

Morphological variation, and latitudinal and altitudinal distribution of *Eothenomys chinensis*, *E. wardi*, *E. custos*, *E. proditor*, and *E. olitor* (Rodentia, Arvicolidae) in China

Yukibumi KANEKO

Biological Laboratory, Faculty of Education, Kagawa University, Takamatsu 760, Japan
Fax. 0878-36-1652

Abstract. A total of 308 museum specimens of the genus *Eothenomys* from five separate areas in Sichuan (Szechwan) and Yunnan Provinces, China, were categorized by the relationship between condylobasal length (CBL) and tail length (TL). These specimens were allocated to three larger species, *E. chinensis*, *E. wardi* and *E. proditor*, and two smaller ones, *E. custos* and *E. olitor*.

E. chinensis and *E. wardi* are allopatric, and their distributions separated by about 240 km in northern high mountain areas (28-30° N). *E. chinensis* lives at altitudes above 1500 m, whereas *E. wardi* was found above 2300 m. Lengths of bulla (BL), tail (TL) and hind foot (HFL) were slightly larger in *E. chinensis* than in *E. wardi*.

E. custos has a large latitudinal range between 26° and 29° N in Sichuan and Yunnan Provinces, whereas *E. proditor* occurs near the borders of Sichuan and Yunnan (27-28° N). The latitudinal range of *E. custos* overlaps with that of *E. proditor* in the areas of 26-28° N and 100-102° E, but *E. custos* was found at slightly higher altitudes (2500-4800 m) than *E. proditor* (2500-4200 m).

The distance between the anterior-most point on the upper incisor to the posterior-most edge of the third upper molar (I-M3) and BL of *E. custos* tended to increase from south to north, whereas those of *E. proditor* tended to decrease. *E. custos* had longer tails in localities around 29° N and 101.5° E than in other areas.

E. olitor was recorded from two widely separated localities (ca. 23.5° N and 99.5° E, and ca. 27° N and 104° E).

Key words: distribution, *Eothenomys*, identification, southwest China, taxonomy.

The classification and identification of the genus *Eothenomys* (Rodentia, Arvicolidae) have remained confused, because no study on morphological variation has been carried out over the entire geographical range of the genus. Furthermore, a number of nominated species have all been identified as *Clethrionomys rufocanus* (Hinton 1926, Allen 1940, Tokuda 1941, Ellerman 1941,

Ellerman and Morrison-Scott 1951, Jones and Johnson 1965, Gromov and Polyakov 1977). Kaneko (1990, 1992) has already documented the morphological variation, identification, and geographical distribution of *E. regulus*, *E. shansei*, *E. inez*, and *E. eva* on the Korean Peninsula and in northern and central China, all of which proved to be distinct from *C. rufocanus*.

The classification of, and keys for the identification of other species of *Eothenomys* living in central and southern China, Taiwan, Vietnam, Thailand, Burma, and India, have not been well established yet, and only crude distribution maps have been provided (Allen 1940, Corbet 1978, Corbet and Hill 1992).

In Sichuan and Yunnan Provinces, China, with the exception of the *E. melanogaster* group (which includes *fidelis*, *eleusis*, and *miletus*), some taxonomists recognize four species of *Eothenomys* (*chinensis*, *custos*, *proditor* and *olitor*) (Allen 1940, Ellerman and Morrison-Scott 1951, Corbet 1978, Honacki *et al.* 1982, Corbet and Hill 1991, Musser and Carleton 1993), whereas others recognize five (*chinensis*, *wardi*, *custos*, *proditor* and *olitor*) (Hinton 1926, Ellerman 1941, Gromov and Polyakov 1977, Corbet and Hill 1992).

The purpose of this paper is to describe identification methods and to establish the geographical distribution of *Eothenomys* spp. in Sichuan and Yunnan Provinces, China, based on the morphological variation in external and skull measurements, and in molar characteristics.

MATERIALS AND METHODS

A total of 308 specimens were examined in the following institutions: the Natural History Museum, London (BM); the United States National Museum of Natural History (USNM); the American Museum of Natural History (AMNH); the Museum of Comparative Zoology, Harvard University (MCZ); the Field Museum of Natural History (FMNH); the Zoological Institute, Academia Sinica (ASZI); and the Kunming Institute of Zoology, Academia Sinica (ASKZI).

The localities from which specimens were collected, and their reference numbers, are shown in Fig. 1, while the latitude, longitude, altitude, date collected, museum and registration number of all specimens examined can be found listed in the Appendix. The latitude and longitude of each locality were determined from gazetteers (Zhuang 1983, Su 1984) and from accounts of collecting expeditions (Kingdon Ward 1923, Roosevelt and Roosevelt 1929). Altitudes and distances were obtained from labels attached to specimens, and those recorded in feet and miles were converted to meters and kilometers. Some of these specimens had previously been described or identified by other researchers (Thomas 1891, 1911a, b, 1912a, b, 1914, 1923, Miller 1896, Allen 1912, 1924, 1940, Hinton 1923, 1926, Howell 1929, Osgood 1932, Pen *et al.* 1962, Lu *et al.* 1965).

It is difficult to appreciate the variation among these vole species at first glance, because of the great variation among the 42 localities from which they were collected. These localities were grouped into five geographical areas:

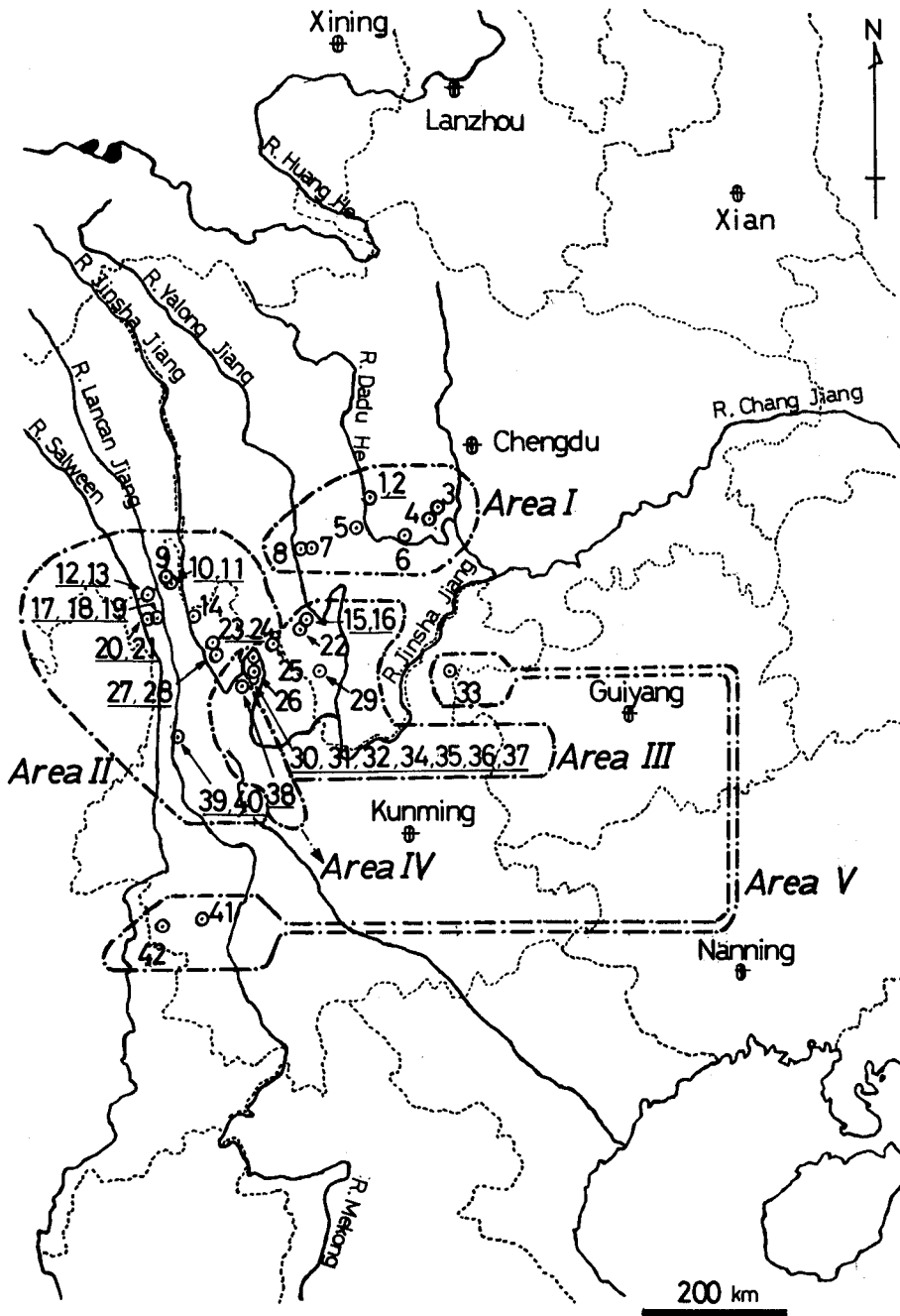


Fig. 1. Sichuan and Yunnan Provinces, China, showing Localities 1-42 grouped into Areas I-V, as defined in this study.

Area I, Localities 1-8; Area II, Localities 9-14, 17-21, 23-24, 27-28, and 39-40; Area III, Localities 15-16, 22, 25-26, 29-32, and 34-37; Area IV, Locality 38; and Area V, Localities 33, and 41-42. Locality 38 (the Lichiang Range) was divided into ten different altitudinal zones.

Measurements of head and body length (H & BL), tail length (TL), and hind foot length (HFL), were obtained from labels attached to specimens. The presence of mammae was checked for on the skins of females. Condylbasal length (CBL), incisor-third upper molar length (I-M3), condyle-first upper molar length (C-M1), the length of bulla (BL), and the interorbital width (IOW), were measured to the nearest 0.1 mm with a dial caliper by the author (the minimum accuracy = 0.05 mm).

These measurements are defined as follows: the CBL is the distance between the occipital condyle and the anterior point of the premaxillae; I-M3 is the distance from the anterior-most point on the upper incisor to the posterior-most edge of the third upper molar; C-M1 is the distance between the occipital condyle and the anterior edge of the first upper molar; BL is the longest length of the auditory bulla, and IOW is the shortest measurement of the frontal bones between the orbits.

Where specimens skulls had been damaged, CBL was estimated from regression lines between I-M3 and CBL or between C-M1 and CBL, using data from specimens with undamaged skulls. The regression lines were calculated separately for four geographical areas: Area I ($n=49$) $CBL=1.492(I-M3)+2.644$, $CBL=1.482(C-M1)+1.171$; Area II ($n=45$) $CBL=1.551(I-M3)+1.514$; Area III ($n=31$) $CBL=1.537(I-M3)+1.543$, $CBL=1.693(C-M1)-1.955$; and Area IV ($n=64$) $CBL=1.422(I-M3)+3.193$, $CBL=1.671(C-M1)-1.596$. Regression coefficients of these lines ranged from 0.906 to 0.982 ($p<0.05$).

Specimens were identified as adult by the presence of mammae, or as young by the presence of minute skull perforations and the absence of full ossification.

