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Morphometric Analysis of Shell and Operculum Variations in the Viviparid Snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan

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Yuh-Wen Chiu, Hon-Cheng Chen, Sin-Che Lee and Chaolun Allen Chen (2002) Morphometric analysis of shell and operculum variations in the viviparid snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan. *Zoological Studies* **41**(3): 321-331. The viviparid snail, *Cipangopaludina chinensis*, is one of the widely distributed freshwater gastropods in Asia, whose intraspecific variations in shell morphology and operculum were thought to be due to ontogenetic allometric growth or environmental effects. In this study, morphometric analyses were applied to discriminate shell and operculum variations in 251 individuals of *C. chinensis* from 5 populations, including Chutzuhu, Laumay, Lantan, and Wanda in Taiwan, and 1, Kwangju, in Korea. The allometric shell growth pattern in *C. chinensis* was identified using linear regression analysis. Thirteen shell and operculum characters were measured and examined using multidimensional scaling (MDS) and canonical discriminate analysis (CDA). These 2 analyses clearly demonstrated that 2 morphotypes, namely a tall-spired form and a short-spired form, exist among the 5 populations. MDS indicated that snails with the shorter shell spire in Chutzuhu and Laumay were morphologically related. CDA suggested that spire height is the most important character contributing to variation between these populations. One of the factors causing variation in spire height within and between populations is allometric growth. Different growth rates between the spire and other portions of the shell result in the shell changing shape with growth. Linear regression demonstrated that the spire of the tall-spired form lengthens at a faster rate than that of the short-spired form. Different growth rates in the spire thus contributed to the major difference in shell shape between the 2 morphotypes. Ontogenetic allometric growth and environmental factors that contribute to the configuration of the 2 morphotypes in *C. chinensis* are discussed. http://www.sinica.edu.tw/zool/zoolstud/41.3/321.pdf

Key words: Morphometric analysis, Viviparid snail, Allometric growth, Morphotype.

The genus *Cipangopaludina* is a common but archaic group of viviparid gastropods distributed throughout Eurasia (Yen 1941, Pace 1973). Members of this genus inhabit various natural and artificial freshwater environments, including shallow lakes, streams, wetlands, and ponds, as well as rice and taro farms (Pace 1973, Chen 1990). Many morphotypes and subspecies have been described for Asian *Cipangopaludina* based on shell shape and external color patterns (Yen 1943, reviewed in Pace 1973). Two species of *Cipangopaludina*, *C. miyagii* (Kuroda) and *C. chinensis* (J. E. Gray), have been recorded in Taiwan (Kuroda 1941, Pace 1973). *Cipangopaludina miyagii* is endemic to Taiwan and has only been recorded from wetlands of southern Taiwan (Taki 1941, Pace 1973). However, it may now be extinct due to habitat destruction caused by urbanization (Chiu unpubl. data). In contrast, *C. chinensis* has a wide geographic distribution, including East China, Taiwan, Korea, and Japan (Pace 1973, Liu et al. 1995). This species has also been introduced to North America by humans over the last 2 centuries (Abbot 1950). Nevertheless, habitat fragmentation has also resulted in its patchy distribution in lakes, dams, and taro farms in Taiwan (Chiu unpubl. data).

The taxonomic status of *C. chinensis* is still

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uncertain. Pace (1973) reviewed the Chinese viviparid members of the genus *Cipangopaludina* and concluded that there were 17 subspecies for *C. chinensis*, although the taxonomic status of the viviparids in Taiwan remained in doubt (Pace 1973). On the contrary, 4 subspecies, *C. c. aubryana*, *C. c. fluminalis*, *C. c. longispira*, and *C. c. hanianensis*, were recognized for *C. chinensis* by Brandt (1974). Liu et al. (1995) clarified the distribution and taxonomy of this genus and raised most subspecies recognized by Pace (1973) to the species level. Interestingly, most of the species described by Liu et al. (1995) were restricted or endemic to a narrow range, and *C. chinensis* was the only species that was distributed widely, even to southern Taiwan. These contradictary views of the taxonomic status of *C. chinensis* indicate that a comprehensive study of the morphology of this species is needed and may contribute to our understanding of species or subspecies delineation in the genus *Cipangopaludina*.

Shell shape of *C. chinensis* is characterized by a longer shell length than shell width and a longer spire in relation to aperture height (Pace 1973, Liu et al. 1979). However, intraspecific variation in shell shape is frequently observed due to allometric growth between juvenile and adult snails, or different environmental conditions (e.g., dams vs. taro farms) experienced by habitat fragmentation which can result in isolated populations. Allometric growth is defined as different proportions correlated with changes in the absolute magnitude of an organism or a specific part under consideration (Gould 1966). Differences in allometric growth have been documented in individuals of *C. chinensis* introduced to North America with 2 ecomorphs being proposed (Jokinen 1982). Unequal growth rates between shell length and shell width have also been documented in the confamilial genus *Sinotaia*, because juveniles have a discoidal shell form which changes to a globular form in adults (Calow and Calow 1983). It is generally recognized that viviparid snails have a tendency to express a discoidal shell shape in immature stages. Although shells of viviparid gastropods have traditionally been used as an informative source of systematic characters, intraspecific morphological variations due to allometric growth and environmental effects have impeded species delineation.

