Geographic Variation of Chromosomes and External Morphology in the montanum-subgroup of the Leiobunum curvipalpe-group (Arachnida, Opiliones, Phalangiidae) with Special Reference to Its Presumable Process of Raciation

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ABSTRACT—The montanum-subgroup of the Leiobunum curvipalpe-group (Opiliones, Phalangiidae, Leiobuninae) is revised based on analyses of external morphology, genitalia, and karyotypes. The constituents of this subgroup are regarded as a single polytypic species, L. montanum Suzuki, comprised of six geographic races. Leiobunum virgeum Suzuki is considered as a synonym of L. montanum. Five of the races were chromosomally surveyed. It was found that karyotypes of these races exhibit a wide range of variation in chromosome number from 2n = 18 to 26. Component chromosomes in these karyotypes were invariably meta- or submetacentric in structure. Therefore, this numerical variation cannot be ascribed to Robertsonian rearrangement alone. Presumable process of raciation in this species is presented. My interpretation of the spatial patterns of geographic variation in this species is in accordance with the stasipatric model of speciation.

INTRODUCTION
This paper is the second in a series dealing with the taxonomy of harvestmen belonging to the Leiobunum curvipalpe-group. The curvipalpe-group and its subgroups are defined in the first paper of this series [1]. The montanum-subgroup is comprised by only one species, L. montanum Suzuki. It is found in several limited mountainous areas of western Japan, extending from Mt. Sobo in Kyushu to Mt. Shirouma in the Northern Japanese Alps [1, 2]. This subgroup abounds in geographic variations in external morphology, male genitalia, and karyotypes [2, 3] and has been divided into four taxa [2]. In this paper this subgroup is redescribed as one species comprising six geographic races, together with various new information, especially concerning karyotypes.

The most interesting feature of this polytypic species, from the standpoint of evolutionary biology, is its geographic pattern of karyotypic variation; which follows the stasipatric model of speciation advocated by White [4]. The raciation process within this subgroup will be inferred from this geographic pattern of variation.

MATERIALS AND METHODS
A total of 538 specimens collected from 13 localities were used in the comparison of external morphology. They are listed under “Specimens examined” together with their depositories (unless otherwise noted specimens are in my personal collection). Acronyms for other depositories are listed below under “Species Description”. Chromosome observations were made from 41 specimens covering five races by squash method using acetocarmine (1981 preparations) and the air-drying method (1982 preparations). The air-drying technique used is described in detail by Tsurusaki [1].
**SPECIES DESCRIPTION**

The format of the descriptions follows Tsurusaki [1]. All the measurements are in millimeters. Abbreviation used: ZLHU = Zoological Laboratory, Faculty of Science, Hiroshima University, SC = Dr. Seisho Suzuki’s personal collection, NT = N. Tsurusaki, BL = body length, CL = cephalothorax length, FIL = femur one length, PL = palp length, Fe = femur, Pa = patella, Ti = tibia, Ta = tarsus.

**montanum-subgroup (1 species, 6 races)**

**Leiobunum montanum** Suzuki (Figs. 1-10)

*Leiobunum montanum* Suzuki, 1953 [5], p. 188, figs. 6-7 (type: Mt. Ishizuchi, Shikoku, Japan; in ZLHU, not examined).

**Leiobunum montanum**: Suzuki and Kunita, 1972 [6], p. 89; Suzuki, 1976 [3], p. 134, figs. 3-7.


**Leiobunum montanum sobosanum** Suzuki, 1976 [2], p. 212, figs. 36-37, 104, 172, 181-183, 313-314 (type: Mt. Sobo-san, Miyabaru route, at 800-1000 m alt., Oita Pref., Kyushu; in ZLHU, not examined).


**Diagnosis**

Separable from all other species of *curvipalpe* group by its aciculate penis (Figs. 5-7; see also [1]).