Enamel patterns on the occlusal surfaces of the upper molars, were drawn from pictures taken of the molar rows using a Nikon SMZ-10 stereo microscope at $6.6\times$ magnification. Original close-up photographs were taken of the museum specimens using an accessory close-up lens ($1.75\times$ magnification) attached to an Olympus camera. The enamel patterns on the third upper molar were classified into five types (A-E; see Fig. 2). Type A has three salient and two re-entrant folds on the lingual side. It also has a posterior loop in which the inner enamel lamellae has either a straight or concave outline which does not protrude posteriorly beyond line "h" which crosses perpendicularly to the longitudinal axis of the tooth on the lingual side of the posterior loop (Fig. 2); Type B has four salient and three re-entrant folds on the lingual side, where the base line of the enamel lamellae of the third re-entrant fold protrudes beyond line "h"; Type C has four salient and four re-entrant folds with a posterior loop where the inner enamel lamellae has either a straight or concave outline but does not protrude line "h" (compared with Type A); Type D has five salient and four re-entrant folds on the lingual side where the outline

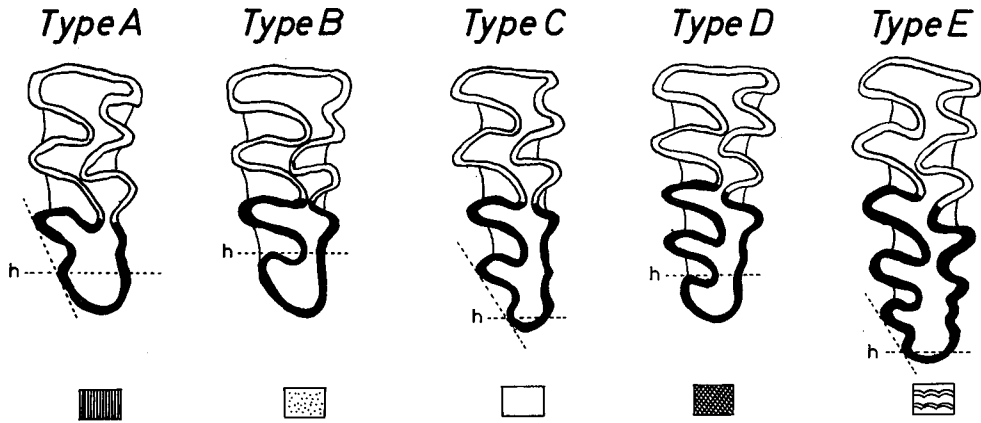


Fig. 2. Types A-E enamel patterns on the third upper molar. These patterns differ in the number of re-entrant angles and the shape of the posterior loop. The line (h), crossing at a right angle to the longitudinal line of the tooth at the antero-external margin of the last re-entrant angle, shows whether the concavity of the re-entrant angle exceeds the line posteriorly or not. Patterns of five rectangles below the molars of Types A-E are used in Figs. 4, 6, 8, 9 and 11.

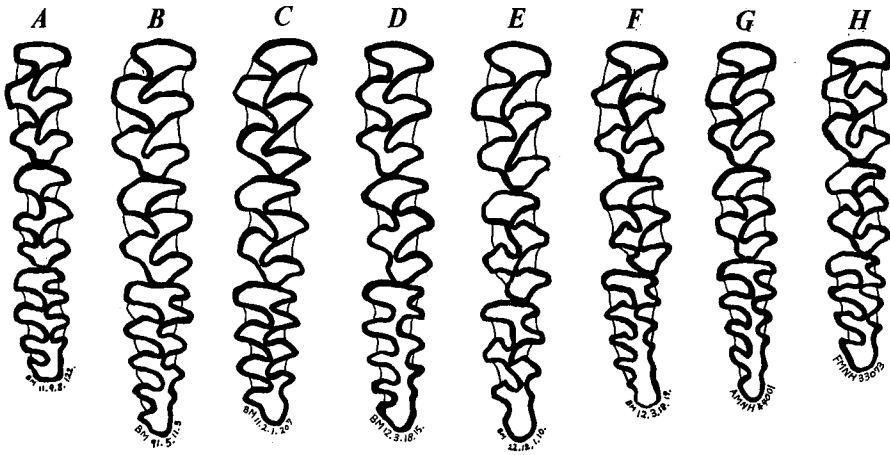


Fig. 3. Enamel patterns on the third upper molar of the *Eothenomys* holotypes examined in this study. A=MEo=*Microtus (Eothenomys) olitor* Thomas, 1911 (BM 11. 9. 8. 122), B=Mc=*Microtus chinensis* Thomas, 1891 (BM 91. 5. 11. 3), C=MAct=*Microtus (Anteliomys) chinensis tarquinius* Thomas, 1912 (BM 11. 2. 1. 207), D=MAw=*Microtus (Anteliomys) wardi* Thomas, 1912 (BM 12. 3. 18. 15), E=MAc=*Microtus (Anteliomys) custos* Thomas, 1912 (BM 12. 3. 18. 19), F=MAcr=*Microtus (Anteliomys) custos rubellus* Allen, 1924 (AMNH 44001), G=EACH=*Eothenomys (Anteliomys) custos hintoni* Osgood, 1932 (FMNH 33073), H=Ep=*Eothenomys proditor* Hinton, 1926 (BM 22. 12. 1. 10).

of the enamel lamellae of the fourth re-entrant fold protrudes beyond line "h" (compared with Type B); and Type E has five salient and four re-entrant folds with a posterior loop where the inner enamel lamellae appear as in Type A.

RESULTS

1. Variation among specimens from Sichuan and Yunnan

Thomas (1911b, 1912a) described *Eothenomys olitor* having a prominent inner salient angle on the second upper molar, and lacking supplementary postero-internal salient projection on the first upper molar (Fig. 3-A). Six specimens, collected from Area V (Localities 33, 41 and 42), were identified as *E. olitor*, with a TL of 35 mm, a HFL of 14-18 mm, and a CBL ranging from 20.9 to 24.1 mm ($n=5$; Fig. 4). The dominant enamel pattern on the third upper molar was of Type B (Table 1).

Except for those of *E. olitor*, all specimens examined were provisionally identified as belonging to one of four groups, according to the relationship between CBL and TL, and according to the geographical areas where they were collected (see Fig. 5). Specimens for which CBL was measured could be grouped into two clusters in each area. Some specimens for which CBL could be estimated were also included in, or were scattered close to their respective clusters (except for several young specimens). Adults were included in the respective clusters in each area except for one Area III cluster, in which no adults appeared. In Areas I and II, there were two clusters of specimens with longer CBL and longer TL (CI-L in Area I and CII-L in Area II) and with

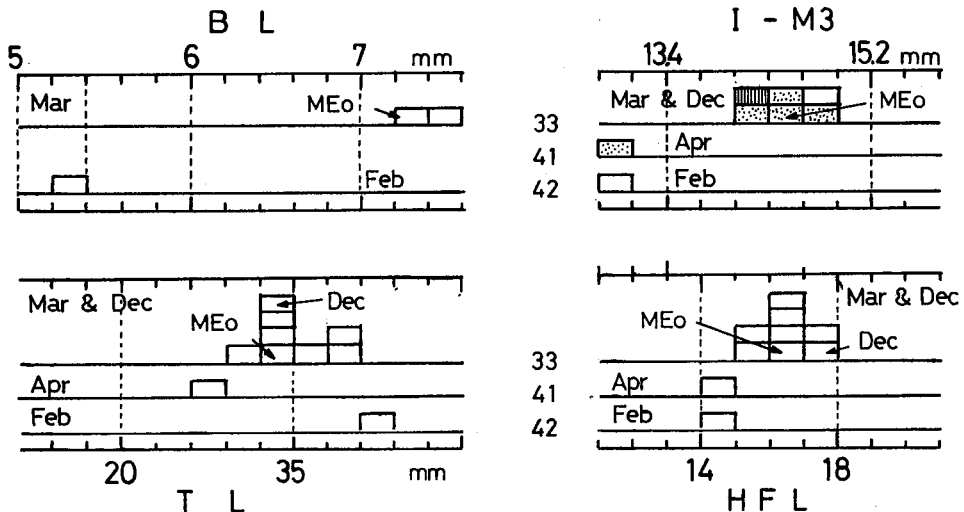


Fig. 4. Geographical variation in BL, I-M3, TL and HFL in *Eothenomys olitor*. One square refers to one specimen. Month indicates collecting month of specimens examined. For details of Localities #33, and #41-42, see the Appendix. For enamel patterns and abbreviation of the holotype, see Figs. 2 and 3.

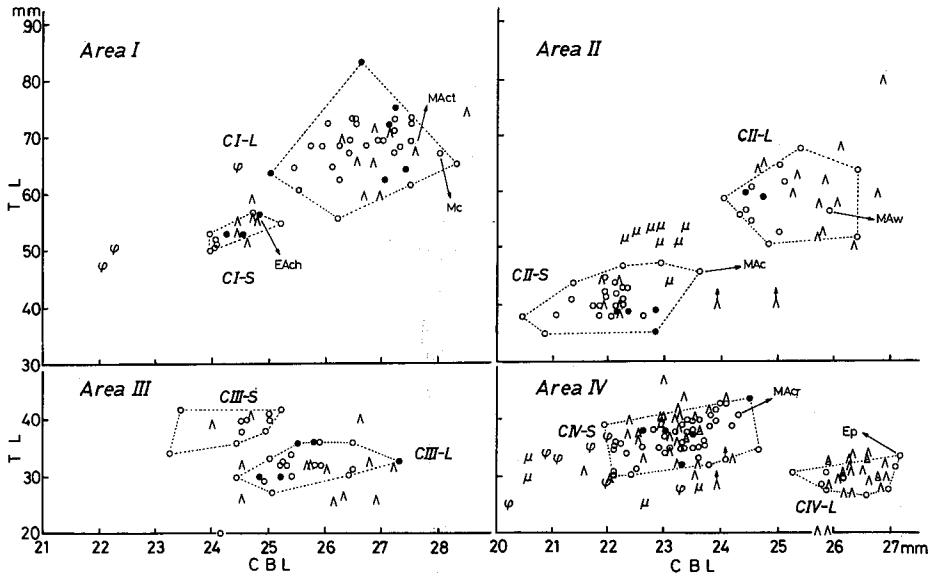


Fig. 5. Relationships between CBL and TL in Areas I-IV. For abbreviation of the holotypes (EAcH, Ep, MAC, MAcr, MAct, MAw and Mc), see Fig. 3. In each area, young individuals were located to the left of a cluster of adults. Symbols: young= φ ; young with estimated CBL= μ ; adult= \bullet ; adult with estimated CBL= Δ ; individual not clearly adults or young= \circ ; individual not clearly adult or young with estimated CBL= \triangle ; individual missing the tip of the tail= \uparrow . It will be shown later that clusters CI-S, CII-S, CIII-S and CIV-S correspond to *Eothenomys custos*; CIII-L and CIV-L to *E. proditor*; CI-L to *E. chinensis*; and CII-L to *E. wardi*.

shorter CBL and shorter TL (CI-S in Area I and CII-S in Area II). In Areas III and IV, there were two clusters of individulas with longer CBL and shorter TL (CIII-L in Area III and CIV-L in Area IV) and with shorter CBL and longer TL (CIII-S in Area III and CIV-S in Area IV). In each area, young individuals were found to the left of a cluster of adults: *i. e.* young in Area I=CI-L, young in Area II=CII-L, young with 20-22 mm in CBL in Area IV=CIV-S, and young with 22-24 mm in CBL in Area IV=CIV-L.

Geographical and monthly variations in two external and two skull characters (TL, HFL, BL and I-M3) along with the enamel patterns of the third upper molar, were examined for each of CI-L, CI-S, CII-L, CII-S, CIII-L, CIII-S, CIV-L, and CIV-S clusters (see Figs. 6-12). A marked difference was observed between CI-L and CII-L in the sizes of BL, TL and HFL, with only slight overlap between the two clusters in the relationship between CBL and TL (Fig. 5). TL, HFL, BL and I-M3 were slightly longer in CI-L than in CII-L and there was no clinal variation in these dimensions (see Figs. 6 and 7). In clusters

CI-L and CII-L, BL, I-M3, TL and HFL did not vary over the geographical range (Figs. 6 and 7). Molar enamel patterns differed between clusters CI-L and CII-L (Table 1), with Type C more common in CI-L (87%) than in CII-L (68%), and Types D and E less common in CI-L (2.2%) than in CII-L (24%).

The clusters CIII-L and CIV-L overlapped (Fig. 5). The sizes of I-M3, BL, and HFL tended to increase from north to south (Fig. 8). Type A molar enamel was commonest in CIV-L than in CIII-L (Table 1).

