

Relationships of the Red-backed Voles of Japan

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EASTERN ASIA is particularly rich in genera and species of microtine rodents, some of which are more or less intermediate between *Microtus* on the one hand and *Clethrionomys* on the other. Where species of only these two genera are concerned, there is no problem of identity because there are differences in the color, in the structure of the palate, and in the skull in general. The age of the specimen changes strikingly the condition of the cheek teeth, in which there are some of the most important generic features. Molars of immature specimens of *Clethrionomys*, for example, are rootless, and resemble in this respect the molars of adult individuals of *Microtus*. In eastern Asia there are a number of species which resemble the species of *Clethrionomys* in the palate, which terminates in a shelf, and are like *Microtus s. str.* in having rootless molars. For these forms which combine some of the structural characteristics of *Clethrionomys* and *Microtus* there are a number of generic names. A reviewer naturally wonders if his material contains mature individuals, and this doubt has caused some disagreement as to the proper generic allocation of red-backed voles of the Far East.

The red-backed voles in Japan have been discussed by Hinton (1926), whose conclusions have been accepted by Ellerman (1941) and by Ellerman and Morrison-Scott (1951). Hinton (1926: 259-262) judged that several different forms were all based on immature specimens and placed *bedfordiae*, *andersoni*, and *niigatae* as synonyms of *smithi*. He very carefully explained the pitfalls in separating voles on a small series and he emphasized the early age at which voles breed (and are apparently adult). In the Japanese forms in question, the age of the specimens is of great importance because these names were proposed for individuals in which the mo-

lars are rootless, and Hinton's conclusion was that they are all immature specimens. His caution is certainly justified but can be carried to misleading extremes, for by combining several distinct forms as one, it is not difficult to show that a given character, in this case the condition of the molar roots, is indeed remarkably variable. There are remarks in Hinton's appraisal of the situation that raise some doubts as to its application to the specimens he had at hand. For example, in reference to the small vole called *smithi*, he stated (1926: 260) that the type was a young male and added that "...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." It is possible, of course, to sample a population and obtain a series in which immature specimens predominate; but it is incredible that such an experienced collector as Anderson would have preserved 53 specimens of *smithi* from at least three widely separated localities and fail to include a single adult. Hinton added:

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. (Crasomys) bedfordiae*. But two specimens of this original series of *E. bedfordiae* are immature, and these are not distinguishable from the material upon which *E. smithii* was founded.

These two presumably immature specimens could possibly belong to *Clethrionomys rutilus*, which is not uncommon in some parts of Hokkaido; and, in this region, *rutilus* is a small bright short-tailed form somewhat like *smithii*. On the same page he dismissed the form described as *E. (C.) andersoni* with the comment, "...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

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as *E. smithii*." Lastly, "Anderson's *E. niigatae* also has been founded upon an adolescent animal. . . ."

Apparently Hinton attached no importance to the occurrence of immature *smithii* on Kyushu, Shikoku, and Honshu, and the absence of adult *smithii* everywhere but on Hokkaido. It is surprising that he did not consider that these forms with rootless molars might actually be adults, for on the mainland of Asia and on Taiwan are genera of red-backed voles in which the molars are rootless in the adults. Hinton recognized *Eothenomys*, *Antelionomys*, and *Aschizomys*, genera in which the molars are rootless; but failed to suggest any similarities between *smithii* and the species of these genera.

The classification of these voles by Japanese mammalogists differs considerably from the recent presentation of Ellerman (1941) and of Ellerman and Morrison-Scott (1951). In the latter work the authors were apparently unaware of the very careful study on Japanese murid rodents by Tokuda (1941).

In his monograph, Tokuda (1941) followed Oldfield Thomas in general in the classification of the Japanese red-backed voles. He considered *smithii* as a separate species in the genus *Clethrionomys*, *bedfordiae* was retained as a subspecies of *Clethrionomys rufocanus*, and *andersoni* was judged to be a distinct species but closely allied to *rufocanus*. Tokuda (1941: 51) followed Hanaoka in placing *Craseomys niigatae* as a synonym of *Clethrionomys andersoni*. Tokuda did not suggest at this time that *smithii* had affinities except in the genus *Clethrionomys*.

The first to suggest a different position for *smithii* was Imaizumi (1949), who placed it in the genus *Eothenomys*. Subsequently, Tokuda (1955) presented evidence for considering *smithii* a species of *Antelionomys*. Imaizumi (1957), considering *Antelionomys* a synonym of *Eothenomys*, continued to use the latter name, and described a second species, *Eothenomys kageus*, from the northern part of Honshu.

The most recent classification of the red-backed voles in Japan is by Imaizumi (1960). In this arrangement there are *Eothenomys*: *smithii* and *kageus*; and three species of *Clethrionomys*: *rutilus*, *rufocanus*, and *sikotanensis*;

in contrast to Tokuda, Hinton, and other recent students, Imaizumi maintained *niigatae* as a species distinct from *andersoni*, and placed both in *Aschizomys*.

