Geographical Variations of Shell Morphology in the Land Snail *Ainohelix editha*: A Review of Factual Evidence

By

Haruo Katakura, Yasuhiro Kuwahara[1] **and Tôru Udagawa**[2]

Zoological Institute, Hokkaido University

(*With 5 Test-figures and 3 Tables*)

The aim of the present paper is to show the degree and extent of geographical variations in shell morphology in a series of Japanese land snails here tentatively referred to as *Ainohelix editha* (A. Adams) (Japanese name: 'Hime-maimai', cf. Habe, 1977). These snails are common in various parts of Hokkaido, the northernmost large island of Japan, dwelling in relatively mesic woodland habitats. The fact that *A. editha* includes diverse forms of land snails has been well known among Japanese malacologists (Iijima, 1892; Habe, 1977; Ito and Habe, 1983; Maeda *et al.*, 1983). Nevertheless, no intensive studies have so far been made on these land snails. In the present paper, we review factual evidence of their geographical variations gathered by ourselves since 1985. We show below only an outline of the geographical variations, leaving detailed analyses of various aspects elsewhere.

Owing to their diverse shell morphology, members of *A. editha* have been called by various names. Although entities of snails treated under some old names are still ambiguous, our *A. editha* probably includes the following snails:

1) The snails which Habe (1977) treated as the synonyms of *A. editha*. Namely, *Helix blakei* Kobelt, *Helix pallida* Iijima, *Helix shirawoi* Iijima, *Eulota luna* Pilsbry, *Eulota sericea* Gude.

2) Snails referred to by the following Japanese names: 'Hime-maimai', 'Hira-maimai', 'Miyabe-maimai', 'Jinbo-maimai', 'Bureiki-maimai'. All these names were used by Iijima (1892) for the first time, and subsequently used by

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1) Present address: Hokkaido Wakkanai Fisheries Experiment Station, Wakkanai, 097 Japan

2) Present address: Department of Zoology, Faculty of Agriculture, Hokkaido University, Sapporo, 060 Japan

various authors. The so-called 'Teshio-maimai' (Iijima, 1892) which has usually been acknowledged as a local variety of *Karaftohelix blakeana* (Newcomb) seems to be a local variety of *A. editha*, judging from the collected locality and the figure provided by Iijima (1892).

3) *Ainohelix io* Minato. Japanese name: 'Akebono-maimai' (Fig. 2, No. 10). This form was said to be discriminated from *A. editha* in its small body size, and the shell with minute scaly folds and without indented spiral lines (Minato, 1983). As shown later, however, the former two characters were variable among the members of our *A. editha*, and we could not discriminate this form from other members with these characters. Furthermore, a check of some specimens showed that conditions of spiral lines were also variable, though this character was not treated in the present study. Although *A. io* might really be a distinct species, for the time being, we treat it as a member of *A. editha*.

4) "*Ainohelix editha* A. Adams var?" in Ito and Habe (1983). Japanese name: 'Kadobari-hime-maimai' (Fig. 2, Nos. 11, 21).

Our *A. editha* also includes some so far undescribed populations that have conspicuous morphological characteristics.

The reason why we treated, though tentatively, these diverse forms of land snails as a single species will be given in "Concluding Remarks" section.

Geographical Distribution

On the basis of our collection records, a map was drawn to show the known geographical distribution range of *A. editha* (Fig. 1). In this map, more than one adjacent localities may be combined and represented by a single dot. Previous distributional records by other authors are not plotted on the map because exact localities are in most cases unknown.

A. editha has so far been recorded from the Hokkaido mainland and its four satellite islands (Rishiri and Rebun Islands off Soya, and Yagishiri and Teuri Islands off Rumoi). An apparent concentration of our collection records to Ishikari district and the eastern part of Shiribeshi district simply means that intensive surveys have been made in these regions. We have relatively good collections for the northern part of Soya district, too. However, we have still poor and scattered collection records in other regions. In particular, we know virtually nothing about *A. editha* in Oshima peninsula (Oshima and Hiyama districts) and eastern Hokkaido (Nemuro and Kushiro districts), though some previous records indicate the occurrence of *A. editha* at least in some localities of Oshima district (Wenz and Zilch, 1959-1960; Maeda *et al.*, 1983).