Clusters CII-S, CIII-S and CIV-S all overlapped one another, but were mostly segregated from cluster CI-S (Fig. 5). TL differed discontinuously

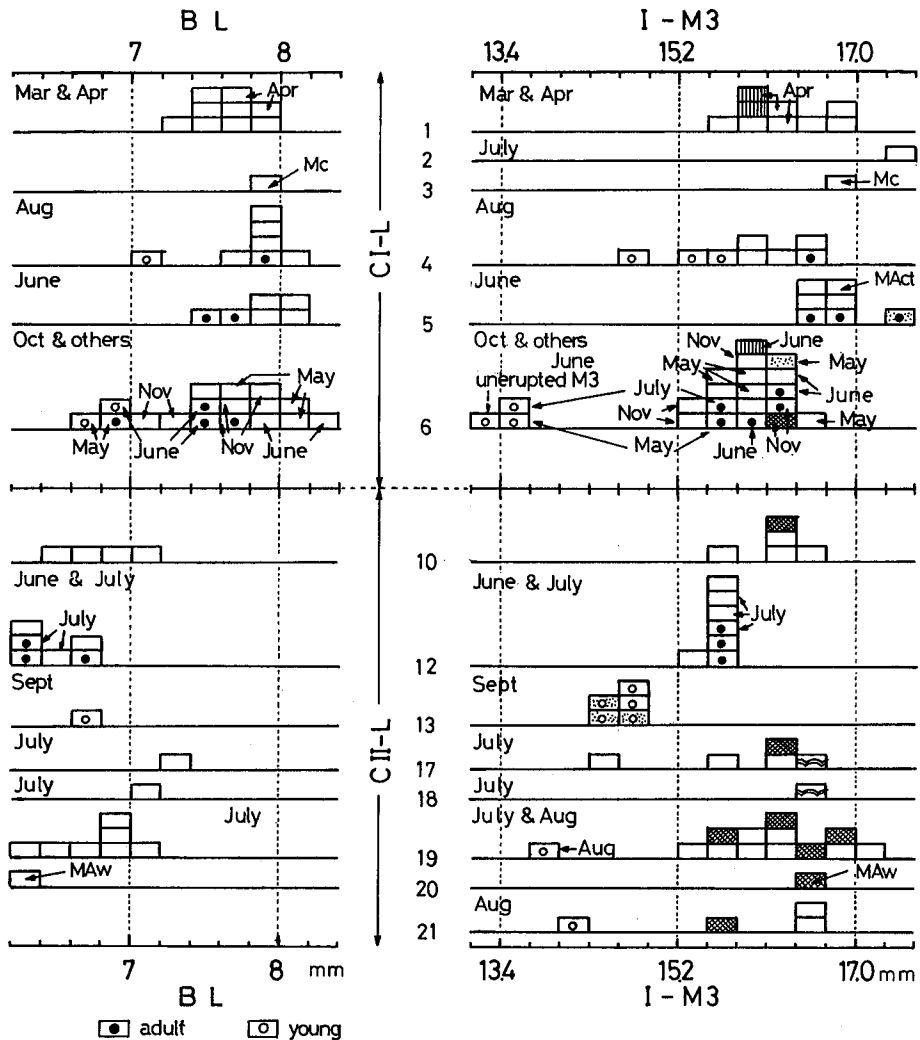


Fig. 6. Geographical variation in BL and I-M3 in *Eothenomys chinensis* (CI-L) and *E. wardi* (CII-L). One square represents one specimen. Month indicates collecting month of specimens examined. For details of Localities 1-6, 10, 12-13, and 17-21, see the Appendix. For enamel patterns and abbreviations of the holotypes, see Figs. 2 and 3.

between clusters CI-S, CII-S and CIII-S. In cluster CII-S, I-M3 and BL decreased in size clinally from north to south, while TL and HFL did not differ among localities (Figs. 9-10). Type C molar enamel predominated in all four clusters (Table 1).

The length of I-M3 varied according to the elevation on the Lichiang Range (Locality 38), where R. C. Andrews and E. Heller (the Asiatic Expedition in 1916) and G. Forrest in 1921-22 collected specimens (Figs. 11 and 12). Both I-M3 and HFL increased in size from higher to lower elevations in cluster CIV-S, whereas they did not show a clinal change in CIV-L. Type A molar enamel

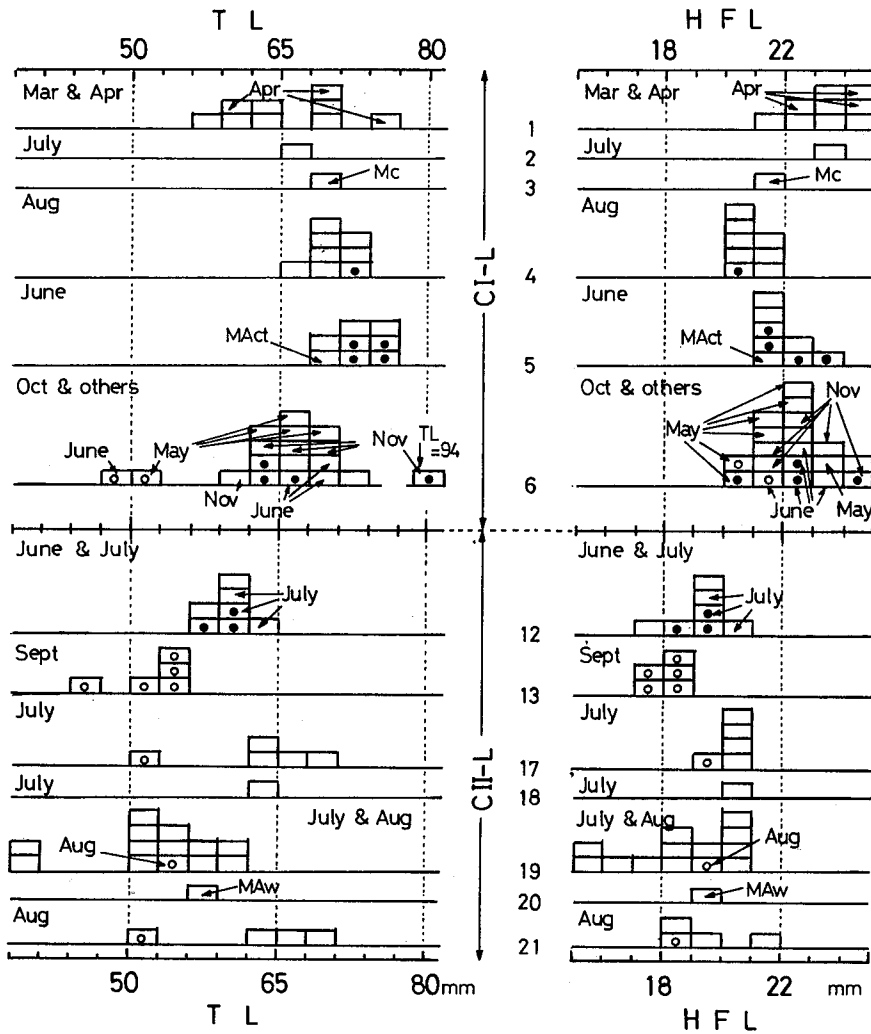


Fig. 7. Geographical variation in TL and HFL in *Eothenomys chinensis* (CI-L) and *E. wardi* (CII-L). Month indicates collecting month of specimens examined.

Table 1. Variations in the enamel patterns on the third upper molar in *Eothenomys chinensis* (ECHI), *E. wardi* (EW), *E. proditor* (EP), *E. custos* (EC), and *E. olitor* (EO).

	Type A	Type B	Type C	Type D	Type E	Total
ECHI (Area I: CI-L)	3 (6.5%)	2 (4.3%)	40 (87.0%)	1 (2.2%)	0	46
EW (Area II: CII-L)	0	3 (7.3%)	28 (68.3%)	8 (19.5%)	2 (4.9%)	41
EP (Area III: CIII-L)	13 (43.3%)	11 (36.7%)	5 (16.7%)	1 (3.3%)	0	30
EP (Area IV: CIV-L)	33 (97.1%)	1 (2.9%)	0	0	0	34
EC (Area I: CI-S)	0	1 (5.9%)	13 (76.5%)	3 (17.6%)	0	17
EC (Area II: CII-S)	0	1 (3.2%)	18 (58.1%)	12 (38.7%)	0	31
EC (Area III: CIII-S)	0	1 (8.3%)	6 (50.0%)	4 (33.3%)	1 (8.3%)	12
EC (Area IV: CIV-S)	2 (2.3%)	22 (25.3%)	55 (63.2%)	8 (9.2%)	0	87
EO (Area V)	1 (12.5%)	5 (62.5%)	2 (25.0%)	0	0	8

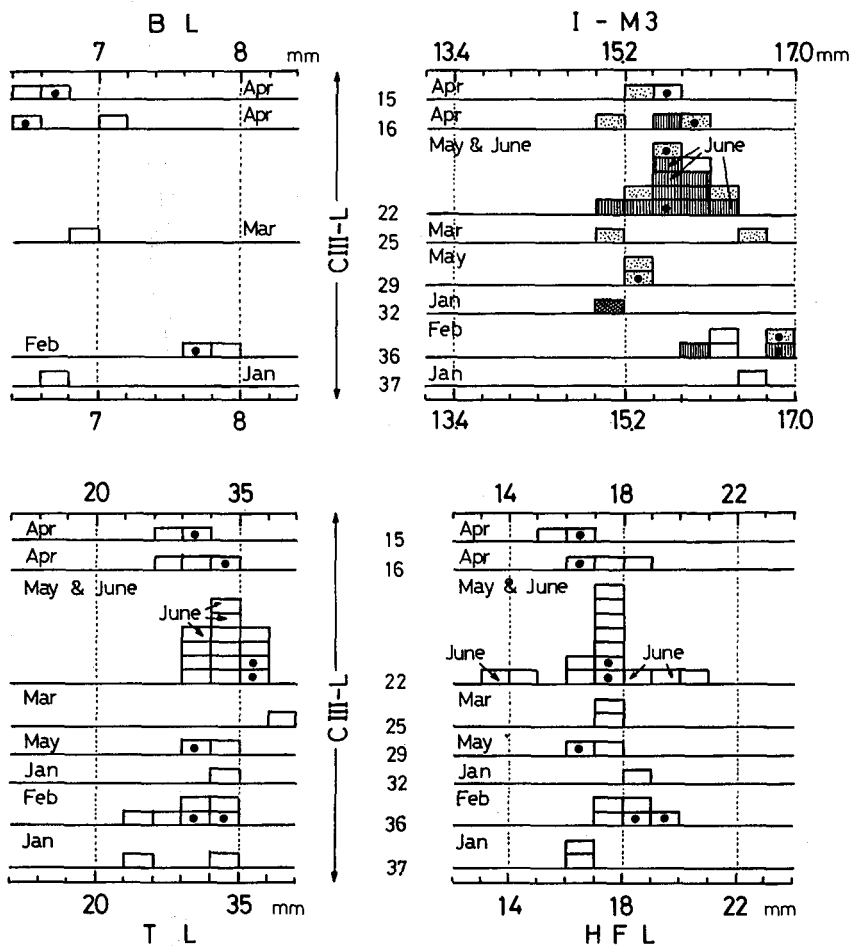


Fig. 8. Geographical variation in BL, I-M3, TL and HFL in *Eothenomys proditor* in Area III (CIII-L). Month indicates collecting month of specimens examined.

For details of Localities 15-16, 22, 25, 29, 32, and 36-37, see the Appendix.

was commonest in CIV-L, whereas Type C predominated in CIV-S (Table 1). Specimens from CIV-S were collected at rather higher elevations than those of CIV-L.