**Description**

**Male:** Body medium-sized. Genital operculum as in Figure 1B, posterior margin relatively distinct and straight. Labrum (Fig. 2) considerably extended and swollen, widest at middle in ventral view, laterally with several teeth. Chelicera (Fig. 1D) with several teeth on distomesal surface of distal segment. Palp (Fig. 1E-F) normal in size for *curvipalpe* group; femur prominently curved below; patella widened distally with a small distomesal lobe; tibia (Fig. 3) with a cluster of several dark-colored teeth on ventromesal surface of distal half, or on whole mesal side (Mt. Daisen race); tarsus always with two distinct rows of dark-colored teeth ventrally (Fig. 4A).
Penis (Figs. 5-7) very slender and aciculate, with widened basal portion; shaft distally with well-developed alates; alate part consisting of two abreast pairs of thin membraneous processes, i.e. ventral alates and lateral alates (Fig. 5); glans, dorsoventrally movable, distally with two pairs of short setae; stylus also dorsoventrally movable (Figs. 5 and 7H).

Female: Labrum small, tapered distally, without armaments (Fig. 1C). Palp (Fig. 4B) typical of the curvipalpe-group, with well-developed lobes on both distomesal margins of patella and tibia, covering entire mesal surfaces of these two segments and especially dense on and around the lobes. Each hair with a socket on the base and with numerous villous processes on approximately distal half of its body (Fig. 4C). Seminal receptacle as in Figure 1G-J, not significantly variable geographically.

Karyotypes

Chromosome observation was carried out during the summers in 1981 and 1982 for specimens taken from five localities representing different geographical range. Materials examined and the results are summarized in Table 1 and karyotypes are shown in Figure 8.

Number of chromosomes fluctuated among populations between 2n=18 and 26. In spite of this wide range of variation in number, chromosomes were invariably meta- or submetacentric. The X chromosome was always largest, but morphologically variable among localities; i.e. the X was a metacentric in specimens from Mt. Ontake and Mt. Daisen (Fig. 8B-C), whereas it was a submetacentric in the other three populations. This suggests the occurrence of pericentric inversion in X chromosome in some populations. On the other hand, the Y chromosome was invariably the smallest and submetacentric.

Geographic Variation and Races

1. Geographic variation in some metrical characters

Means, ranges and standard deviations for total body length (BL) and length of first femur (FIL) in various populations of this species are presented in Figure 9. Since female specimens were scarce, only males were used for these measurements. Although mean of BL varied considerably among populations, no evidence of a geographic or altitudinalcline was indicated. On the other hand, occurrence of an altitudinal cline was suggested in FIL, although no prominent latitudinal cline was found. Namely, within the areas occupied by each race, FIL became shorter with increasing altitudes (e.g. compare 2,000–2,200 m and 2,200–2,400 m populations in Mt. Tsukabukuro). Similar geographic variation, that is a cline in leg length but not in body length, was reported in Leiobunum bracchiolum McGhee and Leiobunum politum Weed by McGhee [7] and in Leiobunum cretatum Crosby and Bishop by Cokendolpher and Rapp [6].

2. Races

Suzuki [2] recognized four taxa in the montanum-subgroup on the basis of genital morphology, and divided these taxa into two species by the difference of chromosome number between Mt. Hōkidaisen (=Mt. Daisen) (2n=18) and Mt. Ishizuchi (2n=24) populations (cf. [3]). In this study, six geographic forms are distinguished that are clearly assignable to the montanum-subgroup, based on external (including genital) characters. In addition, karyotypes of these taxa, except one (Mt. Tsurugi race) whose chromosomes have not yet been studied, are unique and separable from each other. These taxa can be regarded as distinct species if we rely on karyotypic difference as the criterion of "species" as in Suzuki [2, 3]. However, in the present paper, I treat these six taxa provisionally as "races" of a single species for reasons mentioned in the preceding paper [1] and because the degree of divergence in external morphology among these six taxa is small compared with those among the other species of the curvi-

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Table 1. Chromosome numbers in five populations of Leiobunum montanum

<table>
<thead>
<tr>
<th>Locality</th>
<th>Date</th>
<th>Number of individuals observed</th>
<th>Chromosome number (2n)</th>
<th>FN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mt. Tsukaburo</td>
<td>20–VIII–1981</td>
<td>6*</td>
<td>26*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>18–VIII–1982</td>
<td>7j (3*/4+1*)</td>
<td>26</td>
<td>52</td>
</tr>
<tr>
<td>Mt. Ontake</td>
<td>30–VII–1981</td>
<td>6j (7*)</td>
<td>24*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16–VIII–1982</td>
<td>1/8j (5*/4+1*)</td>
<td>24 24</td>
<td>48</td>
</tr>
<tr>
<td>Mt. Daisen</td>
<td>9–VIII–1982</td>
<td>3*</td>
<td>18</td>
<td>36</td>
</tr>
<tr>
<td>Mt. Ishizuchi</td>
<td>5–VIII–1982</td>
<td>7*</td>
<td>24 24</td>
<td></td>
</tr>
<tr>
<td>Mt. Sobo</td>
<td>2–VIII–1982</td>
<td>3*</td>
<td>26</td>
<td>52</td>
</tr>
</tbody>
</table>

Asterisked: Results obtained by squash method.