During 1952 I spent 10 months in Japan and made a small collection of voles. In 1958 and 1959 I was able to trap additional specimens of all but one (*Clethrionomys sikotanensis*) of the forms of red-backed voles in Japan, and from these specimens and the excellent discussions of Tokuda and Imaizumi, it is apparent that the original descriptions of Oldfield Thomas and the recent researches of Tokuda and Imaizumi more accurately express the relationships of these voles. The work of Hinton was executed apparently with little knowledge of the geologic history of the Japanese archipelago and without the advantage of having studied these Japanese voles in the field. The arrangement given below is, in most respects, like that accepted by Japanese mammalogists today. Because of the stature of Hinton's monograph, his conclusions have been followed by European and American zoologists, and reiterated, in regard to the rodents in question, by Ellerman (1941) and Ellerman and Morrison-Scott (1951). The environmental distributions and economic importance of these voles is discussed by Ota and Jameson (in press).

GENUS *Clethrionomys* Tilesius

Originally all the red-backed voles in Japan were placed in *Clethrionomys*. The Japanese *C. rutilus mikado* exists only on the island of Hokkaido. In general appearance and in most details *rutilus* closely resembles the other species of *Clethrionomys s. str.* The skull is light with rounded contours, the palate is abnormal (differing from *Microtus*), the cheek teeth are relatively light and are rooted in the adult. The mammae are in four pairs. The species in this genus are characterized by other features but the above are sufficient to separate *rutilus* from the other species of microtine rodents in Japan.

The species *rufocanus* has long been known as a rather aberrant species of *Clethrionomys*. Miller (1898a: 360) treated in some detail the distinctive characters of this vole:

So divergent is the animal that it may well be questioned whether it is to be regarded as a true

Evotomys (= *Clethrionomys*). Its heavy and apparently imperfectly rooted teeth more closely resemble those of many species of typical *Microtus* than they do the weak, perfectly rooted teeth of true *Evotomys*. The relationship of the root of the lower incisor and the posterior lower molar, while not typical of either genus are clearly suggestive of *Microtus* rather than *Evotomys*. The palate structure, on the other hand, appears to agree with that of *Evotomys*.

Also, in a key to the Arctic species of red-backed voles Miller (1898a: 359) separated *rufocanus* by the comment: "Teeth large and heavy as in *Microtus* (never perfectly rooted?) . . ." In characterizing *rufocanus*, Hinton (1926: 245) also emphasized its approach to the species of *Microtus* and on page 215 pointed out that individuals look mature "long before the molars show the slightest sign of rooting." To distinguish *rufocanus* from the other species of *Clethrionomys* Miller (1900) created the subgenus *Craseomys* with the following characters:

Skull as strongly angular as in *Microtus*, the postorbital processes well developed; teeth relatively as large as in *Microtus*, the molar row about equal to the diastema; roots of molars developed late in life; root of posterior lower molar lying in a distinct capsule on the lingual side of incisor root.

Soon after Thomas (1905) placed the Japanese forms *bedfordiae* and *andersoni* in the subgenus *Craseomys*. Later (1907), he used *Craseomys* as a genus for *Craseomys regulus* (= *Clethrionomys rufocanus regulus*) from Korea and noted that not even the oldest in the series of 18 specimens showed any trace of roots on the molars.

Aschizomys lemminus was described as a new genus and species by Miller (1898b) on the basis of a single specimen and was characterized in these terms: "Palate as in *Clethrionomys*. Molars small and weak, as in *Clethrionomys*, but teeth growing from a persistent pulp as in *Microtus*" which strongly displaces root of large posterior lower molar. Plantar tubercles six. Number of mammae unknown." The illustrations accompanying the original description indicate other features common to both *lemminus* and *rufocanus*: the encapsulated roots of the upper second molar and the lower third molar

and the reduced lateral tubercles on the rostrum. The upper third molar of *lemminus* is longer than in *rufocanus* and there is little doubt that the two species are separate. The third upper molar of *Clethrionomys niigatae* of northern Honshu is long and similar to *lemminus*. In the original description of *Aschizomys* Miller recommended that *rufocanus* was allied to *lemminus* and later Imaizumi (1957: 199) suggested that *Clethrionomys niigatae* might well be placed in *Aschizomys*. Also, Hinton (1926: 43) stated that *lemminus* seemed to be very close to *rufocanus*. However, as Miller suggested (1898a: 359), the molars of *rufocanus* form roots very late in life; it is quite possible that *rufocanus* and *lemminus* are alike in this respect as well, and that a large series of *Aschizomys lemminus* would probably contain a few individuals old enough to have partly rooted molars. Granting this supposition, a reasonable arrangement would be to place *rufocanus* with *lemminus* in *Aschizomys*.