Intraspecific morphological variations caused by environmental differences can also lead to ambiguous identification of closely related viviparid gastropods. These environmental differences include the long-term stability of habitats (such as lakes vs. farms), the availability and concentrations of calcium sources, and the presence of predators. Analysis of the shell shape of the *Viviparus georgianus* species complex revealed intraspecific differences possibly due to environmental factors (Katoh and Foltz 1994). The shell morphology of the African freshwater snail, *Biomphalaria pfeifferi*, is affected by ecological factors, such as the stability of the African Great Lakes over a long period of time, since populations in these lakes tend to develop their own characteristics, such as blunt keels and deflected apertures (Dupouy et al. 1993). Individual variation in the shell shape of *Physa gyrina* reflects the presence of predators in local populations (Dewitt et al. 1999).

In this study, morphometric analyses of shell and operculum variations were conducted on *C. chinensis* (Fig. 1) collected from 4 isolated popula-

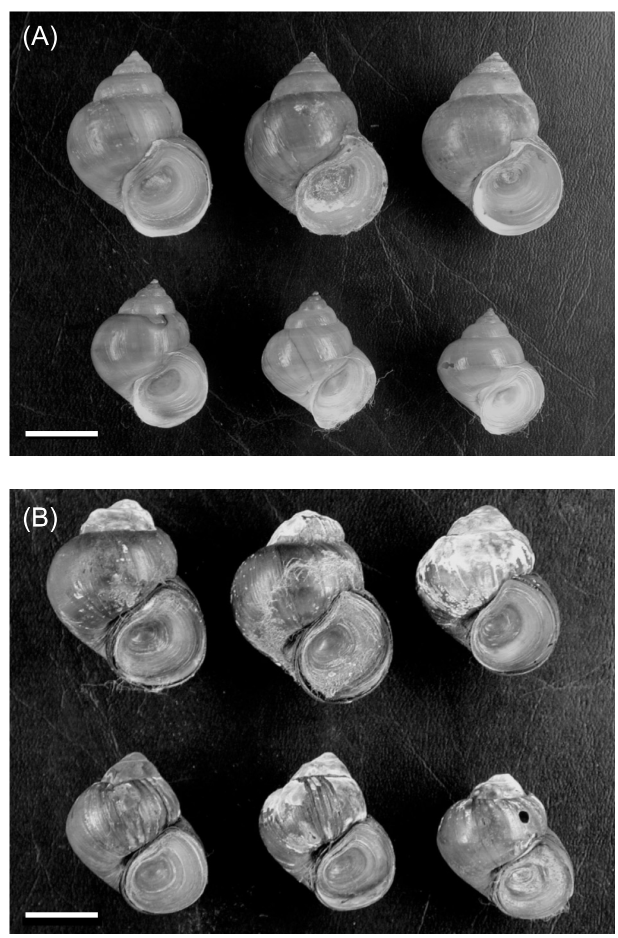

Fig. 1. Shells of *Cipangopaludina chinensis* from different habitats. (A) Lantan, the tall-spired form; and (B) Laumay, the short-spired form. Bar = 10 mm.

tions in Taiwan. The 4 localities represent 2 distinct habitats, taro farms and dams, for *C. chinensis* (Table 1). Since *C. chinensis* is widely distributed in the East Asian region, snails purchased from a traditional market in Kwangju, Korea were also included for morphometric comparison. First, we investigated the effect of allometric growth on shell morphology using linear regression. A minimum shell size of the adult shell shape was determined, and juveniles were excluded from subsequent analyses. Second, multidimensional scaling (MDS) and canonical discriminate analysis (CDA) were utilized to reveal if variations in shell and operculum measurements correspond with distinctly different morphotypes within *C. chinensis*. Both multivariate analyses indicated that 2 morphotypes exist in populations of *C. chinensis* in Taiwan, with each corresponding to environmental conditions of their respective habitats.

MATERIALS AND METHODS

Sample collection and habitat characteristics

Two hundred and fifty-one *Cipangopaludina chinensis* snails (Fig. 1) were collected from 4 localities in Taiwan from August 1997 to October

Table 1. *Cipangopaludina chinensis*. Localities, habitat, number of snails, and measurements of 13 shell and operculum characters used for multivariate analyses

