Revision of the Asian Moles of the Genus *Mogera*

Hisashi ABE

*Laboratory of Applied Zoology, Faculty of Agriculture, Hokkaido University, Sapporo 060, Japan*

(Accepted 28 April 1995)

**Abstract.** In order to resolve taxonomic problems among the Japanese moles, *Mogera* spp., I compared the five main diagnostic skull characters among all the known taxa in the genus using, as a basis, the previous work by Abe (1967). A total of 612 specimens were examined, including the type specimens of *M. wogura*, *M. w. kobeae*, and *M. w. kanai* of Japan, those of *M. w. coreana* of Korea, *M. hainana* of Hainan and *M. latouchei* of south-east China, and others from the Far East maritime region of Siberia and Taiwan R.O.C. It was concluded that the mole ranging across the southern half of Japan, previously known as *M. kobeae*, is in fact a synonym of *M. wogura* and should be referred to as such. The mole previously called *M. wogura* with its main range to the northern half of Honshu is henceforth called *M. minor*. Four species of the genus *Mogera*: *M. wogura, M. minor, M. tokudae*, and *M. insularis*, are thus recognized as occurring in east Asia.

**Key words:** *Mogera*; Asian moles; Taxonomic revision; Skull characters

The Japanese mole was first described by Temminck (1842) as *Talpa wogura* with no specified type locality given other than "Japan", then moved to a new genus, *Mogera*, by Pomel (1848). Five subspecies from Japan and Korea were subsequently recognized as belonging to this species by Thomas (1905, 1906) and Kuroda (1936, 1940). Schwarz (1948), however, lumped many Eurasian mole species and reduced all the Japanese moles to subspecies of *Talpa micrura*, a revision that was also followed by Ellerman and Morrison-Scott (1951). Imaizumi (1960, 1970), however, separated the Japanese moles into two species, *M. wogura* and *M. kobeae*, each with three subspecies. Abe (1967), who examined the age, geographical, and sexual variation of 445 specimens he collected from many scattered localities in Japan, recognized three Japanese mole species: *M. wogura, M. kobeae*, and *M. tokudae*. Abe’s (1967) classification of *M. kobeae* differed from that of Imaizumi (1960, 1970), who regarded *tokudae* as a subspecies of *M. kobeae*. Ecological, distributional, and karyological information all supported classification of the moles of Japan into three species (Abe 1967, 1985; Tsuchiya 1988). This classification has been further supported by isozyme analysis of 20 loci (Okamoto and Abe unpubl.). Recently, Corbet and Hill (1980, 1986, 1991), Rossolimo et al. (1982) and Hutterer (1993) have all referred to differing combinations of mole species in Japan. The domains of species, i.e. the local populations they included, and the distribution of species they defined, however, differ greatly from those of Abe (1967) even when they
used the same specific names. As a result, the classification of the Japanese moles remains in disarray and requires clarification.

Although there have been discrepancies in the published classification of moles in Japan, it seems clear that three species are involved. The most significant problem remaining is the current use of specific names including those of Abe (1967); a problem originally caused by the restriction of the type locality of *M. wogura* to Yokohama by Kuroda (1940).

The main purpose of this paper is to correct the confusion over the current names of the Japanese moles and also to compare them taxonomically with other Asian moles of the genus *Mogera*.

**Materials and Methods**

A total of 612 mole specimens were examined, 585 collected by the author: 313 *M. wogura* collected from Honshu, Shikoku, Kyushu, Okinoshima, Tsushima, Tanegashima and Yakushima, Japan; 25 "*M. w. coreana*" from Korea; 206 *M. minor* from Honshu, Shikoku and Awashima, Japan; 41 *M. tokudae* from Honshu and Sado, Japan. One specimen of "*M. robusta*" was collected from the Far East maritime region of Russia by M. B. Okhotina; two specimens of *M. insularis* were collected from Taiwan by S. Shiraishi; and 49 specimens of *Mogera* spp., including the type specimens of *M. wogura*, *M. w. kobeae*, *M. w. kanai*, *M. w. coreana*, *M. hainana* and *Talpa (Mogera) latouchei*, were examined in the Rijksmuseum van Natuurlijke Historie (RNH) in Leiden, the British Museum (Natural History) (BM) in London, and the American Museum of Natural History (AMNH) in New York (see Appendix 1).