Table 2. Synopsis of the systems adopted by Suzuki (1976 [2]) and present paper

<table>
<thead>
<tr>
<th>Suzuki (1976)</th>
<th>Tsurusaki</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. virgatum ontakense</td>
<td>Mt. Tsukaburo race</td>
</tr>
<tr>
<td></td>
<td>Mt. Ontake race</td>
</tr>
<tr>
<td>L. virgatum virgatum</td>
<td>Mt. Daisen race</td>
</tr>
<tr>
<td>L. montanum montanum</td>
<td>Mt. Tsurugi race</td>
</tr>
<tr>
<td></td>
<td>Mt. Ishizuchi race</td>
</tr>
<tr>
<td>L. montanum sobosanum</td>
<td>Mt. Sobo race</td>
</tr>
</tbody>
</table>

Corresponding forms are connected by line(s).
palpe-group. The system proposed by Suzuki [2] and that adopted in the present paper are listed in Table 2.

The holotype of *L. montanum* Suzuki belongs to the Mt. Ishizuchi race. Diagnosis of each race is separately mentioned below with notes on distribution and biology.

(1) Mt. Tsubakuro race
(Figs. 1A, 2A, 3A, 5A, 6A-B, 8A, 9, 10)


**Diagnosis:** Separable from all other races of *L. montanum* except Mt. Tsubakuro race, in the size and shape of male labrum (Fig. 2B); i.e. football-shaped in ventral view and the apex is less sharply angulated than the other races. Distin-

**Measurements:** Mt. Shirouma, 2,200 m alt. (♂): BL, 4.0; CL, 1.40; Mt. Tsubakuro, 2,200–2,400 m alt. (♂): BL, 3.7–5.1 (4.24); CL, 0.96–1.56 (1.20); FIL, 4.8–6.4 (5.71); PL: Fe, 0.97–1.25 (1.178); Pa, 0.72–0.82 (0.780); Ti, 0.83–0.95 (0.880); Ta, 1.14–1.56 (1.406).

**Karyotype:** 2n(♂)=26, FN=52 (Fig. 8A).

**Distribution:** So far known from only two localities (Mt. Shirouma, Mt. Tsubakuro) in the Northern Japanese Alps (=Hida Mountains), central Honshu (Fig. 10). In Mt. Tsubakuro occurrence of this race is confined to the coniferous forest (Marie's fir, *Abies Mariesii* Masters) of subalpine zone (ca. 2,000–2,500 m in alt.).

**Biology:** Usually found during day on the canopies of shrubs (mainly *Rhododendron* or trunks of trees. Adults emerge during mid to late August at Mt. Tsubakuro. At this locality *L. montanum* may be sympatric with *L. hiraiwai* (Kamikochi race) of the curvilapalpe-group near the lower limit of former species’ vertical distribution (ca. 1,950 m).

(2) Mt. Ontake race
(Figs. 1B and H, 2B, 3B, 6C, 8B, 9, 10)


**Diagnosis:** Distinguished from all other races of *L. montanum*, except Mt. Tsubakuro race, in the size and shape of male labrum (Fig. 2B); i.e. football-shaped in ventral view and the apex is less sharply angulated than the other races. Distin-

**Measurements:** Mt. Ontake, Tanohara, 2,190–2,250 m alt. (♂): BL, 4.9; CL, 1.66; FIL, 5.3; PL: Fe, 1.24; Pa, 0.81; Ti, 0.84; Ta, 1.47.

**Karyotype:** 2n(♂)=24, FN=48 (Fig. 8B).

**Distribution:** So far known from only Marie's fir forest in subalpine zone (2,000–2,300 m) of Mt. Ontake (=Mt. Kiso-Ontake), central Honshu (Fig. 10).

