every specimen used for the present study was directly examined to see whether or not roots were formed in their molars, but in no case was either a root or an incipient root found.

The crown patterns (Table 7-8) and isthmuses (Table 9) on both the upper and lower molars were examined. The result is as follows:

M^1 — The anterior wall of the enamel is usually single-lobed or bilobed, and rarely trilobed. The size of the anterolabial conule usually approximates to that of the anterolingual conule. The second minor fold is always developed, and the second secondary fold is usually seen. The frequency of the closed dentinal isthmus in isthmus no. 1 is significantly different ($.01 < P < .05$) in the collection from Mt. Yatsugatake compared to that from Mt. Chokai. Differences in frequencies of the others are not significant among the collections.

M^2 — The anterior wall of the enamel is usually single-lobed. The second minor fold is developed, and the second secondary fold is usually developed.

M^3 — The anterior wall of the enamel is bilobed or single-lobed. The third minor fold is developed. The fourth minor fold is usually undeveloped. The second secondary fold is developed. The third secondary fold is variable. The posteroloph is well developed. The posterior posteroconule is developed.

M_1 — The anterior wall of the enamel is single-lobed. The size of the anterolingual conulid is smaller than that of the anterolabial conulid in Mt. Chokai specimens, but in Shiga Heights specimens this is reversed. In Mt. Yatsugatake specimens these two are nearly the same in size. The posterior wall of the enamel is single-lobed.

M_2 — The first secondary fold is developed. The anterior labial fold is seen. The posterior wall of the enamel is single-lobed.

M_3 — The first secondary fold is developed. The anterior labial fold is variable. The second minor fold is not well developed. The posteroconulid is not developed.

REMARKS: Concerning the classification of the present species, *Eothenomys andersoni*, much debate has arisen not only on the generic allocation but also on the

Table 7. Frequency distribution of upper molar pattern in samples of *Eothenomys andersoni* collected at three localities.

Molar	Classified character*	Mt. Chokai N=23	Shiga Heights N=29	Mt. Yatsugatake N=436
M ¹	T	0	1	10
	B	3	15	130
	S	20	13	296
	8>7	3	4	69
	8=7	20	20	335
	8<7	0	5	32
NF2	D	23	29	436
	M	0	0	0
	U	0	0	0
SF2	D	19	22	345
	M	0	5	62
	U	4	2	29
M ²	B	5	3	70
	S	18	26	366
NF2	D	23	29	435
	M	0	0	1
	U	0	0	0
SF2	D	17	18	315
	M	2	3	71
	U	4	8	50
M ³	B	7	17	282
	S	16	12	154
NF3	D	23	27	433
	M	0	2	3
	U	0	0	0
NF4	D	2	3	13
	M	4	4	51
	U	17	22	372
SF2	D	23	29	436
	M	0	0	0
	U	0	0	0
SF3	D	12	14	119
	M	2	6	121
	U	9	9	196
9	D	21	27	424
	M	2	2	12
	U	0	0	0
11	D	21	26	429
	M	2	3	7
	U	0	0	0

* For explanation see the text and Fig. 3.

division at the species level. The generic allocation will be discussed later.

As stated before, Anderson described *niigatae* as a species distinct from *andersoni* which had been first described by Thomas. The cranial diagnostic characters of *niigatae* are as follows:

Table 8. Frequency distribution of lower molar pattern in samples of *Eothenomys andersoni* collected at three localities.

Molar	Classified character*	Mt. Chokai N=23	Shiga Heights N=29	Mt. Yatsugatake N=436
M ₁	T	0	0	40
	B	0	2	41
	S	23	27	355
	7>8	3	2	29
	7=8	4	20	218
	7<8	16	7	189
		B	4	9
M ₂ SD1	S	19	20	328
	D	22	29	432
	M	1	0	4
	U	0	0	0
ABF	D	11	15	241
	M	5	5	108
	U	7	9	87
	B	1	0	17
	S	22	29	419
M ₃ SF1	D	17	19	371
	M	3	6	41
	U	3	4	24
ABF	D	6	11	118
	M	7	8	105
	U	10	10	213
NF2	D	3	0	126
	M	1	5	75
	U	19	24	235
10	D	1	0	4
	M	0	0	1
	U	22	29	431

* For explanation see the text and Fig. 3.

1. Skull is much shorter, but very nearly as broad as that of *Craseomys andersoni*.
2. The nasals is shorter, but equally broad; the interorbital region is broader.
3. The palatal foramina is longer.
4. The diastema is longer than in *C. andersoni*.

Afterwards Hanaoka (1937) examined twelve specimens collected from Mt. Yatsugatake, all of which by external characters could be identified as *niigatae*. Based on the cranial characters, however, some of their skulls were similar to the skull of *andersoni*, while others resembled that of *niigatae*. Therefore, he concluded that *niigatae* was a synonym of *andersoni*. More recently Imaizumi (1960) again separated *niigatae* from *andersoni*. Diagnostic characters in the skull that distinguished these two forms were differences in dimensions of overall length, rostrum, molar row, and

Table 9. Frequency distribution of closed dentinal isthmuses in samples of *Eothenomys andersoni* collected at three localities.

Isthmus no.*	Mt. Chokai N=23	Shiga Heights N=29	Mt. Yatsugatake N=436
1	5	7	62
2	15	17	216
3	9	9	119
4	7	14	174
5	21	21	304
6	15	20	276
7	6	16	245
8	13	24	273
9	9	18	227
10	8	15	262
11	9	10	203
12	0	1	25
13	0	0	0
14	0	0	0
15	1	3	15
16	0	4	12
17	8	9	181
18	8	18	236
19	6	5	105
20	13	23	307
21	0	0	1
22	18	27	356
23	1	1	53
24	20	27	361
25	0	0	1
26	19	25	360
27	0	1	5
28	21	24	368

* For explanation see the text and Fig. 4.

auditory bulla. Moreover, Imaizumi (1965) added another diagnostic character to them; the fact that the first and second dentinal spaces of M^3 are constricted in *andersoni*, while they are confluent in *niigatae*.

According to Imaizumi (1960), the specimens from Mt. Chokai refers to *andersoni*, and those from Mt. Yatsugatake and Shiga Heights to *niigatae*. In the present study, it has become clear that there are significant positional differences ($P < .01$) among

the three collections in rostral width, zygomatic width, braincase length, and auditory bulla width, but there is no significant difference in slope. This fact means that morphological differences among the three collections are attributable to differences in size, and not to differences in shape. Furthermore, the direction of the variation in size is always in the sequence of Mt. Chokai — Shiga Heights — Mt. Yatsugatake; in other words, the variation is clinal. This is true of parietal width, too. In the condition of the dentinal isthmuses, there are no clear differences among the three collections. For these reasons, the existence of *niigatae* is doubtful as far as the examined characters are concerned.

On the other hand, Jameson (1961) described a new species, *Clethrionomys imaizumii*, collected from Nachi, Kii Peninsula, Honshu. Diagnostic characters he listed were as follows: salient angles of all cheekteeth rounded or irregular, their triangles often open, the auditory bullae relatively small. Aimi (1967) examined two new specimens that he had collected from Nachi, with the result that the difference was not so great as to establish a species distinct from the specimens of Mt. Yatsugatake. Accordingly, he ranked *imaizumii* as a subspecies under *andersoni* because of its isolated distribution. It is evident from the present study that the ranges of variation of skull dimensions and dental characters of the specimens from Nachi and from Mt. Ohdaigahara is included within that of specimens from Mt. Yatsugatake. The present study does not give the slightest support to the validity of *imaizumii* as a distinct species, and therefore, it follows that *imaizumii* is a synonym of *andersoni*.

There are many controversies on the generic allocation of *andersoni*. Thomas (1905b) placed *andersoni* in the genus *Evotomys*; Palmer (1928) considered *Evotomys* as a synonym of *Clethrionomys*; Hanaoka (1937) adopted *Clethrionomys* for *andersoni* according to Palmer's interpretation.

Imaizumi (1960) placed *andersoni* in the genus *Aschizomys* because the molars of *andersoni* were rootless, while those of *Clethrionomys* were rooted. On the other hand, Jameson (1961) examined nine adult specimens of "*niigatae*" and reported that one of the specimens had closed pulp cavities and incipient roots. He wrote: "If I am correct in presuming that very old specimens of *Aschizomys lemminus* will tend to develop roots on the molars, then *Aschizomys* is more appropriately placed with *Clethrionomys*. Inasmuch as a few old individuals of *rufocanus* and *niigatae* have partly rooted molars, it seems best to place *Aschizomys* as a subgenus under *Clethrionomys*." As a result, he placed *andersoni* in *Aschizomys* which in turn he ranked a subgenus of the genus *Clethrionomys*.

Aimi (1971) examined about 700 skulls of *andersoni* but could not find any specimens even with incipient molar roots. On that occasion, the material included the specimens used in this study. Furthermore, Aimi (unpublished) caught three adult

specimens of *andersoni* (body weight over 28 g) alive at Mt. Goyo, Iwate Prefecture, Honshu, in August of 1970, and after having fed them for five months, sacrificed them for study. He found no roots or sign of roots in any molar of their skulls. Taking into consideration the fact that in *Clethrionomys rufocanus* root formation starts within 100 days of birth (Abe, 1973), it is likely that *andersoni* does not develop roots on the molars even in the slightest degree.

Again Bol'shakov (1966) studied molar root formation of "*Aschizomys lemminus*." He examined 46 specimens including nine over-wintered individuals and found that the molars develop no roots in any specimens. Consequently it is not reasonable to accept the classification proposed by Jameson (1961) regarding *Aschizomys* as a subgenus under the genus *Clethrionomys*.