In this case *Craseomys* Miller, 1900 will become a synonym of *Aschizomys* Miller 1898. Recent authors have regarded *Craseomys* a synonym of *Clethrionomys*; perhaps because they considered it unnecessary to retain a subgenus which contained but a single species. In placing *rufocanus*, *niigatae*, *andersoni*, and a new species from Honshu together with *lemminus* all in *Aschizomys*, one must decide the proper position of this group. Although Miller preferred to call it a genus, he did consider that *Aschizomys* could be placed with *Eothenomys* and *Antelionomys*. *Eothenomys* combines characters of *Microtus* and *Clethrionomys*; and *Aschizomys* (including *rufocanus* and *andersoni*) bridges the gap between *Eothenomys* and *Clethrionomys*.

As pointed out by Ellerman and Morrison-Scott (1951: 670), Russian authors place *Aschizomys* as a subgenus of *Alticola*. The two groups are certainly very close; but, 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*, and the forms known in Japan can be separated by the key below.

KEY TO SPECIES OF *Clethrionomys* IN JAPAN

1. Molars developing long roots in adults; postorbital crests poorly developed or absent; second upper molar and third lower molar not encapsulated in adults: (subgenus *Clethrionomys*)
.....*rutilus*
Molars rootless except in very old adults; postorbital crests well developed; second upper molar and third lower molar usually encapsulated in adults (subgenus *Aschizomys*)..... 2
2. Third upper molar with three inner salient angles (Fig. 1); tail less than one-half the body length; on Hokkaido.....*rufocanus bedfordiae*
Third upper molar with more than three inner salient angles or loops although some projections may be irregular or rounded (Fig. 1); on Honshu..... 3
3. Salient angles of all cheek teeth rounded or irregular, and triangles often open (Fig. 1); auditory bullae relatively small; in low elevation evergreen broad leaved forests of extreme southern Honshu.....*imaizumii*
Salient angles more or less pointed, and triangles usually closed; auditory bullae relatively large; in coniferous forests of the northern half of Honshu..... 4
4. Rostrum relatively long; anterior palatine foramina arise from about level of anterior molar alveolae; upper molar tooth row more than 6.0 mm.....*niigatae*
Rostrum shorter; anterior palatine foramina arise from a point distinctly anterior to the level of anterior molar alveolae; upper molar row less than 6.0 mm.....*andersoni*

Clethrionomys rufocanus bedfordiae (Thomas, 1905)

Evotomys bedfordiae Thomas, 1905, Abstracts, Proceedings, Zoological Society of London, no. 23. (Holotype from Shinshinotsu, near Sapporo, Hokkaido.)

This is the form of *rufocanus* which occurs on the northern island, Hokkaido. It is a large, richly colored species with a tail of moderate length. It is difficult to compare *bedfordiae* with the other named subspecies: the illustrations of *rufocanus shanseius* (of the adjacent mainland) in Hinton (1926) are made from specimens which perhaps are not *rufocanus* and may not even belong in *Clethrionomys*. Presumably the nearest relatives live on the island of Sakhalin and the adjacent mainland. *Clethrionomys sikotanensis* (Tokuda, 1935) seems to be quite distinct from, although allied to, *rufocanus*; *sikotanensis* is known from the Southern Kuriles and may be more closely related to *lemminus*.

The skull of *bedfordiae* resembles the illustration of *C. r. rufocanus* in Hinton (1926: fig. 80); the depicted specimen is from an un-

specified locality. Hinton's illustration of *C. r. shanseius* (1926: fig. 83) is from the type series of *Caromys inez*; *shanseius* (from China) should be closer to *bedfordiae* than is typical *rufocanus* (from Sweden), but there is little doubt that Hinton's illustration of *shanseius* represents a form at least specifically distinct from *rufocanus*. The enamel pattern (Fig. 1) is typical of *C. r. bedfordiae* and the third upper molar is especially characteristic. In 22 adults examined, 2 have distinctly rooted molars; in 8, the pulp cavities are more or less closed off, indicating that roots would probably have formed later in life. The anterior palatine foramina are expanded anteriorly and quite narrow posteriorly and resemble *C. r. rufocanus* in this respect. The tail is less than one-half the body length.

C. rufocanus bedfordiae is the most abundant microtine mouse on Hokkaido and is almost always more common than *C. rutilus*. In the absence of any competing species of *Microtus* (which does not occur on Hokkaido), *rufocanus* is sometimes a common inhabitant of open meadows and is of considerable economic importance (Ota and Jameson, in press).