Locality	Chutyuhu 121°31'E 25°11'N	Laumay 121°32'E 25°16'N	Lantan 120°28'E 23°23'N	Wanda 121°07'E 23°58'N	Kwangju 127°31'E 36°39'N
Habitat	taro farm	taro farm	dam	dam	unknown
No. of snails[a]	52	32	20	42	19
Character[b]					
SL	2.80 ± 0.36[c] (2.17 − 3.57)	2.60 ± 0.24 (1.94 − 2.97)	2.53 ± 0.98 (1.57 − 4.19)	3.10 ± 0.80 (1.51 − 4.16)	4.02 ± 0.69 (2.87 − 5.02)
SW	2.28 ± 0.27 (1.71 − 2.89)	2.17 ± 0.23 (1.62 − 2.49)	1.87 ± 0.71 (1.00 − 3.05)	2.39 ± 0.49 (1.06 − 3.13)	3.03 ± 0.41 (2.32 − 3.60)
AL	1.74 ± 0.18 (1.32 − 2.11)	1.66 ± 0.15 (1.28 − 1.85)	1.45 ± 0.57 (1.08 − 2.39)	1.82 ± 0.36 (1.05 − 2.31)	2.35 ± 0.350 (1.77 − 2.89)
AW	1.30 ± 0.14 (1.05 − 1.63)	1.26 ± 0.10 (1.02 − 1.44)	1.05 ± 0.36 (0.67 − 1.67)	1.38 ± 0.27 (0.88 − 1.77)	1.80 ± 0.25 (1.37 − 2.20)
WL	2.33 ± 0.35 (1.19 − 3.02)	2.27 ± 0.24 (1.67 − 2.72)	2.02 ± 0.81 (1.07 − 3.38)	2.48 ± 0.60 (0.95 − 3.25)	3.23 ± 0.55 (2.34 − 4.02)
P1	0.76 ± 0.12 (0.48 − 1.00)	0.71 ± 0.08 (0.50 − 0.83)	0.66 ± 0.26 (0.31 − 1.11)	0.80 ± 0.23 (0.27 − 1.12)	1.05 ± 0.20 (0.71 − 1.42)
PL	1.45 ± 0.23 (1.09 − 1.98)	1.27 ± 0.13 (0.95 − 1.47)	1.38 ± 0.52 (0.74 − 2.30)	1.67 ± 0.49 (0.53 − 2.36)	2.21 ± 0.41 (1.57 − 2.77)
OL	1.66 ± 0.19 (1.22 − 2.10)	1.56 ± 0.19 (0.85 − 1.87)	1.31 ± 0.57 (0.65 − 2.20)	1.73 ± 0.37 (0.61 − 2.18)	2.25 ± 0.32 (1.75 − 2.72)
OW	1.20 ± 0.15 (0.80 − 1.52)	1.15 ± 0.17 (0.68 − 1.73)	0.93 ± 0.39 (0.41 − 1.54)	1.24 ± 0.27 (0.46 − 1.62)	1.58 ± 0.23 (1.17 − 1.97)
LC	0.36 ± 0.05 (0.24 − 0.44)	0.28 ± 0.04 (0.18 − 0.35)	0.27 ± 0.11 (0.12 − 0.54)	0.37 ± 0.07 (0.16 − 0.53)	0.46 ± 0.08 (0.33 − 0.59)
RC	0.86 ± 0.10 (0.61 − 1.09)	0.87 ± 0.09 (0.67 − 1.05)	0.68 ± 0.29 (0.32 − 1.15)	0.90 ± 0.18 (0.31 − 1.17)	1.15 ± 0.18 (0.88 − 1.54)
TC	0.84 ± 0.10 (0.66 − 1.03)	0.79 ± 0.09 (0.60 − 0.94)	0.65 ± 0.28 (0.31 − 1.10)	0.84 ± 0.19 (0.32 − 1.12)	1.10 ± 0.18 (0.79 − 1.35)
BC	0.88 ± 0.10 (0.66 − 1.08)	1.11 ± 1.49 (0.65 − 9.25)	0.72 ± 0.31 (0.34 − 1.21)	0.94 ± 0.18 (0.39 − 1.19)	1.21 ± 0.18 (0.91 − 1.55)

[a]Juvenile snails were excluded from the multivariate analyses after RSMAL was determined to be 1.0 cm for apertural length (AL).

[b]For codes of each character listed in the 1st column see text and figure 2 for details.

[c]Unit for measurements is in centimeters. The range of each character from each location is given in parentheses.

1998. Locality descriptions and codes of populations are listed in table 1. An additional 19 individuals were also purchased from a traditional market in Kwangju, Korea for geographic comparison. In total, 270 individuals were measured and used in the present study. The Chutzuhu and Laumay collection sites are located on Yangmingshan, northern Taiwan, which is characterized as a volcanic area (Yen et al. 1984). The viviparid snails in these locations were collected from taro farms and wetlands in shallow water (< 0.3 m deep). The water quality was characterized by a low pH level (4.0-5.8) and low calcium ion concentrations (< 0.1 meq/l) (Chen and Wang 1997, Chiu unpubl. data). Some of the snails collected from these 2 sites showed erosion of the spire top, probably due to the low pH and low calcium ion concentrations. In order to avoid measurement bias derived from the erosion of the spire top, only individuals having an apparent apical portion were chosen for morphometric measurement. The collecting sites at both Lantan and Wanda were originally natural lakes, but dams were constructed for hydropower generation several decades ago. Nevertheless, the ecological and geological characteristics of these 2 sites are still similar to those of a natural lake. The viviparid snail populations were collected from an area of a greater depth (> 1 m), and snails were collected by capturing them in bamboo traps. The water quality was characterized by high pH levels (7.7-9.0) and high calcium ion concentrations (> 1.0 meq/l), especially at Lantan (Chen and Wang 1997). Habitat characteristics are summarized in table 2. Specimens from all locations, except Chutzuhu, were collected for identification and morphometric measurements. Snails from Chutzuhu were identified and measured on site and then released, because this collecting site is located within the protected area of Yangmingshan National Park.

