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Morphometric Variation Analyses and Revision of the Japanese Toads (Genus *Bufo*, Bufonidae)[1]

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Abstract

Two problems have been involved in the classification of the Japanese toads: (1) relationships with the continental forms, and (2) relationships among forms hitherto described within the islands. The present study was undertaken with the purpose of resolving the latter problem, and to achieve this, morphometric variation analyses were made of a large number of preserved specimens. The results were synthesized with the hitherto accumulated non-metrical and non-morphological information so as to taxonomically revise the Japanese toads. A historical review of the classification of the Japanese toads revealed that the most complex problems were involved in the still-water breeding forms from the main islands (=the Japanese common toad), and that the taxonomic confusion was caused mainly by previous authors' classification through examination of a small number of specimens notwithstanding the great variability of external morphometric characters of the toads. The critical points for measurements for each character, and problems with measurement errors due to variant fixation and preservation are discussed. Allomorphic relations of 30 characters to SVL were analyzed for four age/sex groups of 147 Japanese common toads from Momoyama, Kyoto, with the result that many characters should be treated separately for three groups, i.e., young, adult males, and adult females. Besides, it was determined that simple ratios to SVL should not be calculated for many characters. For the Japanese common toad, SVL and relative value (ACV=theoretical value calculated by the allomorphic relationship of each character to SVL) of 10 selected characters for each of 2,525 specimens belonging to 96 populations were analyzed, and the presence or absence of intrapopulational age and sexual variations and of interpopulational variations was noted. From these analyses, the Japanese common toad was divided into northeastern (A) and southwestern (B) types chiefly by the relative size of the tympanum diameter. For the two types of the Japanese common toad, presence of morphometric clines in relation to geographical and/or climatological parameters was investigated. Clear clinal tendencies were found mostly in type A, whereas few clear trends were detected in type B. Taxonomical meaning of the clines was discussed, and it was suggested that the Japanese common toad should be split into taxa below the species level. Similar morphometric analyses were made on the still-water breeding Miyako toad from the Ryukyu Archipelago. The results for 176 specimens from 4 populations indicated that this form was very uniform in external morphometry, that it greatly differed from the Japanese common toad in several characters, and that the differences were greater between this form and geographically adjacent type B Japanese common toads in some characters. Similar analyses were also performed on 265 specimens of 13 populations of the stream-breeding Japanese stream toad. Interpopulation variation in this form was very small. Comparisons with sympatric and allopatric populations of the Japanese common toad were made with the result that the two forms were found to be morphometrically almost completely separated, showing greatest differentiation in the zone of sympatry. Taxonomic conclusions were drawn with these results in mind. For the Japanese common toad, the type series or topotypes of each of the hitherto described forms were compared with the other populations and it was determined that neither type A nor type B can be split further. The syntypes of *Bufo*

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vulgaris japonicus, which is the oldest of all the described forms from Japan and is now kept in Leiden, were examined and a lectotype was designated and described. This form clearly belonged to type B. The nature of the intergradation of morphometric variations between type A and type B is discussed, and special attention is paid to the sudden change in the morphocline in the tympanum diameter. From this discussion, the relation of the two types is regarded as subspecific, and they are treated as *B. japonicus formosus* (type A) and *B. j. japonicus* (type B). For the Miyako toad, the morphometric difference from the Japanese common toad in the adjacent distribution range was studied, and the two forms are regarded as belonging to the different lineages. In addition, the known results of artificial hybridization support this idea, and therefore, the form is regarded as specifically different from *japonicus* and is treated as a subspecies (*miyakonis*) of the northeastern Chinese species *B. gargarizans*. The Japanese stream toad has been shown to have strong genetic compatibility with the Japanese common toad. Therefore, from the viewpoint of evolutionary taxonomy, the taxonomic value of the evidence from genetical sources is discussed. The two forms are distributed sympatrically, but are judged to seldom interbreed or show morphological intergradation in nature. Thus, notwithstanding the strong genetic compatibility of the artificial hybrids, the Japanese stream toad is regarded as a full species, *B. torrenticola*, as was originally described. In conclusion, the Japanese toads are taxonomically divided into three species, *Bufo japonicus* (*j. japonicus* Schlegel, 1838 and *j. formosus* Boulenger, 1883), *B. gargarizans miyakonis* Okada, 1931, and *B. torrenticola* M. Matsui, 1976.

Contents

Introduction

The family Bufonidae is a large group of anuran amphibians consisting of more than 18 genera (Trueb, 1971; Pillai and Yazdani, 1973; Gorham, 1974; Ruiz and Hernández, 1976), among which the genus *Bufo* is predominant both in the range of distribution and in the number of species included.

The genus is almost cosmopolitan and is distributed in all the main land masses except Greenland, Australia, New Guinea, and New Zealand (Goin et al., 1978). At least 187 species were known some ten years ago (Gorham, 1974), and the number is still increasing (e.g., Tandy et al., 1976; Matsui, 1976a; Ye, 1977; Andrén and Nilson, 1979; Duellman and Toft, 1979), since, as pointed out by Blair (1972), there are many undescribed cryptic species, and there still remain areas not yet thoroughly surveyed.