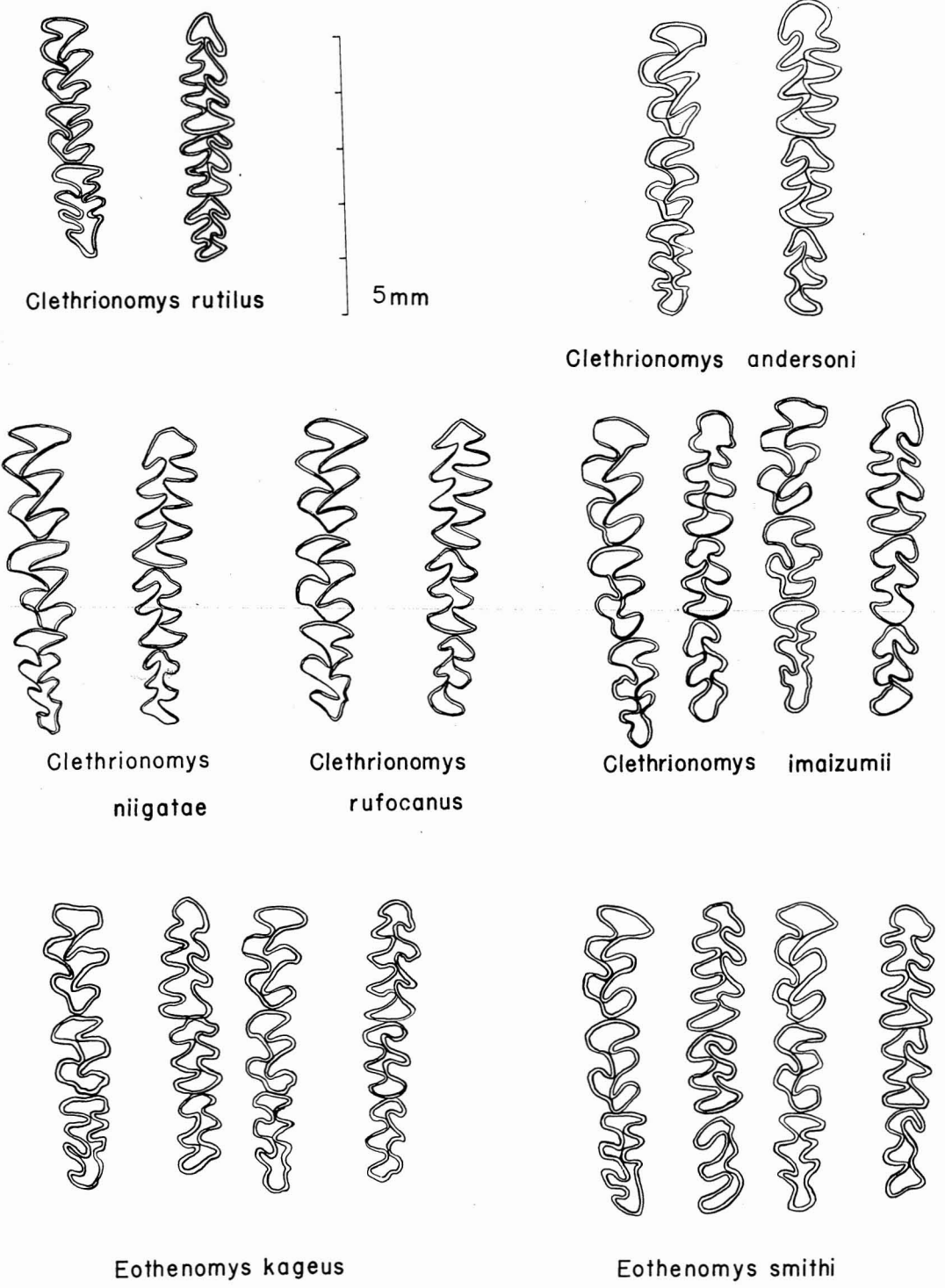


FIG. 1. Enamel patterns of Japanese red-backed voles.

Clethrionomys andersoni (Thomas, 1905)

Evotomys andersoni Thomas, 1905, Abstracts, Proceedings, Zoological Society of London, no. 28. (Holotype, from Tsunagi, Iwate-ken, Honshu.)

This form is sometimes considered to be a subspecies of *rufocanus*, to which it is closely related. *C. andersoni* is easily separable from *C. rufocanus bedfordiae* by the longer third upper molar, which has four inner salient angles. *C. andersoni* is close also to *C. niigatae*, which is sometimes considered to be the same. Examination of specimens of the type series of both *andersoni* and *niigatae* indicated that the two are distinct and that adults can be identified by the above key.

C. andersoni is an inhabitant of coniferous forests in northern Honshu, in Aomori-ken, Fukushima-ken, and Iwate-ken, according to Imaizumi (1960: 134).

Clethrionomys niigatae (Anderson, 1909)

Craseomys niigatae Anderson, 1909, The Annals and Magazine of Natural History, vol. 4, ser. 8: 317. (Holotype from Akakura, Niigata-ken, Honshu.)