External measurements were made in the field or recorded from specimen labels. Fifteen skull dimensions, as defined by Abe (1967), were measured to the nearest 0.01 mm using dial calipers. Specimens with skulls were assessed as belonging to one of four age classes (I-IV) on the basis of tooth wear, following the methods of Hoslett and Imaizumi (1966) and Abe (1967).

During previous work on variation and taxonomy (Abe 1967), I found that:

1. Japanese moles were geographically so variable in size that size itself was not a useful taxonomic character, because of the wide overlap of size between species.
2. The shape of the upper incisor row (UIR) was the most useful and almost the only diagnostic character necessary in order to separate the two sibling species *M. wogura* and *M. kobeae*, defined at that time. The UIR is projected forward and arranged in a V or U shape in *M. wogura*, and is round and arc–like in *M. kobeae*. For the comparison of this character two values were taken: firstly the difference between the length of the upper tooth row (I1–M3) and the length from the canine to the last molar (C–M3), and secondly the proportion (%) of the difference between I1–M3 and C–M3 to the rostral breadth (RB), which indicated the degree of projection of the UIR. 
3. The proportion (%) of RB to the interorbital breadth (IB), the palatal length (PL) and the breadth across the molars (BAM) were also effective diagnostic characters for certain mole species.
4. The difference between I1–M3 and C–M3, the degree of
projection of the UIR and the proportion of RB to IB varied remarkably, but with a particular tendency, with advancing age.

From these conclusions, only seven of the measurements concerned above were employed as meristic skull characters and only five combinations were actually used for the taxonomic comparison in the present study. These seven were:

1) Greatest length of skull (GLS): The overall length from the anterior tip of the premaxilla to the posterior bulge of the braincase.
2) I\textsuperscript{1}-M\textsuperscript{3}: The distance between the outer margins of the first incisor and the last molar on the left side of the upper jaw.
3) C-M\textsuperscript{3}: The distance between the anterior margin of the canine and the posterior margin of the last molar on the left side of the upper jaw.
4) RB: The breadth of the rostrum across the canines.
5) IB: The greatest breadth of the outer protrusions of the inner orbital margins.
6) PL: Length, in the mid-ventral line of the skull, from the anterior most point of the posterior border of the palate to the posterior most margin of the alveoli of the first upper incisor.
7) BAM: The greatest distance between the outer surfaces of the molars.

As stated above, some skull characters vary greatly with age. In the present work, therefore, I have used, unless otherwise noted, only samples of age class I, consisting of young individuals less than one year old, in the graphical and statistical analyses of skull characters.

For the statistical analyses, relative variables were subjected to arcsin-root transformation as a precaution against the trends of non-normal distribution.

The colors of specimens were described according to Ridgway (1912).

Results

Two values of UTR, the difference between I\textsuperscript{1}-M\textsuperscript{3} and C-M\textsuperscript{3} (Fig. 1) and the degree of projection of the incisor row (Fig. 2) proved particularly important in identifying specimens. When the measurements of three type specimens of *M. wogura* (small solid circles) were added, they coincided with a group of other individuals (Fig. 1 and 2). This group was confirmed as *M. wogura*, which occurs throughout the southern half of Japan (Fig. 3).

The measurements of the type specimens of *M. w. kobeae, M. w. kanai, M. w. coreana* and various other specimens of *M. w. coreana* from Korea also fall clearly within the range of measurements of *M. wogura*.

