

# Geographical Variations of Rana sauteri (Anura: Ranidae) in Taiwan

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**Wen-Hao Chou and Jun-Yi Lin (1997)** Geographical variations of *Rana sauteri* (Anura: Ranidae) in Taiwan. *Zoological Studies* **36**(3): 201-221. *Rana sauteri* is widely distributed in hills and mountains of Taiwan from 100 to 3000 m in elevation, a range including subtropical to cool temperate climatic zones. Both the gastromyzophorous tadpoles and adults have distinct geographical variations in morphology. Clinal variation in the shape of the upper jaw sheath and the number of labial tooth rows occurs from the foothills of western Taiwan eastward through the Central Mountain Range to the eastern slopes of the Central Mountain Range. This geographical pattern is supported and validated by multivariate analyses of adult morphology. According to the dispersal hypothesis, this geographical pattern may suggest that the dispersal center (= initial range of the ancestral group) was located in the western foothills, and it may indicate that the population expanded radially through the clinally variable transition zone to areas adjacent to the ridge of the Central Mountain Range (= range of the derived group). However, the establishment of the geographical pattern of *R. sauteri* seems to be better explained by the vicariance hypothesis which supports the occurrence of isolation-based dichotomous divergence within this grossly defined taxon.

Key words: Rana sauteri, Biogeography, Clinal variation, Tadpole, Taiwan.

In recent decades, some studies dealing with actual and causal aspects of within-island geographical variation in organisms used Asian island amphibians as a model (e.g., Nishioka et al. 1981, Chen 1984, Matsui 1984, Hayashi and Matsui 1988, Yang et al. 1994). *Rana sauteri* occurs in Taiwan on hills and mountains up to 3000-3500 m throughout almost the entire island (Lue et al. 1990). The considerable climatic variation and complicated geomorphology of Taiwan raises the possibility of local adaptation and geographical morphological variation in this species.

Rana sauteri was initially described from Kanshirei Village (= Quantzelin, Tainan Co.), Taiwan (Boulenger 1909). Smith (1921) described the Vietnamese population as a subspecies, *R. s. johnsi*. The distributional range of *R. sauteri* was further reported to cover Guangxi Province, China (Tien and Jian 1986, Zhao and Adler 1993), but the taxonomic status of the populations both outside and within Taiwan remains uncertain (Kuramoto et al. 1984, Zhao and Adler 1993).

The natural history of Taiwanese R. sauteri had been ignored until Kuramoto et al. (1984) described its life history and ecology. The tadpole of R. sauteri occurs in fast running water and is characterized by having a relatively depressed body, an enlarged oral disc with increased rows of labial teeth, an abdominal sucker, a robust caudal muscle, and lower fins. The larval morphology of R. sauteri, typifying the gastromyzophorus type (Altig and Johnston 1989), is unique among the anuran tadpoles of Taiwan. To date, the larval morphology and ecology of R. s. johnsi is only briefly documented (Smith 1924) but some features, e.g., the depressed head and body, supero-lateral eyes, and widened oral disc with numerous labial tooth rows (5/5), suggest that it belongs to the lotic form. The abdominal sucker and the central notch on the upper jaw sheath evident in R. s. sauteri have

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not been described previously.

In general, subdivisions of biogeography include descriptive and interpretive perspectives. The former deals with the distributional ranges of taxa, taxic compositions, and the formulation of biogeographical regions; whereas the latter elucidates the historical and ecological aspects of the taxa using base line data provided by the former (Wiley 1981). In a global view of interpretive zoogeography of ranids (Savage 1973), the temporaria and esculenta groups represent the northern line of dispersal from the African radiation center via Europe to eastern Asia and into North America. Nearly 2/3 of the species of brown frogs (= temporaria group) occur in eastern Asia, and the group may have had a secondary radiation center there (Kuramoto et al. 1984). These frogs are widely distributed in the Holarctic region except for R. sauteri, R. longicrus, and some Chinese populations of R. japonica (i.e., R. zhenhaiensis, sensu Ye et al. 1995) that occur in the Oriental region (Kuramoto et al. 1984, Frost 1985). In contrast to the view of Kuramoto et al. (1984) who recognized R. sauteri and R. longicrus as closely related brown frogs, Dubois (1992) removed the former from the subgenus Rana and assigned it to the subgenus Pseudorana together with R. sangzhiensis and R. weiningensis, and retained the latter, R. longicrus, in the subgenus Rana while assigning it to the japonica group which is separated from the temporaria group (see also Duellman 1993). These treatments of classification blur the hypothesis that R. sauteri may originate from one of the subgroups of the northern line of dispersal from African radiation. This large-scale historical issue certainly needs further clarification, so therefore, we began concentrating on the Taiwanese R. sauteri by providing a quantitative description of its geographical variation and discussing its historical biogeography in this paper.

In addition, we also have addressed the question of whether speciation occurs within *R. sauteri*, since speciation is commonly associated with a geographical extension of population range (e.g., Moore 1975, Hillis et al. 1983, Jacobs 1987, Hillis and de Sá 1988, Platz 1989). Kuramoto et al. (1984) speculated that divergence had occurred within *R. sauteri* to a degree equivalent to speciation between frogs from lowlands (i.e., Quantzelin, type locality, ca. 300 m) and those from highlands (i.e., Alisan, Chiayi Co., at 2200 m elev.). The patterns of geographical variation of *R. sauteri* provided here yield insights into this issue.

## MATERIALS AND METHODS

#### **Distribution survey**

Distribution surveys were conducted mainly during the breeding season. Preliminary data provided by Kuramoto et al. (1984) suggest that *Rana sauteri* breeds from October to April. However, we found tadpoles almost year round; larval records constitute the most extensive data for our study of the distributional range. We surveyed 170 locations but made no attempt at complete coverage of Taiwan (Fig. 1). Because other authors (e.g., Kuramoto et al. 1984) stated that this species mainly breeds in mountain streams, our survey efforts



Fig. 1. Locations in Taiwan where *Rana sauteri* were (solid dots) or were not (open circle) found. Triangles denote literature records, broken lines delimit the geographical climate districts of Maa (1956). E = Eastern District; M = Montane District; N = Northern District; NE = Northeastern District; S = Southern District; and W = Western District. Scale = 50 km.

focused on such areas. Sampling locations were plotted onto a predefined geographical climatic map to reveal the relationship between climatic factors and the range of the frogs.

Taiwan has been divided into several geographical regions based on climate and vegetation. Lin (1990) described the characteristics of climate, biota, geomorphology, and vegetation of the 6 districts defined by Maa (1956), while Su (1992) proposed a similar system. We adopt Maa's (1956) system (Fig. 1) because of its simplicity, but also consider Su's (1992) climatological interpretation of the relevant districts in the discussion.

#### Larval variations

A total of 1033 larvae from 44 locations (Fig. 3, Appendix I) were examined for 4 oral features; 16 body measurements were also taken for tadpoles at Gosner's (1960) stages 26-38. Oral features include upper jaw sheath form, and counts of continuous tooth rows on the anterior and posterior labia, and of discontinuous tooth rows on the anterior labial tooth rows independent of length.

For the multivariate analysis of morphometric characters, tadpoles from Chihtwan (location 6, N = 10), Wuling (10, N = 30), Madalahsi (11, N =5), Chiayan (18, N = 12), Chiapaotai (19, N = 5), Takeng (21, N = 2), Alisan (30, N = 16), Tsukou (32, N = 8), Quantzelin (33, N = 15), Tapu (34, 10)N = 10, Paolai (36, N = 15), and Machia (42, N = 15) were measured. The following measurements were taken (Altig 1970): 1) head-body length (HBL); 2) tail length (TL)-posterior end of body to tip of tail; 3) tail height (TH); 4) body width (BW)--width at the spiracle; 5) body height (BH); 6) maximum caudal muscle height (CMH); 7) maximum caudal muscle width (CMW); 8) internarial distance (IND)-distance between inner edges of nostrils; 9) interorbital distance (IOD)-distance between inner edges of orbits; 10) eyeball diameter (EBD)diameter parallel to body axis; 11) mouth width (MW)-maximum width of oral disc; 12) snoutspiracle distance (SSD)-tip of snout to insertion of spiracle; 13) snout-nostril distance (SND)-tip of snout to anterior edge of right nostril; 14) eyenostril distance (END)-anterior edge of right eye to posterior edge of right nostril; 15) sucker length (SL)-posterior edge of oral disc to highest point of the posterior edge of sucker; and 16) sucker width (SW)-maximum width of the highest points of both sides. Except for IND, IOD, END, SND, and ED that were measured with an ocular meter, measurements were taken using dial calipers to the greatest 0.01 mm. Canonical discriminant analyses (CANDISC procedure of SAS, the Statistical Analysis System; SAS Institute Inc. 1988) were performed to evaluate variations among samples using log-transformed variables as input data.