Variations in Shell Morphology

In this paper, we treat only the variations in shell morphology, although we have detected certain degree of interpopulational variation in other characters

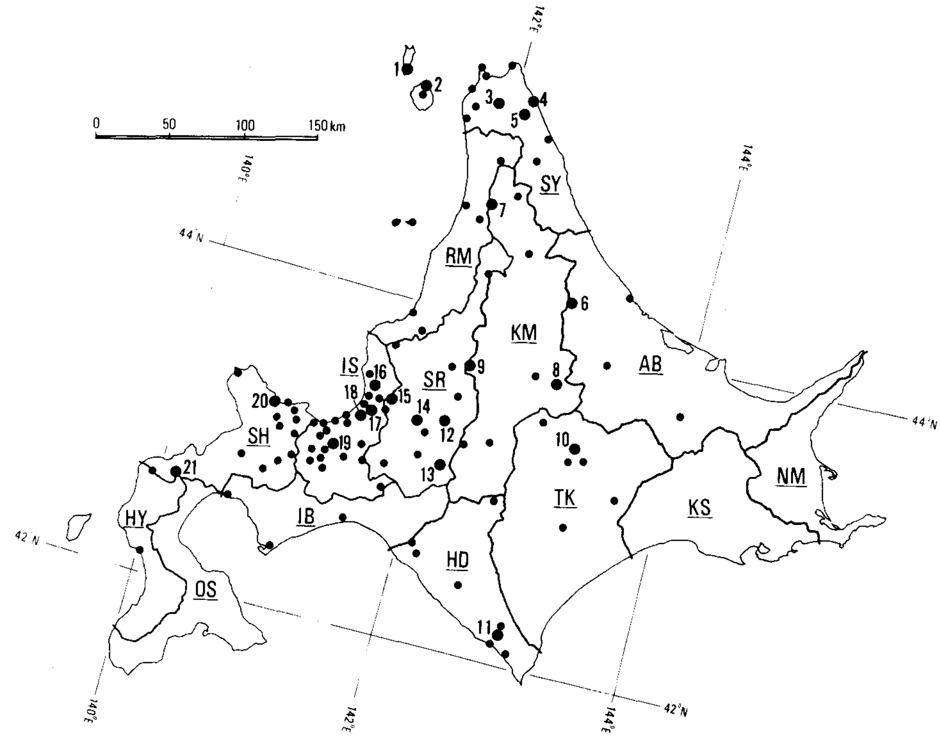

Fig. 1. Distribution of *Ainohelix editha*. Large dots with Roman numerals denote the provenance of 25 representative population samples examined in the present study (see, Table 1). District names are abbreviated as: SY (Soya), AB (Abashiri), NM (Nemuro), KS (Kushiro), KM (Kamikawa), TK (Tokachi), RM (Rumoi), SR (Sorachi), HD (Hidaka), IS (Ishikari), IB (Iburi), SH (Shiribeshi), HY (Hiyama), OS (Oshima).

such as mantle color, some internal structures, and also egg size (unpublished observations).

The following shell characters are treated herewith: 1) Size, 2) shape, 3) banding pattern, and 4) surface condition.

To show the diversity of shell morphology, we chose a total of 25 populations (Table 1) representing various phenotypes (Fig. 2) and various geographical origins (Fig. 1). Three to twenty-four adult shells (determined by their reflected lips) were then chosen for each of the 25 representative populations. For each shell, the width and height excluding the reflected part of lip were measured, and the banding pattern and the condition of shell surface (either hirsute or not) were recorded. Results are summarized in Table 1.