**Biology:** This race matures in late August at Mt. Ontake.
Leiobunum montanum: Suzuki and Kunita, 1972 [6], p. 89. 


Diagnosis: The general appearance of penis of this race is similar to both Mt. Daisen and Mt. Ontake races, but separable from those by having relatively shorter alate parts.

Measurements: Mt. Ishizuchi race (A, Mt. Kamegamori; D, Mt. Ishizuchi; E, Mt. Saragamine; F, Odamiyama). G, Mt. Sobo race (Mt. Sobo). H, A scheme of the terminal part of penis showing movable ranges of stylus (st) and glans (gl), not to scale.

Karyotype: 2n(♀)=18 ([3] and present study), FN=36 (Fig. 8C).

Distribution: Mountainous areas (above ca. 700 m alt.) of Tottori Pref., western Honshu (Fig. 10).

Biology: This race matures in early July in Mt. Daisen.

Remarks: Specimens from Tatsumi Pass and those from two localities on Mt. Daisen differ enormously from each other in size of various external parts (compare Figs. 2C and D-E, 3C and D-E, 6D and E-F). However, both populations are treated here as a single race because no significant difference was detected in the ratio of penis L / body L as well as the other major characters between the two (e.g., distribution pattern of denticles on palpal tibia or general structure of alate part of penis).

(5) Mt. Ishizuchi race
(Figs. 1A, D-F and J, 2H-K, 3H-K, 4, 5D, 7C-F, 8D, 9, 10)

Leiobunum montanum Suzuki, 1953 [5], p. 188 (in part), figs. 6B-C, 7A-E.

Geographic Variation of L. montanum. However, a close examination of L. m. montanum specimens from six localities in Shikoku revealed that the specimens from two localities in Tokushima Pref. (the present race) are distinct from the other four from Ehime Pref. (Mt. Ishizuchi race) in the shape and size of penis.

Leiobunum montanum: Suzuki and Kunita, 1972 [6], p. 89.


Diagnosis: The general appearance of penis of this race is similar to both Mt. Daisen and Mt. Ontake races, but separable from those by having relatively shorter alate parts.

Measurements: Mt. Ishizuchi (Tsuchiyogawa—Mt. Iwakuro), 1,490-1,745 m alt. (31 ° N, means in parentheses): BL, 3.6-4.9 (4.28); CL, 1.12-1.59 (1.356); FIL, 5.0-6.6 (5.66). PL: Fe, 1.22-1.40
Geographic Variation of *L. montanum*

Loc. No. Race

1. Mt. Tsubakuro (2n=26)
2. Mt. Ontake (2n=24)
3. Mt. Daisen (2n=21)
4. Mt. Tsurugi (2n=18)
5. Mt. Ishizuchi (2n=24)
6. Mt. Sobo (2n=26)

--Tottori Pref.-Tatsumi Pass, 780m, 12-1-1977, 8-VIII-1982, H. Komatsu and NT (SC).

Figs. 8, 9. Male karyotypes of *Leiobunum montanum*. A, Mt. Tsubakuro (2n=26); B, Mt. Ontake (2n=24); C, Mt. Daisen, Natsumaya route (2n=18); D, Mt. Ishizuchi (2n=24); E, Mt. Sobo (2n=26).

(1.300); Pa, 0.82-0.97 (0.877); Ti, 0.80-0.94 (0.856); Ta, 1.33-1.55 (1.444).

Karyotype: 2n(♂)=24, FN=48 (Fig. 8D).

Contrary to the description by Suzuki [3], in which he stated that “the complement consisted of 12 acrocentrics and 12 metacentrics”, no acrocentric chromosome was found in the present study.

Distribution: Mountainous areas (above ca. 800 m alt.) of Ehime Pref., western Shikoku (Fig. 10).

**Biology:** This race inhabits both beech (*Fagus crenata* Blume) forest and coniferous forests (Japanese red cedar, *Cryptomeria japonica* L.; Nikko fir, *Abies homolepis* Sieb. and Zucc., Veitch's silver fir, *Abies Veitchii* Lindley). Adults are usually found on the trunks of trees during day. This race matures in mid July at about 1,500 m alt. on Mt. Ishizuchi. On 5 August 1982 (12:40-16:00) in the Nikko fir forest from Tsuchigoya (1,492 m) to the peak of Mt. Iwakuro (1,745.6 m), located in the Ishizuchi area, five copulating pairs of *L. montanum* were observed (four pairs on trunks of Nikko fir, one pair on the leaves of climber, *Hydrangea petiolaris* Sieb. and Zucc.).