#### Adults

The following statistical analyses of selected characters are similar to those used in Matsui (1986). Twenty-five measurements were taken (0.1 mm, dial calipers) from 440 mature frogs (374 males, 66 females) from locations 10-12, 16-19, 21-22, 32-33, and 44-46 in Fig. 7. The mensural characters are: 1) snout-vent length (SVL); 2) head length (HL); 3) snout-tympanum distance (STD); 4) snout-nostril distance (SND); 5) nostril-eve distance (NED); 6) nostril-tympanum distance (NTD); 7) snout-eye distance (SED); 8) eye length (EL); 9) eve-tympanum distance (ETD); 10) tympanum diameter (TD); 11) head width (HW); 12) internarial distance (IND); 13) interorbital distance (IOD); 14) evelid width (EW): 15) head and lower arm length (HLAL); 16) 3rd finger length (TFL); 17) outer palmar tubercle length (OPTL); 18) inner palmar tubercle length (IPTL; for males); 19) thenar tubercle length (TTL; for females); 20) thigh length (THIGH); 21) tibia length (TiL); 22) foot length (FL); 23) tarsus length (TaL); 24) 4th toe length (FTL); and 25) inner metatarsal tubercle length (IMTL).

Individuals from the same sampling site were assigned to the same OTU, but because of sexual dimorphism, males and females were treated separately. Preliminary analyses using ratios to SVL and log-transformed variables as input data vielded similar results, therefore, we only present results for the log-transformed variables herein. Stepwise discriminant analysis (STEPDISC procedure of SAS) selected variables for subsequent analyses. Twenty-one variables in males and 12 variables in females with significant F's-to-enter (p < 0.05) were selected out of the 24 variables. To determine group separations, canonical variate scores of each individual of the OTUs were plotted on their respective axes with canonical discriminant analysis (CANDISC procedure of SAS). OTUs were subsequently pooled according to the grouping of the plots and the analyses of variance that described the significant differences among groups. Pooled groups were then re-tested by a canonical discriminant analysis from which the major contributing variables of each axis were obtained.

The neighbor-joining method (Saitou and Nei 1987) of the NTSYS-pc 1.8 (Rohlf 1993) was used to inspect the membership of pooled groups using distance matrices developed by canonical discriminant analyses.

Geographic and climatic correlates of morphological variation were assessed by methods of Burnett (1983). We used elevation (ELV) to represent the geographical factor, and mean January temperature (M1T), mean July temperature (M7T), mean annual temperature (ANT), mean January precipitation (M1P), mean July precipitation (M7P), and mean annual precipitation (ANP) to represent climatic factors. Principal component analyses (PRICOMP procedure of SAS) of the logtransformed climatic characters and morphological characters were used to reduce the number of independent morphological and climatic variables. A stepwise multiple regression (REG procedure of SAS) established predictive models for morphological variables by incorporating climatic and geological variables. Correlations among the morphological and geoclimatic variables were also obtained by use of the CORR procedure of SAS.

### RESULTS

#### Summary of distribution and habitats

Rana sauteri inhabits hilly and mountainous districts of Taiwan (Fig. 1). The distribution with features of climate, vegetation, and geology are as follows: (I) Northeastern District (similar to Northeast Coastal Region of Su 1992): high annual precipitation with an especially high intensity in winter; vegetation mainly of the Machilus-Castanopsis type; frog uncommon. Larvae were recorded only from Tsukeng (100 m elev.; 7 km southwest of Yuansan, Ilan Co.), on the boundary of this district and the Montane District. This location represents the lowest elevation of occurrence. Lue et al. (1990) discovered R. sauteri at 3 locations (i.e., Chiaohsi, Keelung, and Yangmingshan National Park) within this district. The population sizes at these 3 locations remain unknown, but the frog seems to be extremely rare in Yangmingshan National Park (Lue et al. 1987). (II) Northern District, including Taipei Basin (= Northwest Coastal and the northern corner of the Central West Inland Region of Su 1992): low annual precipitation with relatively high summer precipitation and moderate winter precipitation; vegetation mainly of the Machilus-Castanopsis type near the foothills;

under 500 m elev. with intensive agriculture and dense populations in most areas. The 3 records of R. sauteri occur near the foothills (e.g., Taping, 3 km south of Peipu, Hsinchu Co., 180 m elev.; Wenshuei, Miaoli Co., 350 m elev.; and Shichiao, 3 km southeast of Tungshi, Taichung Co., 350 m elev.), which are adjacent to the Montane District. Lue et al. (1990) found R. sauteri from Yingko, Taoyuan Co. (III) Western District (= Central West Coastal Region and the area under 500 m elev. of the Central West Inland Region and Southwest Region except the southern part of Pingtung Co. of Su 1992): accommodating large areas of agricultural plains, very low annual precipitation with relatively high summer precipitation and especially low winter precipitation; and vegetation mainly of the Ficus-Machilus type near the foothills. Several records from the hilly areas around 300 m elev. are known from our survey (e.g., Takeng and Toubenkeng near Taichung City; Chusan, Nantou Co.; Tsukou, Chungpu, and Tapu, Chiayi Co.; and Quantzelin, Tainan Co. within Su's [1992] Inland Region where the annual precipitation is higher). (IV) Southern District, mainly the area under 500 m



Fig. 2. Upper jaw sheath forms of larval *Rana sauteri*: boomerang form (**B**), deep-notched form (**D**) and shallow-notched form (**S**). See text for definitions.

elev. of the Hengchun Peninsula: summer rain with medium annual precipitation and very low winter precipitation; vegetation near the foothills is the *Ficus-Machilus* type and lowlands are agriculturalized; dramatically windy in winter. Su (1992) separated the Hengchun Peninsula into eastern and western parts based on different climates. *R. sauteri* was not found here. (V) Eastern District, including the Taitung Longitudinal Valley and to the east, the Coastal Mountain Range. Geologically, the Coastal Mountain Range represents the leading edge of the Philippine Sea Plate, and the Longitudinal Valley is the collision suture between the Central Mountain Range and the Coastal Mountain Range (Ho 1982). *R. sauteri* was not found here. (VI) Montane District, including the mountainous areas in the central part of Taiwan that include most inland regions and the area near the Central Mountain Range of the East region defined by Su (1992): various types of climate and vegetation and complicated geomorphology; medium to high annual and winter precipitation. The Central Mountains extend north-south through this district and divide it into western and eastern slopes with dramatically different climates. Most rivers originate in the Central Mountains and then flow east or west. Our data suggest that *R. sauteri* is widely distributed in this district from the foothills to the "upper montane zone". The highest breeding population was at Dayuling (2560 m), Taichung



Fig. 3. Frequency distribution of upper jaw sheath forms for larval *Rana sauteri* at each sampling location. Broken lines represent postulated borderlines of isofrequency zones—Left of the left line: 100% S form; between left and middle lines: 100% D form and/or with S form; between middle and right lines: combination of B and D forms; right of the right line: 100% B form. **B**: boomerang; **D**: deep-notched; and **S**: shallow-notched forms. The pie diagram size is proportional to sample size. Refer to Appendix I for detailed description of and sample size in each numbered locality. Jaw sheath forms of Fig. 2S-c (\*) and Fig. 2S-a (\*\*) were found in the samples. Scale = 50 km.

Co. within the *Tsuga-Picea* vegetation zone. Lue et al. (1990) gave a record between 3000 and 3500 m elev. which is in the "subalpine zone". This district extends partly to the Hengchun Peninsula where *R. sauteri* was not found. The southernmost record was from Dahansan (1400 m), Pingtung Co. at the southern end of the Central Mountain Range.

River drainages create various stream habitats in which *R. sauteri* mates and breeds. Tadpoles are usually associated with fast-flowing waters that range from rivers in wide, open valleys (width ca. 7-8 m, with pebble, cobble, or small boulder bottom, usually with low or high gradient riffles) to steep streams in dense forests (width ca. 0.5 m, with gravel bottom). Eggs were usually found under the downstream side of rocks at a depth of 10-15 cm. Tadpoles were also found in secondary channels, backwater pools, plunge pools, and behind stream dams where the current was slow or absent. Tadpoles and eggs were occasionally observed in ponds in highland forests and seepage habitats with trickling water. In the lowlands, tadpoles were never found in ponds.