Adult females and young were collected in May, June, July, August and November in cluster CI-L; in August and September in CII-L; in February, April, and May in CIII-L; and in May, June, and July in CI-S, CII-S and CIII-S, respectively (Figs. 6, 8 and 9). On the Lichiang Range, adult females and young were collected in August (4200 and 3300 m), September (4200 and 3900 m) and October (4500-4800, 3900 and 3600 m) in CIV-S, whereas they were captured in May (4200-3900 and 3900 m) and September (4200 and 2700 m) in CIV-L. One pregnant female collected in October in CIV-S (Locality 38,

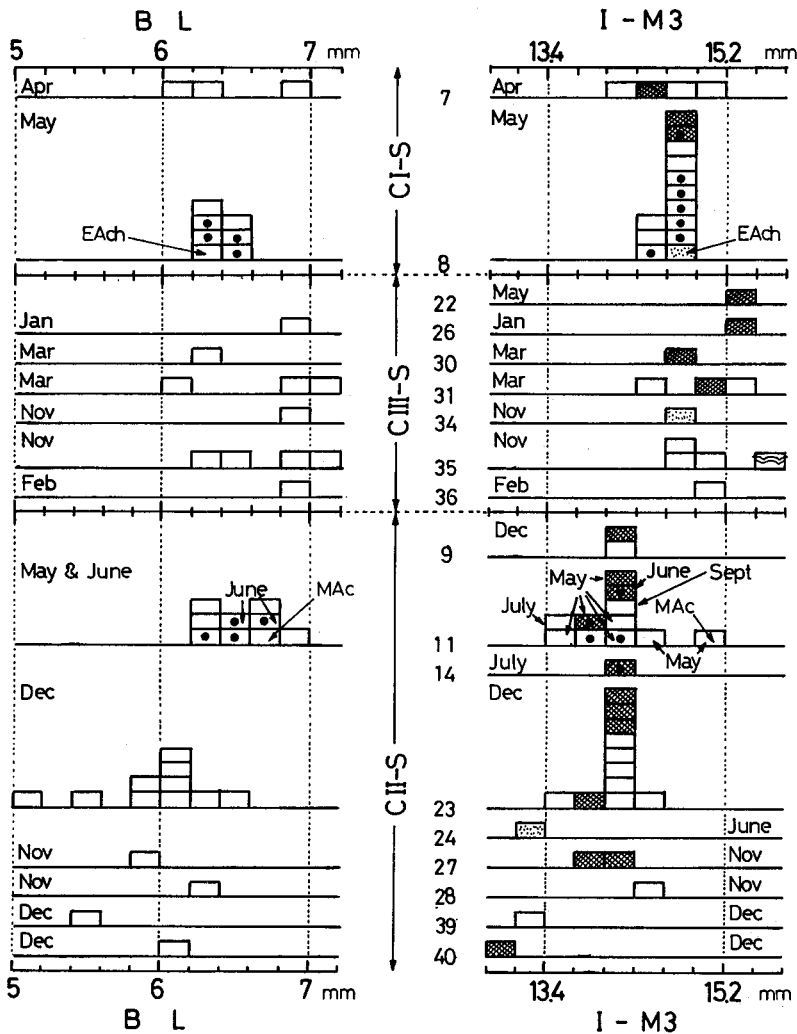


Fig. 9. Geographical variation in BL and I-M3 in *Eothenomys custos* in Areas I-III (CI-S, CIII-S, and CII-S). Month indicates collecting month of specimens examined. For details of Localities 7-9, 11, 14, 22-24, 26-28, 30-31, 34-36, and 39-40, see the Appendix.

3600 m) contained two embryos (FMNH 33792).

2. Taxonomic conclusion

All 308 specimens examined in this study were found to have : i) a palatal shelf construction as in the genus *Clethrionomys* ; ii) rootless molars even in old age, and iii) narrower re-entrant folds on the molars than in the genus *Alticola* (which has little cement in the folds). All three of these characteristics are diagnostic traits for *Eothenomys*, to which consequently they were allocated (Hinton 1926, Ellerman 1941, Corbet 1978).

Some holotypes were re-presented in the respective clusters (L and S in CI-CIV) of Areas I, II and IV (Fig. 5). In Area I, specimens within cluster CI-

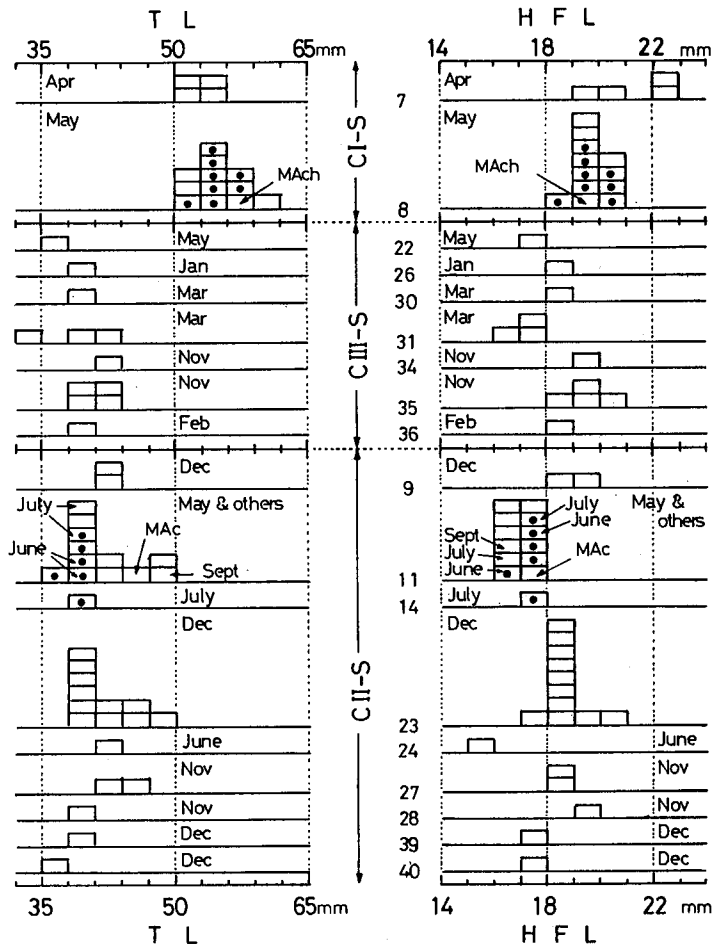


Fig. 10. Geographical variation in TL and HFL in *Eothenomys custos* in Areas I-III (CI-S, CIII-S, and CII-S). Month indicates collecting month of specimens examined.

L were identified as *Eothenomys chinensis* (Thomas, 1891) because the holotypes of *Microtus (Antelionomys) chinensis* Thomas, 1891 and *Microtus (Antelionomys) chinensis tarquinius* Thomas, 1912 were both included in CI-V. The latter name *Microtus (Antelionomys) chinensis tarquinius* is a junior synonym of *E. chinensis* (Thomas, 1891).

Specimens within cluster CII-L were identified as *Eothenomys wardi* (Thomas, 1912) in Area II, because the holotype of *Microtus (Antelionomys) wardi* Thomas, 1912 occurred within the cluster.

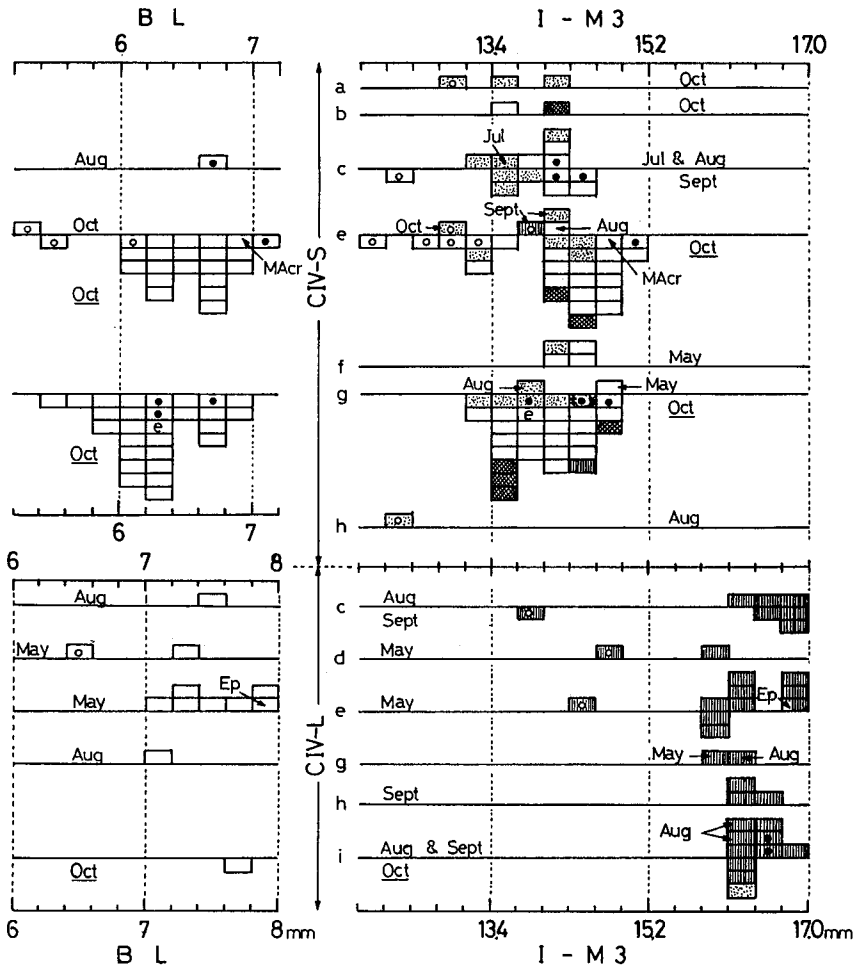


Fig. 11. Altitudinal variation in BL and I-M3 in *Eothenomys custos* (CIV-S) and *E. proditor* (CIV-L) in the Lichiang Range (locality 38). Month indicates collecting month of specimens examined. a=4500–4800 m; b=4200–4500 m; c=4200 m; d=3900–4200 m; e=3900 m; f=3600–3900 m; g=3600 m; h=3300 m; i=2700 m. Underlined records from October indicate specimens collected by R. C. Andrews and E. Heller. All other specimens were collected by G. Forrest.

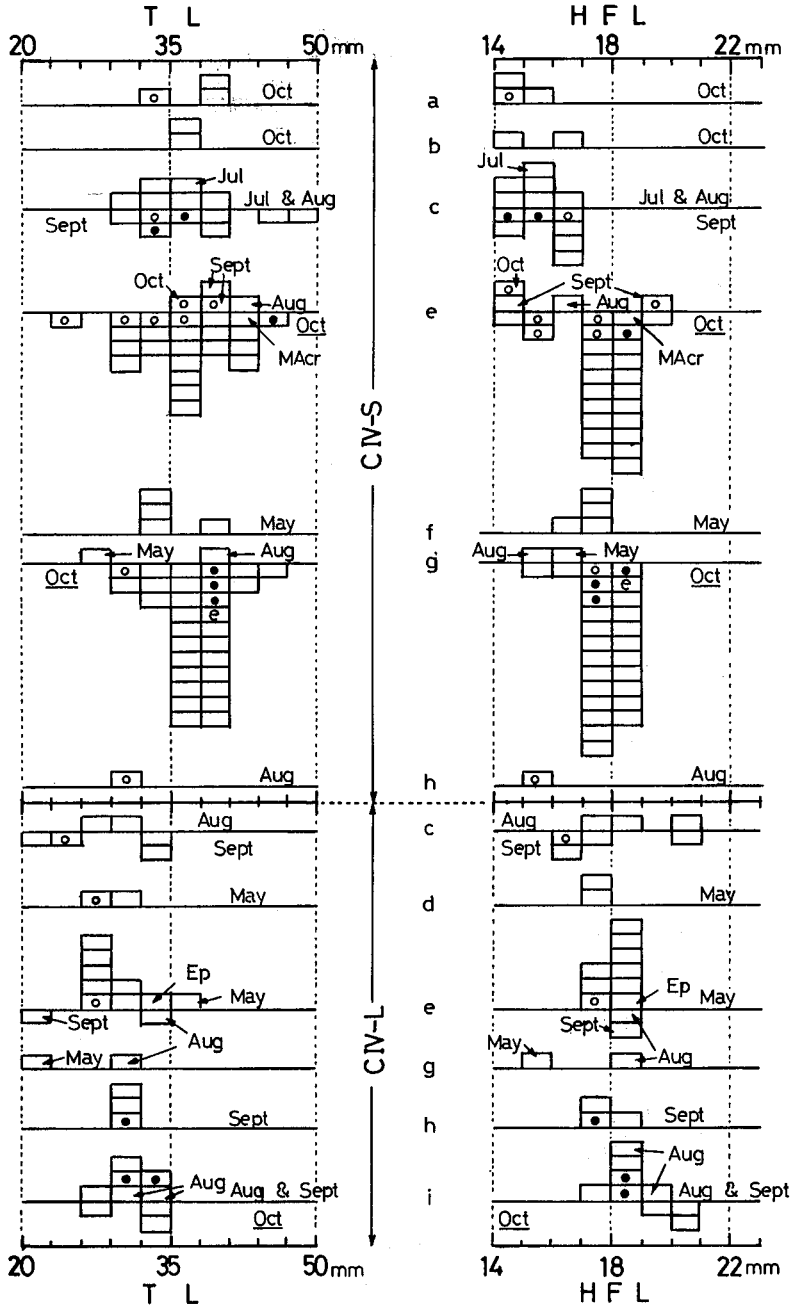


Fig. 12. Altitudinal variation in TL and HFL in *Eothenomys custos* (CIV-S) and *E. proditor* (CIV-L). Month indicates collecting month of specimens examined.