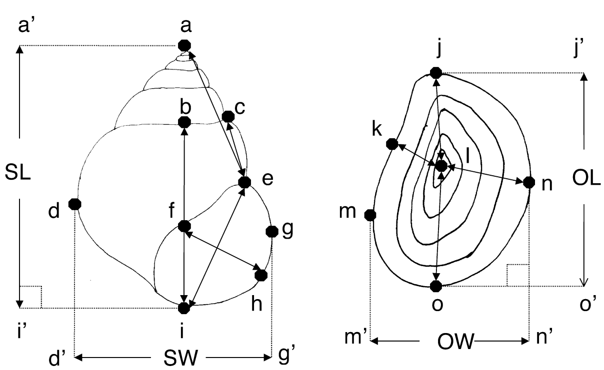

Fig. 2. Measurements made on shells (left) and operculum (right) of viviparid snails.

Characters selected for morphometric analysis

To select characters for use in morphometric analyses, we reviewed the available taxonomic descriptions from the literature (Pace 1973, Brandt 1974, Liu et al. 1979, Burch 1980) and adopted characters of the shell and operculum that were practical for use in identification. The results of morphometric analyses might directly reflect the importance and effect of each character. A total of 13 continuous shell and operculum measurements was taken with calipers made along imaginary straight lines as shown in figure 2. Shell length (SL) was measured along an axis passing through the apex (a) to the bottom (i) of the shell. Shell width (SW) is the maximum width perpendicular to the shell length distance (d'-g'). Aperture length (AL) is the length from the beginning of the 1st suture (e) to the bottom of the aperture (i). Aperture width (AW) is the maximum diameter perpendicular to the aperture length (f-h). The body whorl length (WL) was measured from the intersection of the axis passing through the apex (b) to the bottom of the shell (i). The penultimate whorl

Table 2. Summary of habitat characteristics of collection sites. Data were obtained from Chen and Wang (1997)

Location	Morphotype	Habitat	Depth	Water level	pH	Conductivity (μs/cm)	Total Ca^{2+} (meq/l)	Total cations (meq/l)	Total anions (meq/l)
Wanda / Lantan	tall-spired	dam	deep	stable	> 7.7	> 195	> 1	> 2.5	> 2.6
Laumay / Chutyuhu	short-spired	taro farm	shallow	unstable	< 5.8	< 30	< 0.1	< 0.4	< 0.5

length (P1) is the length between the beginning of the 1st suture (e) to the beginning of the 2nd suture (c). Spire height (PL) was measured from the beginning of the 1st suture (e) to the apex of the shell (a). Operculum length (OL) is the maximum longitudinal length of the operculum (j'-o'). Operculum width (OW) is the maximum length measured at 90° to the operculum length (m'-n'). RC is the length between the nucleus (l) to the right margin (n) of the operculum. LC is the shortest length between the nucleus (l) and the left margin (k) of the operculum. TC is from the upper margin (j) to the nucleus of the operculum (l). BC is the distance from the nucleus (l) to the lowest margin (o) of the operculum.

Allometric shell growth

The ontogenetic effect of allometric growth has been documented in several groups of molluscs that have usually caused confusion in morphometric analyses, and those individuals within the range of allometric growth were eventually excluded before multivariate analyses (Valovirta and Vaisanen 1986, Urabe 1992, Armbruster 1995, Mylonas et al. 1995). Therefore, the effect of allometric shell growth on *C. chinensis* was examined prior to conducting the multivariate analyses. Since the present-day distribution of *C. chinensis* in Taiwan is fragmented, this would eventually increase the difficulties for us to obtain snails of all size classes from each population and examine the allometric shell growth under reasonable sampling effects. Under these circumstances, allometric shell growth was only examined in snails from the Wanda (n = 70) and Laumay (n = 109) populations, which provided sufficient individuals to cover different size ranges (Fig. 3). Any findings of allometric shell growth in these 2 populations should be applicable to the remaining *C. chinensis*. The ratios, AL/SW and SL/SW, representing different proportions of growth rates in shells, were analyzed against aperture length (AL) (representing the size category) using linear regression. If allometric shell growth exists in this species, the correlation coefficient, R^2, of both regressions will significantly differ. Furthermore, the minimum shell aperture length of the 2 populations can be obtained from the intersection of the 2 linear regression equations of SL/SW vs. AL. Snails were not used for the following multivariate analyses when the aperture length was smaller than the minimum shell aperture length. We therefore excluded small-sized individuals from the following morphometric analysis to avoid bias due to allometric growth in shell morphological variation. The general linear regression option was utilized in SPSS 10 (SPSS 1999).