"*Aschizomys lemminus*" was first described by Miller (1898) on the basis of one specimen collected from the eastern coast of Siberia. Afterwards, he (1940) re-examined the type specimen and concluded that this form was "nothing more than an alcohol-discolored specimen of the extreme East Asian representative of *Clethrionomys rufocanus*." In Russia, however, the classification of this vole differs from that of Miller. Vinogradov (1927), on the basis of four specimens, came to the conclusion that *Aschizomys lemminus* is a valid species. Recently, Ognev (1956) placed *Aschizomys* as a subgenus under the genus *Alticola*. More recently, Gromov et al. (1963) studied the variation of molar patterns, one of the principal characters that distinguish "*lemminus*" from other species of *Alticola*, and concluded that "*lemminus*" is merely a subgenus of *Alticola macrotis*. From a detailed study of geographic variation, Geptner and Rossolimo (1968) have agreed with the conclusion of Gromov et al. (1963). Since then "*lemminus*" has been regarded as a subspecies of *Alticola macrotis* among Russian students, and up to now there have been no data available to disprove this view. Accordingly, the use of the genus "*Aschizomys*" should be discontinued. It follows that it is unreasonable to place *andersoni* in "*Aschizomys*" as Imaizumi (1960) did on the basis of the rootless molars and resemblance of the molar pattern to that of "*lemminus*." i.e. the fact that both M³ first outer reentrant angle is as deep as the inner one. These are the common features of *Alticola macrotis*. *Alticola* has been regarded as being not widely separated from *Eothenomys* (e. g. Ellerman & Morrison-Scott, 1951). In addition, the folds of the cheekteeth are always noticeably wide in *Alticola* and develop little cementum (Hinton, 1926; Ellerman, 1941). In these characters, *andersoni* differs from *Alticola*. On the other hand, *Eothenomys* still retains primitive enamel patterns on the molars — in most species of this genus an additional posterior cusp (anterior posteroconule) is well developed on M¹ and M² (Hinton, 1926). To place *andersoni* in the genus *Eothenomys*, the only difficulty lies on the number of mammae because the mammary formula of *andersoni* is 2-2=8, while that of *Eothenomys* is 0-2=4. However, as

the number of mammae is variable within a genus (Arvy, 1974) and even within a species (e. g. *smithi*), it is considered that this character is of little importance for a generic diagnosis. Therefore, it would be reasonable to place *andersoni* in the genus *Eothenomys*.

*Eothenomys smithi** (Thomas, 1905)

Evotomys (Phaulomys) smithii Thomas, *Ann. Mag. Nat. Hist.*, Ser. 7, 15: 493.

[type: Kobe, Hyogo Prefecture, Honshu, Japan; British Mus. (Nat. Hist.)]

Evotomys rufocanus smithii Hinton (in part), 1926, *Monogr. Voles & Lemmings*, 1: 257.

Clethrionomys rufocanus okiensis Tokuda, 1932, *Annot. Zool. Jap.*, 13: 578.

Clethrionomys smithii Watanabe (in part), 1937, *Occ. Pap. Ibaraki Agr. St.*, 2: 20.

Clethrionomys rufocanus smithii Hanaoka, 1937, *Zool. Mag. (Jap.)*, 49: 274.

Clethrionomys smithii smithii Tokuda, 1941, *Trans. Biogeogr. Soc. Jap.*, 4: 45.

Clethrionomys rufocanus smithii Ellerman (in part), 1941, *Fam. & Genera Living Rodents*, 2: 572.

Eothenomys (Phaulomys) smithii smithii Imaizumi, 1949, *Nat. Hist. Jap. Mamm.*: 244.

Anteliomys smithii Tokuda, 1955, *Bull. Biogeogr. Soc. Jap.*, 16–19: 338.

Eothenomys (Phaulomys) smithi Imaizumi, 1957, *Bull. Nation. Sci. Mus.*, 3: 209

Eothenomys (Eothenomys) kageus Imaizumi, 1957, *Bull. Nation. Sci. Mus.*, 3: 204. [type: Yamuramachi, Yamanashi Prefecture, Honshu, Japan; Nation. Sci. Mus. (Tokyo)]

Eothenomys smithi Miyao et al., 1964, *Zool. Mag. (Jap.)*, 73: 189.

Phaulomys smithi Tanaka, 1971, *Jap. J. Zool.*, 16: 175.

As in the case of *andersoni*, geographic variation was analysed for the skull dimensions and dental characters of specimens of *smithi* collected from four localities and one district: Mt. Yatsugatake, Mt. Fuji, Mt. Gozaisho, Shikoku, and Mt. Hiko (Fig. 1).

For the skull dimensions regression lines were calculated on logarithmic scales (Table 10) and the data were compared among the five collections statistically, and *F*-values for slope and positional differences were examined (Table 11). No significant difference ($P > .05$) in slope is found between any pair of lines, whereas differences in position are significant for rostral width, braincase length, and width of

* The International Code of Zoological Nomenclature (1961) recommends the spelling *smithi* rather than *smithii* for the species-group name based on Smith.

Table 10. Equilibrium constants (a) and initial growth indices (b) for skull measurements in samples of *Eothenomys smithi* collected at five localities.

Dimension		Mt. Hiko (22.6–25.4)*		Shikoku (21.7–25.8)*		Mt. Gozaisho (20.9–23.7)*		Mt. Fuji (21.0–24.1)*		Mt. Yatsugatake (19.6–22.3)*	
		t _{.05}	S.E.	t _{.05}	S.E.	t _{.05}	S.E.	t _{.05}	S.E.	t _{.05}	S.E.
Nasal length	a	0.9467	0.3871	0.9029	0.3435	1.1465	0.4096	1.3011	0.5815	0.8290	0.3418
	b	-0.4288	0.5326	-0.3715	0.4754	-0.7068	0.5546	-0.9190	0.7887	-0.2762	0.4521
Rostral width	a	0.8398	0.5735	0.9190	0.3251	0.9188	0.5262	1.0111	0.4644	0.4305	0.4063
	b	-0.5677	0.7881	-0.6577	0.4495	-0.6705	0.7124	-0.8062	0.6299	-0.0267	0.5374
Zygomatic width	a	0.9680	0.4739	1.0476	0.3631	1.0030	0.3426	1.0000	0.2440	1.1775	0.3254
	b	-0.1925	0.6522	-0.3004	0.5040	-0.2393	0.4639	-0.2461	0.3307	-0.4675	0.4305
Braincase length	a	0.7810	0.4184	0.3894	0.2142	0.7217	0.4096	0.4402	0.2187	0.4132	0.2634
	b	-0.0086	0.5749	0.5362	0.2963	0.0738	0.5545	0.4518	0.2954	0.4764	0.3484
Auditory bulla width	a	0.3309	0.7245	0.7316	0.2108	0.5469	0.3776	0.6026	0.3531	0.6633	0.3594
	b	0.2869	0.9956	-0.2759	0.2915	-0.0243	0.5113	-0.1027	0.4789	-0.2029	0.4755
Length of upper molar row	a	0.8681	0.7319	1.1491	0.3205	0.5839	0.4535	0.9095	0.4069	0.6206	0.3771
	b	-0.4651	1.0057	-0.8451	0.4432	-0.0734	0.6140	-0.5251	0.5529	-0.1477	0.4992

* Range of condylobasal length (in mm).

Table 11. *F*-values for slope and positional differences among samples of *Eothenomys smithi* collected at Mt. Yatsugatake, Mt. Fuji, Mt. Gozaisho, Shikoku, and Mt. Hiko.

Difference	NL N=134	RW N=144	ZW N=114	BL N=141	AW N=142	ML N=137
Slope differences	0.928	1.245	0.280	1.270	0.654	1.579
Positional differences	0.887	7.164**	3.476*	6.491**	10.291**	2.856*

* .01 < P < .05

** P < .01

auditory bulla at the level of .01, and in zygomatic width and length of upper molar row at the level of .05. Positional differences in nasal length are not significant ($P > .05$).

The mean values of parietal width of these collections (Table 4, Fig. 5) indicate a clinal feature, and the sequence of localities is: Mt. Yatsugatake — Mt. Fuji — Mt. Gozaisho — Shikoku — Mt. Hiko, from the smallest to the largest. There is no significant difference in this dimension ($P > .05$) between any pair of the neighbouring localities.

Dental characters

All of the specimens used for the present study were directly examined to look for root formation of the molars, but neither roots nor signs of roots were found in

any case.

Crown patterns (Tables 12–13) and isthmuses (Table 14) were examined on both upper and lower molars. The observations are as follows:

Table 12. Frequency distribution of upper molar pattern in samples of *Eothenomys smithi* collected at five localities.

Molar	Classified character*	Mt. Yatsugatake N=25	Mt. Fuji N=19	Mt. Gozaisho N=27	Shikoku N=63	Mt. Hiko N=18
M ¹	T	0	0	0	10	0
	B	7	4	7	21	6
	S	18	15	20	32	12
	8>7	2	3	2	2	2
	8=7	16	7	17	44	14
	8<7	7	9	8	17	2
NF2	D	24	19	27	63	18
	M	0	0	0	0	0
	U	1	0	0	0	0
SF2	D	15	14	21	55	14
	M	6	4	5	8	3
	U	4	1	1	0	1
M ²	B	6	3	7	6	2
	S	19	16	20	57	16
NF2	D	24	19	27	63	18
	M	1	0	0	0	0
	U	0	0	0	0	0
SF2	D	15	12	18	53	13
	M	7	2	5	8	3
	U	3	5	4	2	2
M ³	B	19	10	14	36	12
	S	6	9	13	27	6
NF3	D	25	18	26	63	18
	M	0	1	1	0	0
	U	0	0	0	0	0
NF4	D	0	0	0	0	0
	M	1	0	0	3	1
	U	24	19	27	60	17
SF2	D	25	18	27	63	18
	M	0	0	0	0	0
	U	0	1	0	0	0
SF3	D	7	8	8	41	9
	M	6	1	6	14	6
	U	12	10	13	8	3
9	D	20	15	24	60	16
	M	5	3	3	3	2
	U	0	1	0	0	0
11	D	20	15	22	60	15
	M	5	4	4	3	2
	U	0	0	1	0	1

* For explanation see the text and Fig. 3.

Table 13. Frequency distribution of lower molar pattern in samples of *Eothenomys smithi* collected at five localities.

Molar	Classified character*	Mt. Yatsugatake N=25	Mt. Fuji N=19	Mt. Gozaisho N=27	Shikoku N=63	Mt. Hiko N=18	
M ₁	T	1	0	1	16	0	
	B	3	2	1	4	0	
	S	21	17	25	43	18	
	7>8	0	1	0	2	1	
	7=8	11	2	5	31	5	
	7<8	14	16	22	30	12	
	B	4	2	7	9	4	
M ₂ SF1	S	21	17	20	54	14	
	D	22	18	24	63	17	
	M	3	0	3	0	1	
	U	0	1	0	0	0	
	ABF	D	16	13	16	38	13
		M	1	3	7	15	1
		U	8	3	4	10	4
		B	0	0	0	8	0
		S	25	19	27	55	18
	M ₃ SF1	D	13	9	16	57	14
M		8	5	5	4	4	
U		4	5	6	2	0	
ABF		D	9	4	14	32	8
		M	8	4	4	12	5
		U	8	11	9	19	5
NF2	D	4	0	3	17	2	
	M	4	2	9	6	0	
	U	17	17	15	40	16	
I0	D	0	0	0	0	0	
	M	0	0	0	0	0	
	U	25	19	27	63	18	

* For explanation see the text and Fig. 3.

M¹ — The anterior wall of the enamel is usually single-lobed. The size of the anterolabial conule is nearly the same as that of the anterolingual conule. The second minor fold is always developed. The second secondary fold is also usually developed.