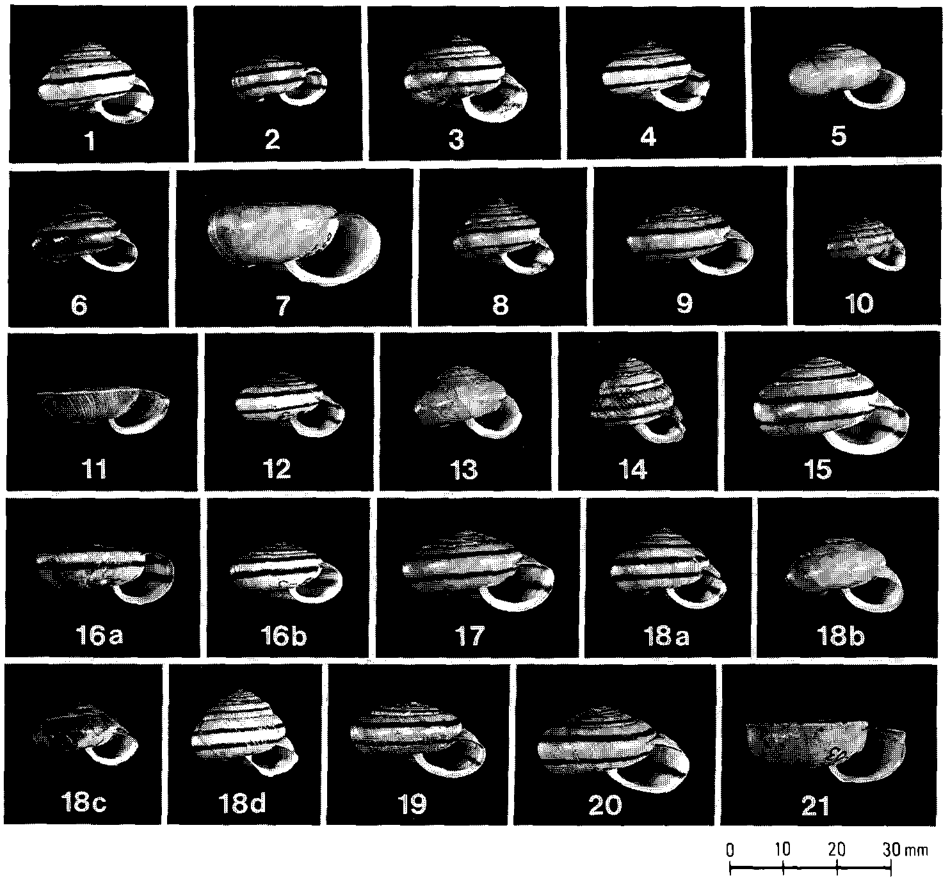

Fig. 2. Side views of adult shells selected from the 25 representative population samples. Numerals denote the sample codes.

1. Size. Interpopulational size variation was conspicuous. As shown in Table 1, the mean shell widths of the 25 representative population samples ranged from 14 mm (Sample No. 10) to 31 mm (No. 7), and the mean heights from 8 mm (No. 11) to 18 mm (No. 15). Individual shell sizes ranged from 13.7 mm (No. 10) to 32.5 mm (No. 7) in width, and 6.8 mm (No. 11) to 20.5 mm (No. 15) in height. Thus, the largest shell was nearly three times larger than the smallest shell in both dimensions. On the other hand, degree of intrapopulational size variation was far less conspicuous, as indicated by the SD values in Table 1 (also see, Fig. 5).

2. Shape. Variation in shell shape was also remarkable. Shell shape varied from flat (Sample Nos. 11 and 21, the height/width ratio being approxi-

Table 1. A summary of the studied shell characters in the 25 representative population samples of *A. editha*.