I was unable to examine the type specimen of *M. robusta*, but measurements of other specimens of this mole from the Russian Far East suggest that it is just a large local form of *M. wogura* (Figs. 1 and 2). The Russian specimens were very similar to the largest forms of *M. wogura* from Japan with a GLS of longer than 41 mm, with the exception of the relatively short, narrow palate (Figs. 4 and 5).
Greatest length of skull (mm)

Fig. 1. The relationship of the difference between $1'-M^3$ and $C-M^3$ and the greatest length of the skull of four species of moles. • = type series of *M. wogura*; ○ = type of *M. w. kanai*, age class II; ● = type of *M. w. coreana*; ■ = type of *M. w. kobeae*; ○ = *M. wogura*; □ = *M. w. coreana*; ■ = "M. robusta"; △ = *M. tokudae*; + = *M. minor*; ▲ = *M. insularis*; "H" = type of "*M. hainana"; "L" = "*M. latouchei" (bold letters = type specimens).

Greatest length of skull (mm)

Fig. 2. The relationship between the arcsine transformed degree of projection of the incisor row and the greatest length of the skull (see Fig. 1 for legend).
Fig. 3. The distribution map of the four species of the Asian moles. The western limit of the distribution of *Mogera insularis* is not included in this map.

Fig. 4. The relationship between the palatal length and the greatest length of the skull (see Fig. 1 for legend).
Greatest length of skull (mm)

Fig. 5. The relationship between the breadth across molars and the greatest length of the skull (see Fig. 1 for legend).

Table 1. ANCOVA test for each of five skull characters of four mole species and for age variation in the degree of projection of the incisor row in *M. wogura*. W = *M. wogura*, T = *M. tokudae*, M = *M. minor*, I = *M. insularis*. Right upper cells for each character indicate significance levels (*p < 0.05*) of the difference of the regression coefficients. Left lower cells show those of the *Y*-intercepts when the equality between regression coefficients was accepted. Data have been revised by the sequential Bonferroni method (Rice 1989).

<table>
<thead>
<tr>
<th>Difference between (I1-M3) and (C-M3): GLS</th>
<th>Degree of projection of incisor row: GLS</th>
<th>Proportion of breadth of rostrum to interorbital breadth: GLS</th>
</tr>
</thead>
<tbody>
<tr>
<td>W T M I</td>
<td>W T M I</td>
<td>W T M I</td>
</tr>
<tr>
<td>W * * ns</td>
<td>* * *</td>
<td>* * *</td>
</tr>
<tr>
<td>T * ns</td>
<td>* *</td>
<td>* *</td>
</tr>
<tr>
<td>M *</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>I *</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Palatal length:</th>
<th>Breadth across molars: GLS</th>
<th>Age variation of degree of project. of UIR in <em>M. wog.</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>W T M I</td>
<td>W T M I</td>
<td>Age I II III</td>
</tr>
<tr>
<td>W * * *</td>
<td>ns ns ns</td>
<td>ns</td>
</tr>
<tr>
<td>T ns ns</td>
<td>* * ns</td>
<td>II * ns</td>
</tr>
<tr>
<td>M * *</td>
<td>*</td>
<td>III * *</td>
</tr>
<tr>
<td>I ns</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>
Ta~ononzic
Revisiolz
of
Asian
Moles

5

Moles from the northern half of Honshu, Japan, and with scattered small relict populations in southern regions of Honshu and in Shikoku have a relatively large degree of projection of the UIR. The grouping of their measurements (as shown in Figs. 1 and 2 by cross marks) indicates that they belong to a distinct species (Table 1). The specific name that should be assigned to this group of small moles is *M. minor*, first used in the form *M. w. minor* by Kuroda (1940) for specimens from Shiobara, northern Kanto, Honshu. The type specimen could not be examined unfortunately, because it was destroyed by fire in 1945 (Imaizumi 1962). The type locality, however, is within the central part of the main range of this species as defined here. Specimens from Yokohama, originally assigned to typical *M. wogura* by Thomas (1905) must in fact be *M. minor* as Yokohama is located well within the range of *M. minor* and because no other specimens fitting the definition of *M. wogura* have been reported from the area. In his work Thomas (1905) relied entirely on skull size to assess his specimens and did not take into account the important diagnostic characters of the UIR.