### **Tadpole** variation

Upper jaw sheath: Three categories of upper jaw sheath are based on the contour of the cutting edge (Fig. 2). The inverted V-shaped "boomerang form" (Fig. 2B), characterized by finely serrated, relatively straight cutting edges that form a nearly



Fig. 4. Frequency distribution of the number of anterior continuous labial tooth rows for larval *Rana sauteri* at each sampling location. Broken lines represent postulated borderlines of isofrequency zones—Left of left line: 100% with 2 rows; between lines: combination of 2 and 3 rows; right of right line: 100% with 3 and/or 4 rows. The legend denotes the number of rows. The pie diagram size is proportional to sample size. Refer to Appendix I for detailed description of and sample size in each numbered location. Scale = 50 km.

right angle, was most common among samples from the eastern and western slopes of the Central Mountain Range (Fig. 3). There is a large scraping surface inside the cutting edge at the angle. The 2nd "deep-notched" form had a large central notch. curvy cutting edges, and an evident scraper, with variation in contour shape of the cutting edge (Fig. 2D). Most individuals showing this condition were from the foothills near the border of the Northern and Montane Districts (Fig. 3; Neipu [location 12], Taian [13] and Wensuei [14]) and mid-elevations of the central and southern Montane District (e.g., Chiapaotai [19], Hopin [20], Lienhwachih [23], Hsitou [27], Fengchihu [31], Paolai [36], Tsuyunsan [37], and Machia [42]). In specimens from the foothill regions of the Western District (e.g., Takeng [21], Toubenkeng [22], Tsukou [32], Quantzelin [33], Tapu [34], and Sanmin [35]), upper jaw sheaths were "shallow-notched" with a small central notch (Fig. 2S). The scraping surface described above was not evident. The size and contour of cutting edges vary slightly. The jaw sheath form of Fig. 2S-a was found only at Sanmin [35]. Some tadpoles collected from Tsukou [32] had the jaw sheath form of Fig. 2S-c.

The 3 major forms of the upper jaw sheath and their variants illustrated in Fig. 2 may constitute a hypothetical transformation series, of which the central notches range from ones as in Fig. 2S-c through the inverted V-shaped form by gradual changes of the notch size and the contour of the cutting edges.

**Fig. 5.** Frequency distribution of the number of anterior discontinuous labial tooth rows for larval *Rana sauteri* at each sampling location. Broken lines represent postulated borderlines of isofrequency zones—Left of left line: 100% with 3 rows; between lines: combination of 3 and 4 rows; right of right line: 100% with 4 and/or 5 rows. The legend denotes the number of rows. The pie diagram size is proportional to sample size. Refer to Appendix I for detailed description of and sample size in each numbered locality. Scale = 50 km.

Labial tooth rows: The number of continuous anterior labial tooth rows varied from 2 to 4 (Fig. 4). Only a few individuals from Nansan [8] and Chiayan [18] in the northern Montane District had 4 rows. Most samples from the vicinity of the Central Mountain Range had 3 continuous anterior labial tooth rows. On the contrary, tadpoles from the foot hills and most mid-elevation (i.e., 500 to 1500 m) samples had 2 continuous anterior labial tooth rows. Several samples from locations at mid-elevations (Taian [13], Chiapaotai [19], Hsitou [27], and Fengchihu [31]) included both individuals having 2 and 3 continuous anterior rows of labial teeth.

Like the continuous anterior row, there was a trend in which the samples from the vicinity of the

Central Mountain Range in the Montane District had more discontinuous anterior labial tooth rows (Fig. 5) than those of other areas; most individuals had 4 pairs, yet some from the highlands and lowlands on the eastern slope had 5. All individuals from Takeng [21], Toubenkeng [22], Tsukou [32], Quantzelin [33], and Tapu [34] had 3 pairs. Most mid-elevation samples had combinations of individuals with either 3 or 4 pairs. The number of continuous posterior labial tooth rows varied greatly from 4 in samples from the foothills of the Western District (at Takeng [21], Toubenkeng [22], Quantzelin [33], and Tapu [34]) to 9 in samples from the eastern and western slopes of the Central Mountain Range (Fig. 6).



**Fig. 6.** Frequency distribution of the number of posterior continuous labial tooth rows for larval *Rana sauteri* at each sampling location. Broken lines represent postulated borderlines of isofrequency zone—Left of left line: > 50% with 4 rows; between left and middle left lines:  $\ge 50\%$  with 5 rows; between middle lines: > 50% with 6 rows; between middle right and right lines:  $\ge 50\%$  with 7 rows; right of right line:  $\ge 50\%$  with 8 and/or 9 rows. The legend denotes the number of rows. The pie diagram size is proportional to sample size. Refer to Appendix I for detailed description of and sample size in each numbered location. Scale = 50 km.

Integrated examination of the geographical variation in oral disc characters (Figs. 3-6) allowed the samples to be classified into 3 groups. Samples 21-22 and 32-34 from the western foothills included all individuals with shallow-notched sheaths, all of which had 2 continuous anterior labial tooth rows. 3 pairs of discontinuous anterior labial tooth rows, and 4 or 5 (mostly 4) posterior labial tooth rows (group I, Table 1). The collective labial tooth row formula (= semi-condensed collective keratodont formula, SCCKF; Dubois 1995) for this group is  $5[A_3-A_5]/5-6[P_1]$ . Group II, consisting of the samples 12-14, 19-20, 23, 27, 31, 35-37, and 42, was characterized by various sheath forms and an SCCKF of 5-7[(A<sub>3</sub>-A<sub>5</sub>)-(A<sub>3</sub>-A<sub>7</sub>)]/6-9[P<sub>1</sub>]; the association of the number of labial tooth rows and upper sheath form is complicated in this group (Table 1). Samples 1-11, 15-18, 24-26, 28-30, 38-41, and 43-44 included all individuals with boomerangshaped sheaths, all of which had more than 3 continuous anterior labial tooth rows, more than 4 pairs of discontinuous anterior labial tooth rows (but there were 6 specimens from samples 8 and 10 that had only 3 pairs), and more than 6 (mostly 7 or 8) posterior labial tooth rows. Samples coming from the Central Range comprised group III (Table 1). The SCCKF can be written as 6-8[(A<sub>4</sub>-A<sub>6</sub>)-(A<sub>5</sub>-A<sub>8</sub>)]/7-10[P<sub>1</sub>]. Note that groups I and III differ from each other in having disparate upper sheath forms at the extremes of the hypothetical transformation series (Fig. 2) and the absence of overlap in any labial tooth row character. The geographic range of group II is considered to constitute a transitional zone between those of groups I and III. The possible limits of the 3 groups are given in Fig. 7, in which the line dividing groups II and III passes through Taian [13], Hsitou [27], and Fengchihu [31] where both larval forms were collected. Although the sample from Sanmin [35] invariably had shallow-notched sheaths, it contained

Group	Upp sheat	er jaw h form	Cont anteri to	Continuous anterior labial tooth		Discontinuous anterior labial tooth		inuous ior labial oth	Dental structure	
	form	%	row	%	row	%	row	%	formula	%
	В	0.0	2	100.0	3	100.0	4	96.1	5[A <sub>3</sub> -A <sub>3</sub> ]/5[P <sub>1</sub> ]	96.1
I	D	0.0	3	0.0	4	0.0	5	3.9	5[A <sub>4</sub> -A <sub>5</sub> ]/6[P <sub>1</sub> ]	3.9
	5	100.0	4	0.0	5	0.0	6	0.0		
	form	%	row	%	row	%	row	%	formula	%
	В	31.5	2	77.2	3	46.5	4	3.8	5[A <sub>3</sub> -A <sub>5</sub> ]/6-7[P <sub>1</sub> ](B)	1.6
	D	62.8	3	22.3	4	53.3	5	56.3	6[A <sub>3</sub> -A <sub>6</sub> ]/6-7[P <sub>1</sub> ](B)	11.9
	S	5.7	4	0.0	5	0.2	6	26.9	7[A <sub>3</sub> -A <sub>7</sub> ]/6[P <sub>1</sub> ](B)	0.2
							7	11.6	6[A <sub>4</sub> -A <sub>6</sub> ]/6-7[P <sub>1</sub> ](B)	4.6
							8	1.4	6[A <sub>4</sub> -A <sub>6</sub> ]/8-9[P <sub>1</sub> ](B)	3.4
							9	0.0	7[A <sub>4</sub> -A <sub>7</sub> ]/6-7[P <sub>1</sub> ](B)	0.9
									7[A <sub>4</sub> -A <sub>7</sub> ]/8-9[P <sub>1</sub> ](B)	8.9
									5[A <sub>3</sub> -A <sub>5</sub> ]/5[P <sub>1</sub> ](D)	2.7
II .									5[A <sub>3</sub> -A <sub>5</sub> ]/6-7[P <sub>1</sub> ](D)	19.1
									6[A <sub>3</sub> -A <sub>6</sub> ]/6-7[P <sub>1</sub> ](D)	30.8
									6[A <sub>4</sub> -A <sub>6</sub> ]/6-7[P <sub>1</sub> ](D)	9.3
									7[A <sub>4</sub> -A <sub>7</sub> ]/7[P <sub>1</sub> ](D)	0.2
									7[A <sub>4</sub> -A <sub>7</sub> ]/8-9[P <sub>1</sub> ](D)	0.7
									5[A <sub>3</sub> -A <sub>5</sub> ]/6-7[P <sub>1</sub> ](S)	1.1
									5[A <sub>3</sub> -A <sub>5</sub> ]/6-7[P <sub>1</sub> ](S)	4.1
									6[A <sub>3</sub> -A <sub>6</sub> ]/6-7[P <sub>1</sub> ](S)	0.5
	form	%	row	%	row	%	row	%	formula	%
	В	100.0	2	0.0	3	1.0	4	0.0	6[A <sub>4</sub> -A <sub>6</sub> ]/8-10[P <sub>1</sub> ]	0.7
	D	0.0	3	99.3	4	95.0	5	0.0	7[A <sub>4</sub> -A <sub>7</sub> ]/7[P <sub>1</sub> ]	0.7
III	S	0.0	4	0.7	5	4.0	6	0.7	7[A <sub>4</sub> -A <sub>7</sub> ]/8-10[P <sub>1</sub> ]	93.9
							7	39.3	8[A <sub>4</sub> -A <sub>8</sub> ]/8-10[P <sub>1</sub> ]	4.0
							8	55.7	7[A <sub>5</sub> -A <sub>7</sub> ]/8-10[P <sub>1</sub> ]	0.3
							9	4.3	8[A <sub>5</sub> -A <sub>8</sub> ]/8-10[P <sub>1</sub> ]	0.4