Code No.	Locality* (cf. Fig. 1)	Sample size	Width (W) Mean±SD	Height (H) Mean±SD	H/W Mean±SD	% banded	Remarks
1	Rebun (SY)	9	21.0±1.1	14.1±1.0	0.67±0.03	100.0	
2	Rishiri (SY)	23	17.8±1.1	9.9±0.9	0.55±0.04	100.0	
3	Wakkanai (SY)	10	21.4±0.8	14.8±0.4	0.69±0.02	90.0	
4	Sarufutsu (SY)	4	21.0±0.4	12.9±0.7	0.61±0.03	0.0	
5	Karibetsu (SY)	3	20.3±0.5	13.3±0.6	0.66±0.02	100.0	
6	Mt. Uenshiri (AB)	3	18.3±1.0	11.3±1.0	0.62±0.05	100.0	
7	Nakagawa (KM)	9	30.7±1.6	13.9±1.4	0.45±0.03	11.1	
8	Sounkyo (KM)	11	17.8±1.1	12.5±1.2	0.70±0.06	81.8	
9	Kamuikotan (KM)	9	24.5±1.1	14.5±1.1	0.59±0.03	55.6	
10	Nukabira (TK)	5	14.1±0.5	10.0±0.5	0.71±0.03	100.0	
11	Samani (HD)	16	23.0±1.7	7.7±0.6	0.34±0.03	75.0	Keeled
12	Ashibetsu (SR)	3	19.9±0.7	11.4±0.1	0.57±0.01	33.3	
13	Yubari (SR)	9	20.0±0.7	13.5±0.8	0.67±0.04	55.6	
14	Bibai (SR)	8	17.3±1.0	14.9±0.8	0.87±0.06	100.0	Hirsute
15	Tsukigata (SR)	18	26.7±1.0	17.7±1.4	0.66±0.04	77.8	
16a	Atsuta-A (IS)	19	23.5±1.5	9.6±0.7	0.41±0.02	63.2	Hirsute
16b	Atsuta-B (IS)	24	20.8±0.8	10.7±0.6	0.52±0.03	83.3	Hirsute
17	Penkebetsu (IS)	20	27.6±1.0	14.2±1.0	0.52±0.04	90.0	
18a	Shishinai-A (IS)	10	23.2±1.5	16.5±1.1	0.71±0.04	70.0	
18b	Shishinai-B (IS)	24	21.3±0.9	13.9±0.9	0.65±0.03	25.0	
18c	Shishinai-C (IS)	11	20.5±0.7	12.4±0.8	0.60±0.03	36.4	Hirsute
18d	Shishinai-D (IS)	13	19.7±1.1	14.5±1.1	0.71±0.04	53.8	
19	Moiwa (IS)	6	25.4±1.1	14.6±0.5	0.58±0.03	83.3	
20	Yoichi (SH)	10	26.9±1.2	16.0±0.9	0.59±0.03	100.0	
21	Oobira (SH)	10	29.6±1.3	10.7±1.1	0.36±0.02	90.0	Keeled
	Average and SD of sample means		22.1±4.0	13.0±2.4	0.60±0.12	71.0±30.0	

* District name are abbreviated in parentheses as follows: SY (Soya), AB (Abashiri), KM (Kamikawa), TK (Tokachi), SR (Sorachi), HD (Hidaka), IS (Ishikari), SH (Shiribeshi).

Table 2. Frequency of banded shells in the 25 representative population samples of *A. editha.*