Specimens within cluster CIV-L were identified as *Eothenomys proditor* Hinton, 1923, because the holotype of *E. proditor* Hinton, 1923 was also in the cluster. In Area III, although there was no holotype, cluster CIII-L overlapped with, and was consequently regarded as conspecific with cluster CIV-L, that is *E. proditor* (Fig. 5).

Specimens within cluster CII-S were identified as *Eothenomys custos* (Thomas, 1912), because the holotype of *Microtus (Anteliomys) custos* Thomas, 1912 was included in the cluster. Clusters CIII-S and CIV-S overlapped cluster CII-S (Fig. 5); and all the specimens were identified as *Eothenomys custos* (Thomas, 1912). *Microtus (Anteliomys) custos rubellus* Allen, 1924 is a junior synonym of *E. custos* (Thomas, 1912).

It was noticeable that cluster CI-S did not overlap clusters CII-S, CIII-S or CIV-S (Fig. 5), and TL in CI-S was clearly different from those in CII-S and CIII-S (Fig. 7). However, I-M3, BL and HFL tended to either decrease or increase in size clinally, or varied continuously from north to south among these clusters. Therefore, the taxonomic position of CI-S is considered to be the same as CII-S and CIII-S, which were identified as *E. custos*. Consequently, *Eothenomys (Anteliomys) custos hintoni* Osgood, 1932, included in cluster CI-S (Fig. 5), is a junior synonym of *E. custos* (Thomas, 1912).

The relationship between H & BL and TL (tail ratio=100TL/H & BL) varied from 55-85% in *E. chinesis*, from 40-65% in *E. wardi*, from 50-65% in *E.*

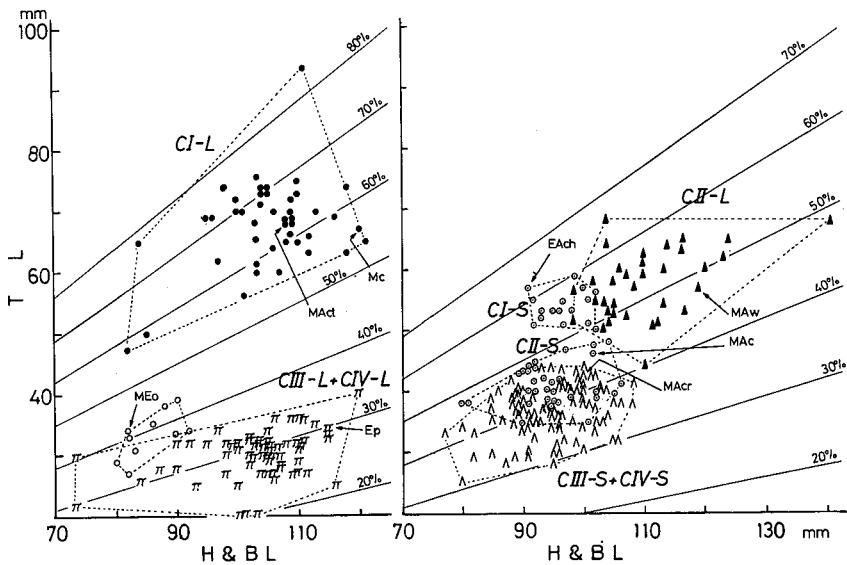


Fig. 13. The relationship between H & BL and TL in five species of *Eothenomys*. The ratio of TL to H & BL is shown with lines and percentages. ● = *E. chinesis* (CI-S); ○ = *E. olitor*; π = *E. proditor* (CIII-L+CIV-L); ▲ = *E. wardi* (CII-L); ⊙ = *E. custos* in Areas I (CI-S) and II (CII-S); △ = *E. custos* in Areas III and IV (CIII-S+CIV-S). For abbreviations of the holotypes, see Fig. 3.

custos from Area I, and 30–50% in *E. custos* from Areas II–IV, from 30–45% in *E. olitor*, and from 20–40% in *E. proditor* (see Fig. 13). Thus, on the basis of this character alone, it is difficult to segregate specimens of *E. chinensis* and *E. custos hintoni* from Area I, specimens of *E. custos* and *E. wardi* from Area II, or specimens of *E. custos* and *E. proditor* from Areas III and IV.

3. Latitudinal and altitudinal distributions

Eothenomys chinensis was found on both sides of the River Datu He near Omei Shan, Sichuan Province at 29–30° N. *E. wardi* was found to occur from the Jinsha Jiang River to the Salween River around 28° N and 99° E. *E. chinensis* and *E. wardi* have allopatric ranges separated by about 240 km. *E. custos* was found from the Yalong Jiang River to the areas between the Jinsha Jiang and Lancan Jiang (=Mekong) Rivers from 26° N to 29° N. *E. proditor* was found along the borders of Sichuan and Yunnan Provinces, from the Yalong Jiang River to the Jinsha Jiang River around 27–28° N. *E. olitor* was recorded from a fragmented range in Zhangton (Localities 41 and 42; 23° N) and Lincang (Locality 33; 27° N) districts in Yunnan Province. The latitudinal distribution of *E. custos* proved to be rather larger than those of either *E. chinensis*, *E. wardi* or *E. proditor* (Fig. 14).

With the exception of the fragmented range of *E. olitor*, the lower altitudinal limit of these four species of *Eothenomys* increased from north to south (see Fig. 15). The altitudinal range of *E. chinensis*, which extends down to 1500 m, was found to be slightly lower than that of *E. wardi* which occurs above 2300 m. *E. custos* was found at slightly higher altitudes (2500–4800 m) than *E. proditor* (2500–4200 m), though the latitudinal range of *E. custos* overlapped that of *E. proditor* in the areas of 26–28° N and 100–102° E (Fig. 14). The lower limit of *E. custos*, range was approximately the same, at about 2500 m, in Areas I, III and IV, but in Area II it decreased from 3500 m to 2700 m from north to south.

Some information on the habitats of *Eothenomys* spp. was available from specimen labels. *E. wardi* was noted as occurring along the banks of streams (Locality 12), in narrow valleys in forest (Locality 18), in alpine meadows, open meadows and among rocks (Locality 13), and in alpine meadows and alpine rocks (Locality 21). *E. custos* was noted as occurring along forested banks, in holes under trees with runs under moss (Locality 11), under roots of large trees in very damp forests (Locality 11), in alpine meadows, rocky meadows, forests, and open coniferous forests (Locality 38; 3300 m), and under logs (Locality 38; 3150 m). *E. proditor* was found in open meadows and open rocky meadows (Locality 38), on mountain slopes (Locality 36), and under logs (Locality 37). Thus, the main habitat differences appear to be that *E. chinensis* lives in both forests and meadows, whereas *E. wardi* and *E. proditor* inhabit meadows and rock areas.

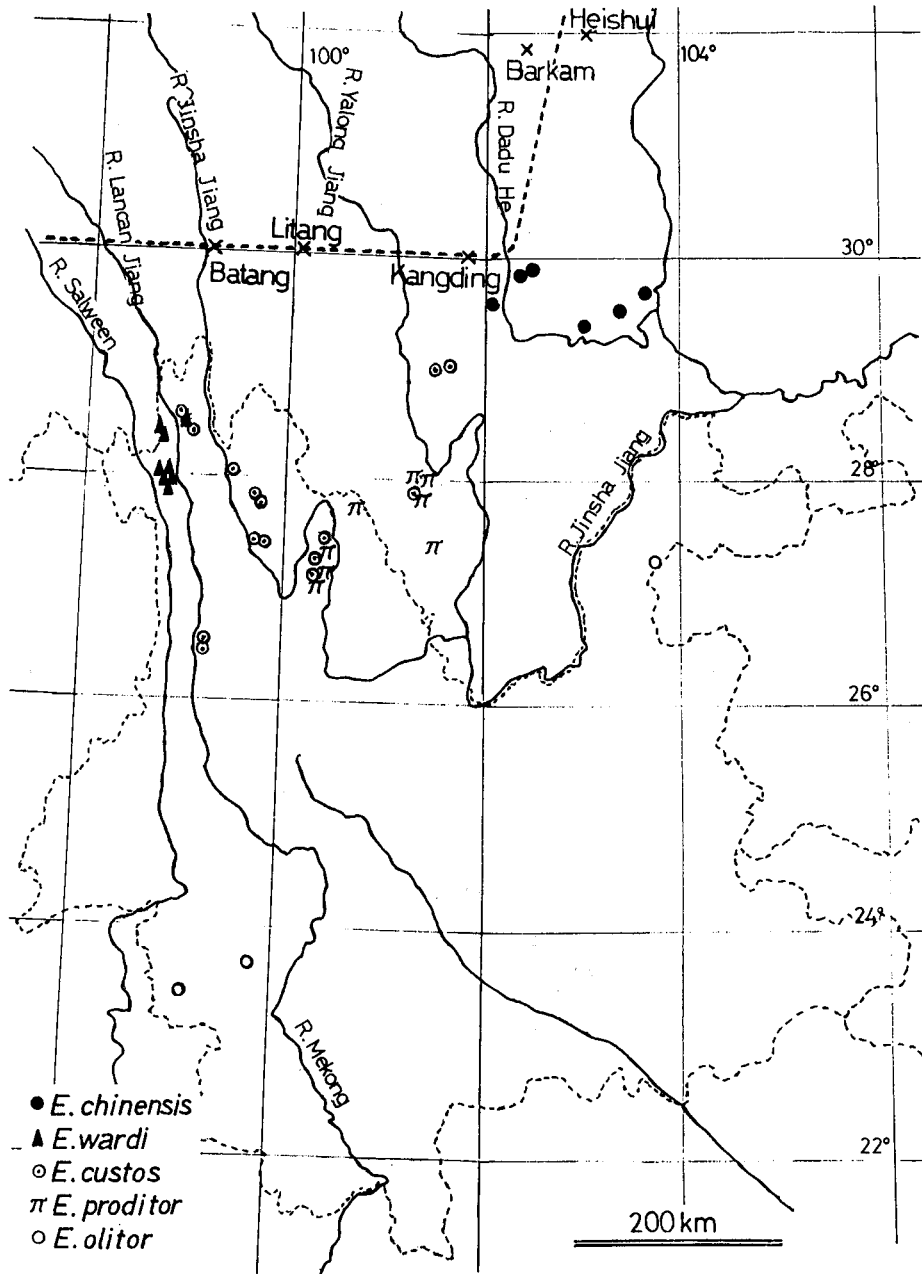


Fig. 14. Summary of the geographical distribution of *Eothenomys chinensis*, *E. wardi*, *E. proditor*, *E. custos*, and *E. olitor*. The broad dotted line indicates the demarcation line between the Palearctic and Oriental regions based on mammals and birds (Zhang 1979), which passes from Zoige (33.5°N, 102.9°E), through Heishui, Barkam, Kangding and Litang, and to Batang in Sichuan Province.