Table 1. Variation of oral disc structure in larval Rana sauteri. See text for definitions of groups

Upper jaw sheath forms are: boomerang form (B), deep-notched form (D), and shallow-notched form (S).

12% of individuals with 4 discontinuous anterior labial tooth rows and 83% with 5 continuous posterior labial tooth rows. We assigned this sample to group II. This jaw sheath form (Fig. 2S-a) is considered to represent an intermediate condition between the shallow-notched and deep-notched forms. Figure 8 gives the 3 representative oral disks which had the highest proportions in samples of groups I, II, and III, respectively (Table 1).

Multivariate analysis of larval morphometric characters: The values for the 4 criteria in this



analysis (e.g., Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root Statistics) were significant at the p < 0.0001 level which indicates significant geographical correlations. Figure 9 illustrates plots of the canonical variables of tadpoles representing groups I (N =35, pooled from samples from Takeng [21], Tsukou [32], Quantzelin [33], and Tapu [34]), II (N = 45,



Fig. 7. Zoogeographical divisions of larval *Rana sauteri*. Broken lines delineate ranges of larval groups I, II, and III. See text for classification of groups. Refer to Appendix I for detailed description of and sample size in each numbered location. Scale = 50 km.

**Fig. 8.** Three representative oral disc forms of larval *Rana* sauteri: group I form (bottom), group II form (middle), and group III form (top). Scale = 1 mm.

pooled from samples from Chiapaotai [19], Paolai [36], and Machia [42]), and III (N = 73, pooled from samples from Chihtwan [6], Wuling [10], Madalahsi [11], Chiayan [18], and Alisan [30]). The 1st canonical variable (CAN 1) separates group III from groups I and II with a slight overlap. Groups I and II can be separated by the 2nd canonical variable (CAN 2) but with a substantial overlap.

Table 2 gives the standardized canonical coefficients of the 1st and 2nd variables that describe 84.5% and 15.5% of the total variance, respectively. The best discriminant variables for CAN 1 are eyeball diameter, snout-spiracle distance, tail length, mouth width, head-body length, and sucker length in that order, while those for CAN 2 are body depth, snout-nostril distance, eyeball diameter, and body width. In general, group III tadpoles differ from tadpoles of groups I and II by having a relatively small eye, wide mouth, short HBL, long snout-spiracle distance, long abdominal sucker, and long tail. Group II tadpoles have a relatively deep and narrow body, small eye, and long snoutnostril distance compared to group I tadpoles.

# Multivariate analyses of adult morphometric characters

Canonical discriminant analyses: Figure 10



**Fig. 9.** Canonical plots of the first 2 axes for larval *Rana sauteri*. Open circles, open triangles, and solid dots denote samples from the range of larval groups I, II, and III, respectively.

illustrates both exploratory and confirmatory plots of the canonical variables of adult males and females. The values of the 4 criteria in each analysis (e.g., Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root Statistics) were significant at the p < 0.0001 level which indicates significant geographical correlations to variation.

In the exploratory analysis of males, the first 3 axes accounted for 59.1%, 13.2%, and 7.7% of the variance in the data, respectively. We present the plot of the first 2 axes (Fig. 10a) for 3 reasons: (1) Plots of the first 2 canonical variables and that of the 1st against the 3rd canonical variable gave similar patterns of sample separation. (2) No clear separation was displayed in the plot of the 2nd against the 3rd canonical variables. (3) The first 2 axes interpreted jointly account for more than 2/3 of the entire dispersion. The 1st canonical variable (CAN 1) may not completely separate samples into distinct groups. The 3 best discriminant variables are NTD, HLAL, and HL in that order (Table 3). Samples collected from the range of larval group I (Fig. 10a; e.g., Takeng [21], Toubenkeng [22], Tsukou [32], and Quantzelin [33]), while showing extensive overlaps with each other, were collectively separated from those from the range of larval group III (e.g., Chihtwan [6], Wuling [10], Madalahsi [11], Davuling [17], Chiavan [18],

**Table 2.** Standardized canonical coefficients ofthe first 2 variables in multivariate analyses forlarval Rana sauteri

Larval characters	CAN1	CAN2
Head-body length	-0.784 <sup>a</sup>	-0.402
Tail length	-1.035 <sup>a</sup>	-0.234
Tail height	0.343	-0.030
Body width	0.276	-0.697
Body depth	0.069	1.748 <sup>a</sup>
Caudal muscle height	0.162	0.049
Caudal muscle width	-0.015	0.351
Internarial distance	-0.184	-0.224
Interorbital distance	0.360	0.295
Eyeball diameter	1.488 <sup>a</sup>	–0.939 <sup>a</sup>
Mouth width	-0.841 <sup>a</sup>	-0.403
Snout-spiracle distance	-1.267 <sup>a</sup>	0.397
Snout-naris distance	0.261	1.040 <sup>a</sup>
Eye-naris distance	0.216	-0.372
Sucker length	-0.716 <sup>a</sup>	-0.129
Sucker width	-0.081	0.344
Eigenvalue	3.39	0.61
Proportion (%)	84.5	15.5

<sup>a</sup>Bold face indicates the values of best discriminating variables.

and Alisan [30]). The latter samples also exhibited extensive within-group overlaps. Samples from Neipu [12], Chiapaotai [19], and Machia [42] that exemplify larval group II exhibited expansive dispersion, and the Machia sample [42], while being disparate from group II members, falls within the range of group I. The 2nd canonical variable (CAN 2), predominated by TiL, SVL, NTD, and FTL in that order (Table 3), shows inevident separation. Group I is not clearly separated from the remainder, either, along the CAN 2 axis.

The pattern of sample dispersion in females is similar to that of males (Fig. 10c). The 1st canonical variable, accounting for 52.7% of the dispersion, discriminates the group of samples from larval Group III (e.g., Wuling [10], Alisan [30], and Yunhai [46]) from the remaining samples with certain overlaps with the sample from Quantzelin [33]. The 2nd axis, accounting for 21.0% of the dispersion, further isolates the Chiapaotai [19] sample of larval Group II from the others. Analysis of the standardized canonical coefficients (Table 3) revealed that NTD made the greatest contribution to the separation on the 1st axis, followed by SVL and FL in that order. Regarding the separation along the 2nd axis, THIGH, FL, EW, STD, and TaL made the greatest contributions in that order.

Based on these groups, we pooled the samples belonging to the same larval group into 1 OTU for discriminant analyses. Plots of canonical variables for pooled OTUs in males showed discrete dispersion between groups I and III (Fig. 10b). The major contributing characters with dominant standardized canonical coefficients were similar to those for the original analyses (Table 3). Linear discriminant function analysis (Table 4) misclassified



Fig. 10. Exploratory canonical plots (a, c) and confirmatory plots (b, d) of the first 2 axes for adult *Rana sauteri*. In plots a and c, thin lines, broken lines, and bold lines denote samples from the distribution divisions of larval groups I, II, and III, respectively. Refer to Appendix I for description of the numbered location. In plots b and d, open circles, open triangles, and solid dots denote samples from the range of larval groups I, II, and III, respectively.

only 7 out of 158 (4.4%) belonging to group I, 19 of 80 (23.8%) in group II, and 2 of 136 (1.5%) in group III for adult males. No misclassifications occurred between groups I and III. Group II males were more frequently misclassified into group I (15.0%) than to group III (8.8%). In females, the

discriminant plot shows a slight overlap between groups I and III (Fig. 10d) with less than 5% misclassification between them (Table 4).