The ranges of *M. wogura* and *M. minor* are contiguous, and sharply segregated in central Honshu (Fig. 3).

Moles from the Echigo Plain, Honshu, and from Sado Island in the Sea of Japan are large bodied and have a number of distinctive characters, particularly in the UIR, the proportion of RB to IB, PL, and BAM which distinguish them as a full species *M. tokudae* (Figs. 1, 2, 4, 5, and 6). Despite its recent assignment to *M. robusta* (Corbet and Hill 1986) and partly to *M. etigo* (Yoshiyuki and Imaizumi 1991) this is clearly the species for which Kuroda (1940) collected the type specimen and which he initially described as *M. w. tokudae*. This species appears to be a primitive member of the genus *Mogera*, because in its UIR, in its vertebral formula and in the structure of its ear bones it resembles the primitive, probably ancestral mole, *Euroscaptor mizura* (Abe 1967, Yoshiyuki 1986).

Moles from Taiwan, southeast China and Hainan, though previously regarded by some authors as full species, all have relatively large degrees of projection of UIR and large proportions of RB to IB, and appear to form a single group, although their overall sizes do differ from each other (Figs. 1, 2, and 6). On the basis of their similarities moles from all three of these areas, therefore, were assigned to *M. insularis*.

Of the five main diagnostic skull characters subjected to ANCOVA testing, four characters showed that each of the four species differed significantly from the others either in regression coefficient or in Y–intercept (Table 1). Neither the regression coefficients nor the Y–intercepts of palatal length of *M. tokudae* and *M. insularis* were significantly different, indicating a very close relationship in this character.

On the basis of this analysis, therefore, four species of moles in the genus *Mogera* in Asia should be recognized. Brief descriptions of their histories and characteristics are as follows.
Fig. 6. The relationship between the arcsine transformed proportion of the breadth of the rostrum to interorbital breadth and the greatest length of the skull (see Fig. 1 for legend).

**Mogera wogura** (Temminck)


**Type:** *Talpa wogura* Temminck, from Japan (probably from Nagasaki Prefecture or somewhere else where relatively small-bodied moles are found in west or south Kyushu).

**Description of the species:** Body size is very variable geographically, from medium to large. Individuals from wide alluvial plains with deep soils are usually larger than those from mountainous regions or from narrow valleys. The smallest are from the southernmost, Tanegashima, population (head and body length 138.4 ± 4.9 (SD) mm, n = 18; GLS 34.44 ± 0.54 mm, n = 18) while the largest are from the northernmost, Tatsuno−Shiojiri (Nagano), population (HBL 178.2 ± 3.7 mm, n = 13; GLS 41.49 ± 0.40 mm, n = 13).

The summer pelage is bistre or mars brown above; slightly paler than back or near Prout's brown below; the throat and upper chest are ochraceous tawny or orange in adults. In winter the pelage is much darker than in summer.

The skull is usually distinguishable from those of the other species by the following characters: broader rostrum, narrow and nearly cylindrical interorbital portion, angular and shorter braincase, obtuse and rounded postero-inferior angle of the infraorbital foramen, and rounded arc-like UIR. The degree of projection of the UIR is significantly smaller than in any other species, even in relatively young animals or in small local forms (Fig. 2). The difference between 1−M and C−M is relatively small (Fig. 1). The three upper incisors are approximately equal in height.

In ear bones, the apophysis orbicularis of the malleus is usually present; the lamina forms a thin externally convex plate; the cavum lamina is broad and long triangular; the capitulum mallei is not a globular formation but only a well developed thickening of the articular surface. The processus longus of
the incus is relatively very short.

The other skull characters resemble those of *M. minor*.

The vertebral formula, the number of cervical, thoracic, lumbar, sacral and caudal vertebrae is: 7+14+5+6+12.