Chiefly by the shape of the frontoparietals, the toads of this genus can be divided into broad-skulled and narrow-skulled types (Martin, 1972). The former type is considered to be adapted to warmer climates and the latter to colder climates (Blair, 1963, 1972).

The Japanese toads treated in the present paper are regarded as members of the *Bufo bufo* species group (=complex) which belongs to the narrow-skulled type (Inger, 1972; Matsui, 1976d, 1980a, b). The distribution range of the *Bufo bufo* complex is rather wide compared with that of the other species groups of the genus and includes most of Europe, western North Africa, northern Asia Minor, central Asia, northeastern

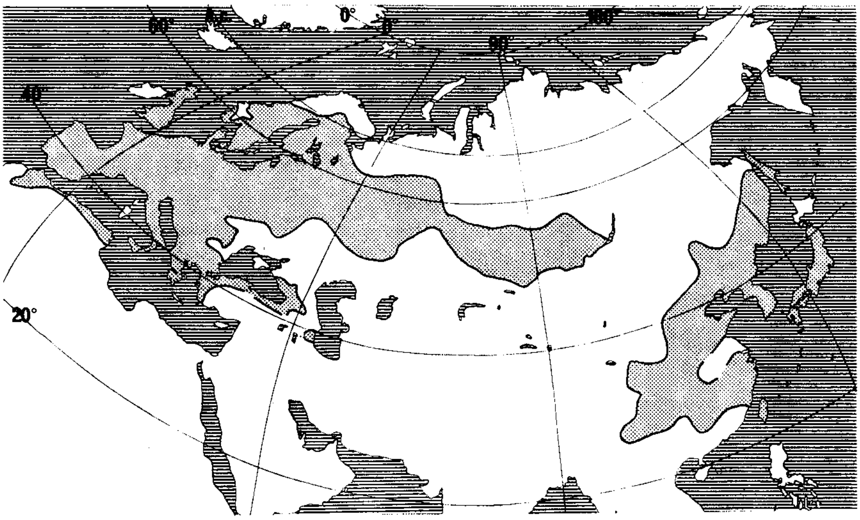

Fig. 1. Map of Eurasia showing distribution range of the *Bufo bufo* complex, from data by Arnold and Burton (1978), Bannikov et al. (1977), Borkin and Roshchin (1981), Fuhn (1960), Liu and Hu (1961), Matsui (1976d), Pasteur and Bons (1959), Schmidtler and Schmidler (1969), Schneider (1974), and Terhivuo (1981).

Asia, Taiwan, Japan, and Sakhalin (Inger, 1972; Matsui, 1976d; Fig. 1). The toads of this complex, as a whole, are different from members of the largely sympatric *Bufo viridis* complex in some morphological features (Inger, 1972; Matsui, 1980b), forming a somewhat uniform group. On the other hand, geographic variation in some morphological characters in this complex is pronounced and this makes the classification within the complex not easy (Inger, 1972; Matsui, 1980a).

The complex from Japan has been regarded as represented by two species: the Japanese common toad and Miyako toad (*Bufo bufo* ssp.), and the Japanese stream toad (*Bufo torrenticola*). The distribution range of the former species within the Japanese Islands includes the southernmost part of Hokkaido and most parts of Honshu, Shikoku, and Kyushu. It also occurs in Goto, Yakushima, and Tane-gashima Islands, but has never been reported from Sado, Oki, and Tsushima islands. In the Ryukyu Archipelago, it naturally occurs only in Miyakojima Is. and has been artificially introduced into Okinawajima Is. (Yashiro, 1938) and Kita- and Minami-Daitojima Islands. (Matsui, 1975b). By contrast, the distribution of *Bufo torrenticola* is much more limited; it is found only in some parts of Honshu (Matsui, 1976a, 1980e). As many as five forms (subspecies), i.e., *hokkaidoensis*, *montanus*, *formosus*, *japonicus*, and *yakushimensis* have been reported for Japanese common toad (Okada, 1966). This number is extremely large compared with that of the other Japanese anuran species (of the 31 other species, only four are currently divided into more than two forms; *Hyla hallowellii* (2 spp.), *Rana porosa* (2 spp.), *Rana tagoi* (3 spp.) and *Rhacophorus viridis* (2 spp.)), and this suggests that the Japanese common toad is far more variable than the other species. On the other hand, the number also suggests that the Japanese common toad tends to have been split into too many forms compared with the toads of this complex in the continental regions: only four subspecies in Europe (*bufo*, *spinosus*, *gredosicola*, and *verrucosissimus*) and three in China (*gargarizans*, *andrewsi*, and *minshanicus*) are generally recognized as valid (Liu and Hu, 1961; Mertens and Wermuth, 1960), though the forms of China have not yet been thoroughly surveyed (Matsui, 1980a).

Most of the Japanese forms have been classified and described on the basis of only several morphological characteristics on small number of samples, and therefore, the classifications made so far stand on taxonomically weak grounds. In the current systematics of anurans, much attention has been paid to characters other than morphological ones, and data from many biological aspects, such as ecological, physiological, genetical and ethological, have become increasingly emphasized (Blair, 1962).