*Cluster analyses*: In males, the midpoint-rooted neighbor-joining tree (Fig. 11a) shows that the 1st dichotomy is located between samples from Takeng

**Table 3.** Standardized canonical coefficients of the first 2 variables in exploratory and confirmatory multivariate analyses for adult male and female *Rana sauteri*. See Appendix II for character abbreviations

		MA	LE	#t_	FEMALE				
	Explo	oratory	Confir	matory	Explo	Exploratory		matory	
	CAN1	CAN2	CAN1	CAN2	CAN1	CAN2	CAN1	CAN2	
NTD	1.143 <sup>a</sup>	-1.019 <sup>a</sup>	1.228 <sup>a</sup>	-0.502	2.144 <sup>a</sup>	0.456	2.272 <sup>a</sup>	-0.284	
TiL	0.300	1.046 <sup>a</sup>	-0.185	-0.038					
TaL	-0.445	0.403	-0.290	0.867 <sup>a</sup>	0.240	-0.935	0.100	1.025 <sup>a</sup>	
OPTL	0.383	0.108	0.362	0.010	-0.023	-0.620	0.157	0.488	
SVL	0.647	-1.031 <sup>a</sup>	0.499	–0.790 <sup>a</sup>				,	
SND	-0.130	0.263	-0.214	0.113	-0.411	0.159	-0.105	-0.264	
ETD	0.033	-0.191	-0.059	-0.293					
HLAL	0.995 <sup>a</sup>	-0.292	0.613 <sup>a</sup>	-0.170					
TFL	-0.303	0.443	-0.472	0.302	0.231	0.768	0.122	-0.370	
ED	0.052	-0.126	0.040	-0.167					
HW	-0.444	0.591	-0.432	0.096					
TD	0.061	0.284	-0.152	0.159	1.879 <sup>a</sup>	0.021	1.441 <sup>a</sup>	-0.169	
IPTL	0.004	0.453	-0.128	0.068					
EW	0.216	-0.102	0.374	0.294	-0.252	1.291 <sup>a</sup>	-0.057	-1.110 <sup>a</sup>	
THIGH	-0.276	-0.062	-0.074	0.726 <sup>a</sup>	-0.246	-1.830 <sup>a</sup>	–1.380 <sup>a</sup>	1.647 <sup>a</sup>	
FTL	-0.311	-0.727 <sup>a</sup>	-0.027	-0.408					
NED	-0.106	-0.186	0.124	0.165					
HL	0.704 <sup>a</sup>	0.313	0.442	0.716 <sup>a</sup>					
IOD	-0.106	0.188	-0.006	0.202					
IND	-0.067	0.413	-0.142	0.479	-0.366	0.423	-0.312	-0.406	
FL	0.238	0.325	0.229	0.430	-1.299 <sup>a</sup>	1.654 <sup>a</sup>	-0.842	–2.062 <sup>a</sup>	
STD			•		0.262	–1.020 <sup>a</sup>	0.467	1.302 <sup>a</sup>	
IMTL	•				-0.674	0.044	-0.436	-0.057	
Eigenvalue Proportion	6.57	1.47	3.53	0.63	6.02	2.40	4.65	2.07	
(%)	59.1	13.2	84.5	15.1	52.7	21.0	69.2	30.8	

<sup>a</sup>Bold face indicates values of best discriminating variables.

Table 4.	Misclassification	rates in	confirmatory	canonical	discriminant	analyses	for	adult
male and	female Rana sau	ıteri						

	<u> </u>	Ma	ale	Female				
From Group	i	11		Total		II		Total
I	151 (95.6)	7 (4.4)	0 (0)	158	24 (96)	0 (0)	1 (4.0)	25
II	12 (15.0)	61 (76.2)	7 (8.8)	80	0 (0)	3 (100)	0 (0)	3
III	0 (0)	2 (1.5)	134 (98.5)	134	1 (2.6)	0 (0)	36 (97.4)	37

[21], Toubenkeng [22], Tsukou [32], Quantzelin [33], and Machia [42] and the remaining samples, and the former represents populations classified into larval group I, except for the Machia [42] sample which was preassigned to group II. In the



**Fig. 11.** Phenograms of adult male (a) and female (b) resulting from the neighbor-joining method using Mahalanobis distances obtained from canonical analyses.

other cluster including samples of larval groups II and III, the 1st dichotomy separates the samples of Wulai [45; group III] and Neipu [12; group II] from those of group III and the sample Chiapaotai [19; group II]. These results are congruent with the dispersion pattern in the canonical discriminant analysis.

In the midpoint-rooted neighbor-joining tree of females (Fig. 11b), the 1st dichotomy separates the Chiapaotai sample [19; group II] from the other samples, in which samples from locations within the range of larval group III (i.e., Wuling [10], Alisan [30], and Yunhai [46]) and ones within group I tend to cluster together, respectively.

Geoclimatic correlates: Table 5 summarizes the character loadings, eigenvalues, and the proportion of variance of the morphological principal components. In males, the 1st principal component of head (PC1H) is a factor expressing a longitudinal dimension and shape with STD, HL, NTD, HW, and SED having high loadings. PC2H, on which the loadings in order of importance are ETD, SND, and IND, represents a variable of distance between the tympanum and eye and the triangular area between the snout and nostrils. The 1st principal component of limb (PC1L) in males is a general factor of limbs and body, and PC2L is the factor of limb tubercles. In females, PC1H, like in males, is a factor representing the longitudinal dimension, and PC2H tends to describe the distance between snout and nostril. Similar

**Table 5.** Loadings of morphological variables in adult *Rana sauteri* with eigenvalues and percentage of variance explained on principal component analyses. See Appendix II for character abbreviations

Head	Ma	ale	Fer	Female		M	ale	Fer	nale
character	PC1H	PC2H	PC1H	PC2H	character	PC1L	PC2L	PC1L	PC2L
HL	0.337 <sup>a</sup>	0.054	0.325 <sup>a</sup>	-0.075	SVL	0.336 <sup>a</sup>	0.046	0.339 <sup>a</sup>	-0.025
STD	0.342 <sup>a</sup>	0.068	0.303 <sup>a</sup>	-0.258	HLAL	0.350 <sup>a</sup>	-0.111	0.326 <sup>a</sup>	-0.144
SND	0.187	–0.549 <sup>a</sup>	0.105	0.834 <sup>a</sup>	TFL	0.285	-0.147	0.328 <sup>ª</sup>	-0.080
NED	0.271	0.267	0.312 <sup>a</sup>	-0.046	OPTL	0.232	0.522 <sup>ª</sup>	0.200	0.482 <sup>a</sup>
NTD	0.330 <sup>a</sup>	0.203	0.319 <sup>a</sup>	-0.135	IPTL	0.147	0.738 <sup>a</sup>		
SED	0.312 <sup>a</sup>	-0.086	0.311 <sup>ª</sup>	0.077	THIGH	0.328 <sup>a</sup>	-0.013	0.348 <sup>a</sup>	-0.029
ED	0.288	0.026	0.278	-0.285	TiL	$0.350^{a}$	-0.020	0.347 <sup>a</sup>	-0.089
ETD	0.107	0.614 <sup>a</sup>	0.252	0.027	FL	0.343 <sup>a</sup>	-0.172	0.342 <sup>a</sup>	-0.115
TD	0.296	0.025	0.287	-0.069	TaL	0.302 <sup>a</sup>	- 0.194	0.331 <sup>a</sup>	-0.039
HW	0.319 <sup>a</sup>	-0.033	0.314 <sup>a</sup>	-0.003	FTL	0.335 <sup>a</sup>	-0.171	0.312 <sup>ª</sup>	-0.005
IND	0.239	-0.421 <sup>a</sup>	0.216	0.200	IMTL	0.237	0.223	0.242	0.043
IOD	0.195	-0.105	0.228	0.142	TTL			0.082	0.845 <sup>a</sup>
EW	0.274	0.050	0.272	0.245					
Eigenvalue	7.93	1.14	9.07	1.18		7.25	1.14	7.38	1.09
Proportion (%)	61.0	8.8	69.8	7.9		66.9	10.3	67.1	1.0

<sup>a</sup>Bold face indicates relatively important values.

to males, PC1L and PC2L of females represent limb length and limb tubercles, respectively. In the principal component analyses of climatic factors, those with eigenvalues > 1 were extracted (Table 6). PC1Ts of both sexes were general temperature variables that explained approximately 96% and 99% of the total variance. PC1P and PC2P of both sexes represented general rainfall, mean January precipitation, and annual precipitation. In males PC1P explained 57.3% of the variance and PC2P explained 39.6%, whereas PC1P explained 64.1% and PC2P 33.2% of the total variance in females.