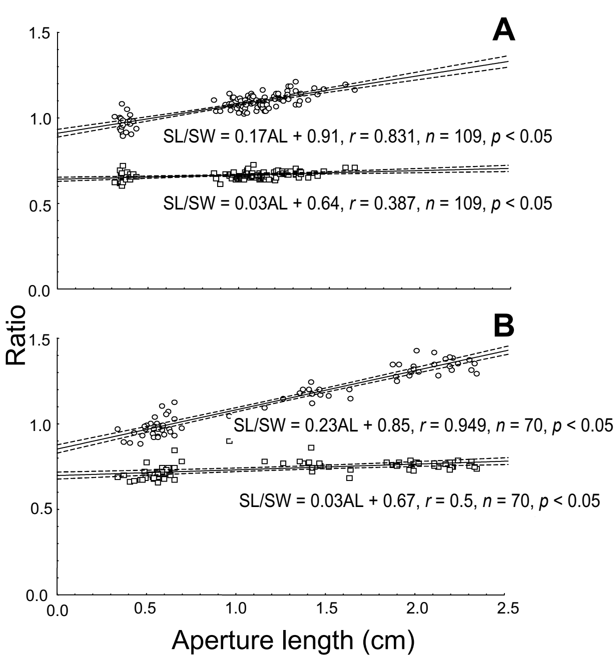

Fig. 3. Allometric growth of populations of 2 morphotypes of *Cipangopaludina chinensis*. (A) Laumay population, short-spired form; and (B) Wanda population, tall-spired form. Solid lines are regression lines; dashed lines are 95% confidence intervals. ○ shell length/shell width; □ aperture length/aperture width.

Multivariate analyses

Two multivariate methods were used to char-

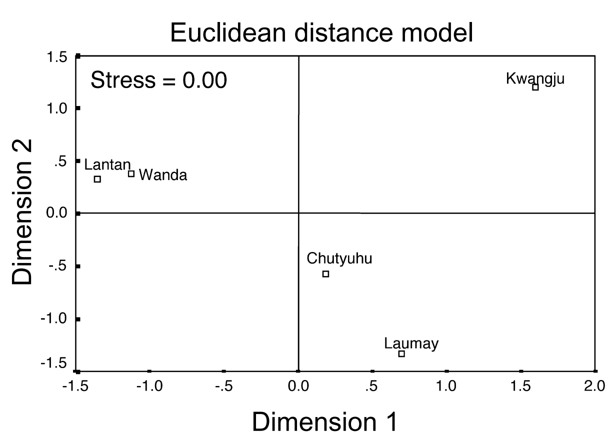

Fig. 4. Two-dimensional plot of shell and operculum character sets analyzed by metric multidimensional scaling.

acterize the morphometric data: multidimensional scaling (MDS), which gives a general overview of the data and is used for illuminating relationships among populations; and canonical discriminate analysis (CDA), which provides maximum discrimination among groups using linear combinations of variables. A similarity matrix of 5 populations was obtained from the mean of each morphological measurement from each population. An MDS map of Euclidean distances was created. The lower stress value suggests the preferable metric scaling (Manly 1994). We refer to populations as a priori groups in the canonical discriminate analysis (CDA). Canonical discriminate analysis quantifies characters of the shell and operculum and assesses how successful the characters are at allocating individuals to their a priori groups. Data were pre-examined for homogeneity and log-transformed in order to reduce the correlation of the measurement means and variances (Sokal and Rohlf 1995) before CDA. The contribution of each morphometric value to the CDA varieties was visualized by plotting canonical variable 1 (CV1) against CV2 on a bi-plot chart. MDS and CDA were performed using SPSS 10 (SPSS 1999).

RESULTS

Viviparid snails from several sampled populations represent 2 distinct habitats, taro farms and dams, for *Cipangopaludina chinensis* (Table 1). Individuals from Wanda and Lantan bear the typical shell shape of *C. chinensis*, i.e., spiral portions taller than the aperture portion (Fig. 1A). The shell is yellow brown. These 2 populations exist in deeper habitats such as behind dams with stable environmental conditions (Table 2). Individuals from Laumay and Chutzuhu show a shorter spiral portion in shape and a thin, fragile shell in texture (Fig. 1B). We selected unworn individuals with a clear apical portion even though shell dissolution and a worn-off periostracum were common in many individuals. The apical portion had thicker deposited conchiolin layers. The shell is dark brown. Snails collected from Kwangju, Korea possessed the largest shell size with a mean SL of 4.02 cm, even though only 19 individuals were measured. In general, larger sizes always appear in the Kwangju, Lantan, and Wanda populations.