Code No.	Locality	Sample size	Unbanded	Banded*		% banded
				Two-bands	Others	
1	Rebun	9	0	9	0	100.0
2	Rishiri	23	0	23	0	100.0
3	Wakkanai	10	1	7	2	90.0
4	Sarufutsu	4	4	0	0	0.0
5	Karibetsu	3	0	1	2	100.0
6	Mt. Uenshiri	3	0	3	0	100.0
7	Nakagawa	9	8	0	1	11.1
8	Sounkyo	11	2	7	2	81.8
9	Kamuikotan	9	4	5	0	55.6
10	Nukabira	5	0	5	0	100.0
11	Samani	16	4	10	2	75.0
12	Ashibetsu	3	2	1	0	33.3
13	Yubari	9	4	5	0	55.6
14	Bibai	8	0	8	0	100.0
15	Tsukigata	18	4	10	4	77.8
16a	Atsuta-A	19	7	10	2	63.2
16b	Atsuta-B	24	4	13	7	83.3
17	Penkebetsu	20	2	18	0	90.0
18a	Shishinai-A	10	3	6	1	70.0
18b	Shishinai-B	24	18	3	3	25.0
18c	Shishinai-C	11	7	2	2	36.4
18d	Shishinai-D	13	6	4	3	53.8
19	Moiwa	6	1	5	0	83.3
20	Yoichi	10	0	8	2	100.0
21	Oobira	10	9	0	1	90.0
	Average	—	—	—	—	71.0±30.0
	Total	287	90	163	34	
	Percentage		31.4	56.8	11.8	68.6

* Others included three types of one-banded shells and one type of three-banded shells. Bands were counted even if they were faint. Two neighbouring bands fused into one thick band were treated as two distinct bands.

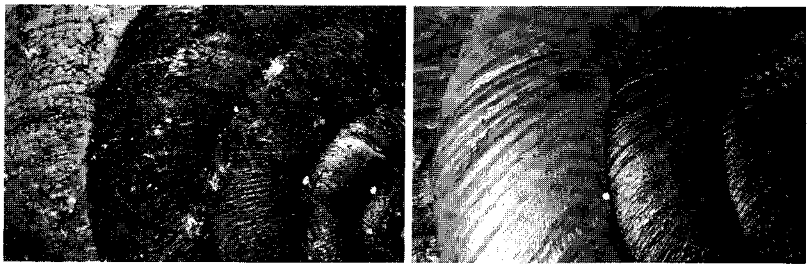

Fig. 3. Comparison of hirsute (left) and not-hirsute (right) shell surface.

mately 0.35) to considerably conical (No. 14, H/W ratio 0.87) (Fig. 2, Table 1). Various degrees of intermediate states between these two extremes were found (Fig. 2, Table 1). Moreover, in the two populations having most flat shells, every shell was also provided with an angular peripheral "keel" at the upper corner (the so-called 'Kadobari-hime-maimai', Sample Nos. 11 and 21). Infrapopulational variations were again far less conspicuous than the interpopulational variations.

3. Banding pattern. Shells were usually pale yellowish white, sometimes somewhat reddish, and in most cases with no or two dark bands (Table 2, also cf. Fig. 2; both no and two banded individuals combined occupied ca. 90% of total specimens examined). Although the number of specimens examined for each population was not many, there was a considerable local variation in the frequency of banded individuals, the mean of 71.0% with the range from 0 to 100%.

4. Shell surface condition. Although young shells of *A. editha* were often partly covered with minute scaly folds, adult shells are usually devoid of such folds, or only with their vestige. What Minato (1983) reported for *A. io* are probably of this type of scaly folds. There were, however, populations that were characterized by adult shells having distinctly hirsute surfaces (Fig. 3). Our representative samples include four such populations (Nos. 14, 16a, 16b, 18c; Table 1, Fig. 4).

Correlations Among Variable Characters

From the data given in Table 1, we calculated Kendall's coefficient of rank correlation (τ) for every pair among four variable characters, i.e. width, height, H/W ratio and percentage banded. Correlation coefficient (r) was also calculated for every pair among width, height and H/W ratio. As shown in Table 3, the mean body widths and mean H/W ratios as well as the mean body heights and mean H/W ratios correlated significantly. Namely, there are tendencies that the narrower or higher the mean shell sizes of populations are, the more conical the shell shapes are (Fig. 4). On the other hand, the correlation between the mean body width and mean body height was not significant. Frequency of banded

Table 3. Kendall's coefficients of rank correlation (τ) and correlation coefficients (r, given in parentheses) for paired characters except for surface condition, calculated from the data given im Table 1.