According to Tsuchiya (1988), the karyotype of this mole shows no variation in Japan, but individuals from South Korea differ somewhat from those from Japan; 2n=36; Japanese specimens have autosomes of four pairs of metacentrics, three pairs of submetacentrics, two pairs of subtelocecntrics and eight pairs of acrocentrics; the Korean specimens have five pairs of submetacentrics, three pairs of subtelocecntrics and five pairs of acrocentrics. The X and Y sex chromosomes consist of a submetacentric element and a microchromosome, respectively.

**Distribution**: South Japan: Kyushu and many small islands such as Tanegashima, Yakushima, Tsushima, and Goto islands; Shikoku except for the high mountain areas of Mt. Tsurugi, Mt. Ishizuchi and Mt. Ohtaki; part of Shodoshima, Kagawa Prefecture; the southern half of Honshu north to a line connecting Shizuoka, Nagano, Gifu and Ishikawa Prefectures, except for the mountainous regions of Kyoto, Hiroshima and the southern parts of the Kii Peninsula; and Okinoshima. Beyond Japan, *M. wogura* also occurs on the Korean Peninsula, in northeastern China and in the southern maritime region of Siberia (Fig. 3).

In Nagano Prefecture, Japan, one of the northernmost limits of the range of *M. wogura* is reached in the narrow Agematsu valley where its range is contiguous with that of *M. minor*. Between 1959 and 1979, *M. wogura* has displaced *M. minor* by about 3.6 km (Abe 1985). Another limit is found at Ueda (Ono), Shiojiri, Nagano Prefecture. There, the border between the two species had not changed at all between 1959 and 1979, but by 1983 *M. wogura* had advanced about 0.4 km into the range of *M. minor* (Abe 1985).

*Mogera minor* Kuroda


**Type**: *Mogera wogura minor* Kuroda, from Shiobara, Tochigi Prefecture, Honshu, Japan.

*Description of the species*: Body size is very variable geographically, from small to medium. It is usually larger in wide alluvial plains than in mountainous regions or narrow valleys. The largest population (HBL 152.3±3.9 (SD) mm, n=20; GLS 36.81±0.85 mm, n=20) occurs on the Sendai Plain (e.g. the Semine population), Miyagi Prefecture, Honshu, and the smallest (HBL 123.7 mm, n=4; GLS 31.69 mm, n=4) occurs on Mt. Tsurugi in Shikoku.

The pelage is variable in color, but usually darker in the small forms from mountainous regions, and lighter brown in the large forms from plains. The summer pelage of the large local form varies between mars brown and clove brown above, and is nearly cinnamon brown below. The back of the small local forms is nearly clove brown, and the belly is slightly paler. In winter the pelage is usually darker than in summer.

The skull has a relatively narrow rostrum and a wide interorbital region; the braincase is smooth, less angular than in *M. wogura*. The postero-inferior angle of the infraorbital foramen is usually acute. The UIR usually projects well forward and is markedly V- or U-shaped in small local forms, though only broadly V-shaped in the large local forms. The degree of projection is clearly larger, therefore, than that of *M. wogura*, but resembles that of the much larger *M. tokudae*. The difference between I1-M3 and C-M3 is relatively long (Fig. 1). The three upper incisors gradually diminish in height from the first to the third in small forms, whereas they are approximately equal in height in large forms.

The characters of the ear bones resemble those of *M. wogura*, and the vertebral formula (7+14+5+6+12) is the same as that of *M. wogura*.

According to Tsuchiya (1988), the karyotype is 2n=36; the autosomes consist of four pairs of metacentrics, three pairs of submetacentrics, three pairs of subtelocentrics and seven pairs of acrocentrics. In a variant form from the Kii Peninsula there are four pairs of submetacentrics and six pairs of acrocentrics. A submetacentric and a microchromosome form the X and Y sex elements.