For a very long period *C. niigatae* had been considered to be a synonym of *C. andersoni*; but, after studying specimens from the type series of both species, I agree with Imaizumi (1960) that the two are distinct species. In the nine adults examined, one specimen has closed pulp cavities and incipient roots. This is in contrast to the specimens examined by Imaizumi (1957 and 1960); the series in the National Science Museum in Tokyo all possess rootless molars. *C. niigatae* lives in the higher elevations of central Honshu. In Nagano-ken, it is found at approximately 1900 m. and higher among boulders both in virgin forests of fir and spruce and in rather open tangles of wild raspberries and currants.

Clethrionomys imaizumii, new species

TYPE: Adult male, skin and skull. Collected 13 Feb. 1959, Nachi Falls, 300 feet elevation, Wakayama-ken, Honshu, Japan; E. W. Jameson, Jr., no. 1083.

RANGE: Probably in broadleaved forests at low elevations in extreme southern Wakayama-ken (Kii Peninsula).

DIAGNOSIS: A rather large, brightly colored, long-tailed species of the subgenus *Aschizomys*. Dorsum Rood's Brown; venter Sayal Brown; tail bicolor, thinly haired, as in *rufocanus* and *andersoni* (color from Ridgway, 1912). Skull with rather small auditory bullae. Molars with angles rounded.

MEASUREMENTS (in mm.): Holotype (and paratype): Total length, 194 (184); tail, 67 (61); hind foot, 22 (21). Skull: condylobasilar length, 29.1 (skull of paratype damaged); zygomatic breadth, 15.6 (15.1); interorbital breadth, 4.3 (4.4); lambdoidal breadth 12.5 (—); alveolar length of upper molar row, 6.9 (6.3); diastema, 8.3 (7.7).

This species is most nearly like *C. niigatae*, but differs strikingly in the color and dentition. The molars are rootless with open dentine spaces in the two adult males seen. The enamel pattern is quite different, however: the triangles are rounded and indistinct and frequently open (Fig. 1). The auditory bullae are markedly smaller.

This species inhabits the luxuriant hardwood forests of the southern part of the Kii Peninsula in Wakayama-ken, the southernmost part of Honshu. Specimens were first collected by Dr. R. Kano; and Dr. Yoshinori Imaizumi kindly directed me to collecting localities.

These four forms of the subgenus *Aschizomys* are separable on external characters, and these features are substantiated by constant dental and other cranial morphology. The relative proportions of the tail and body lengths are rather different for *rufocanus*, on the one hand, and for *andersoni*, *niigatae*, and *imaizumii* on the other hand. *C. niigatae* and *C. imaizumii* are long tailed. In nine specimens of *niigatae* from the upper slopes of Yatsugatake, the tail is from 58 to 66 mm. in actual length, and the tail length is from 51 to 62 per cent of the body length. In a series of 22 adults of *C. rufocanus bedfordiae* from various localities in Hokkaido, the tail is from 34 to 56 mm., and the tail length is from 28 to 46 per cent of the body length. It is quite possible that large series of both species would show some

overlap in this character but the difference is nevertheless real and fairly constant. *C. imaizumii* is a long-tailed animal like *niigatae*. The general fascies of the enamel patterns of *C. rufocanus bedfordiae*, *C. niigatae*, and *C. andersoni* are angular (Fig. 1), but *andersoni* and *niigatae* are distinct in having four inner salient angles in the third upper molar, whereas *rufocanus bedfordiae* has three. The enamel pattern of *imaizumii* is quite different in having the angles rounded, and there is a tendency for the loops and triangles to remain open (Fig. 1). The four species differ also in the form of the anterior palatine foramina. The hind foot of *rufocanus bedfordiae* is more densely furred than that of *niigatae*, *imaizumii*, and *andersoni*, but all species are alike in possessing six plantar tubercles between which there are tiny projections.

Imaizumi (1957) intimated that *niigatae* might be generically distinct from *rufocanus bedfordiae* because the molars are rarely rooted in *bedfordiae* and seemed never to be rooted in *niigatae*. In one specimen of *niigatae* examined by me, the pulp cavities are closed and there are incipient roots. Later (1960) Imaizumi placed *niigatae* and *andersoni* in *Aschizomys* and kept *rufocanus* in *Clethrionomys*; but such an arrangement does not indicate the nearness of these three species. As will be pointed out later in this paper, *andersoni* and *niigatae* almost certainly emigrated from Hokkaido from a stock close to *rufocanus*. Imaizumi's suggestion, reasonable as it may seem, simply emphasizes the weakness of the presence or absence of molar roots as a generic character in this case.

Clethrionomys rutilus mikado (Thomas, 1905)

Evotomys mikado Thomas, 1905, Abstract, Proceedings, Zoological Society of London, no. 23, p. 19. (Holotype from Aoyama, Hokkaido.)