M² — The anterior wall of the enamel is usually single-lobed. The second minor fold is developed. The second secondary fold is also usually developed.

M³ — The anterior wall of the enamel is generally bilobed, but often single-lobed. The third minor fold is developed. The fourth minor fold is not developed. The second secondary fold is developed. The third secondary fold is variable. The posteroloph is developed. The posteroconule is developed.

M₁ — The anterior wall of the enamel is usually single-lobed. The anterolingual conulid is smaller than the anterolabial conulid except in the specimens from Shikoku. In the specimens from Shikoku, the anterolingual conulid is sometimes smaller than,

Table 14. Frequency distribution of closed dentinal isthmuses in samples of *Eothenomys smithi* collected at five localities.

Isthmus no.*	Mt. Yatsugatake N=25	Mt. Fuji N=19	Mt. Gozaisho N=27	Shikoku N=63	Mt. Hiko N=18
1	2	3	6	25	4
2	3	3	12	28	6
3	1	3	2	26	6
4	4	1	7	24	5
5	11	9	19	44	13
6	5	4	3	30	8
7	2	4	13	21	7
8	8	8	14	32	14
9	0	1	0	8	0
10	5	4	17	28	8
11	0	0	1	12	2
12	0	0	0	0	0
13	0	0	0	1	0
14	0	0	0	0	0
15	0	0	0	0	0
16	1	0	2	0	0
17	0	0	0	17	2
18	6	6	15	22	9
19	0	1	0	4	0
20	11	12	24	44	17
21	0	0	0	0	0
22	11	12	25	48	17
23	0	0	0	0	0
24	11	14	24	56	18
25	0	0	0	0	0
26	13	14	25	55	16
27	0	0	0	0	0
28	12	10	27	59	16

* For explanation see the text and Fig. 4.

or nearly the same as, the anterolabial conulid. Posterior wall of the enamel is usually single-lobed.

M₂ — The first secondary fold is developed. The anterior labial fold is usually developed. The posterior wall of the enamel is single-lobed.

M₃ — The first secondary fold is generally developed. The anterior labial fold is variable, but often developed. The second minor fold is frequently not developed.

The posteroconulid is not developed.

As for the dentinal isthmuses in all the specimens examined, nos. 9, 11, 12, 14, 15, 16, 17, 19, 21, 23, 25, and 27 are very rarely closed. In general, the isthmuses tend to be open in specimens from Mt. Yatsugatake and Mt. Fuji in comparison with those from Mt. Gozaisho, Shikoku, and Mt. Hiko.

REMARKS: Imaizumi (1957) found two types of mammary formulae within *smithi* which was then regarded as a single species. One of them was $1-2=6$, which was seen in specimens from the western half of Honshu, Shikoku, Kyushu, and Dogo Island. The other was $0-2=4$, which was seen in the eastern half of Honshu, and he named this latter form *Eothenomys kageus*. This classification was accepted by Jameson (1961), though with the reservation that "future studies may reveal that *E. kageus* is a subspecies of *E. smithi*." Later Miyao et al. (1964) found two types of mammary formulae, $1-2=6$ and $0-2=4$, in the collection from Mt. Yatsugatake. Miyao (1967) further studied geographic variation in the number of mammae of this form and ascertained that the number varied from two to four pairs and that this character was quite variable even within specimens from the same locality. For example, 29 out of 38 specimens had two pairs, and the others three pairs at Mt. Yatsugatake. He suggested that this character showed a tendency to decrease in number as the location moved from south to north. Furthermore, he examined the variation of external dimensions such as hind foot length and tail length, and found that they also showed a clinal variation. For these reasons, he concluded that this form consisted of a single species, *Eothenomys smithi*, contrary to Imaizumi. Subsequently Tanaka (1971) examined the mammary formulae of the specimens collected from Mt. Tsurugi, Shikoku, with the result that five out of 17 specimens were found to have $0-2=4$, and the others, $1-2=6$. Putting together this feature and the traits in dental and external characters, he proposed that this form should be placed in the genus *Phaulomys*, which had been established by Thomas (1905a), and named it *Phaulomys smithi*. According to Imaizumi (1957) specimens from Mt. Gozaisho, Shikoku, and Mt. Hiko are referred to *smithi*, and those from Mt. Fuji and Mt. Yatsugatake to *kageus*. In the present study, among the specimens of these localities, there are significant positional differences in rostral width, braincase length, and auditory bulla width ($P < .01$), and in zygomatic width and length of upper molar row ($.01 < P < .05$), but no significant difference in slope. The mean value of parietal width shows a gradual reduction with localities in the sequence: Mt. Hiko — Mt. Gozaisho — Mt. Fuji — Mt. Yatsugatake. Furthermore, dental characters show no clear difference that this form constitutes a single species and should not be divided into two species, as far as these characters are concerned.

There has been confusion in the generic allocation of this form. After Thomas

(1905a) described this form as *Evotomys (Phaulomys) smithii*, Imaizumi (1949) transferred this form to the genus *Eothenomys* on the basis of the presence of rootless molars and two pairs of mammae. Subsequently Tokuda (1955) placed this form in the genus *Anteliomys*, but this shift was of little significance, because there has been general agreement that *Anteliomys* is a synonym of *Eothenomys* (Osgood, 1932). More recently, as mentioned above, Tanaka (1971) placed *smithii* in the genus *Phaulomys*. Regarding characters that distinguished *smithii* from the genus *Eothenomys*, he wrote: "As for *Eothenomys*, the enamel pattern of the upper molars shows salient angles which are altogether opposed rather than alternating, and peculiar and complex in M¹ with a well developed fourth inner (posterointernal) angle and in M² with a similar (third) angle, while as to *Anteliomys*, a vestigial trace of posterointernal one in M¹ and M² each is present, but M³ is very complex and peculiar in that the anterior loop is followed by 7 or 8 alternating triangles and the first outer infold is shallow leaving the first triangle confluent with the anterior loop." According to Allen (1940), however, *Eothenomys inez* and *E. eva* are very similar to *smithii* in their tooth pattern. It follows that *Phaulomys* is not so distinct as to warrant a separate genus, and therefore, it seems that the use of the name *Phaulomys* is not pertinent. For the above reasons, the name of this form should be *Eothenomys smithii* (Thomas, 1905).

Genus *Clethrionomys*

Clethrionomys rufocanus bedfordiae (Thomas, 1905)

Evotomys bedfordiae Thomas, 1905, *Abstr. Proc. Zool. Soc. London*: 18. [type:

Shinshinotsu, near Sapporo, Hokkaido, Japan; British Mus. (Nat. Hist.)]

Evotomys (Craseomys) bedfordiae Thomas, 1905, *Proc. Zool. Soc. London*: 353.

Craseomys bedfordiae Thomas, 1907, *Proc. Zool. Soc. London*: 413.

Evotomys rufocanus smithii Hinton (in part), 1926, *Monogr. Voles & Lemmings*, 1: 257.

Evotomys rufocanus bedfordiae Kuroda, 1931, *Zool. Mag. (Jap.)*, 43: 661.

Clethrionomys rufocanus bedfordiae Tokuda, 1932, *Trans. Sapporo Nat. Hist. Soc.*, 12: 208.

Neoschizomys sikotanensis Tokuda, 1935, *Mem. Coll. Sci. Kyoto Imp. Univ.*, Ser. B, 10: 241. [type: Sikotan Isl., Kuril Isls., USSR; Kyoto Univ.]

Clethrionomys sikotanensis Tokuda, 1941, *Trans. Biogeogr. Soc. Jap.*, 4: 49.

Clethrionomys rufocanus smithii Ellerman (in part), 1941, *Fam. & Genera Living Rodents*, 2: 572.

Neoschizomys sikotanensis akkeshii Imaizumi, 1949, *Illustrated Jap. Mamm.*: 241.

Clethrionomys rufocanus bedfordiae Ota, 1956, *Mem. Fac. Agr. Hokkaido Univ.*, 2: 123.

Clethrionomys sikotanensis Imaizumi, 1960, *Colored Illustrations Mamm. Jap.*: 131.

Clethrionomys rex Imaizumi, 1971, *Jap. J. Mamm.*, 5: 99. [type: Mt. Rishiri, Rishiri Is., Hokkaido, Japan; Nation. Sci. Mus. (Tokyo)]

Clethrionomys bedfordiae Imaizumi, 1972, *Mem. Nation. Sci. Mus.*, 5: 138.

Clethrionomys montanus Imaizumi, 1972, *Mem. Nation. Sci. Mus.*, 5: 144. [type: Mt. Poroshiri, Hidaka Mts., Hokkaido, Japan; Nation. Sci. Mus. (Tokyo)]

Imaizumi (1971) described a new form collected from the Rishiri Island, off the northwestern coast of Hokkaido, and named it *Clethrionomys rex*. According to him, the characters that distinguish this form from *C. rufocanus bedfordiae* are as follows: larger size; auditory bulla relatively small; lateral bridges of palatine incomplete; third upper molar with three deep reentrant and four prominent salient angles both on inner and outer sides; closed triangle rarely seen in front of posterior loop in second lower molar.

In the present study three of these diagnostic characters were used in order to examine the validity of *C. rex* (Table 15). Only four out of nine specimens bear three characters constantly. The others, however, bear one or two characters only.

Table 15. Appearance of principal diagnostic characters in voles from Rishiri Island.

Specimen no.	Sex*	No. of inner salient angles in M ³	Closed triangles in M ³ **	Lateral bridge of bony palate	Condylobasal length (mm)
441	F	4	+	incomplete	27.8
442	M	4	—	incomplete	26.7
446	M	3	—	complete	27.4
447	F	4	+	complete	27.4
448	M	3	—	incomplete	26.1
449	F	3	—	complete	29.9
450	M	4	—	incomplete	30.6
451	M	4	—	incomplete	29.4
452	M	3	—	incomplete	27.1
453	F	3	—	incomplete	27.3
458	M	4	—	incomplete	26.9
459	M	4	+	complete	—
462	M	3	—	incomplete	25.8

* M: male, F: female

** +: present, —: absent.

From this result, the validity of *C. rex* is doubtful, and therefore, it seems safe to treat "rex" not as a distinct species but as a form of *C. rufocanus* living on the Rishiri Island.

Geographic variation was analysed in the skull dimensions of the specimens collected from Hokkaido (Nopporo, Ishikarifutomi, and Shibecha), Rishiri Island, and Eurasian Continent. Dental characters were compared among the specimens from Nopporo, Shibecha, and Rishiri Island.

For the skull dimensions regression lines were calculated on logarithmic scales (Table 16). The data were compared among the collections statistically, and *F*-values for slope and positional differences were examined (Table 17). In this case too, no significant difference ($P > .05$) in slope is found between any pair of lines, but differences in position are significant ($P < .01$) in all dimensions.