**Measurements:** Mt. Sobo, 1,420–1,650 m alt. (7♂♂, means in parentheses): BL (n=6), 3.4–4.3 (3.80); CL (n=6), 1.39–1.45 (1.350); FIL, 5.2–6.0 (5.47). PL: Fe, 1.16–1.28 (1.234); Pa, 0.79–0.85 (0.809); Ti, 0.82–0.90 (0.859); Ta, 1.40–1.49 (1.457).

Karyotype: 2n(♂)=26, FN=52 (Fig. 8E).

Distribution: So far known only from Mt. Sobo (above ca. 700 m alt.), Kyushu (Fig. 10).

Specimens Examined

- Mt. Tsubakuro race.—Nagano Pref.—Mt. Shirouma, 1,950–2,200 m, 3♂♂, 6♀♀, 15–21-VIII-1968, H. Sako and N. Nakamura (SC). Mt. Tsubakuro, Maries's fir forest: 2,000–2,200 m,

7♂♂♂ 3 juv. (6♂♂ Chrom. Obs.); 2,200–2,400 m, 20♀♀; 17♀♀ 11 juv., 20-VIII-1981, NT; 1,990–2,300 m, 1♀♂ 10 juv. (7 juv. Chrom. Obs.). 18-VIII-1982, NT.

- Mt. Ontake race.—Nagano Pref.—Mt. Ontake, 1970–2,200 m, 1♀♂ 18 juv. (1♂ 7 juv. Chrom. Obs.). 15/16-VIII-1982, NT.

**Specimens Examined**

- Mt. Daisen race.—Tottori Pref.—Tatsumi Pass, 780 m, 1♀♂ 8–VIII-1977, H. Komatsu. Mt. Ontake, Tanohe, Maries's fir forest: 2,200 m, NT (SC). Mt. Daisen: Ninosawa, 970 m.
Leiobunum montanum

13, 6–VIII–1977, S. Suzuki, M. Kunimoto, H. Komatsu, and NT (SC); Daisenji–Natsuyama route, 500–1,100 m, 3 n=32 (3 n Chrom. Obs.), 9–VIII–1982, NT.


Discussed

Spatial pattern of variation in L. montanum

As already stated, karyotypic variation in this species is profound. However, a more salient aspect of its karyotype evolution is the pattern of its spatial distribution. Namely, chromosome number is smallest, 2n=18, in the center of the distributional range was studied (hiraiwai-subgroup 2n=18, 20, 22; curvipalpe-subgroup 2n=20, 22, 24: Tsurusaki, in prep.). Obviously, chromosomal rearrangements which result in a change in diploid number have occurred very frequently in the evolutionary history of this group. Suzuki, who is the person that first recognized karyotypic variation in these animals, explained this diversity in chromosome number by centric fusion on the basis of his observation on concomitant increase and decrease in numbers between metacentrics and acrocentrics [3]. However, differing from his descriptions, chromosomes in various races of L. montanum were invariably meta- or submetacentric and no acrocentrics or telocentrics were observed in the present study using current air-drying method. Likewise, the chromosomes were always meta- or submetacentrics in all other species of the curvipalpe-group ([1] and Tsurusaki, in prep.). Therefore, centric fusions or simple Robertsonian translocations alone do not explain the chromosomal evolution of this group. There are two possible interpretations for this type of change in chromosome number: (1) it resulted from a number of pericentric inversions followed by fusions (including tandem fusions), or fissions followed by inversions; (2) the acrocentrics are by unknown reasons unstable in this group of animals and soon become metacentrics by acquiring heterochromatic arms, or inversely two metacentrics whose one-sided arms are heterochromatized fused into a fully euchromatic single metacentric chromosome. The latter phenomenon is reported in the lady bird beetle genus Chilocorus [9]. Of these two interpretations, the latter is indubitably more parsimonious since the former explanation postulates that several sequences of more than one kind of rearrangement progressively arise in very short time. The fact that no heterozygosity for pericentric inversion has been found in any forms of the curvipalpe-group, except for only one example in Mt. Bunagatake population of L. hiraiwai (Tsurusaki, in prep.), strongly suggests that the former explanation is unlikely. However, the detailed structure of each chromosome in the montanum-subgroup was not revealed in the present study. A C-banding analysis might provide a more definitive explanation of the karyotypic evolution of this group, and such an analysis is currently undertaken by the author.