This bright red little vole is quite unlike any other species in Japan. The color, rounded enamel pattern (Fig. 1), well-developed molar roots, and small size separate *rutilus* from *rufocanus*, the only other vole in Hokkaido. The molar row is rather short, as in *Eothenomys smithi* and *E. kageus*, and the enamel patterns are similar, but the angles are less rounded. In

C. rutilus there are four pairs of mammae. One specimen was examined.

C. rutilus mikado is a rather uncommon dweller of the forests of Hokkaido and is not known to occur elsewhere in Japan.

GENUS *Eothenomys* Miller

The other genus of red-backed voles in Japan is *Eothenomys*; most of the species occur in China and one (*melanogaster*, the type of the genus) is found also on Taiwan. These species are quite close to *Clethrionomys* in general and some of them are perhaps related to the species of the subgenus *Aschizomys* in particular. In *Eothenomys* the color is highly variable, but some species are reddish and so resemble the species of *Clethrionomys*, with which they have been confused on more than one occasion. *Eothenomys* differs in possessing rootless molars and only two or three pairs of mammae. Even in the oldest specimens there is no closure of the pulp cavities. The skull of *Eothenomys* is light and delicate and tends to be rounded; and the palate terminates in a shelf, as in *Clethrionomys*.

KEY TO SPECIES OF *Eothenomys* IN JAPAN

1. Mammae four.....*kageus*
Mammae six.....*smithi*

Eothenomys smithi (Thomas, 1905)

Evotomys smithi Thomas, 1905, Annals and Magazine of Natural History, series 7, vol. 15, p. 493. (Holotype from Kobe, Honshu.)

In Japan, the species *smithi* was described from specimens from Kobe, on the island of Honshu; *smithi* is also a common species on Shikoku and Kyushu, and a shorter-tailed subspecies (*okiensis*) was described from the island of Dogo in the Oki Group. The species *smithi* was described by Thomas in 1905, who at that time placed it in *Evotomys* (= *Clethrionomys*); and, noting some differences from the morphology of most species of that genus, he erected the subgenus *Phaulomys*. Thomas stated then that *smithi* showed characters of *Evotomys*, *Eothenomys*, and *Anteliomys*. Externally *smithi* is similar to species of *Clethrionomys*, except that there are two or three pairs of mammae

instead of four pairs. The form of the skull resembles that of *C. rutilus* and the other species of *Clethrionomys s. str.* (not including *rufocanus*, *andersoni*, *imaizumii*, and *niigatae*): the skull is delicate and rounded and the postorbital projections are barely developed. The enamel pattern tends to be rounded rather than angular; Thomas noted that the closed triangles tend to be little broader than long (Fig. 1). *Phaulomys* stands apart from *Clethrionomys* because the molars are rootless in the adult. Thomas also pointed out the encapsulated root of the second upper molar which projects into the orbital fossa; this invariably occurs in microtine rodents when the molars are not rooted and is simply another way of stating this condition. Since the description of *smithi*, many hundred of specimens have been collected and the molars are known to be rootless even in old adults. (Hinton's [1926] observation to the contrary resulted from his confusing *Clethrionomys rufocanus bedfordiae* and perhaps *C. rutilus mikado* with *smithi*.) Recent studies by Japanese workers (e.g., Tokuda, 1955, and Imaizumi, 1957) indicated that *smithi* is allied to the Chinese species of *Antelionomys* (a synonym or subgenus of *Eothenomys*), and the proper name for this species is *Eothenomys smithi*. Nineteen specimens were examined.

Eothenomys kageus Imaizumi, 1957

Eothenomys kageus Imaizumi, 1957, Bulletin, National Science Museum (Tokyo), vol. 3, no. 3, p. 204. (Holotype from Yamuramachi, Minamitsuru-gun, Yamanashi-ken, Honshu.)

Imaizumi (1957) named the form from the northeastern part of Honshu as *E. kageus*. From the detailed description of *kageus*, it is apparent that *kageus* and *smithi* are very close. *E. kageus* has two pairs of mammae whereas in *smithi* there are three pairs. The size, color, and body measurements of *E. kageus* are very close to those of *E. smithi*. The enamel patterns of the two species are also very similar (Fig. 1). The original description of *E. kageus* included a difference in the posterior angle of the zygomatic arch; but the explanatory drawing (Imaizumi, 1957: fig. 3) indicated that the angle measured on *E. kageus* was different from that taken from

E. smithi, and the data are not comparable. The differences in the bacula of *E. kageus* and *E. smithi* may be due to individual variation: specimens of both species are extremely variable and there seem to be no constant differences in the bacula of the two named forms (Fig. 2). Six specimens were examined. Future studies may reveal that *E. kageus* is a subspecies of *E. smithi*.