Among the mean values of parietal width of the collections (Table 4, Fig. 5), that of the Rishiri specimens is significantly greater than those of specimens from

Table 16. Equilibrium constants (a) and initial growth indices (b) for the skull measurements in samples of *Clethrionomys rufocanus*.

Dimension		Nopporo (21.4–28.8)*	Ishikarifutomi (21.0–27.8)*	Shibecha (20.2–27.4)*	Rishiri Is. (24.8–30.6)*	Continental (23.5–27.0)*
		$t_{.05}$ S.E.	$t_{.05}$ S.E.	$t_{.05}$ S.E.	$t_{.05}$ S.E.	$t_{.05}$ S.E.
Nasal length	a	1.1315 0.0824	1.2127 0.2220	1.1289 0.1729	1.2404 0.2675	1.1599 0.4600
	b	-0.7207 0.1164	-0.8445 0.3123	-0.7021 0.2404	-0.8655 0.3862	-0.7610 0.6416
Rostral width	a	0.7728 0.0698	0.9869 0.2006	0.8941 0.1483	1.0155 0.1719	0.7527 0.5471
	b	-0.4758 0.0985	-0.7678 0.2822	-0.6342 0.2062	-0.8132 0.2480	-0.4634 0.7631
Zygomatic width	a	0.9587 0.0495	0.9996 0.1424	0.9281 0.1405	1.2021 0.1582	1.0671 0.3928
	b	-0.1795 0.0699	-0.2351 0.2005	-0.1525 0.1953	-0.5460 0.2283	-0.3389 0.5478
Braincase length	a	0.6500 0.0415	0.6773 0.1039	0.6627 0.1042	0.6404 0.1391	0.7533 0.3496
	b	0.1879 0.0586	0.1451 0.1463	0.1709 0.1449	0.2015 0.2008	0.0357 0.4875
Auditory bulla width	a	0.6992 0.0608	0.8339 0.1874	0.7318 0.1418	0.4668 0.1936	0.6434 0.5280
	b	-0.2140 0.0858	-0.4126 0.2638	-0.2590 0.1972	0.1013 0.2796	-0.1298 0.7364
Length of upper molar row	a	0.6846 0.0666	0.8442 0.1748	0.6673 0.1605	0.8753 0.1787	0.7962 0.4242
	b	-0.1853 0.0940	-0.4146 0.2460	-0.1585 0.2231	-0.4510 0.2578	-0.3588 0.5916

* Range of condylobasal length (in mm).

Table 17. *F*-values for slope and positional differences among samples of *Clethrionomys rufocanus*.

Difference	NL N=326	RW N=338	ZW N=329	BL N=339	AW N=335	ML N=338
Slope differences	0.282	2.348	1.982	0.229	1.912	1.535
Positional differences	11.137**	12.601**	23.912**	3.956**	14.987**	8.254**

** $P < .01$

other localities ($P < .01$), but no significant difference ($P > .05$) in this value is found among the specimens from the other localities.

Dental characters

Crown patterns (Tables 18–19) and isthmuses (Table 20) were observed both

Table 18. Frequency distribution of upper molar pattern in samples of *Clethrionomys rufocanus* collected at three localities.

Molar	Classified character*	Nopporo N=203	Shibechea N=27	Rishiri Is. N=27
M ¹	T	1	6	0
	B	73	3	16
	S	129	18	11
	8>7	105	10	9
	8=7	80	14	11
	8<7	18	3	7
NF2	D	203	25	26
	M	0	1	1
	U	0	1	0
SF2	D	180	22	25
	M	14	1	1
	U	9	4	1
M ²	B	60	11	9
	S	143	16	18
	D	202	26	27
NF2	M	1	0	0
	U	0	1	0
	D	165	21	23
SF2	M	22	3	2
	U	16	3	2
	B	120	15	14
M ³	S	83	12	13
	D	132	23	27
	M	44	2	0
NF3	U	27	2	0
	D	0	0	5
	M	0	0	2
NF4	U	203	27	20
	D	203	27	27
	M	0	0	0
SF2	U	0	0	0
	D	84	11	22
	M	7	0	1
SF3	U	112	16	4
	D	24	2	16
	M	179	25	11
9	U	0	0	0
	D	13	2	17
	M	161	23	10
11	U	29	2	0

* For explanation see the text and Fig. 3.

in the upper and lower molars of the specimens from Nopporo, Shibecha, and the Rishiri Island. The result was as follows:

M¹ — The anterior wall of the enamel is single-lobed or bilobed. Size of the anterolabial conule exceeds, or is the same as, that of the anterolingual conule. The second minor fold is developed. The second secondary fold is also developed.

M² — The anterior wall of the enamel is often single-lobed. The second minor fold is developed. The second secondary fold is usually developed.

M³ — The anterior wall of the enamel is often bilobed. The third minor fold is developed. The fourth minor fold is not developed. The second secondary fold is developed. The third secondary fold is variable. In the Nopporo and Shibecha specimens the third secondary fold may be either developed or undeveloped but in the Rishiri Island voles this fold is usually developed. The posteroloph and posterior

Table 19. Frequency distribution of lower molar pattern in samples of *Clethrionomys rufocanus* collected at three localities.

Molar	Classified character*	Nopporo N=203	Shibecha N=27	Rishiri Is. N=27
M ₁	T	50	8	7
	B	52	1	6
	S	101	18	14
	7>8	32	2	2
	7=8	86	14	10
	7<8	85	11	15
M ₂ SF1	B	23	3	8
	S	180	24	19
ABF	D	202	26	27
	M	1	0	0
	U	0	1	0
M ₃ SF1	D	165	22	22
	M	26	2	2
	U	12	3	3
	B	10	2	1
	S	193	25	26
ABF	D	172	21	24
	M	9	0	1
	U	22	6	2
NF2	D	99	16	21
	M	35	1	3
	U	69	10	3
10	D	1	2	2
	M	12	3	10
	U	190	22	15
10	D	0	0	0
	M	1	0	0
	U	202	27	27

* For explanation see the text and Fig. 3.

Table 20. Frequency distribution of closed dentinal isthmuses in samples of *Clethrionomys rufocanus* collected at three localities.

Isthmus no.*	Nopporo N=203	Shibechea N=27	Rishiri Is. N=27
1	131	21	9
2	147	24	12
3	159	23	7
4	151	22	5
5	185	24	12
6	186	25	11
7	175	24	7
8	152	19	13
9	174	22	9
10	131	19	6
11	21	5	4
12	0	0	0
13	0	0	0
14	0	0	0
15	47	6	0
16	115	19	0
17	139	19	2
18	176	22	5
19	141	19	6
20	182	25	12
21	0	0	0
22	191	25	12
23	55	14	2
24	198	26	13
25	0	0	0
26	192	23	24
27	0	0	0
28	196	25	18

* For explanation see the text and Fig. 4.

conule are moderate in the Nopporo and Shibechea specimens, but often well developed in the Rishiri specimens.

M_1 — The anterior wall of the enamel is often single-lobed. The size of the anterolabial conulid is smaller than, or nearly equal to, that of the anterolabial conulid. The posterior wall of the enamel is usually single-lobed.

M₂ — The first secondary fold is developed. The anterior labial fold is usually developed. The posterior wall of the enamel is single-lobed.

M₃ — The first secondary fold is usually developed. The anterior labial fold is often developed. The second minor fold is usually not developed. The posteroconulid is not well developed.

As for the dentinal isthmuses, nos. 12, 13, 14, 21, 25, and 27 were always open in all the specimens examined, and nos. 11 and 15 were open in most cases. In general, this character tends to be open in the Rishiri specimens compared with that of the Nopporo and Shibechea specimens.

REMARKS: In connection with the red-backed voles of Hokkaido and its adjacent islands, Tokuda (1935) studied a new form collected from the Shikotan Island of the Kuril Islands and named it *Neoschizomys sikotanensis*, but afterwards he (1941) transferred this form to the genus *Clethrionomys*. Imaizumi (1949), however, described a new form collected from Daikoku Isle, off the southeastern coast of Hokkaido, as its subspecies, *Neoschizomys sikotanensis akkeshii*. Subsequently, Ota (1956) studied external, cranial, and dental characters of the voles from Daikoku Isle and the main island of Hokkaido, as well as the morphology of their glans penes, with the result that he found no distinct difference between them and instead, he noted that some specimens from the main island closely resembled Tokuda's "*sikotanensis*." Consequently he concluded that *Neoschizomys sikotanensis* and *Clethrionomys sikotanensis* were synonyms of *Clethrionomys rufocanus bedfordiae*, this view being accepted by Abe (1968).

As already mentioned, Imaizumi (1971) described *Clethrionomys rex*, a form collected from the Rishiri Island. Soon after he (1972) reported another new form, *C. montanus*, which was collected from Hidaka Mountains, Hokkaido. One of the principal diagnostic characters distinguishing this form from *bedfordiae* was that this form had four inner salient angles on M³. Abe (1973a, b) considered that *rufocanus bedfordiae*, *sikotanensis*, and *rex* were distinct from one another but *montanus* was synonymous with *rex*.

A similar circumstance has been reported concerning *Clethrionomys glareolus* of Europe: two forms, one with three inner salient angles and the other with four on M³, occur in the same area (Miller, 1912; Zejda, 1960; Corbet, 1963, 1964). Steven (1953) proved that the two forms interbreed freely and concluded that they are conspecific.

It is clear from the present study that the vole of the Rishiri Island is larger in size than that of the main island of Hokkaido. Miyao (1968) has already pointed out that not only the voles of the Rishiri Island but also those of the Daikoku Isle and Rebun Isle, located near the Rishiri Island, were generally larger in overall size than

voles of the main island of Hokkaido. Prior to this, gigantism in insular forms has been reported in *C. glareolus* (Delany & Bishop, 1960; Corbet, 1964), and Foster (1964) noted that this type of gigantism is very common in rodents in general.

Differences in the skull dimensions among the collections are all due to differences in size and not to those of shape. Based on the result obtained from this study and on the above discussions, it is clear that the rather subtle characteristics of *C. sikotanensis*, *C. rex*, and *C. montanus* are not enough to warrant them a rank of distinct species. Therefore, the use of all these scientific names should be discarded, though future work may establish subspecific allocations of these forms.

Clethrionomys rutilus mikado (Thomas, 1905)

Evotomys mikado Thomas, 1905, *Abstr. Proc. Zool. Soc. London*: 19. [type: Aoyama, Hokkaido, Japan; British Mus. (Nat. Hist.)]

Evotomys amurensis mikado Aoki, 1915, *Nipponzan Nezumika*: 24.