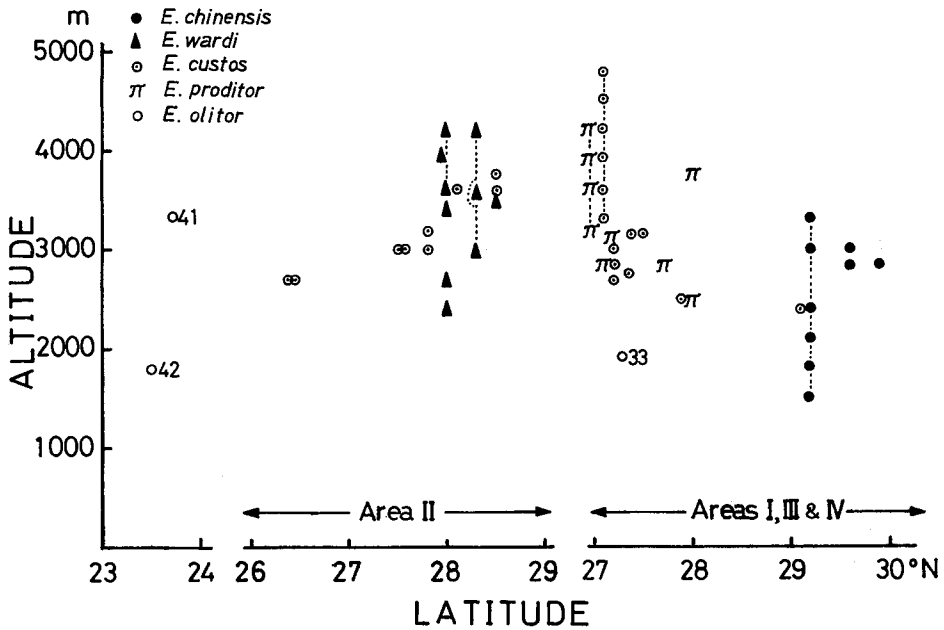


Fig. 15. Summary of the altitudinal distribution of the five species of *Eothenomys* examined in this study. Numbers with open circles indicates the localities of *E. olitor* listed in the Appendix. A dotted line shows the same locality.

DISCUSSION

Hinton (1926), Ellerman (1941), and Gromov and Polyakov (1977) all considered *Anteliomys* to be a distinct genus, separate from *Eothenomys*, whereas Osgood (1932) and Allen (1940) designated *Anteliomys* as a subgenus of *Eothenomys*. In the present study, I have followed the opinions of Ellerman (1949), Ellerman and Morrison-Scott (1951), Corbet (1978), Honacki *et al.* (1982), Corbet and Hill (1992), Musser and Carleton (1993) in regarding *Anteliomys* as a synonym of *Eothenomys*.

Two distinct groups of species belonging to the genus *Eothenomys* have been identified as occurring in the provinces of Sichuan and Yunnan. The first is the *E. melanogaster* group, which includes *confinii*, *eleusis*, *fidelis*, *miletus* and *mucronatus*, and is characterized by the fourth salient angle on the first upper molar and the third salient angle on the second upper molar on the lingual side. The second group consists either of the four species *E. custos*, *E. chinensis*, *E. olitor* and *E. proditor* (Allen 1940, Ellerman and Morrison-Scott 1951, Corbet 1978, Honacki *et al.* 1982, Corbet and Hill 1991, Musser and Carleton 1993) or of the five species *E. custos*, *E. chinensis*, *E. wardi*, *E. olitor*, and *E. proditor* (Hinton 1926, Ellerman 1941, Gromov and Polyakov 1977, Corbet and Hill 1992),

all of which lack the inner salient angles on the first and second upper molars as found in the former group.

However, *Eothenomys* identification has remained confused due to a lack of research into morphological variation, and because only crude distribution maps have been published (Hinton 1926, Allen 1940, Corbet 1978, Corbet and Hill 1992). During research for this paper it became apparent that Allen's (1940) identification key for this species group was rather difficult to apply because of the discrepancies in the number of outer salient angles and in CBL between *E. proditor* and *E. olitor* (Figs. 3 and 5) and in TL between *E. chinensis* and *E. custos* (Fig. 13). The ratio of TL to H & BL (Hinton 1926, Corbet 1978) was not sufficient for identification because of the great overlap between the two sympatric species of *E. custos* and *E. chinensis* (or *E. wardi*) and between *E. custos* and *E. proditor* (Fig. 13). Furthermore, this study showed that the ranges of HFL and the ratio of TL to H&BL, and the number of inner re-entrant folds on the third upper molars given by Corbet and Hill (1992; Table 262) were erroneous for the five species.

The first basic taxonomic debate is over whether *wardi* is a distinct species or just a subspecies of *Eothenomys chinensis*. Thomas (1891) originally described *Microtus chinensis* from a specimen collected from Kia-ting-fu (=Le-shan; Locality 3). Later, Thomas (1911a) identified 23 specimens collected from 23 miles (=36.8km) SE of Ta-t sien-lu (=Moxi; Locality 5) and Emei Shan (Locality 4) as the same species. Subsequently, Thomas (1912b) described *Microtus (Antelionomys) wardi* from a specimen from Chamutong (=Tra-mutang; Kingdon Ward 1923; p. 193; Locality 20), W. of Atuntsi, Yunnan, and differentiated it from *chinensis* on the basis of its much smaller bullae. Hinton (1926) followed this classification, but Allen (1940) changed the taxonomic status of *wardi* to that of a subspecies of *chinensis*, because the third upper molar was the same as that of *chinensis*. Ellerman and Morrison-Scott (1951), Corbet (1978), Honacki *et al.* (1982), and Musser and Carleton (1993) followed Allen (1940), whereas Corbet and Hill (1992) followed Thomas (1912b) and Hinton (1926). Corbet and Hill (1992) distinguished *wardi* from *chinensis* on the basis of *wardi*'s shorter tail and smaller auditory bulla, and remarked on the length of the bulla (BL=6.7 mm in *wardi*, and 9.1 mm in *chinensis*) as a distinguishing character. From this study, however, it is clear that in *wardi* BL ranged from 6.2 to 7.4 mm, and from 6.6 to 8.4 mm in *chinensis*. The length of 9.1 mm referred to by Corbet and Hill (1992) for *chinensis* may well be in error. I also regard *wardi* as a full species, but because not only does it have a smaller bulla but also a shorter tail and hind foot than *chinensis* (Fig. 7), and because its latitudinal distribution is isolated from that of *chinensis* (Fig. 14).

The second basic taxonomic debate is over whether *custos* is best regarded as full species or as a subspecies of *Eothenomys chinensis*. Thomas (1912b) originally described *E. (Antelionomys) custos*, based on two specimens from A-tun-tsi, Yunnan (Locality 11), which had a small bulla, and a shorter tail than either *chinensis* or *wardi*. Hinton (1926; p. 296 and p. 298-299 in the footnote), however, remarked that *custos*, was a small form very closely related mor-

phologically and geographically to the larger forms *chinensis* and *wardi*, and is best regarded as a subspecies of *Antelionomys* (=now *Eothenomys*) *chinensis*, because neither the holotype of *custos* nor the other *custos* skulls examined were "old", though Hinton (1926) retained the taxonomic position of *custos* as a full species as did Thomas (1912b) and Allen (1924). In Areas I and II, some adult females were included into clusters composed of both large (CI-L and CII-L) and small specimens (CI-S and CII-S), the last of which were clearly identified as *E. custos* (Figs. 4 and 5). Therefore, the original specimens of *custos* are neither young *chinensis* nor *wardi* as suggested by Hinton (1926).

Two subspecies of *Eothenomys custos* have been described, excluding the nominotypical subspecies. Allen (1924) described one as *Microtus (Antelionomys) custos rubellus*, collected from Ssu-shan (=Snow Mountain), in the Lichiang Range, Yunnan (Locality 38-e), on the basis that *rubellus* was a little larger on average than typical *custos*. Osgood (1932) described a second subspecies, *Eothenomys (Antelionomys) custos hintoni*, from Wushi (Wu-chi on the holotype label; Locality 8), south-west of Tatsienlu, Sichuan, because it has a slightly longer hind foot and longer tail than *custos*. My examination showed that although the tail was longer in the specimens described by Osgood (1932), the hind foot length was not (see Fig. 10). Furthermore, Osgood (1932) stated that the interorbital width (IOW) was relatively greater in *hintoni* than in *chinensis*, and that the third inner angle of the third upper molar was usually confluent with the fourth outer one in *hintoni* but not in *chinensis*. On further examination, however, I was unable to confirm these differences: IOW ($X + SD$) of *hintoni* (Localities 7-8) was 4.38 ± 0.11 mm ($n=16$), while that of *chinensis* (Localities 1-6) was 4.33 ± 0.21 mm ($n=44$), ($t=0.784$, $0.5 < p < 0.6$, $df=58$). Most specimens of *chinensis* (7/9) from Locality 1, and the holotype of *chinensis tarquinius*, had enamel lamellae contacting the third inner and the fourth outer triangles, whereas other specimens of *chinensis* from Localities 2-6, and of *custos* from Localities 7-8, did not.

The range of *Eothenomys chinensis* was shown to be distinct from but parallel to that of *E. custos* in Sichuan (Allen 1940). That the two species are allopatric in distribution has been further confirmed by the present study. The distribution of *E. chinensis* is also known to be distinct from that of *E. eva* (Kaneko 1992).

Eothenomys custos has been recorded from the extreme north-west of Yunnan, the Likiang Range, the loop of the Jinsha Jiang River, and from central Sichuan (Hinton 1926, Allen 1940). Yang (1985), added Lanping (26.4° N, 99.2° E), Jianchuan (26.5° N, 99.8° E), and Dali (25.6° N, 100.1° E) to the range of *E. custos*, though his means of identification was not clear. Because *E. custos* has been recorded from around 25.5-29° N and from 99-100.5° E (Fig. 14), the latitudinal distribution is the largest among *Eothenomys* species investigated here. *E. custos* was not, however, recorded from the west side of the Lancan Jiang River (Figs. 1 and 14). According to Yang (1985), the lower limit of *E. custos*, range decreases from north to south. The present study supports his finding in Area II, but not in Areas I, III and IV, where the lower limits were

nearly the same (Fig. 15). Therefore, the altitudinal distribution of *custos* probably differs between Sichuan and Yunnan Provinces. The habitat of *custos* studied here was also similar to that reported by Yang (1985); *i. e.* it occurs in shrubs, bamboos, alpine meadows, and in forests.

No taxonomic problems have been associated with *Eothenomys proditor* since Hinton (1923) described it on the basis of its generally smaller size, its shorter tail and peculiar third upper molar (simple form) based on specimens collected from the Lichiang Range (Locality 38). Although there have been no published reports of the geographical range or habitat of this species, I consider *E. proditor* to be restricted to the border between Sichuan and Yunnan, at around 27–28° N and 100–102° E, and that it lives in meadows and in rocky areas.

Eothenomys olitor, the least abundant member of the genus, was described as a new species, *Microtus (Eothenomys) olitor* by Thomas (1911b) on the basis of specimens collected at Chao-tung-fu (Locality 33), in eastern Yunnan. *E. olitor* differs considerably from other forms examined here. On the second upper molar, although a third inner salient angle appears in some specimens of *E. custos*, *E. proditor*, *E. chinensis* and *E. wardi* as a very small form, the salient angle is as large in *E. olitor* as any species of the *E. melanogaster* group (Fig. 3).