*Distribution*: Shikoku: Mt. Ishizuchi, Ehime Prefecture; Mts. Tsurugi and Ohtaki, Tokushima Prefecture; Shodoshima, Kagawa Prefecture. Honshu: Hiwa T., Hiroshima Prefecture; Sakyo-ku, Kyoto; Kozagawa T. and Nachikatsuura T., Wakayama Prefecture; and northern Honshu north of a line connecting Kanagawa (Hakone), Yamanashi, Nagano and Ishikawa Prefectures, except for the lower basins (the Echigo Plain) of the Shinano and Agano rivers, and the island of Awashima, off the plain, Niigata Prefecture (Fig. 3).

In Nagano Prefecture, the southernmost limits of the range of the northern main population of *M. minor* occur at Agematsu and Shiojiri. The ranges of *M. minor* and *M. wogura* are contiguous here, though *M. minor* is slowly retreating northwards and being displaced by larger *M. wogura*. 

---

*Taxonomic Revision of Asian Moles*  
World (Wilson and Reeder, eds.) 1993, 126.
Mogera tokudae Kuroda


**Type:** *Mogera wogura tokudae* Kuroda, from Sado Is., Japan.

**Description of the species:** The body is very large but quite similar in external characteristics to *M. wogzwa* except for the relatively longer tail. The head and body length (170.6 ± 4.9 (SD) mm, n=24) and the greatest length of skull (41.13 ± 1.02 mm, n=24) of the Echigo Plain population are much larger than those of the largest populations of *M. minor* and comparable to those of the largest populations of *M. wogura*.

The summer pelage is mars brown, nearly clove brown, or darker above, and nearly cinnamon brown below.

The skull essentially resembles that of *M. minor* but is much larger. The braincase is wide and short. The UIR is clearly V-shaped and projected forward. The degree of projection is as large as that of *M. minor* (Fig. 2). The difference between I1-M3 and C-M3 is very large (Fig. 1). The palatal part is very long and wide (Figs. 4 and 5). The rostrum is relatively narrow; the interorbital portion is broad (Fig. 6). The upper incisors gradually diminish in size from the first to the third in frontal view.

The ear bones typically differ from those of *M. wogura* and *M. minor* in the larger angle formed between the nanubrium and the collum mallei, and in the ill-defined smooth apophysis orbicularis as is found in *Euroscaptor micrura* (Stroganov 1948) and *E. mizura*.

The vertebral formula (7+13+6+6+13) is different from that of *M. wogura* and *M. minor*, but rather similar to that of the primitive mole, *E. mizura*.

According to Tsuchiya (1988), *M. tokudae* has a particular karyotype 2n=36; the autosomes consist of five pairs of metacentrics, three pairs of submetacentrics, five pairs of subtelocentrics and four pairs of acrocentrics. A submetacentric chromosome and a microchromosome form the X and Y sex elements.

**Distribution:** Sado Island and the Echigo Plain, Niigata Prefecture, Honshu, Japan. The range of this species is contiguous with that of the much smaller *M. minor* in the Echigo Plain where *M. tokudae* appears to be ecologically
inferior to *M. minor* as shown by the gradual retreat of its range with the invasion of the latter (Imaizumi and Imaizumi 1970, Abe unpubl. data).

**Remarks**: Yoshiyuki and Imaizumi (1991) recognized the mainland (Honshu) population of *M. tokudae* as a new species, *M. etigo*, differing from that on Sado Island. As there are no significant differences between the two populations, however, except in overall body size which is larger in the mainland form and in slight other morphological difference occurred with the size variation, and as such variation is common among various mole species, the mainland form is recognized as a local variant.

*Mogera insularis* (Swinhoe)


**Type**: *Talpa insularis* Swinhoe, from the island of Taiwan.

**Description of the species**: The body is the smallest in the genus *Mogera*. Taiwanese moles (*insularis*) are largest (HBL 120.5 ± 10.5 (SD) mm, n = 5; GLS 32.81 ± 0.85 mm, n = 10). The tail is usually shorter than the hind foot in individuals from the islands of Taiwan and Hainan, but longer than the hind foot in those from southeast China.

The pelage is variable in color from dark brown to slate color above, and is tawny brown or dark gray below.