Clethrionomys amurensis mikado Kuroda, 1939, *Shokubutsu oyobi Doöbutsu*, 7: 29.

Clethrionomys yesomontanus Kishida, 1931, *Lansania*, 3: 107.

Clethrionomys rutilus mikado Tokuda, 1941, *Trans. Biogeogr. Soc. Jap.*, 4: 44.

Clethrionomys mikado Ellerman, 1941, *Fam. & Genera Living Rodents*, 2: 571.

Clethrionomys rutilus amurensis Ellerman & Morrison-Scott (in part), 1951, *Checklist Palaearc. & Indian Mamm.*: 661.

Geographic variation was analysed for the skull dimensions of the specimens of *rutilus* collected from Hokkaido (Ishikarifutomi and Oketo) and the Asiatic Continent (eastern Siberia).

For the skull dimensions regression lines were calculated on logarithmic scales (Table 21). The data were compared among the collections statistically, and *F*-values for slope and positional differences were examined (Table 22). It was found that there was no significant difference ($P > .05$) in slope between any pair of lines, but differences in position are significant for rostral width, zygomatic width, auditory bulla width, and length of upper molar row at the level of .01, and for braincase length at the level of .05. Positional differences for nasal length are not significant ($P > .05$).

Among the mean values of parietal width of the collections from the three localities (Table 4, Fig. 5), the mean for Oketo is significantly larger than that for Ishikarifutomi ($.01 < P < .05$), though these are linked by that of the Continental form.

REMARKS: It has become clear from the present study that, as mentioned above, there are significant positional differences in some skull dimensions among the col-

Table 21. Equilibrium constants (a) and initial growth indices (b) for skull measurements of *Clethrionomys rutilus* collected from Hokkaido and the Continent.

Dimension		Ishikarifutomi (18.3–24.7)*		Oketo (19.2–24.6)*		Continental form (18.9–23.2)*	
		t _{.05}	S.E.	t _{.05}	S.E.	t _{.05}	S.E.
Nasal length	a	1.2355	0.1722	1.0738	0.1792	1.4256	0.3719
	b	-0.8445	0.2307	-0.6304	0.2430	-1.0992	0.4982
Rostral width	a	0.6577	0.2749	0.7221	0.2075	0.8599	0.6509
	b	-0.3492	0.3691	-0.4421	0.2813	-0.6426	0.8719
Zygomatic width	a	0.8559	0.1378	0.8246	0.1271	0.5343	0.4966
	b	-0.0542	0.1850	-0.0215	0.1723	-0.3526	0.6652
Braincase length	a	0.5777	0.0822	0.4532	0.1198	0.5625	0.3039
	b	0.2368	0.1103	0.4116	0.1625	0.2626	0.4062
Auditory bulla width	a	0.6180	0.1436	0.4464	0.1479	0.5441	1.2793
	b	-0.1411	0.1929	0.1037	0.2005	-0.0053	1.7137
Length of upper molar row	a	0.7641	0.2307	0.9086	0.1819	0.7384	0.4396
	b	-0.3877	0.3098	-0.5710	0.2469	-0.3480	0.5864

* Range of condylobasal length (in mm).

Table 22. *F*-values for slope and positional differences among samples of *Clethrionomys rutilus*.

Difference	NL N=98	RW N=102	ZW N=95	BL N=100	AW N=102	ML N=69
Slope differences	2.249	0.292	1.775	0.914	0.621	0.695
Positional differences	0.659	4.936**	9.930**	3.078*	10.174**	4.416**

* .01 < P < .05

** P < .01

lections, but no significant differences in slope between any two collections. In this case too, therefore, it follows that these differences are all due to differences in size and not to differences in shape. In addition, the means of parietal width indicate a clinal variation among the three collections. Rossolimo (1962), who studied the variation of *rutilus* on the Continent, received an impression of geographical continuity of the local forms. She wrote: "There are no real differences between the subspecies previously established. The population is characterized by a considerable geographical homogeneity and a great individual variability. The author thinks that none of the forms can be separated to an individual subspecies by the complex of its characters generally accepted as taxonomic ones." Based on such a view, it is very likely that, the larger the number of localities of collection is within one area, the more indistinct the differences will become among the collections.

The subspecific allocation of this form is still an open problem at the present

stage of study. It seems best to accept the recombination by Tokuda (1941), *Clethrionomys rutilus mikado* (Thomas, 1905).

Cranial comparison among species of *Clethrionomys*

Within the genus *Clethrionomys*, there are three extant species known from the Palaearctic Region: *C. rufocanus*, *C. rutilus*, and *C. glareolus*. In the present study, skull dimensions were compared to elucidate the interspecific feature of variation among these voles.

For the skull dimensions regression lines were calculated on logarithmic scales (Table 23). The data were compared among the species statistically, and *F*-values for slope and positional differences were examined (Table 24). Differences in slope are significant ($P < .01$) for zygomatic width and braincase length, and positional differences are significant ($P < .01$) in all dimensions.

Table 23. Equilibrium constants (a) and initial growth indices (b) for skull measurements in three species of *Clethrionomys*.

Dimension		<i>C. rufocanus</i> (20.2–30.6)*		<i>C. rutilus</i> (18.3–24.7)*		<i>C. glareolus</i> (21.4–24.5)*	
		t _{.05}	S.E.	t _{.05}	S.E.	t _{.05}	S.E.
Nasal length	a	1.1512	0.0647	1.1467	0.1104	1.3684	0.4479
	b	-0.7471	0.0914	-0.7278	0.1491	-1.0273	0.6068
Rostral width	a	0.8397	0.0565	0.7266	0.1432	0.8285	0.4869
	b	-0.5682	0.0797	-0.4497	0.1934	-0.5837	0.6596
Zygomatic width	a	0.9738	0.0445	0.8048	0.0965	0.7783	0.2913
	b	-0.2034	0.0627	0.0054	0.1303	0.0413	0.3946
Braincase length	a	0.6602	0.0324	0.5352	0.0718	0.6972	0.3141
	b	0.1728	0.0457	0.2993	0.0970	0.1095	0.4255
Auditory bulla width	a	0.6482	0.0514	0.5384	0.1377	0.6884	0.4032
	b	-0.1439	0.0726	-0.0219	0.1859	-0.1901	0.5462
Length of upper molar row	a	0.7442	0.0523	0.8639	0.1249	0.9270	0.3020
	b	-0.2695	0.0738	-0.5138	0.1688	-0.5726	0.4091

* Range of condylobasal length (in mm).

Table 24. *F*-values for slope and positional differences among samples of *Clethrionomys rufocanus*, *C. rutilus*, and *C. glareolus*.

Difference	NL N=435	RW N=451	ZW N=435	BL N=449	AW N=448	ML N=417
Slope differences	0.362	1.297	5.580**	5.218**	1.488	1.932
Positional differences	14.191**	107.856**	68.968**	505.942**	84.693**	580.435**

** $P < .01$

The result shows clearly the difference between inter- and intra-specific features of variations in the red-backed voles. Among distinct species there are significant differences not only in size but also in shape. On the other hand, within a species there are significant differences only in size and not in shape among the collections from various localities as have been shown in *Eothenomys andersoni*, *E. smithi*, *Clethrionomys rufocanus*, and *C. rutilus*.

Cranial comparison among the Japanese red-backed voles

In the classification of the Japanese red-backed voles there has been dispute as to whether *Eothenomys andersoni*, *E. smithi*, and *Clethrionomys rufocanus bedfordiae* are three distinct species or are conspecific. As an attempt to solve this problem, cranial comparisons were made on these three forms.

For the six skull dimensions regression lines were calculated on logarithmic scales (Table 25). The data for the three forms were compared statistically, and *F*-values for slope and positional differences were examined (Table 26). It was found that there are significant slope differences in rostral width, auditory bulla width, and length of upper molar row at the level of .01, and in nasal length at the level between .01 and .05. In all dimensions significant differences ($P < .01$) in position are found between every pair of lines.

This result indicates that the differences both in size and shape are significant among the three forms. As already mentioned both in *andersoni* and *smithi*, the mean

Table 25. Equilibrium constants (a) and initial growth indices (b) for skull measurements in samples of *Eothenomys andersoni* and *E. smithi*.

Dimension		<i>E. andersoni</i> (19.3–28.5)*		<i>E. smithi</i> (19.6–25.8)*	
			$t_{.05}$ S.E.		$t_{.05}$ S.E.
Nasal length	a	1.1446	0.0776	0.9770	0.0972
	b	-0.7169	0.1091	-0.4747	0.1324
Rostral width	a	0.7573	0.0757	1.0723	0.1141
	b	-0.4755	0.1065	-0.8755	0.1556
Zygomatic width	a	1.0558	0.0504	1.0035	0.0784
	b	-0.3313	0.0709	-0.2406	0.1067
Braincase length	a	0.6688	0.0442	0.7420	0.0719
	b	0.1613	0.0622	0.0458	0.0980
Auditory bulla width	a	0.9641	0.0599	0.8909	0.0856
	b	-0.5595	0.0843	-0.4954	0.1167
Length of upper molar row	a	0.9026	0.0649	1.0696	0.1078
	b	-0.5067	0.0913	-0.7368	0.1472

* Range of condylobasal length (in mm).

Table 26. *F*-value for slope and positional differences among samples of *Eothenomys andersoni*, *E. smithi*, and *Clethrionomys rufocanus bedfordiae*.

Difference	NL N=863	RW N=901	ZW N=845	BL N=893	AW N=898	ML N=896
Slope differences	3.994*	11.837**	2.853	2.581	32.989**	17.776**
Positional differences	177.946**	239.893**	134.782**	158.461**	549.389**	88.418**

* .01 < P < .05

** P < .01

value of parietal width varies clinally from locality to locality (Fig. 5). In *andersoni*, the mean for the Mt. Yatsugatake specimens is the largest, and in *smithi*, contrary to *andersoni*, that of the Mt. Yatsugatake specimens is the smallest. The mean values show significant difference ($P < .01$) between the two forms of Mt. Yatsugatake. Therefore, it is clear that these two clines are distinct from each other.