	Height	H/W	%banded
Width	0.2371 (0.3127)	0.3667* (−0.5800***)	0.1358
Height	—	0.3973** (0.5732***)	0.0244
H/W	—	—	0.1079

*,**,*** : Significant at $p<0.05$, $p<0.01$ and $p<0.005$, respectively.

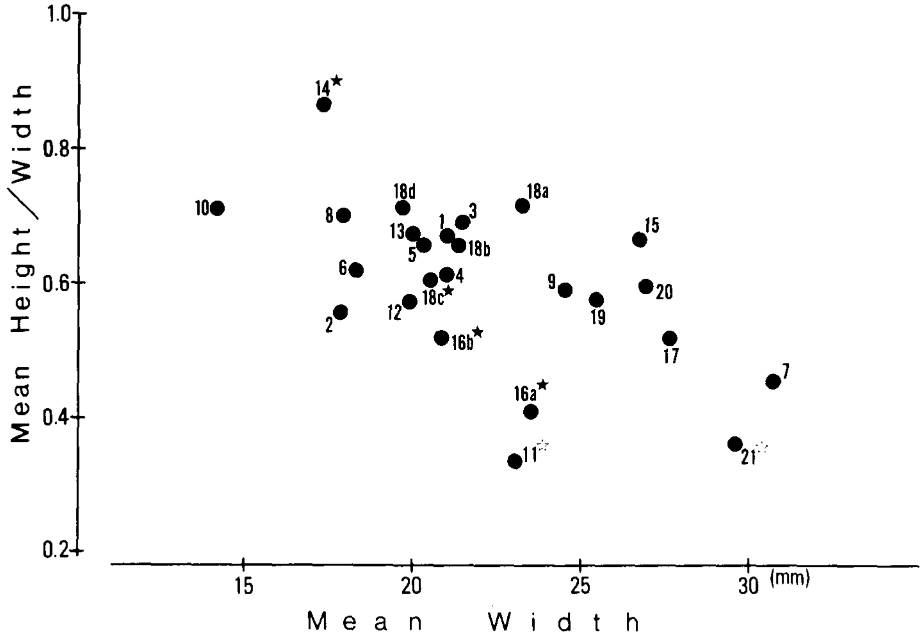

Fig. 4. A scatter diagram showing relation between shape (expressed by height/width ratio) and size (width) of the 25 population samples of *Ainohelix editha*. Numerals denote the sample codes. Open stars, populations with keeled shells; closed stars, populations with hirsute shells.

individuals also varied independent from variations of other characters. Furthermore, no correlation was indicated between the incidence of hirsute shells and other characters (Fig. 4).

Trends of Geographical Variations

It is difficult to point out any trend in the geographical variations of the four variable characters mentioned above. Although no precise analysis has been made yet, there seems to be no noticeable cline in every variable character along