Bivariate correlation coefficients indicate a successful solution to the problem of multicollinearity within sets of morphological variables or climatic variables (Table 7), but significant relationships exist between sets of morphological and the geoclimatic variables. In both sexes, principal components of some head and limb variables were correlated significantly, possibly indicating that variability in these structures depends upon similar sets of environmental variables. Strong correlations among geoclimatic variables (Table 7) suggest that there may be redundancy in the data set; this would make only a few predictors emerge during the selection of stepwise multiple-regression analyses (Table 8). Regression models of PC1H and PC1L in both sexes and PC2L in females had more explanatory power. In males, the 1st principal component of precipitation is the most significant explanatory factor considered for PC1H and PC1L. This suggests that frogs with larger heads, and longer limbs and SVLs occur in environments with more rainfall in July and less in January. Likewise, female frogs with larger heads occur in warmer climates; frogs with longer limbs and SVLs in environments with high rainfall in July and low in January; and frogs with larger palmer tubercles in environments with more rainfall in January and high annual precipitation.

## DISCUSSION

# Descriptive biogeography of Rana sauteri

We conclude that Rana sauteri is a montane

Temperature character	Male	Female	Precipitation character	Ma	ale	Fer	nale
	PC1T				BC2B		
=	POT	FOIT		FOIF	FUZF	FOIR	F UZF
M1T	0.574	0.576	M1P	-0.503	0.673	-0.509	0.695
M7T	0.581	0.579	M7P	0.746	0.021	0.716	0.000
ANT	0.577	0.578	ANP	0.436	0.739	0.492	0.718
Eigenvalue	2.88	2.97	Eigenvalue	1.72	1.19	1.92	1.00
Proportion (%)	96.0	98.9	Proportion (%)	57.3	39.6	64.1	33.2

**Table 6.** Loadings of climatic variables of locations from which adult *Rana sauteri* were collected, with eigenvalues and percentage of variance explained on principal component analyses

**Table 7.** Pearson product-moment correlations among principal components of morphological variation and geoclimatic variation for male ( $\circ \circ \circ$ ) and female ( $\circ \circ \circ$ ) Rana sauteri

	PC1H	PC2H	PC1L	PC2L	ELV	PC1T	PC1P	PC2P	
PC1H		0.001	0.892****	-0.023	-0.590****	0.683****	0.580****	-0.520****	
PC2H	-0.007		-0.005	-0.067	-0.315****	0.368****	-0.060	-0.127**	
PC1L	0.698****	-0.396***		0.002	-0.490****	0.605****	0.639****	0.465****	0° 0'
PC2L	-0.667****	-0.273*	-0.003		0.050	-0.053	0.109*	-0.005	
ELV	0.790****	0.001	-0.451***	0.629****		-0.904****	-0.245****	0.648****	
PC1T	0.967****	-0.035	0.668****	-0.657****	-0.912****		0.358****	-0.717****	
PC1P	0.675****	-0.375**	0.986****	0.018	-0.336**	0.603****		-0.011	
PC2P	-0.667****	-0.273*	-0.003	1.000****	0.629****	-0.657****	0.018		
_			φφ.						

\* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001; \*\*\*\* p < 0.0001; \*\*\*\* p < 0.0001.

species in Taiwan. In spite of outliers in the tropical climatic zone, R. sauteri was found from subtropical areas through areas equivalent to cool temperate zone. This distributional range largely corresponds to the range enclosed within the 20 °C isotherm on the map of normal annual daily temperature and above the 1 600-mm isohyet of normal annual total precipitation (Central Weather Bureau 1990); apparently R. sauteri tends to inhabit cool, humid areas. It is commonly hypothesized that certain Palaearctic animals dispersed to the Oriental region during the glacial age and emigrated into Taiwan via a land bridge that connected Taiwan and southeastern China. After the glacial retreat, these cool-adapted animals persisted in the highlands of Taiwan (Kano 1940, Hachisuka and Udagawa 1950, Lin and Lin 1983). The distribution of R. sauteri in the Montane District of Taiwan may be explained by the same scenario. As currently understood, the closely related species of R. sauteri, R. sangzhiensis, R. weiningensis (Dubois 1992, Duellman 1993), and R. sauteri johnsi mainly occur in areas about 1500 m elev. in the Oriental region of China and Vietnam (Smith 1921, Liu et al. 1962, Shen 1986, Ye et al. 1993). This implys their Palaearctic origin.

The local distributions of amphibians may be determined by their tolerances of moisture or temperature or both (reviewed by Duellman and Trueb 1986). The combination of stream habitat availability, vegetation, and microclimate characteristics, such as temperature and precipitation,

seems to be the primary factor limiting the distribution of R. sauteri in Taiwan. Human activities that disturb their habitats may also affect the present range. Absence of R. sauteri in the lowlands where agricultural and residential areas are common is not surprising. Its absence in the southernmost part of Maa's (1956) Montane District is another example. We made a survey from the foothills in the vicinity of Dahansan (44) at the southern distributional limit to the top of the mountain at 1200 m. Undoubtedly, deforestation has severely altered the original vegetation under 1200 m and has caused the local absence of R. sauteri. Certain amounts of undisturbed vegetation and clear streams still remain in the Southern District. The absence of R. sauteri in this region may be attributed to human activity and to the peculiar tropical climate which features high annual temperatures, rigorous droughts, and severe winds in the winter.

Rana sauteri presumably does not occur in the Eastern District because of the presence of the Longitudinal Valley, a natural barrier that would prohibit the dispersion of a montane frog, rather than because of a lack of appropriate habitats or climate. Rarity of *R. sauteri* in Yangmingshan, Northeastern District, may be explained by a similar situation. Limited dispersal abilities may result in the absence of the frog in regions where conditions appear optimal. For example, this may explain the relatively few populations on the eastern slope of the Central Mountain Range of the Montane District in comparison with the western slope. The

**Table 8.** Results of stepwise multiple-regression analyses of morphological and geoclimatic variables in male and female *Rana sauteri*. For each dependent variable the information given includes: 1) step entered (in parentheses); 2) significance to enter, 3) standardized regression coefficient when all selected variables were included, and 4) coefficients of multiple determination  $(R^2)$ 

		PC1H		PC	PC2H		PC1L		PC2L	
	ELV	(4)NS	-0.14	(1)*	0.64	(4)NS	0.16	(4)NS	-0.19	
	PC1T	(1)****	0.24	(2)****	1.06	(3)*	0.20	(1)*	-0.33	
0, 0,	PC1P	(2)****	0.49	(3)****	0.39	(1)****	0.59	(2)***	0.21	
	PC2P	(3)****	-0.30	(4)****	0.41	(2)****	-0.36	(3)*	-0.19	
		$R^2 = 0.63$		$R^2 = 0.28$		$R^2 = 0$	0.62	$R^2 = 0.04$		
	ELV	(2)****	-1.06	(3)*	2.32	(2)****	-0.65			
	PC1T	(1)****	1.26	(4)*	1.66	(4)***	-0.16			
φç	PC1P	(4)NS	0.04	(1)**	-1.07	(1)****	0.97			
	PC2P	(3)****	-0.11	(2)NS	0.19	(3)****	0.07	(1)****	1.00	
		R <sup>2</sup> =0	).99	$R^2 = 0$	0.29	$R^2 = 0$	0.99	$R^2 = 1$	1.00	

NS p > 0.05; \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001; \*\*\*\* p < 0.001; \*\*\*\* p < 0.0001.

Central Mountain Range inevitably impedes dispersal.

# Interpretive biogeography on larval Rana sauteri variation

The gastromyzophorus larva of Rana sauteri, very peculiar among species of the subgenus Pseudorana (Liu et al. 1962, Shen 1986), inhabits fast running water and maintains its position by use of the abdominal sucker and oral disc. Parts of the oral apparatus of larval *R. sauteri* vary greatly across the distributional range in Taiwan. The number of both anterior and posterior labial tooth rows and the depth of the median notch of the upper jaw sheath (Figs. 3-6) gradually increase, for example, from Takeng [21; 300 m] to Dayuling [17: 2560 m] along the Dachiahsi drainage or from Tsukou [32; 300 m] to Alisan [30; 2200 m] along the Tzenwenhsi drainage. In view of their structure and function, the increased numbers of tooth rows would allow the tadpole a better grasp on substrates, and the deep median notch of the upper sheath, decreasing the thickness of the jaw sheath, allows for increased contact of the oral disc with the substrate. Results of multivariate analysis (Table 2; Fig. 9) demonstrate that the highland (group III) tadpoles have several other external characters with better adaptation to torrential streams. Wider oral discs and larger abdominal suckers suggest that these structures allow tadpoles to maintain position better in faster waters. The tail muscle mass appears to be related to swimming performance, particularly important in running water (Wassersug and Hoff 1985, Altig and Johnston 1989), but clinal variation in the relative size of the caudal muscle is not evident among larval groups.