Hinton (1926) examined specimens of the Japanese red-backed voles and stated: "A careful study of the magnificent material ... leaves no room for doubting that *E. smithii*, *E. 'bedfordiae'*, *E. 'andersoni'*, and '*niigatae*' belong to one form and if the material representing each of these nominal species had arrived on one and the same day all would, in my opinion, have been inevitably treated as one form. ... Throwing the lot into a heap the reviser begins by determining the relative ages of the skulls of all the specimens, and as they arrange themselves in order of length he sees at last that he is not dealing with so many distinct species and subspecies but with so many different stages of growth. ... *E. (Phaulomys) smithii* was based upon a young male, obtained in February 1904; by accident the fifty-three specimens of the series collected in Hondo, Kiushiu, and Shikoku, by M. P. Anderson in the following year are all young too. ... Later on Mr. Anderson collected thirteen in Hokkaido. The majority of these are adult, some even old; in size, skull form and tooth pattern they are strikingly different from the material referred by Thomas to *E. smithii*. These were therefore described as a new species, *E. (Craseomys) bedfordiae*. ... In the same paper *E. (C.) andersoni* was described, from two specimens obtained in North Hondo. Both specimens, however, are merely large adolescents ... Lastly, Anderson's *E. niigatae* also has been founded upon an adolescent animal ... On laying out all the skulls from Japan, whether labelled as '*smithii*,' '*bedfordiae*,' '*andersoni*,' or '*niigatae*,' in order of age, we find that the whole series forms an exact parallel to the series formed by the skulls of *E. r. rufocanus*, *E. r. shanseius*, and *E. r. regulus* when similarly arranged." This conclusion has been accepted by Ellerman (1941), Ognev (1950), and Ellerman and Morrison-Scott (1951).

The result of the present study is incompatible with Hinton's (1926) view that the difference among *smithi*, *bedfordiae*, *andersoni*, and "*niigatae*" is no more than an age

variation within a single species. There are significant differences both in size and shape of the skull among the three forms (“*niigatae*” is synonymous with *andersoni*). The mean values of parietal width show the same tendency of variation both in *andersoni* and *smithi*, that is, the value in the specimens from southern localities is larger than that in the northern specimens. In the specimens from Mt. Yatsugatake, where the distribution of both forms overlaps, their mean values are significantly different. Accordingly, each of *andersoni* and *smithi* consists of an independent clinal variation in parietal width. Further, these three forms, *smithi*, *bedfordiae*, and *andersoni* can easily be identified by means of the key presented in this study.

From these result and discussions, it is clear that *andersoni*, *smithi*, and *bedfordiae* are three distinct species and that Hinton’s interpretation is not correct.

Phylogenetic Relationship of *Eothenomys andersoni*

Many students have discussed the problem of the origin of the Japanese red-backed voles, but there is, at least, no room to doubt the generic allocation of *Eothenomys smithi*, *Clethrionomys rufocanus bedfordiae*, and *C. rutilus mikado*. In the case of *E. andersoni*, there are two different views to account for its origin: one of them links it with the genus *Clethrionomys* and the other with the genus *Aschizomys*. Here the relationship of *andersoni* to other allied species will be discussed on the basis of dental morphology, bacular morphology, comparative karyology, ectoparasites, and fossil evidence, all of which have been considered important in clarifying the phyletic relationships of mammals.

The extant red-backed voles of Eurasia are classified in three genera: *Eothenomys*, *Alticola*, and *Clethrionomys*. They can be divided into two types by their morphology,

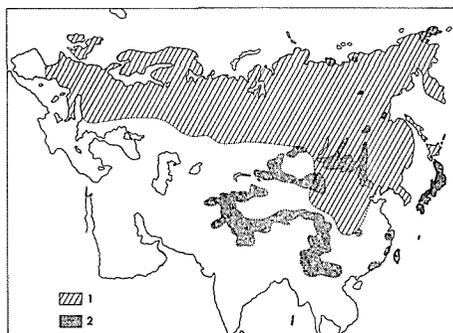


Figure 6. Geographic distribution of red-backed voles in Eurasia.
1: Voles with rooted molars (*Clethrionomys*); 2: Voles with rootless molars (*Eothenomys* and *Alticola*).

one with rootless molars and the other with rooted molars. *Eothenomys* and *Alticola* belong to the former, while *Clethrionomys* belongs to the latter type. The distribution of *Eothenomys* and *Alticola* is restricted to montane regions, while *Clethrionomys* is distributed widely in the northern half of Eurasia (Fig. 6). *E. andersoni* is distributed mainly in the montane region of Honshu.

Dental morphology

Regarding the evolutionary trend of the molar pattern in microtine rodents, Kowalski (1970) has stated that: "It is open to discussion whether the evolution of voles occurred through the simplification of the tooth structure, as accepted by Hinton (1926) and by Zimmermann (1955), or through the complication of the original pattern (Guthrie, 1965)."

In *andersoni*, while the animal is young the postcingulum is well developed, the molar crown bears a more complicated occlusal pattern and its dentinal spaces are confluent with the neighbouring ones (Fig. 7). When occlusion begins, the postcingulum decreases in size and the dentinal isthmuses tend to close. This is the general process of molar attrition in red-backed voles (Zejda, 1960; Abe, 1977a). Thus, it can be presumed on the basis of this ontogenetic change that the molar patterns of red-backed voles decrease their complexity and tend to close their dentinal isthmuses in the course of evolution.

In *andersoni* and *smithi*, the posteroloph and posterior posteroconule of M³ are

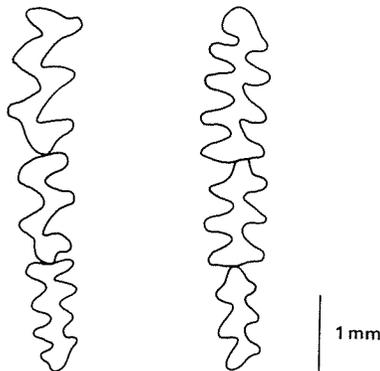


Figure 7. Occlusal surfaces of molars showing M³ not yet fully occluded in one young specimen (No. 52) of *Eothenomys andersoni* collected at Mt. Nyutoh, Akita Prefecture, northern Honshu.

left: upper left molar row; right: lower right molar row.

usually well developed, but in *rufocanus*, these are not so. In the dentinal isthmuses, there is a general tendency for them to be open more often in *smithi* and *andersoni* than in *rufocanus*. In M^1 and M^2 , the second minor fold and second secondary fold are well developed in *andersoni*, though the posteroloph and anterior posteroconule are vestigial. On M^3 the posteroloph and the posterior posteroconule are well developed in *andersoni*. Thus, it can be said that *andersoni* retains a relatively primitive molar pattern.

In the root formation of molars, both *andersoni* and *smithi* have rootless molars, while *rufocanus* has rooted molars. It is generally accepted that rootless molars have differentiated from rooted molars.

As a result, it can be said that *andersoni* and *smithi* share common dental characteristics with each other, and they are more primitive in their occlusal tooth pattern, but more specialized in root formation than *rufocanus*.

Bacular morphology

Jameson (1961) studied bacula of the Japanese red-backed voles and wrote his impression as follows: "The bacula of the red-backed voles in Japan are rather variable within a given species, and provide rather poor taxonomic characters at the specific level. ... There are probably no differences between the bacula of *Clethrionomys niigatae* and *C. rufocanus bedfordiae*, but *C. imaizumii* has relatively larger prongs which are rather divergent." He, however, could not study the baculum of *andersoni* of northern Honshu, so Figure 8 shows a baculum of *andersoni* collected at Mt. Chokai, northern Honshu. This is not distinct from bacula of *andersoni* collected from other localities.

In this character, *andersoni*, *smithi* and *bedfordiae* are not separable, as was pointed out by Jameson (1961).

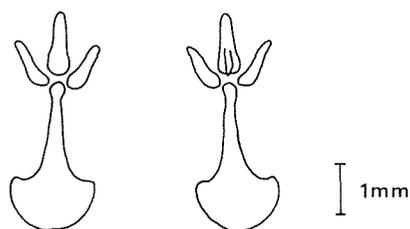


Figure 8. Ventral (left) and dorsal (right) views of baculum of a specimen (No. 301) of *Eothenomys andersoni* collected at Mt. Chokai.

Ectoparasites

It has been said that ectoparasites sometimes give useful information for the

elucidation of phylogeny and the process of distribution of the host animals. Here, host-parasite relations will be discussed only with regard to fleas.

Jameson (1961) suggested a close relationship among “*niigatae*,” *andersoni* (*s. str.*), and *bedfordiae*, partly by reason of the fleas common to them. He ascertained that: “they (“*niigatae*” and *andersoni*) share three species of fleas which are parasites of *C. rufocanus* in Hokkaido; *Catallagia striata*, *Megabothris sokolovi*, and *Rhadinopsylla alphabetica*.” It is, however, evident that these three fleas are parasitic on a wide variety of host species (Table 27). According to Sakaguti (1967), the ranges of distribution of these three fleas are so wide that it is very difficult to find true hosts for each of them. Other fleas may have specific hosts, e.g. *Peromyscopsylla hamifer takahasii*, and *P. h. michinoku*, whose true hosts are *bedfordiae*, *rutilus*, and *Apodemus* spp. for the former, and *andersoni* (*s. str.*) for latter. Therefore, he presumed that *andersoni* (*s. str.*) had reached Honshu via Hokkaido. If this presumption be correct, then the route of migration of “*niigatae*” was different from that of *andersoni* (*s. str.*), since “*niigatae*” does not harbour *P. h. michinoku*. Uchikawa (1967, 1969), who studied fleas parasitic on small mammals at Mt. Yatsugatake, concluded that because fleas change their hosts from locality to locality within the range of their geographic distribution, before discussing host-parasite relationship at the specific level, detailed studies should be done on the range of distribution of the fleas in question.

Table 27. Small mammalian hosts of the three species of fleas, *Catallagia striata*, *Megabothris sokolovi*, and *Rhadinopsylla alphabetica*, recorded from Japan.

Flea	Sakaguti & Jameson (1962)	Sakaguti (1962)	Uchikawa (1967)	Sakaguti (1967)	Uchikawa (1969)
<i>Catallagia striata</i>	<i>rufocanus</i> <i>rutilus</i> “ <i>niigatae</i> ”	<i>rufocanus</i> <i>rutilus</i> “ <i>niigatae</i> ” <i>A. argenteus</i>	<i>andersoni</i> <i>smithi</i> <i>M. montebelli</i>	<i>rufocanus</i> <i>rutilus</i> “ <i>niigatae</i> ”*	<i>andersoni</i> <i>M. montebelli</i>
<i>Megabothris sokolovi</i>	<i>rufocanus</i> “ <i>sikotanensis</i> ” “ <i>niigatae</i> ” <i>Microtus montebelli</i> <i>Rattus norvegicus</i>	<i>rufocanus</i> “ <i>sikotanensis</i> ” <i>M. montebelli</i> <i>R. norvegicus</i>	<i>andersoni</i> <i>smithi</i>	<i>rufocanus</i> “ <i>sikotanesnis</i> ” <i>rutilus</i> <i>M. montebelli</i>	
<i>Rhadinopsylla alphabetica</i>	<i>rufocanus</i> “ <i>niigatae</i> ” <i>Apodemus speciosus</i> <i>A. argenteus</i> <i>Sorex unguiculatus</i>	<i>rufocanus</i> <i>rutilus</i> “ <i>niigatae</i> ” <i>A. argenteus</i> <i>S. unguiculatus</i>	<i>andersoni</i> <i>M. montebelli</i> <i>Dymecodon pilirostris</i>	<i>rufocanus</i> <i>rutilus</i> “ <i>niigatae</i> ” <i>A. speciosus</i> <i>A. argenteus</i>	<i>andersoni</i>

* This was originally described as *andersoni*, but it seems to be “*niigatae*.”