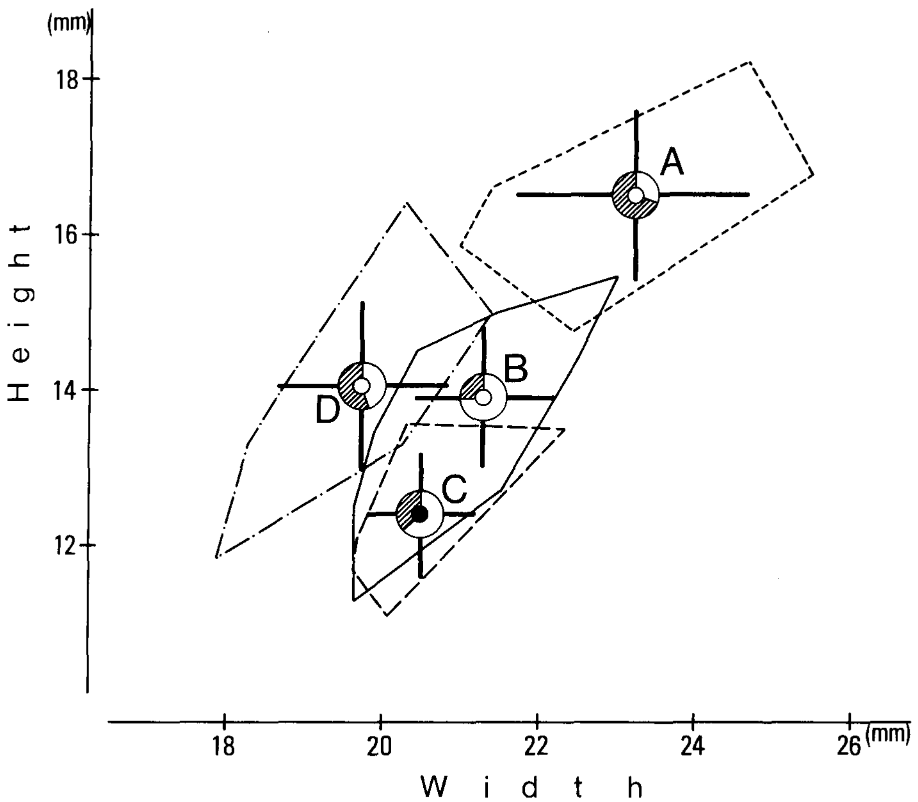

Fig. 5. Comparison of shell characters among four adjacent populations of *Ainohelix editha*. A to D, population samples 18a to 18d. Widths, heights and their relations were shown by polygons constructed from scatter diagrams; thick cross bars denote the mean values and ranges of 1 SD. Frequencies of banded individuals are shown by hatched areas of pie graphs. A hirsute population is indicated by the closed center circle. Distances between sites: A/B, 2,125 m; A/C, 2,325 m: A/D, 4,300 m; B/C, 475 m; B/D, 2,625 m; C/D, 2,125 m.

the changes of climatic conditions, along altitudinal changes or along other ambient changes. Only we are aware concerning this point are, the snails with keeled shells ('Kadobari-hime-maimai') have so far been collected only from calcium rich habitats, and that banded individuals increased in higher altitude in one locality (Udagawa and Kusui, 1987); whether these represent some general trends or not is still uncertain, however.

Consequently, we could not detect any definite trend in the geographical variation of overall shell morphology in *A. editha*. The variations are complex and unpredictable, and while populations with similar appearance are found in very distant localities (e.g., two populations of 'Kadobari-hime-maimai', Nos. 11 and 21), distinctly different phenotypes are distributed in close proximity (e.g., the four populations, Nos. 18a-d, collected within a radius of only 2,150 m in Shishinai and the vicinity; see Fig. 5). In the latter instance, the four populations differ in shell size (No. 18a larger than the rest three, Fig. 5), shape (height/width ratio, 18c < 18b < 18a ≒ 18d, Table 1, Fig. 4), frequency of banding pattern (from 25% in 18b to 70% in 18a, Table 2), or shell surface condition (adult shells distinctly hirsute only in 18c).

Concluding Remarks

To summarize, *A editha* shows conspicuous geographical variations in at least four shell characters, i.e., banding pattern, size, shape, and surface conditions. The geographical variations are complex, unpredictable, and do not show any consistent pattern, as in various other groups of land snails (Komai, 1951).

Since our *A. editha* includes considerably different phenotypes, it is reasonable to question whether it is really a single species or actually an aggregate of more than one species. Still little is known with respect to this question. It must be emphasized, however, that all the populations we have treated as *A. editha* are strictly allopatric. We found no two discrete phenotypes occurring sympatrically.