Dispersal and vicariance hypotheses of biogeography are the major schools in the interpretation of distributional patterns in organisms (Wiley 1981, Nelson and Platnick 1984). The geographical pattern of larval R. sauteri seems to fit Hennig's (1966) Progression Rule, the central hypothesis of dispersal biogeography. We consider the tadpoles in group I of the foothills of the Western District as the basal type for 2 reasons. They have the smallest number of tooth rows (i.e., 5/5-6), which is considered more primitive, because the tooth row formulae in the sister group candidates for Taiwanese R. sauteri populations are 4/5 (as in R. weiningensis: Shen 1986) and 5/5 (as in R. s. johnsi: Smith 1924; R. sangzhiensis: Shen 1986). Also, the form of the upper jaw sheath

that has just a small median notch is more similar to those of out-group larvae having an ordinary wide-arched upper jaw sheath (e.g., R. sangzhiensis, Shen 1986) than the boomerang-shaped form of group III larvae. Larval group I expanded and peripheral demes successfully colonized higher elevations. Eventually, the clinally variable group Il and group III with fixed jaw sheath forms were established, and certain populations of group III invaded eastern Taiwan either by going over or around the Central Mountain Range. Unfortunately, we have no evidence to support either hypothesis. Nevertheless, dispersal biogeography does not perfectly elucidate the geographical pattern of R. sauteri in Taiwan, because it cannot define factors limiting the dispersion of lowland populations (group I and subgroups of group II) along the foothills further northward or southward beyond the current range.

Vicariance biogeography better explains the formation of the geographical pattern of variation in *R. sauteri*, particularly as the dispersal hypothesis has a forced interpretation for the formation of the highly variable group II, which is distributed in a long, narrow, north-south intergradation zone between groups I and III. There may be 2 possible origins of the intergradation zone: primary or secondary contact. It is difficult to distinguish between these concepts (Endler 1977, Barton and Hewitt 1985). In some circumstances, analysis of the range expansion may allow one to directly hypothesize a primary or secondary origin of such a zone (Thorpe 1984 1987). Certain hybrid zones can be accounted for by secondary contact since the last glaciation (Arntzen 1978, Thorpe 1983, Barton and Hewitt 1985, Szymura et al. 1985, Szymura and Barton 1986, Hall 1993). Likewise, distributional patterns of certain small mammals in Taiwan can be better explained by the multipleincursion hypothesis during mid-Pleistocene glaciations (Yu 1995). The vicariant events occurring between China and Taiwan (Lin 1963) allowed animals to reach Taiwan at different periods, providing opportunities for allopatric differentiation in R. sauteri during the isolated periods. The ancestral stock of R. sauteri in China may have re-invaded Taiwan in the following connection events, causing secondary contact with differentiated populations. and producing the highly variable group II as a result of consequent multiple introgressions. This scenario best explains the restricted range of group I to hilly areas of the Western District. This scenario also implies that groups I and III are not monophyletic with each other, but that the former may

have its sister group on the continent.

# Geographical variation in adult morphology

The multivariate analyses of the morphometric characters of adults exhibit geographical variation which largely conforms to larval geographical patterns. In both males and females, samples from the ranges of larval groups I and III are always associated together respectively, and their intergroup mis-classification rates are zero. The samples of group II, however, have diverse associations. In Fig. 11a, each major cluster contains 1 of the 3 group II samples. Two different explanations can be proposed. First, it illustrates a general feature of a wide intergradation zone in which demes located close to one of the parental forms are more predominated by characters of adjacent parental forms (e.g., Arntzen 1978). Oral features of tadpoles from Chiapaotai [19] (Figs. 3-6) support this explanation. Secondly, diverse associations, e.g., samples from Wulai [45; preassigned to group III] with Neipu [12; group II] and samples from Machia [42; group II] with group I, may be of ecological causation. In light of the stepwise multiple-regression analyses of morphological and geoclimatic variables, some discriminating factors in canonical discriminant analyses of geographical patterns (Table 3) seem to be associated with precipitation and temperature (Tables 5-8). For both sexes, frogs with larger heads, and longer limbs and SVLs tend to occur in warmer environments with higher summer precipitation and lower winter rainfall (i.e., the Western District). In addition, female frogs with larger palmer tubercles occur in environments with more rainfall in January and high annual precipitation (i.e., the marginal area of the Montane District near the Northeastern District). In other words, geographical variation in adult morphology can be a consequence of ecogenesis; such possible phenotypic plasticity complicates interpretation of the evolutionary significance of geographical variation among populations (Berven 1982, Berven and Gill 1983).

# **Taxonomic considerations**

In *Rana sauteri*, regardless of possible ecogenetic geographical patterns of adult morphology, the larval geographical pattern of oral variation cannot be regarded as an adaptive type, i.e., having an ecological causation, because selection for current conditions could have resulted in clinal variation on both slopes of the Central Mountain Range. In contrast, larval samples from the eastern slope of the Central Range, irrespective of elevational or climatic differences, all feature the group III larval form (Figs. 3-7). Therefore, larval geographical variation may suggest genetic variation and is significant in systematics. The definitive test would be an analysis of genetic variation, which is not within the scope of this paper.

Taxonomic recognition of clines has been controversial. Allopatric populations that intergrade clinally in a fairly wide contact zone in case of secondary intergradation are usually treated as subspecies (Mayr and Ashlock 1991); however, Frost and Hillis (1990) opposed dividing clines into subspecies and preferred to consider allopatric and clearly diagnosable populations as species based on the recovery of historical relationships. As discussed above, the vicariance hypothesis supports the occurrence of dichotomous divergence within R. sauteri. The diagnosable larval groups I and III represent separate evolutionary lineages, with a clinal zone that may act as a barrier to gene flow, suggesting that they are specifically distinct. Because the range of group I includes Quantzelin, the type locality of R. sauteri, we intend to describe group III as a new species (Chou and Lin 1997).

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## Appendix I:

Examined larval specimens and measured adult specimens. (Note: Locality number refers to Figs. 3-7. NMNS---National Museum of Natural Science, Taiwan, ROC. *Nt*--specimen number of tadpole. *Nm*---specimen number of adult male. *Nf*---specimen number of adult female)