2. Spatial pattern of distribution in L. montanum

Geographic Variation of L. montanum

Fig. 10. Distribution and chromosome numbers of six races of Leiobunum montanum. Localities: 1, Mt. Shirouma; 2, Mt. Tsubakuro; 3, Mt. Onake; 4, Tatsumii Pass; 5, Mt. Daisen; 5, Ninosawa route; 7, Mt. Takaio, 10/12–VIII–1973, NT; Tsuchigoya-Mt. Sobo route, 1,490–1,745 m, 3 n=46 (3 n Chrom. Obs.), 2–VIII–1982, NT. Mt. Sobo race—Miyazaki Pref.–Mt. Sobo, Gokasho route, 1,420–1,950 m, in Japanese larch (Larix Kaempferi Carriere) and beech forests, 7 n=72 (3 n Chrom. Obs.), 2–VIII–1982, NT.

Fig. 11. Possible origin of the present genetic and distributional relations among the races of Leiobunum montanum suggested in the text. Hatched areas denote distribution of supposed derived characters for each stage.

In the present study, remarkable geographic diversity in the chromosome number, ranging from 2n=18 to 26, was detected in L. montanum. This range of variation is as wide as was found in the entire curvipalpe-group except for these two tetraploid forms having 2n=46–52 (Tsurusaki, unpubl.). Geographic variation in chromosome number has been found in the curvipalpe-group whenever a species (or "superspecies") occupying a wide distributional range was studied (hiraiwai-subgroup 2n=18, 20, 22; curvipalpe-subgroup 2n=20, 22, 24: Tsurusaki, in prep.)
distributional range of *L. montanum* and increases toward southwest and northeast, resulting in two very distant races having identical number, 2n = 26 (Mt. Tsukubakuro and Mt. Sobo races, Fig. 10). Further, distribution of two types of X chromosomes in this species is noticeable. One type (metacentric X) occurs in populations occupying the more central part of the species distributional range, whereas other type (submetacentric X) is found in populations that occur in the southern part (Kyushu and Shikoku) and the northernmost part (Northern Japanese Alps). If karyotypes exhibited by both ends of the range of this species are truly homologous for each character state (i.e. "2n = 26" and "submetacentric X"), evolution of these geographic variations in karyotypes may be explained as follows (cf. Fig. 11). Postulates adopted are: Distributional range of the ancestral form of *L. montanum* is approximately identical with the area covered now. It was monotypic and had a karyotype similar to nowadays Mt. Sobo and Mt. Tsukubakuro races, namely 2n = 26 with the X being submetacentric.

**Stage 1** (Fig. 11): By rearrangement, a new chromosomal type with 2n = 24 occurred in the midst of the range and spread over occupied territory, displacing an existing chromosomal type with 2n = 26 by the gradual movement of narrow hybrid zones toward northeast and southwest.

**Stage 2**: Stage 1 was followed by the occurrence of pericentric inversion of the X sex chromosome at some point in Honshu. This rearrangement extended to most parts of the species range in Honshu except for northern part of Chūbu district.

**Stage 3**: Due to the recession of populations to some isolated areas of high elevation, an establishment of unique karyotype having 2n = 18 proceeded in the Chūgoku Mountains. Presumably, this karyotype was derived from a preceding karyotype with 2n = 24, through a series of rearrangement events. Thus the present-day geographic pattern (Fig. 10) of karyotype variation was completed.

The same line of thinking is applicable to geographic variation of external characters when geographic distribution of one character state interwoven between the two isolated areas occupied by another character state. In such cases, the former character state would be ancestral and the latter derived. For two of three external characters of *L. montanum*, showing prominent geographic variation, apomorphic and plesiomorphic states could be identified by such a way. These apomorphic and plesiomorphic states are listed in Table 3 together with those of two chromosomal characters already discussed. In this table, the polarity of one character (male labrum) is unresolved. Remarks on three external characters (3-5 in Table 3) are mentioned below:

1. Denticles of male palpal tibia (3 in Table 3): Populations in Tottori prefecture (Fig. 3C-E) differ from those of other subgroups of the species in having some peculiar traits. The unique geographic patterns, namely, prehistoric populations (Fig. 3A-B) and Shikoku-Kyushu populations (Fig. 3F-L) by having numerous denticles throughout ventromesal surface of tibia. If we adopt the same criterion as was used in karyotypes, a character state exhibited by Tottori populations is assumed to be apomorphic.