Eothenomys smithi and *E. kageus* are similar in habits and habitat. They dwell in forested regions from sea level to elevations of 2500 m. or more, but generally do not occur together with *Clethrionomys niigatae*, *imaizumii*, or *andersoni*. On Yatsugatake, *E. kageus* occurs up to about 2000 m., above which level *C. niigatae* is found; but on the eastern slope of Ontake, where *C. niigatae* does not occur, *E. smithi* extends well above 2000 m. (Tokuda, 1950); and on Mt. Fuji (where *C. niigatae* is absent) *E. kageus* is found to the upper limit of the forest (Imaizumi, 1944). On Kyushu, *E. smithi* is the only red-backed vole, and it lives in wooded areas from at or near sea level to the highest peaks, becoming more abundant at the higher elevations. On Shikoku, where *Microtus montebelloi* is not found, *E. smithi* may move from the forest to relatively open grassy or brushy areas (Ota and Jameson, in press). *Eothenomys* does not occur on Hokkaido.

The bacula of the red-backed voles in Japan (Fig. 2) are rather variable within a given species, and provide rather poor taxonomic characters at the specific level. Some of the smaller bacula are obviously from young animals but even examples of the same size may be remarkably dissimilar. There are differences in both size and shape of the shaft and its base as well as in the three prongs. There seem to be no distinctions between the bacula of *Eothenomys kageus* and *E. smithi* unless the shaft in *kageus* is slightly more slender. 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, and in this respect resembles those of some species of *Microtus*. Most bacula of these voles have a slight keel on the median tyne, a character of the bacula of both *Clethrionomys* and *Microtus*. No bacula of *C. andersoni* were available.

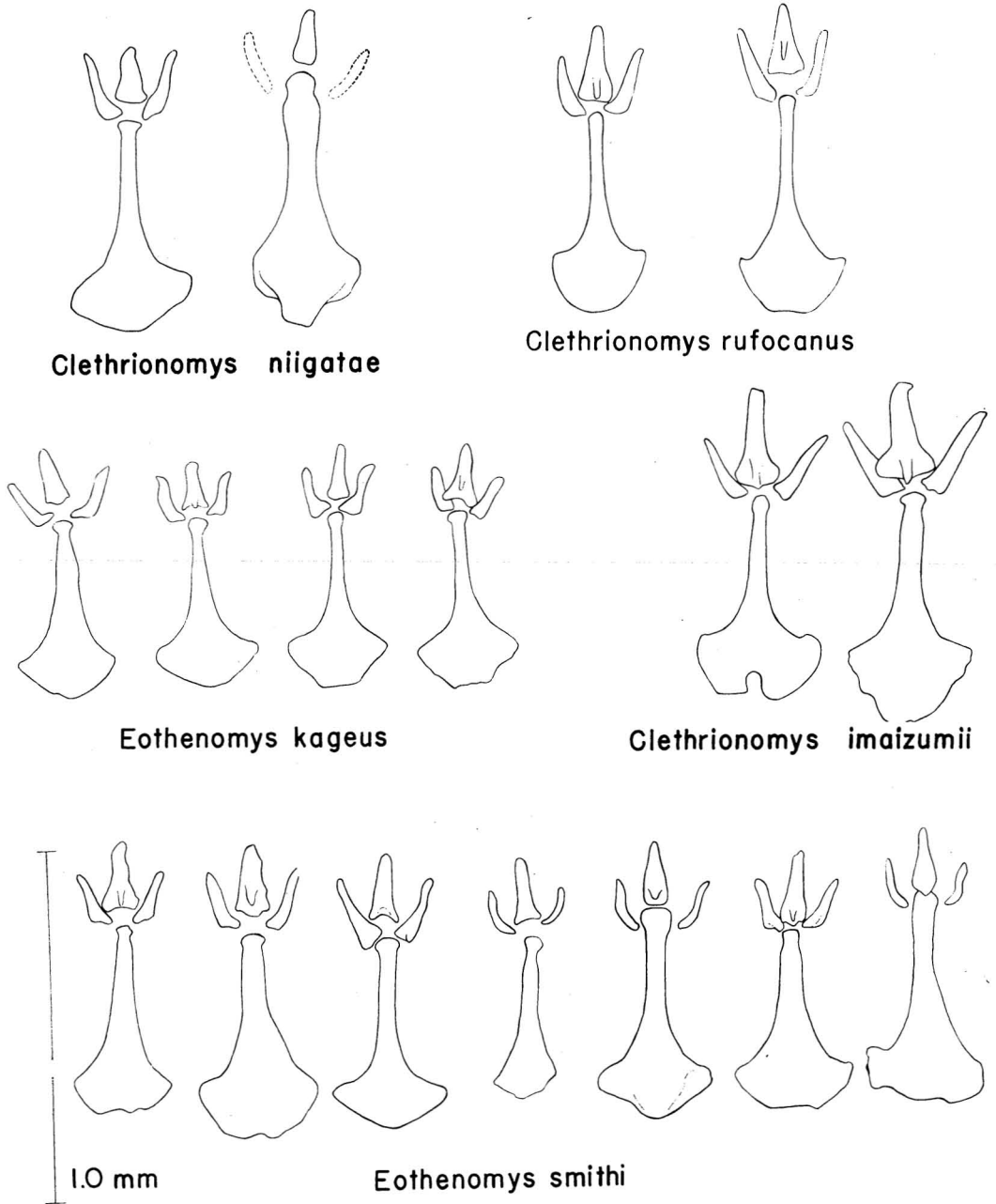


FIG. 2. Bacula of Japanese species of *Eothenomys* and *Clethrionomys* (*Aschizomys*).