The range of *Eothenomys olitor* has been recorded as fragmentary and widely scattered (Fig. 14). Allen (1924) recorded Mucheng, Salween Drainage (2100 m; Locality 42) as a new locality for the species. Later, Allen (1940; p. 820) reported one specimen of *E. olitor* collected from Peitai, 30 miles (= 45 km) south of Chungtien, near Locality 27, from within the range of *E. custos* (Fig. 14). I was not able to locate the specimen in the museums examined here, because Allen (1940) did not record the registration number of the specimen. Two specimens, housed in MCZ and AMNH, belonging to the *E. melanogaster* group, were, however, collected at Peitai on November 26, 1916, by R. C. Andrews. One of them (now MCZ 21298 and originally AMNH 44109) had two re-entrant angles on the lingual side of the third upper molar and the other (AMNH 44233) had three. I think that Allen (1940) misidentified these specimens as *E. olitor*. The latitudinal distribution, therefore, does not include western Yunnan, as described by Allen (1940), but north-eastern and south-western Yunnan, and the altitudinal ranges extends from 1800 to 3350 m. The habitats *E. olitor* occurs in were noted as cultivated plains (Locality 33; Thomas 1912a) and rhododendron shrubs on Daxue Shan (Locality 41; Lu *et al.* 1965).

The altitudinal range of the four species of *Eothenomys* here tended to increase from north to south (Fig. 15). The lower limits of their altitudinal distribution does not, however, coincide with the distribution of vegetation types on the mountains of Sichuan and Yunnan Provinces (Xibei Teachers College and Ditu Chubanshe 1984, Yunnan Province Epidemiology Institution 1978), except for *E. olitor* due to its very fragmented distribution. As an example, *E. custos* was recorded from 1500 to 3300 m on Emei Shan. There, evergreen and deciduous mixed forests occurs from 1500 to 2000 m, coniferous

and broad-leaved mixed forests from 2000 to 2800 m, and subalpine, shrubby, meadowy and coniferous zones above 2800 m (Xibei Teachers College and Ditu Chubanshe 1984). As a second example, *E. wardi* occurs from 2400 to 4200 m around 28° N, however, vegetation in the region changes from *Pinus yunnanensis* and *P. armandii* which grow from 2500 to 3000 m, to mixed forests with *P. yunnanensis*, *Betula* spp. and *Quercus* spp. from 3000 to 3500 m, various *Picea* spp. from 3500 to 4000 m, and to alpine shrubs and meadows with *Rhododendron* spp. above 4000 m (Yunnan Province Epidemiology Institution 1978). It seems likely that the distributions of the four *Eothenomys* species are affected more by topographical barriers, such as rivers running along Hengduan Shan, than by vegetation type.

The length of I-M3 in *Eothenomys custos* increased from south to north (Fig. 9), conversely that of *E. proditor* increased from north to south (Fig. 8). Given the significant correlation between I-M3 and CBL, it also means that body size increases or decreases from south to north, that is an example of Bergmann's rule or of reverse Bergmann's rule. Many mammalian species ranging through wide latitudes follows the rule or the reverse of Bergmann's rule (McNab 1971), thus some species of *Microtus* (Arvicolidae) living in northern latitudes above 50° N obey Bergmann's rule, whereas those living in southern latitudes below 50° N obey the reverse of the rule (Kaneko 1988). It is particularly interesting that two opposite clines in skull length are to be found in closely adjacent areas of Sichuan and Yunnan Provinces.

The breeding seasons of the various voles could be estimated by the occurrence of young and adult females with developed mammae (Figs. 6, 9 and 11). The breeding seasons of *E. chinensis*, *E. wardi*, and *E. custos* were mainly from early summer to late fall, whereas that of *E. proditor* was from February to May in Area III and from spring to fall in Area IV. Thus, *E. proditor* probably breeds slightly earlier than do other species of *Eothenomys*.

Acknowledgments: I gratefully thank the many museum staff who allowed me to examine specimens in their care, particularly: Ian R. Bishop, Jean M. Ingles, Paula D. Jenkins and Daphne M. Hills (BM); Maria E. Rutzmoser (MCZ); Guy G. Musser and the late Wolfgang K. -H. Fuchs (AMNH); Michael C. Carleton (USNM); Bruce B. Patterson (FMNH); Wang Sung, Wang Zongren, and Quan Guoqing (ASZI); and Wu Tehlin (ASKZI). This work was partly supported by a Short Term Visitor Grant from the Smithsonian Institution, by the Karl P. Schmidt Fund of the FMNH, and by an "Overseas Scientific Grant for 1982 (62041089) and 1983 (63043061)" given by the Ministry of Education, Science and Culture of Japan. I also acknowledge the assistance of anonymous referees and Mark Brazil for critically reading and help to improve the manuscript.

REFERENCES

- Allen, G. M. 1912. Some Chinese mammals. Mem. Mus. Comp. Zool. Harvard Coll. 40: 201-247.
Allen, G. M. 1924. Microtines collected by the Asiatic Expeditions. American Mus. Novit. (133): 1-

Kaneko, *Five species of Eothenomys in China*

13.

- Allen, G. M. 1940. Mammals of China and Mongolia. Vol.11, Part 2. Amer. Mus. Nat. Hist., New York, pp. 621–1350.
- Corbet, G. B. 1978. The Mammals of the Palaearctic Region: a Taxonomic Review. Brit. Mus. (Nat. Hist.) & Cornell Univ. Press, London & Ithaca, 314 pp.
- Corbet, G. B. and J. E. Hill. 1991. A World List of Mammalian Species. 3rd ed. Nat. Hist. Publ., Oxford Univ. Press, 243 pp.
- Corbet, G. B. and J. E. Hill. 1992. The Mammals of the Indomalayan Region. Nat. Hist. Mus. Publ., Oxford Univ. Press, 488 pp.
- Ellerman, J. R. 1941. The Families and Genera of Living Rodents. Vol. 2. Family Muridae. Brit. Mus. (Nat. Hist.), London, 690 pp.
- Ellerman, J. R. 1949. The Families and Genera of Living Rodents. Vol. 3. Part 1. Brit. Mus. (Nat. Hist.), London, 210 pp.
- Ellerman, J. R. and T. C. S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian Mammals, 1758 to 1946. Brit. Mus. Nat. Hist., London, 810 pp.
- Gromov, I. M. and I. Ya. Polyakov. 1977. Fauna of the USSR. Mammals. Vol. 3, No. 8. Voles (Microtinae). Nauka Publ., Leningrad. Inst. (Translated for the Smithsonian Inst. Library, Amerind Publishing Co., New Delhi, 1992, 725 pp.)
- Hinton, M. A. C. 1923. On the voles collected by Mr. G. Forrest in Yunnan; with remarks upon the genera *Eothenomys* and *Neodon* and upon their allies. Ann. Mag. Nat. Hist. Ser. 9, 11: 145–162.
- Hinton, M. A. C. 1926. Monographs of Voles and Lemmings (Microtinae) Living and Extinct. Brit. Mus. Nat. Hist., London, 488 pp.
- Honacki, J. H., K. E. Kinman and J. W. Koepl (eds.). 1982. Mammal Species of the World. A Taxonomic and Geographic Reference. Allen Press & Assoc. Syst. Coll., Lawrence, Kansas, 694 pp.
- Howell, A. B. 1929. Mammals from China in the collections of the United States National Museum. Proc. U. S. Natl. Mus. 75: 1–82.
- Jones, J. K., Jr. and D. H. Johnson. 1965. Synopsis of the lagomorphs and rodents of Korea. Univ. Kansas Publ. Mus. Nat. Hist. 16: 357–407.
- Kaneko, Y. 1988. Relationship of skull dimensions with latitude in the Japanese field vole. Acta Theriol. 33: 35–46.
- Kaneko, Y. 1990. Identification and some morphological characters of *Clethrionomys rufocanus* and *Eothenomys regulus* from USSR, northeast China, and Korea in comparison with *C. rufocanus* from Finland. J. Mamm. Soc. Jpn. 14: 129–148.
- Kaneko, Y. 1992. Identification and morphological characteristics of *Clethrionomys rufocanus*, *Eothenomys shanseius*, *E. inez* and *E. eva* from the USSR, Mongolia, and northern and central China. J. Mamm. Soc. Jpn. 16: 71–95.
- Kingdon Ward, F. 1923. Mystery Rivers of Tibet. Seley Service & Co. Ltd. (Cadogan Books Ltd. published in 1986), 316 pp.
- Lu Chang-Kwun, Wang Tsung-Yi, Qian Guo-Qiang, Gin Shan-Ko and Ma Teh-Hwei. 1965. On the mammals from the Lin-Tsang area, western Yunnan. Acta Zootax. Sinica 2: 279–295 (in Chinese with English abstract).
- McNab, B. K. 1971. On the ecological significance of Bergmann's rule. Ecology 52: 845–854.
- Miller, G. S., Jr. 1896. Genera and subgenera of voles and lemmings. North American Fauna 12: 1–85.
- Musser, G. G. and M. D. Carleton. 1993. Family Muridae. In Mammal Species of the World. A Taxonomic and Geographic Reference. 2nd ed. (D. E. Wilson and D. A. M. Reeder, eds.) pp. 501–755, Smithsonian Institution Press, Washington and London.
- Osgood, W. H. 1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic expeditions. Field Mus. Nat. Hist. Zool. Ser. 38: 193–339.
- Pen Hung-Shou, Kao Yueh-Ting, Lu Chang-Kwun, Feng Tso-Chien and Chen Ching-Hsiung. 1962. Report on mammals from southwestern Szechwan and northwestern Yunnan. Acta Zool. Sinica 14: 105–132 (in Chinese with English abstract).

- Roosevelt, T. and K. Roosevelt. 1929. Trailing the Giant Panda. Charles Scribner's Sons, London, 278 pp.
- Su Dei-Rong (ed.). 1984. Gazetteer of the World. Vol. 2. China Encyclopedia Publ. Co., Beijing & Shanghai, pp. 1519–2806.
- Thomas, O. 1891. Description of a new vole from China. Ann. Mag. Nat. Hist. Ser. 6, 8 : 117–119.
- Thomas, O. 1911a. The Duke of Bedford's exploration of eastern Asia. XV. On mammals from the Provinces of Kan-su and Sze-chwan, western China. Proc. Zool. Soc., London 1911 : 158–180.
- Thomas, O. 1911b. Abst. Proc. Zool. Soc., London 100 : 48–50.
- Thomas, O. 1912a. The Duke of Bedford's exploration of eastern Asia. XV. On mammals from the Provinces of Szechwan and Yunnan, western China. Proc. Zool. Soc., London 1912 : 127–141.
- Thomas, O. 1912b. On insectivores and rodents collected by Mr. F. Kingdon Ward in N. W. Yunnan. Ann. Mag. Nat. Hist. Ser. 8, 9 : 513–519.
- Thomas, O. 1914. Second list of small mammals from western Yunnan collected by Mr. F. Kingdon Ward. Ann. Mag. Nat. Hist. Ser. 8, 14 : 472–475.
- Thomas, O. 1923. On mammals from the Li-kiang Range, Yunnan, being a further collection obtained by Mr. George Forrest. Ann. Mag. Nat. Hist. Ser. 9, 11 : 655–663.
- Tokuda, M. 1941. A revised monograph of the Japanese and Manchou-Korean Muridae. Trans. Biogeograph. Soc. Japan 4 : 1–155.
- Xibei Teachers College and Ditu Chubanshe (eds.) 1984. Atlas of Natural Geography of China. Ditu Chubanshe, Beijing, 200 pp (in Chinese).
- Yang Guang-Rong. 1985. Some biological notes on the southwest Chinese vole (*Eothenomys custos*). Acta Sinica Theriol. 5 : 24 and 34 (in Chinese).
- Yunnan Province Epidemiology Institution. 1978. Notes on the vertical distribution of small rodents on Mt. Baimang Shueshan, Yunnan Province. Rep. Biol. Studies for Rodents and its Protection 3 : 133–136 (in Chinese).
- Zhuang Jin-Nan (ed.) 1983. Gazetteer of China. An Index to the Atlas of the People's Republic of China. Atlas Publ. Co., Shanghai, 315 pp.
- Zhang Yongzu (ed.) 1979. Zoogeography in China. Science Publ., Beijing, 121 pp (in Chinese).