Allometric shell growth

Linear regression analyses of the AL/SW ratio vs. AL and the SL/SW ratio vs. AL indicated that allometric shell growth exists in *C. chinensis*. At Laumay, SL/SW ratios increased significantly as AL increased (r = 0.831, p < 0.05), but AL/SW ratios did not increase significantly as AL increased (r = 0.387, p > 0.05). The slopes of both linear regression lines significantly differed (Student t-test, t = 12.24, d.f. = 214, p < 0.001), suggesting that elongation of shell length and enlargement of shell width do not contribute equally to the growth of *C. chinensis* in the Laumay population, with the former significantly faster than the latter (Fig. 3a). The same pattern was also observed in snails from Wanda in which SL/SW ratios increased significantly while AL increased (r = 0.949, p < 0.05), but not for the AL/SW ratios vs. AL regression (r = 0.5, p > 0.05). The slopes of both linear regression lines significantly differed (Student t-test, t = 6.69, d.f. = 136, p < 0.001) (Fig. 3b). The slope of the SL/SW vs. AL regression line for the Wanda population was significantly larger than that of the Laumay (Student t-test, t = 5.6, d.f. = 175, p < 0.001), suggesting that elongation of shell length occurs faster in snails of the Wanda population than in those of Laumay.

In order to reduce the ontogenetic effect of allometric growth on morphometric analyses, we defined the representative minimum shell aperture length (RMSAL) by comparing the 2 regression equations of SL/SW vs. AL from 2 populations and estimating the RMSAL by the intersection of the 2 SL/SW vs. AL regression equations. Lengths smaller than RMSAL were defined as juvenile forms and were excluded from the following multivariate analyses due to effects of ontogenetic changes. In both populations, snails had the same ratio of SL/SW (1.08) and a similar ratio of AL/SW (0.67, 0.70) at an aperture length of 1.0 cm (Fig. 3). We therefore excluded individuals with aperture lengths of less than 1.0 cm from the following analyses. In total, 165 individuals were selected from the 5 populations for multivariate analyses after juvenile individuals were excluded. The means and ranges of 13 measured characters from 165 individual snails are listed in table 1.

Multivariate analyses

Multidimensional scaling (MDS) analysis using 13 characters clearly separated the 5 populations of *C. chinensis* into 3 clusters according to different quadrants (Fig. 4). Lantan and Wanda were clustered in the 1st quadrant, Kwangju in the 2nd quadrant, and Chutzuhu and Laumay in the

4th quadrant (Fig. 4). The MDS map indicates that these 5 populations can be divided into 2 distinct morphotypes: a tall-spired form, including Kwangju, Lantan, and Wanda; and a short-spired form, including Chutzuhu and Laumay. The results of MDS analysis provide a high resolution because of the small stress values (stress = 0). The canonical discriminate analysis (CDA) of 13 shell and operculum characters reveals that 83.7% of total variations in *C. chinensis* are expressed by the 1st (66.1%) and the 2nd (17.6%) canonical variables (Fig. 5a). The canonical variables plot shows an overlapping grouping among the 5 populations, but with a positive trend in the Wanda, Lantan, and Kwangju populations and a negative trend in the Laumay and Chutzuhu populations on the 1st canonical variable. Totally, 89% of positive-trending individuals belonged to the Wanda, Lantan, and Kwangju populations, and 87% of those individuals showing a negative trend belonged to the Laumay and Chutzuhu populations. The contribution of each measurement to the 1st and the 2nd canonical variables can be clearly visualized in the bi-plot (Fig. 5b). The 1st canonical variable shows a positive correlation with spire height (PL) and BC, and a negative correlation with P1 and TC. The 2nd canonical variable has a high positive correlation with AW and RC, and a negative correlation with PL (Fig. 5b). The quantitative result confirms the empirical observation that the tall-spired form is characterized by a longer shell spire and a relatively shorter penultimate whorl length than those seen in the short-spired form.