2. Penis (4 in Table 3): Although shapes of penes differ from race to race, they can be arranged into the following three types by their general structure: A, Tsurugi-Sobo type (Fig. 7A-B, G); characterized by the well-developed lateral alates forming a pair of pouches. B, Onake-Daisen-Ishizuchi type (Figs. 6C-F and 7C-F): relatively narrow and slender alate part sets off penes of these three races from the others. C, Tsukubakuro type (Fig. 6A-B): Characterized by widened proximal half of shaft and relatively short alate part. Of these, state A can be inferred to be plesiomorphic for state B, since areas occupied by state A is divided by one of those of B (cf. Fig. 10). On the other hand, it is unlikely that transformation series proceeded in the order of C-A-B, as state C is far more similar to B in general morphology than to A. Thus, perhaps C is apomorphic relative to A. However, any criterion for the decision in relative apomorphic vs. plesiomorphic states was not obtained.

3. Male labrum (5 in Table 3): As briefly mentioned in the description, populations of the Northern Japanese Alps and Mt. Ontake differ from all other populations in size and shape of male labrum, i.e. in ventral view, football-shaped in the former populations (Fig. 2A-B) and pear-shaped in the latter (Fig. 2C-L). However, decision of the apomorphic vs. plesiomorphic alternative of this character is reserved since the criterion using geographic pattern cannot be applied.

Distribution of these character states in six races is summarized in Figure 12.

These unique geographic patterns, namely, presumably more primitive character state has more peripheral distribution whereas presumably the most derived state is central, are highly reminiscent of the one which is expected from "stasispatic model" of speciation advocated by White [4, 10]. According to White [4, 11], the essential feature in this model is a chromosomal rearrangement, originating somewhere within the area occupied by the ancestral species, which reduces fecundity when heterozygous. If such a rearrangement manages to establish itself (either by drift in a local deme or because it shows "meiotic drive") it can spread gradually throughout a part of the area occupied by the species, because of homoyzgote superiority, and may act as an incipient isolating mechanism between the population homozygous for it and the original population. This speciation process is also characterized by the very narrow hybrid zone (tension zone: [12]) between two contiguous forms. This tension zone is supposed to act like a semipermeable membrane, filtering some advantageous traits but blocking deleterious ones [12, 13]. Some authors believe that this mode of speciation is prevailing in the animals with very low vagility, such as rodents or wingless insects (mormbine grasshoppers [4, 11], stick insects [14, 15], or those having social structure apt to lead inbreeding (some placental mammals, [16, 17]). This mode of evolution may have been prevailing also in the *curvipes*-group. My interpretation about the raciation process of *L. montanum* conforms to this model. Although races of this species are currently confined to geographically isolated areas, in many cases of the other subgroups of the

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**Table 3.** Plesiomorphic and apomorphic alternatives of some characters of *L. montanum* in which geographic variation could be detected

<table>
<thead>
<tr>
<th>Character</th>
<th>Plesiomorphic</th>
<th>Apomorphic</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Chromosome number</td>
<td>26</td>
<td>24, 18 (fully apomorphic)</td>
</tr>
<tr>
<td>2. X chromosome</td>
<td>submetacentric</td>
<td>metacentric</td>
</tr>
<tr>
<td>3. Denticles of male palpal tibia</td>
<td>confined to distal part</td>
<td>spread throughout ventromesal surface</td>
</tr>
<tr>
<td>4. Penis</td>
<td>Tsurugi-Sobo type</td>
<td>a. Onake-Daisen-Ishizuchi type, b. Tsukubakuro type</td>
</tr>
<tr>
<td>(Unresolved character)</td>
<td>a. pear-shaped</td>
<td>b. football-shaped</td>
</tr>
</tbody>
</table>

Two apomorphic states are designated for character 4. Note that the state "b" does not imply that it is apomorphic for state "a". A character, which is unresolved for the relation between the two states, is also presented.
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