At the present stage of study, data are too poor to discuss the phylogeny of red-backed voles on the basis of their ectoparasites. More detailed studies are needed to find a clue to the elucidation of the phylogeny of the host voles.

Comparative karyology

The diploid chromosomal number is constantly 56 in all the species (Table 28). The Japanese red-backed voles are uniform in the chromosomes of the autosomal complements, but sex-chromosomes show intra- and inter-specific variations. Male sex-chromosomes are variable in them, particularly in *Eothenomys andersoni* and *E. smithi*.

Table 28. Karyotypes of the Japanese red-backed voles.

Species	2n	Autosomes*			Sex chromosomes*		
		M	ST	A			
<i>Clethrionomys rutilus mikado</i>	56	2		52	A	M	1, 2, 4, 6
<i>Clethrionomys rufocanus bedfordiae</i>	56	2		52	A	A	1, 2, 3, 4
"rex"	56	2		52	A	M	2, 4, 6
"montanus"	56	2		52	A	A	6
<i>Eothenomys andersoni</i>	56	2		52	ST	M	6
	56	2	2	50	ST	M	7
"niigatae"	56	2		52	A	M	5
	56	2		52	A	A	6
	56	2		52	A	SM	6
	56	2	2	50	A	A	7
"imaizumii"	56	2		52	ST	SM	6
	56	2	2	50	ST	SM	7
<i>Eothenomys smithi</i>	56	2		52	ST	SM	2
	56	2		52	A	SM	4
	56	2		52	A	A	5
	56	2		52	SM	ST	6
"kageus"	56	2		52	ST	ST	4

* M: metacentric, SM: submetacentric, ST: subtelocentric, A: acrocentric.

** 1: Shimba et al. (1969), 2: Tsuchiya (1970), 3: Sonta et al. (1971),

4: Tsuchiya et al. (1971), 5: Hsu et al. (1974), 6: Tsuchiya et al. (1977),

7: Tsuchiya (1977)

Since it is generally known that diploid chromosomal number is constant throughout a species, while sex-chromosomes show great variability within species, karyotype analysis is of little concern for the relationship of *Eothenomys andersoni* with other species.

Fossil evidence

Fossils of microtine rodents have been known from several localities in Japan, except Hokkaido (Kowalski & Hasegawa, 1976; Kawamura & Ishida, 1976; Hasegawa et al., 1978). Unfortunately it is very difficult to know their exact geologic age since

most of them were deposited in fissures, and not in sedimentary beds.

Fossil faunae of the Japanese voles can be divided into three by their elements. The first fauna contains only extinct species such as *Clethrionomys* sp., *Microtus epiratticeps*, and/or *Myopus schisticolor*. The second one contains species which are represented by not only extinct but also surviving voles, such as *Eothenomys* spp. and/or *Microtus montebelli*. The third one consists of surviving species. The oldest of these three should be the first one, and its geologic age is presumed as late middle Pleistocene from the similarity of accompanying elements with those of the locality 1 at Choukoutien (Hasegawa et al., 1978). It would seem possible that after that time the extant species reached Japan.

The possibility of linking the origin of *andersoni* to the genus *Clethrionomys* was conceived by Tokuda (1941). He considered that originally a *rufocanus*-like ancestor inhabited Japan, and after the separation of Honshu from Hokkaido, this form evolved *in situ* to a distinct species, *andersoni*. If this be true, *Clethrionomys* sp. which was unearthed from Ando quarry, Yamaguchi Prefecture, Honshu, and other localities, may have been the ancestor of *andersoni*. This form, however, has relatively simple M³ (Hasegawa et al., 1978). In view of the presumption that, as mentioned before, the ancestor should have had a more complex molar pattern than its descendants, Tokuda's idea is untenable. Another view on the origin of *andersoni* is to link it to the genus *Aschizomys* (= *Alticola*) as was presented by Jameson (1961). He wrote: "*Clethrionomys* (*Aschizomys*) *niigatae* and *C. (A.) andersoni* are almost certainly arrivals via Hokkaido. Although *niigatae* and *andersoni* are close relatives of *C. rufocanus bedfordiae*, they may have been derived from an earlier stock." This is a modification of Tokuda's idea and there are no positive data to support it since no ancestral form of *Alticola* has been found in Japan.

At the present stage of study, it would be most reasonable to regard *andersoni* as evolved from an ancestral form in the genus *Eothenomys*. In consideration of the fact that fossil evidence suggests rather recent appearance of *Eothenomys* in Japanese islands together with *Microtus montebelli* and the fact that these two genera do not inhabit Hokkaido, it would seem possible that they have reached Japan from the Continent via the Korean Peninsula to give rise to *andersoni*, although *Eothenomys* is not found in Korea today. This is the only interpretation that is, at least, not incompatible with the fossil evidence and biogeographical facts.

General conclusion

Based on the dental morphology, bacular morphology, ectoparasites, comparative karyology, and fossil evidence, it seems most reasonable to place *andersoni* in the genus *Eothenomys*.

Summary

The classification of the Japanese red-backed voles is in disorder and diverse interpretations coexist concerning their relationships and allocations. In order to rectify this discordance, the classification was reexamined by means of statistical analyses of craniometric data and of observations of molar patterns, which were obtained from over 1,000 specimens from various localities. For this purpose, the Japanese red-backed voles were divided into four groups, i.e. *andersoni*, *smithi*, *rufocanus*, and *rutilus* groups, and intra-group geographical variations were investigated.

Eight cranial dimensions were selected for craniometry. Among them parietal width showed no increase in absolute size within the range of material available, and therefore, mean values were compared directly. For the other dimensions, their proportions to condylobasal length were compared allometrically among samples from various localities.

First of all, secondary sexual difference was examined craniometrically using the specimens of *Eothenomys andersoni* from Mt. Yatsugatake and it was found that there was no significant difference between the sexes. Accordingly, specimens were treated for further analyses of geographic variation without separation of males and females.

It is concluded that the Japanese red-backed voles are classified into four valid species: *Eothenomys andersoni*, *E. smithi*, *Clethrionomys rufocanus bedfordiae*, and *C. rutilus mikado*. But the propriety of their subspecific arrangement is left for further studies. Furthermore, the phylogenetic relationship of *Eothenomys andersoni* is discussed on the basis of dental morphology, bacular morphology, comparison of karyotypes, ectoparasites, and fossil evidence. From these aspects, too, it is concluded that *andersoni* should be placed in the genus *Eothenomys*, and not in *Clethrionomys* or *Aschizomys*.

In addition, a new diagnostic key for the four species of the Japanese red-backed voles is given for practical use.

Acknowledgments

I am grateful to the following for making it possible for me to examine specimens. They are: Takeo Miyao, Tsutomu Kuwahata, Hisashi Abe, Yuzo Fujimaki, Ryo Tanaka, Masaomi Kanamori, Shoei Otsu, Takeo Ito, and the Yamashina Institute of Ornithology.

I wish to express my deep appreciation to all my colleagues for kindly reading through the manuscript. I am especially indebted to the late Mitosi Tokuda, without whose supervision this study could never have been completed. I am grateful to

Motoö Tasumi, Tsuneaki Kobayashi, and Okimasa Murakami for their useful criticism.

Special thanks are also extended to the following specialists for their kind suggestions on respective field of study: Kohei Sakaguti in parasitology, Kimiyuki Tsuchiya in comparative karyology.

References

- Abe, H., 1968. Growth and development in two forms of *Clethrionomys*. I. External characters, body weight, sexual maturity and behavior. *Bull. Hokkaido Forest Exp. Station*, no. 6: 69–89. [in Japanese with English summary.]
- Abe, H., 1973a. Growth and development in two forms of *Clethrionomys*. II. Tooth characters, with special reference to phylogenetic relationships. *J. Fac. Agr. Hokkaido Univ.*, 57: 229–254.
- Abe, H., 1973b. Growth and development in two forms of *Clethrionomys*. III. Cranial characters, with special reference to phylogenetic relationships. *J. Fac. Agr. Hokkaido Univ.*, 57: 255–274.
- Aimi, M., 1967. Similarity between the voles of Kii Peninsula and of northern part of Honshu. *Zool. Mag. (Japan)*, 76: 44–49. [in Japanese with English summary.]
- Aimi, M., 1971. On the taxonomic status of the red-backed vole of Honshu. In *Symp. "Primates' place in the mammalian evolution."* Inuyama: Primate Research Institute, Kyoto Univ. [in Japanese.]
- Allen, G. M., 1940. Natural history of central Asia, vol. 11, part 2, *The mammals of China and Mongolia*. New York: Amer. Mus. Nat. Hist.
- Anderson, M. P., 1909. Description of a new Japanese vole. *Ann. Mag. N. H.*, ser. 8, 4: 317.
- Aoki, B., 1915. *Nipponzan nezumika (Muridae of Japan)*. Tokyo: Zool. Soc. Tokyo. [in Japanese.]
- Arvy, L., 1974. Contribution à la connaissance de l'appareil mammaire chez les rongeurs. *Mammalia*, 38: 108–138.
- Bol'shakov, V. N., 1966. K voprosu o sistematicheskoi blizosti lemmingovidnoi i krasno-seroi polevok v svyazi s nekotorymi problemami nadvidovoi sistematiki. In S. S. Shvartz(ed.), *Vnutrividovaya izmenchivost' nazemnykh pozvonochnykh zhivotnykh i mikroevolyutsiya*. Sverdlovsk: Akad. Nauk, SSSR. [in Russian.]
- Corbet, G. B., 1963. An isolated population of the bank-vole *Clethrionomys glareolus* with aberrant dental pattern. *Proc. Zool. Soc. London*, 140: 316–319.
- Corbet, G. B., 1964. Regional variation in the bank-vole *Clethrionomys glareolus* in the British isles. *Proc. Zool. Soc. London*, 143: 191–219.
- Delany, M. J. & I. R. Bishop, 1960. The systematics, life history and evolution of the bank-vole *Clethrionomys Tilesius* in north-west Scotland. *Proc. Zool. Soc. London*, 135: 409–422.
- Ellerman, J. R., 1941. *The families and genera of living rodents*. vol. 2, London: British Museum (N.H.).
- Ellerman, J. R. & T. C. S. Morrison-Scott, 1951. *Checklist of Palaearctic and Indian mammals*. London: British Museum (N.H.).
- Foster, J. B., 1964. Evolution of mammals on islands. *Nature, London*, 202: 234–235.
- Geptner, V. G. & O. L. Rossolimo, 1968. Vidovoi sostav i geograficheskaya izmenchivost' aziatskikh gornykh polevok roda *Alticola* Blanford, 1881. *Sb. Trud. Zool. Mus.*, 10: 53–93. [in Russian.]