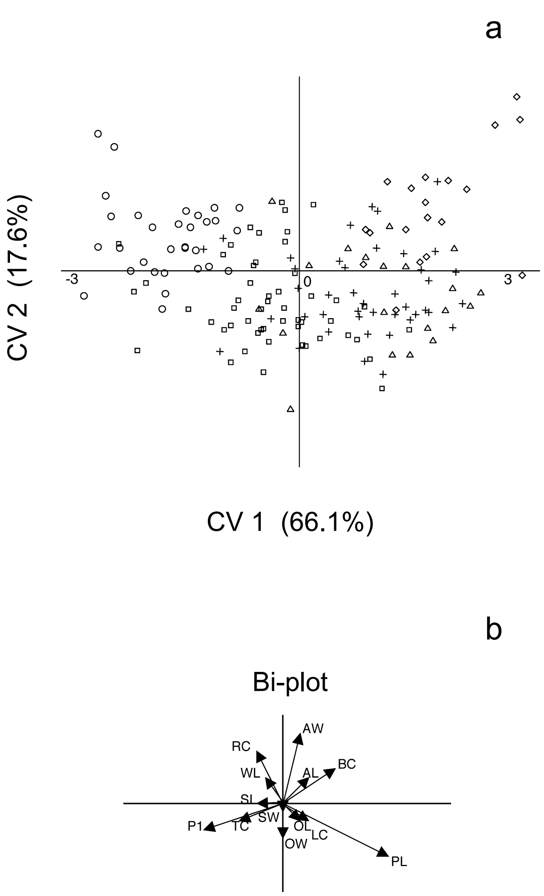

Fig. 5. Plots of the 1st and 2nd variable scores for short-spired-form populations (○ Laumay; □ Chutzuhu) and long-spired-form populations (◇ Korea; △ Lantan; + Wanda).

DISCUSSION

Shells of gastropods contain a rich source of taxonomic information that can be used to interpret evolutionary relationships among taxa. Shell morphological characters are used as primary guidelines for species identification in general handbooks and the taxonomic literature. For example in *Cipangopaludina chinensis*, the most important taxonomic characters are spire height, shell width, and shell shape. However, these morphological characters can be confounded by intrinsic and extrinsic factors, despite the applicability of shell morphology in taxonomic and systematic studies of gastropods.

Ontogenetic effect of allometric shell growth

Allometric growth is the primary intrinsic cause of taxonomic confusion in gastropods. In some species of gastropods, juvenile shell morphology cause difficulties in identification by the overlapping morphological boundaries between related species (Valovirta and Vaisanen 1986). Additionally, the gross morphology of juvenile shells of some species of viviparid snails are so similar that they can only be separated using scanning electron micrographs of shell morphology and shell structure of bristles and lobes formed on embryonic and juvenile shell stages (Falniowski et al. 1996b). Brooding parents are usually scarified to obtain measurements of embryonic juveniles (Falniowski et al. 1996b). In the present study, the representative minimum shell aperture length (RMSAL) was estimated to be 1.0 cm. This statistical result is very important for the following multivariate analyses, because we did not have to scarify brooding parents in order to obtain juvenile snails which we excluded from the multivariate analyses in order to avoid confusing morphological variations produced by shell characters of immature stages of development. The RMSAL is also similar to the minimum aperture length of brooding individuals in populations of *C. chinensis* from Yangmingshan(Chiu unpubl. data), supporting this size limit separating juvenile and adult individuals. The shell shape of the land snail *Helix siphonica* changes allometrically and was correlated to different development of the genital systems as well as habitat differences (Mylonas et al. 1995). The same changing patterns are also present within and between *C. chinensis* populations examined. Different growth rates result in variations between morphotypes as well as in altering the juvenile discoidal shell shape to the globular shape of adults. Anatomically, the spiral portion of viviparid shells mainly houses the visceral mass (Vail 1977). It is also possible that an increased size of the visceral mass is related to reproductive maturation and energy storage for reproduction.

Morphometric analysis

The MDS map indicates 2 pairs of morphotypes from each habitat in Taiwan: the short-spired form of taro farms of Chutzuhu and Laumay, and the tall-spired form at the dams at Lantan and Wanda. The Korean population (Kwangju) is grouped with Lantan and Wanda by Euclidean distances. MDS analysis of the shell data with all characters (without adjustment by shell length) shows an identical pattern to that of the shape data. The shape and shell data cluster populations from similar environments in the same MDS quadrant, suggesting that the occurrence of different morphotypes is probably habitat correlated, and that these different morphotypes can be regarded as ecotypes. It is possible that there is geographic structuring of morphotypes given the clear separation of snails from Korea, although further sampling is necessary to confirm this.

Canonical discriminate analysis identified the important characters that contribute to distinguishing different populations. Spire height was identified as the most important character among the measurements for separating populations. The CDA plot map shows the positive trend of the Wanda, Lantan, and Kwangju populations with the tall-spired form and the negative trend of the Laumay and Chutzuhu populations with the short-spired form along the 1st canonical variable. The data support the difference between the 2 morphotypes being primarily attributed to the spire height. On the other hand, although 6 of the 13 characters measured in the present study were derived from the operculum, the canonical discriminate analysis indicated that the variation in operculum characters has only a small effect on delineating the 2 morphotypes except for the 2 measurements, BC and TC. This is probably reflected in the bi-plot of CDA in which the operculum characters, being highly variable among individual snails, can hardly contribute to either of the canonical variables.