1. Hsiaowulai: Taoyuan Co., 4 km NE Fuhsing; Alt. 350 m (Nt = 14: NMNS 1298, 6 Dec. 1990). 2. Kaoyi: Taoyuan Co., 10 km S Fuhsing; Alt. 500 m (Nt = 18: NMNS 844, 30 Dec. 1989; NMNS 1297, 6 Dec. 1990). 3. Palin: Taoyuan Co., 14 km SE Fuhsing; Alt. 800 m (Nt = 14: NMNS 842, 30 Dec. 1989). 4. Lunpei: Ilan Co., Tatung; Alt. 120 m (Nt = 6: NMNS 833, 836, 29 Dec. 1989). 5. Chilan: Ilan Co., 14 km SW Tatung; Alt. 1100 m (Nt = 16: NMNS 832, 29 Dec. 1989; NMNS 837, 30 Dec. 1989). 6. Chihtwan: Ilan Co., 12 km SW Tatung; Alt. 1100 m (Nt = 25: NMNS 146, 29 Oct. 1986; NMNS 838, 30 Dec. 1989). 7. Taipingshan: Ilan Co., 10.6 km S Chilan; Alt. 1900 m (Nt = 3: NMNS 1295, 5 Dec. 1990). 8. Nansan: Ilan Co., 33 km SW Tatung; Alt. 1050 m (Nt = 29: NMNS 817, 29 Dec. 1989). 9. Siyuan: Taichung Co., 53 km NE Hoping; Alt. 1850 m (Nt = 6: NMNS 814, 29 Dec. 1989). 10. Wuling: Taichung Co., 48 km NE Hoping; Alt. 1650 m (Nm = 40, Nf = 30: NMNS 119, 4 July 1986; NMNS 581, 15 Nov. 1988; NMNS 682, 23 Sep. 1989; NMNS 713, 14 Oct. 1989; NMNS 775, 9 Nov. 1989. Nt = 60: NMNS 537, 15 Nov. 1988; NMNS 551, 10 July 1988). 11. Madalahsi: Miaoli Co., 29 km E Taian; Alt. 1700 m (Nm = 30: NMNS 1180, 1184, 7 Aug. 1990. Nt = 9: NMNS 1182, 7 Aug 1990). 12. Neipu: Hsinchu Co., 5 km SE Peipu; Alt. 300 m (Nm = 26: NMNS 730, 732, 26 Oct. 1989. Nt = 35: NMNS 731, 26 Oct. 1989). 13. Taian: Miaoli Co., 7 km E Taian; Alt. 650 m (Nt = 45: NMNS 785, 23 Nov. 1989). 14. Wensuei: Miaoli Co., 2 km W Taian; Alt. 300 m (Nt = 13: NMNS 798, 8 Dec. 1989). 15. Hsiahsinshan: Hualien Co.; Alt. 1900 m (Nt = 8: NMNS 1102, 11 July 1990). 16. Chihan: Hualien Co., 28 km W Hsiulin; Alt. 2200 m (Nm = 10: NMNS 1280, 8 Nov. 1990. Nt = 12: NMNS 883, 6 Feb. 1990). 17. Dayuling: Nantou Co., 34 km E Hoping; Alt. 2560 m (Nm = 14: NMNS 120. Nt = 19: NMNS 711, 13 Oct. 1989; NMNS 778, 10 Nov. 1989). 18. Chiayan: Taichung Co., 35 km NE Hoping; Alt. 1650 m (Nm = 13: NMNS 708. Nt = 20: NMNS 753, 29 Oct. 1989; NMNS 792, 7 Dec. 1989). 19. Chiapaotai: Taichung Co., 15 km E Hoping; Alt. 800 m (Nm = 28, Nf = 7: NMNS 701, 706, 12 Oct. 1989; NMNS 736, 29 Oct. 1989. Nt = 57: NMNS 565, 2 Jan. 1988). 20. Hoping: Nantou Co.; Alt. 600 m (Nt = 42: NMNS 797, 8 Dec. 1989). 21. Takeng: Taichung City, 20 km NE Taichung City; Alt. 200 m (Nm = 38: NMNS 750, 30 Oct. 1989; NMNS 784, 23 Nov. 1989. Nt = 15: NMNS 790, 7 Dec. 1989). 22. Toubenkeng: Taichung Co., 8 km E Taiping; Alt. 300 m (Nm = 37, Nf = 4: NMNS 583, 27 Oct. 1987. Nt = 39: NMNS 558, 27 Oct 1987). 23. Lienhwachih: Nantou Co., 6 km N Yuchih; Alt. 600 m (Nt = 40: NMNS 1971, 8 Dec. 1992). 24. Chinsueihsi: Nantou Co., 13 km SE Puli; Alt. 900 m (Nt = 17: NMNS 1253, 1 Nov. 1990). 25. Hsilin: Hualien Co., 13 km N Wanjung; Alt. 300 m (Nt = 6: NMNS 896, 7 Feb. 1990). 26. Minli: Hualien Co., 3 km W Wanjung; Alt. 600 m (Nt = 6: NMNS 906, 7 Feb. 1990). 27. Hsitou: Nantou Co., 12 km SE Luku; Alt. 1200 m (Nt = 45: NMNS 547, 15 Feb. 1988; NMNS 729, 24 Oct. 1989; NMNS 1001, 15 May 1990). 28. Shanlinhsi: Nantou Co., 15 km SE Chushan; Alt. 1700 m (Nt = 4: NMNS 1246, 26 Oct. 1990). 29. Tungpu: Nantou Co.; Alt. 1400 m (Nt = 40: NMNS 561, 5 Feb. 1988). 30. Alisan: Chiayi Co., 7.6 km N Wufeng; Alt. 2200 m (Nm = 18, Nf = 3: NMNS 48, 18 Apr. 1986; NMNS 375, 20 Apr. 1989. Nt = 44: NMNS 44, 18 Apr. 1986; NMNS 373, 20 Apr. 1989; NMNS \$80). 31. Fengchihu: Chiayi Co., 14.5 km E Chuchi; Alt. 1200 m (Nt = 40: NMNS 71, 72, 25 Apr. 1986; NMNS 806, 25 Dec. 1989). 32. Tsukou: Chiayi Co., 4.5 km SE Fanlu; Alt. 300 m (Nm = 33, Nf = 13: NMNS 716, 19 Oct. 1989. Nt = 45: NMNS 70, 26 Apr. 1986; NMNS 808, 25 Dec. 1989). 33. Quantzelin: Tainan Co., 10 km E Paiho; Alt. 300 m (Nm = 50, Nf = 7: NMNS 582, 27 Oct. 1988; NMNS 722, 20 Oct. 1989. Nt = 45: NMNS 544, 8 Dec. 1988). 34. Tapu: Chiayi Co., 3 km S Tapu; Alt. 500 m (Nt = 10: NMNS 83, 3 Feb. 1989). 35. Sanmin: Kaohsiung Co.; Alt. 500 m (Nt = 11: NMNS 579). 36. Paolai: Kaohsiung Co., 17 km NE Liukuei; Alt. 400 m (Nt = 42: NMNS 576). 37. Tsuyunsan: Kaohsiung Co., 13 km S Taoyuan; Alt. 600 m (Nt = 5: NMNS 1365, 6 Feb. 1991). 38. Kwaiku: Kaoshjung Co., 36 km NE Taoyuan; Alt. 2400 m (Nt = 7: NMNS 934, 9 Feb. 1990). 39. Sungli: Taitung Co., 26 km NW Haituan; Alt. 2070 m (Nt = 6: NMNS 933, 9 Feb. 1990). 40. Wulu: Taitung Co., 21 km NW Haituan; Alt. 800 m (Nt = 31: NMNS 922, 8 Feb. 1990). 41. Wutai: Pingtung Co., 8 km NE Sandimen; Alt. 1000 m (Nt = 4). 42. Machia: Pingtung Co., 16 km E Machia; Alt. 700 m (Nm = 19: NMNS 724, 20 Oct. 1989. Nt = 64: NMNS 545, 14 Jan. 1989). 43. **Dawu:** Pingtung Co., 8 km E Taiwu; Alt. 1700 m (Nt = 6). 44. **Dahansan:** Pingtung Co., 14 km NE Chunjih; Alt. 1200 m (Nt = 10: NMNS 147, 2 Feb. 1989). 45. **Wulai**: Taipei Co., 11 km S Hsintien; Alt. 300 m (Nm = 9: NMNS 259, 22 Mar. 1987; NMNS 555, 577, 27 Nov. 1988). 46. **Yunhai**: Nantou Co., 10 km E Wushei, Alt. 1800 m (Nf = 3: NMNS 566, 19 Dec. 1987).

#### Appendix II:

Abbreviations of adult morphometric characters.

eye length	NED	nostril-eye distance
eye-tympanum distance	NTD	nostril-tympanum distance
eyelid width	OPTL	outer palmar tubercle length
foot length	SED	snout-eye distance
4th toe length	SND	snout-nostril distance
head length	STD	snout-tympanum distance
head and lower arm length	SVL	snout-vent length
head width	TaL	tarsus length
inner metatarsal tubercle length	TD	tympanum diameter
internarial distance	TFL	3rd finger length
interorbital distance	THIGH	thigh length
inner palmar tubercle length	TiL	tibia length
	TTL	thenar tubercle length
	eye length eye-tympanum distance eyelid width foot length 4th toe length head length head and lower arm length head width inner metatarsal tubercle length internarial distance interorbital distance inner palmar tubercle length	eye lengthNEDeye-tympanum distanceNTDeyelid widthOPTLfoot lengthSED4th toe lengthSNDhead lengthSTDhead and lower arm lengthSVLhead widthTaLinner metatarsal tubercle lengthTDinternarial distanceTFLinner palmar tubercle lengthTiLTTLTTL

# 臺灣產之梭德氏蛙 Rana sauteri (無尾目:赤蛙科) 之地理變異

# 周文豪<sup>1,2</sup> 林俊義<sup>2</sup>

梭德氏蛙廣泛分佈於臺灣海拔 100-3000 公尺的山區,生息環境縱跨亞熱帶到涼溫帶氣候區。蝌蚪是典型 的腹吸型 (gastromyzophorus type),其上喙外形和唇齒列數呈明顯的地理漸變 (clinal variation),由中西部 丘陵向東隨海拔升高到中央山脈臨近地區,並翻越高山到達臺灣東部,上喙中央缺刻增大,唇齒列有漸增的趨 勢,在地理上形成扇狀的變異分佈型。此一地理變異分佈的形成可由播散說 (dispersal) 和分衍說 (vicariance)來解析。播散說推測中西部丘陸族群是分佈起源中心 (祖群 ancestral group 地區),向東呈扇狀播散, 經過渡帶 (transition zone),在中央山脈鄰近地區形成另一族群 (衍群 derived group )。成體的形態多變量分 析也顯示類似的地理變異分佈型。這樣的地理變異更能以分衍說來解釋,表示梭德氏蛙已分岐。

關鍵詞:梭德氏蛙,生物地理,地理漸變,蝌蚪,臺灣。

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