APPENDIX

1. Lu Tsing Shan (=Luding Xian), Sichuan; 29.9° N, 102.3° E; *chinensis* (March, 1931; FMNH 36527–29, 36531–32, 36536, 36538/ April 1931; FMNH 36534–35, 36537).
2. Erlang Shan, Sichuan; 29.9° N, 102.2° E; 2880 m; *chinensis* (July 1962; ASZI 20831).
3. Kia-ting-fu (=Leshan), Sichuan; 29.6° N, 103.7° E; the date of collection remains unknown; BM 91.5.11.3 (the holotype of *Microtus chinensis* Thomas, 1891).
4. Omi-san (=Emei Shan), Sichuan; 29.6° N, 103.4° E; 2850 m; *chinensis* (August 1910; BM 11.2.215–222).
5. 23 miles SE of Ta-tsien-lu (=Moxi), Sichuan; 29.6° N, 102.1° E; 3000 m; June 1910; BM 11.2.1.207 (the holotype of *Microtus (Antelionomys) chinensis tarquinius* Thomas, 1912); *chinensis* (June 1910; BM 11.2.1.208–214).
6. Washan, Sichuan; 29.2° N, 103.0° E; 1500 m, 1800 m, 2100 m, 2400 m, 3000 m, 3300 m; *chinensis* (May 1908, MCZ 7815, 7817, 7819, 7821–23, 7825/ June 1908; MCZ 7812–14, 7820, 7824/ October 1908; MCZ 7805, USNM 175141/ November 1908; MCZ 7806–7809, BM 13.9.13.9/ July 1925; USNM 241279, 241282).
7. Tong Ku or Chung Ku, Chu Liang Shiang (=Jiulong Xian), Sichuan; 29.1° N, 101.6° E; 2400 m; *custos* (April 1934; AMNH 113555–56, 113559–60).
8. Wu-chi (=Wuxu), SW of Tatsienlu, Sichuan; 29.1° N, 101.4° E; May 1929; FMNH 33073 (the holotype of *Eothenomys (Antelionomys) custos hintoni* Osgood, 1932); *custos* (May 1929; FMNH 33072, 33075–76, 33079–80, 33083–33085, 33218; BM 1938.4.1.184–185; USNM 259917–18).
9. Adong, Yunnan; 28.7° N, 98.5° E; *custos* (December, 1979; ASZI 79806–07).
10. E of Atuntzi (=Deqen Xian), Yunnan; 28.5° N, 98.9° E; 3588 m; *wardi* (the date of collection remains unknown; BM 22.10.21.8, 22.10.21.11–13, 22.10.21.15).
11. A-tun-tsi, (=Deqen Xian), Yunnan; 28.5° N, 98.9° E; 3600–3750 m; May 1911; BM 12.3.18.19

- (the holotype of *Microtus (Antelionomys) custos* Thomas, 1912); *custos* (May 1911; BM 12.3.18.16–18, 12.3.18.21–23/ June 1911; BM 12.3.18.24, 14.10.23.31/ September 1911; BM 12.3.18.20/ 3560 m; July 1960; ASZI 17115).
12. Doker-la, Yunnan; 28.3° N, 98.7° E; 3600 m; *wardi* (June 1913; BM 14.10.23–25, 14.10.23.28/ July 1913; BM 14.10.23.26–27, 14.13.23.29–30).
 13. Mekong-Salween Divide (=near Dokerla), Lat. 28° 20' N, Yunnan; 28.3° N, 98.7° E; 3000–4200 m; *wardi* (September 1921; BM 22.12.1.27, 65.3836, 65.3839–41).
 14. Benzilan, Yunnan; 28.1° N, 99.3° E; 3600 m; *custos* (July 1960; ASZI 17186).
 15. Kulu (=I-tse), Szechwan; 28.0° N, 101.3° E; *proditor* (April 1929; FMNH 33064, 33070).
 16. I-tze Camp, Szechwan; 28.0° N, 101.3° E; 3750 m; *proditor* (April 1929; FMNH 33067–69).
 17. Mekong Valley (=near Tzeka), Lat. 28° N, Yunnan; 28.0° N, 98.9° E; 2400–2700 m; *wardi* (July 1921; BM 22.12.1.18–20, 65.3832, 66.1998).
 18. SW side of Si-la pass, Yunnan; 28.0° N, 98.7° E; 3420 m; *wardi* (July 1922; BM 22.10.21.6).
 19. Mekong-Salween Divide, Lat. 28° N, Yunnan; 28.0° N, 98.7° E; 3600–4200 m; *wardi* (July 1921; BM 22.12.1.21–26, 22.12.1.28–30, 65.3834–35, 65.3842/ August 1921; BM 65.3837).
 20. Chamutong (=Tra-mu-tang; Kingdon Ward, 1923), Upper Salween drainage-area, W of A-tuntsi, Yunnan; 28.0° N, 98.6° E; 3900 m; the date of collection remains unknown; BM 12.3.18.15 (the holotype of *Microtus (Antelionomys) wardi* Thomas, 1912).
 21. Kiu-Chiang-Salween Divide (=near Gompa La), Lat. 28° N, Yunnan; 28.0° N, 98.5° E; 3600–4200 m; *wardi* (August 1921; BM 22.12.1.31–33, 65.3838).
 22. Muli, Szechwan; 27.9° N, 101.3° E; 2500 m; *custos* (May 1959; ASZI 17426); *proditor* (May 1959; ASZI 17421, 17425, 17428, 17430–31, 17434, 17439/ May 1960; ASZI 17422, 17424, 17427, 17433/ June 1960; ASZI 17423, 17437, 17440).
 23. To-mu-lang, Chung-tien Dist. (=near Zhongdian Xian), Yunnan; 27.8° N, 99.7° E; 3000 m; *custos* (December 1916; AMNH 44201, 44203–04, 44209–10, MCZ 21303–05, FMNH 33934–36).
 24. Zhongtian Xian, Yunnan; 27.8° N, 99.7° E; 3200 m; *custos* (June 1959; ASZI 17183).
 25. Yun-ning (=Yongning), Yunnan; 27.7° N, 100.8° E; 2850 m; *proditor* (March 1929; FMNH 33019, 33060).
 26. Chang Sung Ping, 60 miles N Lichiang, Yunnan; 27.5° N, 100.4° E; 3150 m; *custos* (January 1929; FMNH 32540).
 27. 20 miles S Chungtien, Tugan-sha, Yunnan; 27.5° N, 99.7° E; 3000 m; *custos* (November 1911; FMNH 33937–38).
 28. Pesu Rusi (=near Xiachongdian), Lichiang, Yunnan; 27.5° N, 99.7° E; 3000 m; *custos* (November 1916; FMNH 33797).
 29. Yannyan, Szechwan; 27.4° N, 101.5° E; *proditor* (May 1959; ASZI 17420, 17432).
 30. Big Bena, Lichiang Range, Yunnan; 27.4° N, 100.4° E; 3180 m; *custos* (March 1929; FMNH 33015).
 31. Lutzulu, Lichiang Range, Yunnan; 27.4° N, 100.4° E; 2790 m; *custos* (March 1929; FMNH 33012–14).
 32. 45 miles N Lichiang, Yunnan; 27.4° N, 100.4° E; *proditor* (January 1929; FMNH 32539).
 33. Chao-tung-fu (=Zhaotong Xian), Yunnan; 27.3° N, 103.7° E; March 1911; 1920 m; BM 11.9.8.122 (the holotype of *Microtus (Eothenomys) olitor* Thomas, 1911); *olitor* (March 1911; BM 11.9.8.121, 11.9.8.123–24, 11.9.8.126/ December 1963; ASKZI 631407).
 34. Peh-hsui (=near Daju), Lichiang, Yunnan; 27.2° N, 100.4° E; 3000 m; *custos* (November 1916; AMNH 44018).
 35. Taku Hills (=near Daju), Lichiang, Yangtze River, Yunnan; 27.2° N, 100.4° E; 2700 m; *custos* (November 1916; FMNH 33798–800, MCZ 21310).
 36. Nguluku, Yunnan; 27.2° N, 100.3° E; 2850 m; *custos* (February 1929; FMNH 33009); *proditor* (February 1929; FMNH 33003–04, 33006–07, 33010, USNM 259908).
 37. 25 miles N Lichiang, Yunnan; 27.2° N, 100.3° E; 3150 m; *proditor* (January 1929; FMNH 32537–38).
 38. Lichiang Range (=Yulongxuen), Yunnan; 27.1° N, 100.2° E.
 - a. 4500–4800 m; *custos* (October 1922; BM 75.645–46, FMNH 28964).
 - b. 4200–4500 m; *custos* (October 1922; BM 75.651, FMNH 28963).

- c. 4200 m; *custos* (July 1922; BM 23.10.11.7/ August 1922; BM 23.10.11.4-5, 75.652-53, 75.655/ September 1922; BM 23.10.11.12, 75.647-49, 75.654, 76.656-58); *proditor* (August 1922; BM 75.682, 75.684-85, FMNH 28967/ September 1922; BM 75.682-683, 75.686-687).
- d. 3900-4200 m; *proditor* (May 1921; BM 22.12.1.11, 22.12.1.12).
- e. 3900 m; October 1916; AMNH 44001 (the holotype of *Microtus (Antelionomys) custos rubellus* Allen, 1924); *custos* (October 1916; AMNH 44003, 44005, 44116-18, 44120, 44123, 44126-28, 44131-33, 44135-36, MCZ 21309, 21311-12, FMNH 31693, 33783, 33784 (the skin is now housed in the AMNH as 44119), 33785-86, 33788, USNM 259928-29/ August 1922; BM 75.662/ September 1922; BM 75.664, 75.678/ October 1922; BM 75.665); May 1921; BM 22.12.1.10 (the holotype of *Eothenomys proditor* Hinton, 1923); *proditor* (May 1921; BM 22.12.1.13-14, 22.12.1.16-17, 65.3828-30, 75.675/ August 1922; BM 75.676/ September 1922; BM 75.681).
- f. 3600-3900 m; *custos* (May 1921; BM 22.12.1.15, 65.3825-26, 75.661).
- g. 3600 m; *custos* (October 1916; AMNH 44007, 44010-11, 44140-43, 44147, 44149-50, 44152, 44154-56, 44158-60, 44163, 44168, FMNH 33789, 33792-96, MCZ 21306-08, USNM 259930, BM 23.3.17.112/ May 1921; BM 75.660/ August 1922; BM 75.663); *proditor* (May 1921; BM 65.3824/ August 1922; BM 23.10.11.2).
- h. 3300 m; *custos* (August 1922; BM 75.666); *proditor* (September 1922; BM 23.10.11.9, 23.10.11.11, 75.671).
- i. 2700 m; *proditor* (October 1916; AMNH 44015, FMNH 31691, MCZ 21293/ August 1922; BM 23.10.11.3, 75.669, 75.674/ September 1922; BM 23.10.11.6, 75.670, 75.674, FMNH 28968-69).
39. La-chu-mi (=near Langpig Xian), Mekong River, Yunnan; 26.4° N, 99.2° E; 2700 m; *custos* (December 1916; MCZ 21302).
40. Ying-pan-kai (=Yingpan), Mekong River, Yunnan; 26.4° N, 99.1° E; 2700 m; *custos* (December 1916; AMNH 44037).
41. Daxue Sahn, Yongde, Yunnan; 23.7° N, 99.7° E; 3350 m; *olitor* (April 1964; ASZI 23960).
42. Mucheng, Salween Drainage (=Megdingjie), Yunnan; 23.5° N, 99.1° E; 1800 m; *olitor* (February 1917; MCZ 21285).

(accepted 21 August 1996)