The skull resembles that of the small local form of *M. minor*, but the rostrum is much broader absolutely and also relatively to the interorbital portion than that of *M. minor* (Fig. 6). The UIR is V-shaped and projected forward, and the degree of projection is larger than in most *M. minor*, although it overlaps that of the small form of *M. minor* (Fig. 2). The difference between I1-M3 and C-M3 is noticeably larger, relative to the size of the skull, than that of *M. minor* (Fig. 1). The upper incisors diminish in size from the first to the third. The first upper premolar is relatively small, and is single rooted in Taiwanese and south-east Chinese moles, whereas in Hainanese moles it is slightly larger and double-rooted.

The ear bones of *M. insularis* resemble those of both *M. minor* and *M.
wogura, with a well-defined apophysis orbicularis.

The vertebral formula varies \((7 + 13 + 6 + 6 + 11)\) or \((7 + 14 + 5 + 6 + 11, n = 2)\) and resembles that of *M. minor* and *M. wogura* (the first specimen) and also that of *M. tokudae* (the second specimen).

**Distribution**: Taiwan R. O. C., the island of Hainan and the provinces of Fujian, Guangdong, Guangxi, and Sichuan in south-east China P. R. O. C (Fig. 3).

**Discussion**

Temminck (1842), in his original description of *Talpa wogura*, gave no detailed type locality, other than "Japan". When Thomas (1905) later described *Mogera wogura kobeae*, he wrote, of the specimens from Yokohama (skulls, range: 34–35 mm), "an example sent in 1843 from the Leiden Museum as representing that form (M. wogura) agrees in size with the Yokohama race, and I have therefore taken that as the typical one. The original figure of the skull is 35 mm in length". It seems clear from his comment that the Yokohama race was of the typical *M. w. wogura*. Kuroda (1940), however, read it as "Thomas restricted the type locality to Yokohama" because he assigned Yokohama as the type locality of *M. wogura* citing Thomas (1905). Some later taxonomists including Imaizumi (1949, 1960, 1970), Abe (1967) and Hutterer (1993) followed this procedure, which caused confusion in the taxonomy of Japanese moles. As a consequence, small moles from northern Honshu were assigned to *M. wogura* (Kuroda 1940, Imaizumi 1949, 1960, 1970, Abe 1967), although they are now correctly assigned to *M. minor* in the present work.

As Thomas (1905) did, many past authors have relied on size as an important character in identifying moles. As Abe (1967) showed, however, size is neither effective nor useful as a single character in assessing the specific identity of moles. *M. tokudae*, for example, is a very large species, comparable in size to the largest form of *M. wogura*; consequently it has often been included as a subspecies of the latter, i.e. as *M. kobeae tokudae* (Imaizumi 1960) or even as *M. robusta* (Rossolimo et al. 1982). *M. tokudae* is, however, a distinct species endemic to Japan, as shown by its morphological, karyological, biochemical, and ecological characteristics.

Some skull features vary greatly with advancing age (Abe 1967). The degree of projection of the UIR, an important diagnostic character, is highly variable according to age and, for instance, the \(Y\)-intercepts of the regression between that projection and GLS in *M. wogura* differ significantly in all the three combinations of age classes (Table 1). The value of the degree of projection of the UIR apparently decreases with age in all species. Older specimens of the larger forms of *M. minor* (e.g. of Semine, Miyagi Prefecture), thus approach in this character younger specimens from small forms of *M. wogura* (e.g. of southern Kyushu) (Abe 1967). Such specimens are sometimes difficult to distinguish, however, specific identification is usually possible when specimens of the same age classes are compared. Furthermore, some large individuals of *M. minor* have, even in age class I, relatively small UIR values,
similar to those of small, but comparable to the size of the former, individuals of *M. wogura* (Figs. 1. and 2). In these cases, it is difficult to distinguish them based only on numerical values, however, the shape of the UIR is usually distinctive, V- or U-shaped in *M. minor* and round and arc-like in *M. wogura*. The two also differ in their geographic distribution. The similar sized forms of the two species are never found contiguously within a close geographic area. Where the ranges of the two species abut, their body sizes and morphologies differ so greatly that it is easy to distinguish them.