Although some previous records exists indicating sympatric occurrence of more than one phenotypes (e.g., three different phenotypes named 'Hira-maimai', 'Miyabe-maimai' and 'Bureiki-maimai', all said to have collected at Shiraoi; Iijima, 1892), we have not yet encountered such a situation. Instead, as shown above, we have found that distinctly different snails often occur in close proximity, even less than several hundreds of meters apart. It is likely that in the above cited instance the three phenotypes were also allopatric on a microgeographical scale, being collected from adjacent but different collecting sites. Thus, we conclude that our *A. editha* does not include sympatric species.

Accordingly, two different possibilities remain as to the taxonomic status of *A. editha*: (1) *A editha* is a very polytypic single species, or (2) it includes more than one allopatric species.

We have yet no direct evidence to accept or reject either of the two alternatives, and many aspects of the geographical variations exhibited by *A. editha* must be clarified before we answer this question. At the present, however, we tentatively treat our *A. editha* as a single polytypic species because the following two points seem to favor this view:

First, as mentioned above, variations of shell morphology in the members of *A. editha* are continuous. For example, the conical and hirsute Bibai population (No. 14) and the flat, keeled and not hirsute Samani population (No. 11) are easily discriminated from each other by a number of diagnostic characters. However, these two populations are united by other populations with various degrees of intermediate conditions between the two. Likewise, the smallest Nukabira population (No. 10) and the largest Nakagawa population (No. 7) are united by a number of populations with intermediate sizes. Thus, we can not discriminate any phenotype from others with sufficiently stable diagnostic characters.

Secondly, in a preliminary study with several populations of *A. editha*, we failed to detect any diagnostic difference in genitalia and radullae (unpublished data), both of which are often used as most reliable characters in land snail taxonomy. This indicates close relationships among the members of *A. editha* in spite of their diverse external morphology.

Summary

Ainohelix editha is a group of closely related allopatric land snails that differ, often drastically, in shell morphology. It is either a very polytypic species or an aggregate of more than one allopatric species. We reviewed factual evidence of its geographical distribution and geographical variations in four shell characters (banding pattern, size, shape, shell surface condition).

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References

Habe, T. 1977. Identity of "*Helix*" *blakeana*. Chiribotan, **9**: 187-188. (In Japanese)

Iijima, I. 1892. Land snails of Hokkaido, II, III. Zoological Magazine (Tokyo), **4**: 187-189, 243-246. (In Japanese)

Ito, K. and T. Habe 1983. Angular periphery form of *Ainohelix editha* (A. Adams). Chiribotan, **14**: 13-14. (In Japanese)

Komai, T. 1951. Geographic variation in the land-snail *Bradybaena similaris*. Jap. J.

Malac., **16**: 87–103. (In Japanese)

Maeda, K., S. Ohta, A. Osato, Y. Shikano and R. Ueshima 1983. Catalogue of the Hirase Collection deposited in the Yokosuka City Museum Part I Terrestrial molluscs (1): Bradybaenidae (Pulmonata). Misc. Rept. Yokosuka City Mus., **8**: 1–60. (In Japanese)

Minato, H. 1983. *Ainohelix io* n. sp. (Bradybaenidae) from Mt. Daisetsu Area, Hokkaido. Venus (Jap. J. Malac.), **42**: 170–173. (In Japanese with English description)

Minato, H. 1988. A Systematic and Bibliographic List of the Japanese Land Snails. 294 pp. "Nihon-rikusan-kairui-soumokuroku- kankoukai", Shirahama.

Udagawa, T. and Y. Kusui 1987. Land snails in the surrounding areas of the Ohirayama Nature Conservation area. In: Conservation Reports of the Ohirayama Nature Conservation Area, Hokkaido, Japan, pp. 307–313. Nature Conservation Bureau, Environment Agency of Japan. (In Japanese with English summary)

Wenz, W. and A. Zilch 1959–1960. Gastropoda-Euthyneura. Handbuch der Palaeozoologie, 6. 834 pp. Berlin.