Environmental factors affecting shell shape

Extrinsic factors due to environmental conditions can induce variations in the shell shape of snails. In addition, environmental changes without genetic change can create distinct non-genetic changes in shell morphology. In a summary of water quality of the 4 collection sites in this study (Table 2), Laumay and Chutzuhu, wetlands and barrier lakes in a volcanic area, are characterized by low pH and soft water (Chen and Wang 1997). The calcium ion content and conductivity are also lower at Laumay and Chutzuhu than at Lantan and Wanda. The calcium value is an important environmental factor for the physiological needs of viviparid snails (Jokinen 1982), because it is necessary for shell construction and repair. The shorter spiral portion may be explained as a constraint of growth due to a low-calcium and acidic environment; dissolved apical portions of shells were commonly observed in *C. chinensis* from Laumay and Chutzuhu. In addition, these individuals were found to have deposited a thicker conchiolin layer which was not found in snails of other populations (Chiu unpubl. data). A thicker conchiolin layer was observed in the unionid bivalves inhabiting acidic waters (pH 4-5) (Kat 1982). On the contrary, *Corbicula fluminea* has a thinner conchiolin layer, and mass morality of this species is usually observed in acidic waters due to shell dissolution, suggesting that the conchiolin layer can provide resistance to acidic environments for bivalves (Kat 1982). Additionally, unionid bivalves are able to survive episodes of relatively low pH levels for up to several weeks because of physiological adaptations to anoxia (Mäkelä and Oikari 1992). A similar scenario of acid resistance may be applicable to *C. chinensis* with the conchiolin layer on the apical portion of the shell in the Laumay and Chutzuhu populations. However, further experimental comparison of physiological responses of the short-spired and tall-spired forms to acidic waters are needed to examine this hypothesis.

Overlap between the 2 morphotypes

Canonical discriminate analysis can not clearly separate the 5 populations examined in this study due to morphological overlap between individuals within and between populations. Closely related species of viviparid snails can be difficult to distinguish because of the overlap in the range of interspecific variability (Falniowski et al. 1996a). Allometry is a possible cause of morphological shell variation within populations, not only due to growth patterns but also to sexual dimorphism. Purchon (1977) noted that sexual dimorphism is rare in mollusks, but when it is present, it can influence shell size in gastropods (Webber 1977, Tupen 1999). For example, significant differences due to sexual dimorphism have been demonstrated in 2 freshwater gastropods, *Pomacea canaliculata* (Ampullariidae) and *Melanoides tuberculata* (Thiaridae) (Brande et al. 1996, Estebenet 1998). Preliminary examination of snails from Kwangju indicated that sexual dimorphism does exist in *C. chinensis* (Chiu unpubl. data). Histogram analysis of size distribution of male and female *C. chinensis* in Taiwan populations is needed to confirm what proportion of the variation observed in allometric shell growth is due to sex-related growth among individuals.

Whether the 2 morphotypes documented in the present study represent population divergence responding to different ecological conditions, or 2 different subspecies of *C. chinensis*, or even 2 species of *Cipangopaludina* is worthy of further investigation. *Cipangopaludina* is one of the widely distributed genera of freshwater gastropods on the Asian continent and major islands along the West Pacific. Different authors have yet to reach a consensus on the number of subspecies or species within the genus because of the ambiguities associated with using simple descriptions of morphological characters or biogeographic information (Pace 1973, Brandt 1974, Liu et al. 1975 1995, Chiu et al. unpubl. data). On the contrary, our approaches provide a robust basis to examine the overall performance of morphological variations in the shell and operculum and can elucidate the major contribution of characters in delineating individual snails. Thus, to resolve the taxonomic status of these 2 morphotypes, morphometric measurements and multivariate statistics of samples from different geographic regions that encompass the distribution of the subspecies or species of *Cipangopaludina* should be conducted. In addition, studies using alternative characters (e.g., allozymes, DNA sequences) are currently in progress and will also help to elucidate the evolutionary relationships among morphotypes within species of *Cipangopaludina* snails.

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臺灣產中國圓田螺（軟體動物：腹足綱）之外殼及口蓋形質測量分析

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中國圓田螺是廣布於亞洲地區的淡水螺，受相對成長與環境因子的影響，常造成種內殼形的變異。本研究以形質測量分析法判別產自包括竹子湖、老梅、蘭潭及萬大四個臺灣的族群，與韓國光州的一個族群之中國圓田螺外殼與口蓋形質的變異。以線性迴歸法分析發現中國圓田螺具有外殼異速成長的現象，依此排除外殼相對成長所產生的變異後，再以多元尺度分析和判別分析檢驗十三個外殼及口蓋的測量形質。由這兩種分析顯示，在五個族群中可區分出兩種形態型，分別為長塔型與短塔型。多元尺度分析將竹子湖和老梅兩短塔型族群分為形態相關的一群，而蘭潭、萬大和韓國光州為形態相關的長塔型。判別分析顯示螺塔高是貢獻於族群間判別函數中最主要的形態測量形質。線性迴歸法分析更進一步的指出，長塔型螺塔增長的速率顯著的比短塔型螺塔增長速率快。因此，螺塔高成長速率上的差別是造成中國圓田螺種內具有兩種形態型的主要原因。本文並討論造成兩種形態型相對成長的模式與環境因子間關係。

關鍵詞：形質分析法，田螺，相對成長，形態型。

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