As stated earlier, the three species in Japan have clear-cut boundaries to their ranges, and severe ecological interactions between species pairs have been found where *M. wogura* and *M. minor*, and where *M. minor* and *M. tokudae* meet (Abe 1985). These facts support the morphological taxonomy presented here.

The characteristics of the UIR of *M. minor* approach, in some of the smaller forms, those of *M. insularis* especially of Taiwan (Figs. 1 and 2). Other characters, such as palatal length and the breadth across molars are also similar, in their pattern of variation, in these two species. Thus the northern species in Japan (*M. minor*) appears to be closer phylogenetically, to the more distant southern species (*M. insularis*), rather than to the contiguously distributed *M. wogura*. The latter species is a newcomer from the Asian continent and the most advanced species among the Japanese moles (Abe 1967, 1985). This type of distribution is also found among subspecies of *Mus musculus* in Japan; the mice from northern Honshu and Hokkaido are phylogenetically more closely related to those of southeast Asia in retaining mitochondrial DNA of the *castaneus* type, rather than to the contiguously distributed mice of the *molossinus (musculus)* type occurring in southern Japan (Moriwaki 1988, Yonekawa *et al.* 1988). These facts suggest that some older species remain in northern Japan as relics. This situation has probably arisen as a result of the invasion of southern Japan, via the past landbridge between Kyushu and the Korean Peninsula, by a dominant congener.

Morphological variation in the three major local forms of *M. insularis* do indicate intraspecific differences, but further analyses from a wide range of specimens are required to clarify this situation.

**Acknowledgments**

I wish to express my cordial thanks to: Drs. J. E. Hill, J. M. Ingles, and P. D. Jenkins of the British Museum (Natural History), London; to Dr. C. Smeenk of Rijksmuseum van Natuurlijke Historie, Leiden; and to Drs. S. Anderson and G. Musser of the American Museum of Natural History, New York for their kindness in permitting me to examine the specimens under their care when I visited those museums in 1987. Thanks are also due to Prof. S. Shiraiishi for the loan of valuable specimens from Taiwan, to Mr. Sang Hoon Han for his kind assistance in the field in Korea, and to Mr. M. Takagi and Dr. S. Kudo for their assistance with the statistical analyses. This study was partly supported...
by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan (no. 05454029).

References

Specimens examined
Locality, giving the third mesh (ca. 1 X 1 km²) code number (LC no.) of the Environment Agency, Japan, for Japanese specimens collected by the author, and the month and year when collected, museum, and the registration number of all specimens examined are listed below (for Japanese specimens at Hokkaido University Abe's collection is numbered: HU, A no.). For Japanese locations V. = village, T. = town, C. = city, and Pref. = prefecture.

M. wogura

M. minor

M. tokudae

M. insularis
Formosa, year?, BM, 62~12~24~19a,b (insularis co-type, no skull); Yan-ming Shan, Taiwan, alt. 650 ft., year?, AMNH, 183146~7; 6 mi N Taipei, Taipei Sien, Taiwan, year?, AMNH, 183178; Taiwan, year?, AMNH, 184537~9; Shou Feng, Hualien Hsien, Taipei, Taiwan, March 1960, AMNH, 184983~4; Taipei, Taiwan, 1980?, coll. by S. Shirashiga; Tanshui, Taiwan, August 1980, coll. by S. Shirashiga; Mt. Wuchi, Hainan, November 1906, BM, 10~4~25~4 (hainana type); Hainan, year?, AMNH, 59914; Kuatan, Fokin, China, year?, BM, 98~8~17~1 (latouchei type); Kuatien, NW Fukien, China, April 1898, BM, 8~7~25~12; Chungau Hsien, Fukien, China, May and July 1926, AMNH, 84805, 84808, 84810~11.