- Gromov, I. M., A. A. Gureev, G. A. Novikov, I. I. Sokolov, P. A. Strelkov, & K. K. Chapskii, 1963. *Mlekopitayuschchie fauny SSSR*. Chast' 1. Moskva-Leningrad: Akad. Nauk, SSSR. [in Russian.]
- Guthrie, R. D., 1965. Variability in characters undergoing rapid evolution, an analysis of *Microtus* molars. *Evolution*, 19: 214–233.
- Hanaoka, T., 1937. Supplementary notes on Muridae in the highlands of central Japan. — On *Clethrionomys rufocanus andersoni* (Thomas) and its taxonomical status. *Zool. Mag. (Japan)*, 49: 429–436. [in Japanese with English summary.]
- Hasegawa, Y., M. Aimi, & G. Okafuji, 1978. Pleistocene Microtinae (Rodentia) from Ando quarry at Ofukudai karst plateau, Yamaguchi Prefecture, Japan. *Quaternary Res.*, 16: 13–17. [in Japanese with English summary.]
- Hershkovitz, P., 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. *Fieldiana Zoology*, 46: 1–524.
- Hinton, M. A. C., 1926. *Monograph of the voles and lemmings, (Microtinae), living and extinct*. London: British Museum (N.H.).
- Hsu, T. C. & K. Benirschke, 1974. Folio 370: *Aschizomys niigatae*, *Aschizomys imaizumi*., Folio 371: *Eothenomys smithi*, *Eothenomys kageus*. In *Atlas of mammalian chromosomes*, vol. 8. New York: Springer-Verlag.
- Imaizumi, Y., 1949. *Nippon honyudobutsu zuzetsu. (Illustrated Japanese mammals)* Tokyo: Yoyoshobo. [in Japanese.]
- Imaizumi, Y., 1957. Taxonomic studies on the red-backed vole from Japan. Part I. Major divisions of the vole and descriptions of *Eothenomys* with a new species. *Bull. National Sci. Mus. Tokyo*, no. 40: 195–216.
- Imaizumi, Y., 1960. *Colored illustrations of mammals of Japan*. Tokyo: Hoikusha. [in Japanese.]
- Imaizumi, Y., 1965. *Shin-Nippon dobutsu zukan. (New illustration book of Japanese animals)*. Tokyo: Hokuryukan. [in Japanese.]
- Imaizumi, Y., 1971. A new vole of the of the *Clethrionomys rufocanus* group from Rishiri Island, Japan. *Japanese J. Mamm.*, 5: 99–103.
- Imaizumi, Y., 1972. Land mammals of the Hidaka Mountains, Hokkaido, Japan, with special reference to the origin of an endemic species of the genus *Clethrionomys*. *Mem. National Sci. Mus. Tokyo*, no. 5: 131–149. [in Japanese with English description.]
- Jameson, E. W. Jr., 1961. Relationships of the red-backed voles of Japan. *Pacific Sci.*, 15: 594–604.
- Kawamura, Y. & S. Ishida, 1976. Preliminary report on the late Pleistocene micro-mammalian fossils from Kumaishi-do Cave, Gifu Prefecture, central Japan. *J. Speleol. Soc. Japan*, 1: 28–34. [in Japanese with English summary.]
- Kowalski, K., 1970. Variation and speciation in fossil voles. *Symp. Zool. Soc. London*, no. 26: 149–161.
- Kowalski, K. & Y. Hasegawa, 1976. Quaternary rodents from Japan. *Bull. National Sci. Mus. Tokyo*, (C), 2: 31–66.
- Kuroda, N., 1931. Yachinezumi no shinsanchi to sonogakumei. (On new locality and name of red-backed vole.) *Zool. Mag. (Japan)*, 43: 661–666. [in Japanese.]
- Miller, G. S. Jr., 1898. Description of a new genus and species of microtine rodent from Siberia. *Proc. Acad. Nat. Sci. Philadelphia*, 50: 368–371.
- Miller, G. S. Jr., 1912. *Catalogue of the mammals of Western Europe*. London: British Museum (N.H.).
- Miller, G. S. Jr., 1940. The status of the genus *Aschizomys* Miller. *J. Mamm.*, 21: 94–95.

- Miyao, T., 1967. Studies on the geographical variation of the small mammals in Japanese Islands. I. Geographical variation of Smith's red-backed vole, *Eothenomys smithi*. (2) Hind-foot length, tail length, number of sacro-caudal vertebrae and breeding activity. *J. Growth*, 6: 7-18. [in Japanese with English summary.]
- Miyao, T., 1968. Rishiri no Ezoyachinezumi. (Red-backed vole on Rishiri Island.) *Hoppingyo*, 20: 169-172. [in Japanese.]
- Miyao, T., T. Morozumi, H. Hanamura, H. Akahane, & A. Sakai, 1964. Small mammals on Mt. Yatsugatake in Honshu. III. Smith's red-backed vole (*Eothenomys smithi*) in the subalpine forest zone on Mt. Yatsugatake. *Zool. Mag. (Japan)*, 73: 189-195.
- Ognev, S. I., 1950. *Zveri SSSR i prilozhaschchikh stran*. 7. Moskva-Leningrad: Akad. Nauk, SSSR. [in Russian.]
- Osgood, W. H., 1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic expeditions. *Field Mus. Nat. Hist.*, Zool. Ser., 18: 193-339.
- Ota, K., 1956. The Muridae of the islands adjacent to Hokkaido. *Mem. Fac. Agr. Hokkaido Univ.*, 2: 123-136. [in Japanese with English summary.]
- Palmer, T. S., 1928. An earlier name for the genus *Evotomys*. *Proc. Biol. Soc. Washington*, 41: 87-88.
- Reeve, E. C. R., 1940. Relative growth in the snout of anteaters. A study in the application of quantitative methods to systematics. *Proc. Zool. Soc. London*, Ser. A, 110: 47-80.
- Rensch, B., 1959. *Evolution above the species level*. London: Methuen.
- Rossolimo, O. L., 1962. O vnutrividovoi izmenchivosti krasnoi polevki (*Clethrionomys rutilus* Pall.). *Zool. Zhur.*, 41: 443-452. [in Russian with English summary.]
- Sakaguti, K., 1962. *A monograph of the Siphonaptera of Japan*. Osaka: Nippon Printing & Publishing Co. Ltd.
- Sakaguti, K., 1967. On the geographical distribution of Japanese fleas with special regard to the distribution of their host mammals. *Mem. Otemae Women's Univ.*, no. 1: 100-115. [in Japanese.]
- Sakaguti, K., & E. W. Jameson, Jr., 1962. The Siphonaptera of Japan. *Pacific Insects Monograph*, 3: 1-169.
- Shimba, H., M. Itoh, Y. Obara, S. Kohno, & T. Kobayashi, 1969. A preliminary survey of the chromosomes in field mice, *Apodemus* and *Clethrionomys*. *J. Fac. Sci. Hokkaido Univ.*, Ser. VI, Zool., 17: 257-262.
- Sonta, S., I. Hayata, & T. Kobayashi, 1971. A chromosome survey of the red-backed mouse, *Clethrionomys rufocanus bedfordiae*, in Hokkaido, with a note of a karyotypically abnormal specimen. *Proc. Japan Acad.*, 47: 679-682.
- Steven, D. M., 1953. Recent evolution in the genus *Clethrionomys*. *Symp. Soc. Exp. Biol.*, 7. *Evolution*: 310-319.
- Tanaka, R., 1971. A research into variation in molar and external features among a population of the Smith's red-backed vole for elucidation of its systematic rank. *Japanese J. Zool.*, 16: 163-176.
- Thomas, O., 1905a. On some new Japanese mammals presented to the British Museum by Mr. R. Gordon-Smith. *Ann. Mag. N. H.*, Ser. 7, 15: 487-495.
- Thomas, O., 1905b. Abstract. *Proc. Zool. Soc. London*, no. 23: 18-19.
- Tokuda, M., 1935. *Neoschizomys*, a new genus of Microtinae from Sikotan, a south Kurile Island. *Mem. Coll. Sci. Kyoto. Imp. Univ.*, Ser. B, 10: 241-250.
- Tokuda, M., 1941. A revised monograph of the Japanese and Manchou-Korean Muridae. *Biogeographica, Transact. Biogeogr. Soc. Japan*, 4: 1-156.

- Tokuda, M., 1955. Congeneric species of voles found in Japan and Yunnan. *Bull. Biogeogr. Soc. Japan*, 16-19: 388-391.
- Tsuchiya, K., 1970. Classification of Japanese voles, rats, and mice based on their karyotypes. *Yama to hakubutsukan. (Mountains and Museum.)*, 15: 2-3. [in Japanese.]
- Tsuchiya, K., 1977. Chromosome studies in three species of the genus *Aschizomys* from Honshu, Japan (Microtinae; Rodentia). *Japanese J. Gen.*, 52: 482. [in Japanese, Abstract only.]
- Tsuchiya, K. & T. H. Yosida, 1971. Chromosome survey of small mammals in Japan. *Annual Rep. National Inst. Gen. (Japan)*, no. 21, 1970: 54-55.
- Uchikawa, K., 1967. An ecological study on the fleas in the Yatsugatake range. (I) On the fleas found on the small mammals trapped in the subalpine forest. *Japanese J. Ecol.*, 17: 43-49.
- Uchikawa, K., 1969. An ecological study on the fleas in the Yatsugatake range. (II) On the fleas found on the small mammals trapped in the mountain zone. *Japanese J. Ecol.*, 19: 48-52.
- Vinogradov, B. S., 1927. Zametki o mlekopitayuschchikh yakutii. I. Lemmingovidnye polevki (rod *Aschizomys*). *Materialy Komissii po izucheniyu Yakutskoi ASS Respubliki*, Vyp. 17. Leningrad: Akad. Nauk, SSSR. [in Russian with English summary.]
- Zejda, J., 1960. The influence of age on the formation of third upper molar in the bank-vole *Clethrionomys glareolus* (Schreber, 1780) (Mammalia: Rodentia). *Zool. Listy*, 9: 159-166.
- Zimmermann, K., 1955. Die Gattung *Arvicola* Lac. im System der Microtinae. *Säugetierk. Mitt.*, 3: 110-112.