GEOGRAPHIC ORIGIN OF RED-BACKED
VOLES IN JAPAN

In the Pleistocene and earlier the present archipelago of Japan was connected to the mainland in the south, between Kyushu and the Korean Peninsula, and in the north, between Hokkaido, Sakhalin, and adjacent Siberia. At approximately the same time, changes resulted in the separation of Kyushu and Korea, and also the formation of the Tsugaru Strait between Hokkaido and Honshu. Consequently, the islands of Kyushu, Shikoku, and Honshu no longer received immigrants from the continent, and they were isolated from the effects of faunal movements on the mainland. Today, the fauna of the old islands of Kyushu, Shikoku, and Honshu is, in many respects, quite different from that of the immediately adjacent mainland, and has its closest affinities to the southwest in China. This faunal difference has been mentioned as early as Thomas' 1905 paper. On the other hand, Hokkaido and Sakhalin remained part of the mainland and were subjected to the faunal changes that affected southeastern Siberia and Korea. There are no land mammals in Hokkaido that are more than subspecifically distinct from those of nearby Siberia and Korea. The important and extensive movements of mammals in this general area during the Pleistocene (see Simpson, 1947: 643) changed the fauna of Hokkaido, replacing with more recent forms the original fauna that now remains in the older Japanese islands.

Eothenomys smithi probably entered Japan on the old route between Korea and Kyushu via a connection which remains today as the islands of Tsushima and Iki. *E. smithi* moved on from Kyushu to Shikoku and is now the only microtine rodent known from the latter island. This vole moved also to Honshu and now occupies a large part of that island, at least to southern Nagano-ken. *E. smithi*, or its progenitor, at one time must have occurred in Korea although the genus is not there now. *E. kageus* may have come from the north via Sakhalin and Hokkaido, although its occurrence is now confined to the northern half of Honshu south to where it abuts the geographic range of *E. smithi*. The changes which resulted in the extinction or the emigration of *Eothenomys* from Korea and Si-

beria apparently affected Hokkaido as well. Actually, it seems likely that *E. smithi* and *E. kageus* are offshoots from a single ancestor which differentiated slightly along the coast from Korea to Siberia so that different subspecies entered Kyushu and Hokkaido. This could account for the great similarity between these two forms that now occupy adjacent but not overlapping geographic areas.

Similarly, the species of *Clethrionomys* came to Japan by two routes. *C. imaizumii*, which is now known only from the low elevations of Wakayama-ken, may have its relatives among one of the many kinds of red-backed voles described from China. This is conjecture, but this vole is now associated with a semitropical flora of broad-leaved hardwoods. This species, moreover, is morphologically quite distinct from *C. andersoni*, *C. niigatae*, and *C. rufocanus bedfordiae*, which are found in forests of fir (*Abies* spp.) and spruce (*Picea* spp.). *C. niigatae* and *C. 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. Hokkaido and Honshu were separated since before the Pleistocene, and *niigatae* and *andersoni* were immune to the immigrants of *C. rufocanus bedfordiae*. Not only are the three species close morphologically, but they share three species of fleas which are parasites of *C. rufocanus* in Hokkaido: *Catallagia striata*, *Megabotbris sokolovi*, and *Rhadimopsylla alphabetica*. One (*Catallagia striata*) occurs also in Siberia and another (*Megabotbris sokolovi*) in the Kuriles.

The occurrence of *C. rutilus* needs little explanation. It is obviously a rather recent arrival in Hokkaido. If it ever extended to Honshu, it did not persist, and it may well have entered Japan after the separation of Hokkaido from Honshu.

SUMMARY

There are seven species of red-backed voles in Japan. *Clethrionomys* (*Clethrionomys*) *rutilus* occurs in Hokkaido. The species *andersoni*, *niigatae*, and *imaizumii* (from Honshu) and *rufocanus* (from Hokkaido) are considered to represent *Aschizomys*, which is placed as a subgenus of *Clethrionomys*. *Eothenomys smithi* in-

habits Kyushu, Shikoku, and Honshu, and *E. kageus* occupies the northern half of Honshu.

ACKNOWLEDGMENTS

The specimens discussed above were collected with the help of Dr. Tatsuo Udagawa, Mr. Kôhei Sakaguti, Dr. Ryo Tanaka, and Dr. Kasio Ota, with whom I made many excursions. To these gentlemen I am most grateful. Dr. Richard van Gelder (American Museum of Natural History), and Dr. John E. Hill (British Museum [Natural History]), generously loaned comparative material. Dr. David H. Johnson graciously read the manuscript.

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