The fundamental ground for reasonable systematics, however, is considered to be morphological data (Zweifel, 1973) which have been well selected and derived from a large collection of samples. Yet morphological investigations of Japanese anurans seem to be less advanced than those in other countries, and morphological variations of only few species have been studied (*Rana nigromaculata-porosa* complex: Moriya, 1954; Kokuryo and Matsui, 1979; *Rana limnocharis*: Kuramoto, 1968). The Japanese toads are supposed to be the most variable among Japanese anurans. Nevertheless, no actual analyses of morphological variation have been made.

With the purpose of establishing reasonable systematics of the toads of *Bufo bufo* complex, I have been studying them from many approaches (Matsui, 1974a, b, 1975a, b, c, d, 1976a, b, c, d, e, f, g, 1977a, b, 1978b, 1979a, c, 1980a, b, c, d, e, f, 1981; Matsui and Satow, 1977; Matsui and Wakana, 1978; Miyamae and Matsui, 1979), and in the present study, I tried to clarify the morphological variations of the Japanese toads so as to revise them systematically.

With this view, 11 metric characters, including most of the hitherto taxonomically stressed ones, were statistically investigated in 2,966 samples from many regions of Japan.

In the course of this study, I paid attention as much as possible to ontogenetic variation, or morphological changes with growth, and to sexual dimorphism in adults, both of which have been almost totally neglected by the previous authors. I analyeed morphometric characters from the standpoint of allomorphic relations between snout-vent length and dimension of each morphometric character and, by calculating the ACV (Thorpe, 1975), I tried to eliminate the errors which might be possibly produced by calculating a simple ratio between two dimensions.

Further, I made analyses on geographic and climatic clines for each character and considered relations between morphological variations and environmental factors for a better understanding of the meaning of variations.

Finally, I made an attempt to revise the classification of the Japanese toads by synthesieing the results of the morphological studies and other non-morphological data hitherto reported (e.g., genetic compatibility, habitat selection, and distribution, etc.).

I

History and Problems of the Taxonomy of the Japanese Toads

1. A Historical Review of Classification of the Japanese Toads

a) 1826–1907

The Japanese common toad was first described in 1826 by Boie under the name of *Bufo praetextatus*, without any indication of the exact type locality. In the next year he assigned this name to the specimens collected by Blomhoff in Nagasaki (Boie, 1827). Boie's type specimens, however, seem to have been lost by the beginning of the 20th century (Stejneger, 1907), and since then the name *praetextatus* has been used only by a few authors (e.g., Slevin, 1930). The oldest type series of the Japanese common toad now existing was collected by Siebold and Bürger in "Japon" and described by Schlegel (1938), and the series is now kept in the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden (Matsui, 1980c).

Schlegel regarded these type specimens as a variety of the European common toad and gave them the name *Bufo vulgaris* var. *japonicus*. Being a typical lumper, he dedicated many pages of his original description of the Japanese common toad to critiques upon splitting with regard to problems of synonymy prevailing at that time in the classification of toads and frogs. As a result, he did not hesitate to believe the Japanese common toad to be a mere climatic variety of the European common toad.

As shown in the upper lines of Table 1, most of the authors before 1882 regarded the Japanese toads either as identical with, or as merely subspecifically separate from the European common toad (Günther, 1858; Bleeker, 1858; Martens, 1876; Boulenger, 1880; Hilgendorf, 1880).

Among these authors, Boulenger (1880), in reviewing the Palaearctic toad species in detail, has admitted that the Japanese and Chinese common toads have some characteristics different from the European common toad. But such characters seemed to him unstable and he concluded that it was unnecessary to separate the former as subspecies from the latter, a view sharply opposed to the opinions of Lataste (1880) and Camerano (1879), who tried to differentiate the Asiatic common toads from the European representative at the species rank.

Boulenger (1883), on the other hand, described a distinct species *Bufo formosus* on the basis of specimens collected from Yokohama and deposited in the British Museum of Natural History (BMNH). Fifteen years later, he regarded the Japanese common toad from Kobe as identical with European common toad— the same treatment as in 1880— and mentioned nothing about the "distinct species" *formosus* (Boulenger, 1898).

These examples clearly indicate that in the early stage of classification of the Japanese toads, there was some confusion with regard to the relationship with the European common toad, and it was Stejneger (1907) who arranged the problems in order. He reviewed in detail the taxonomic history of the Japanese toads by the beginning of the 20th century and summed up the taxonomic problems in the following three points (Stejneger, 1907: 57, parenthesis by me):

(1) Is there more than one species of *Bufo* in Japan?

(2) (If there are more than one species,) is one of these identical with the species on the mainland?

(3) In case of different forms being recognized, what names are to be employed?
He tried to give answers to these problems by comparing available specimens and, as a result, recognized three Japanese forms: *Bufo formosus*, *Bufo bufo japonicus*, and *Bufo smithi*; the last form was newly described by himself.

In his study, Stejneger adopted the "International Rules of Zoological Nomenclature" (1905) which had just been adopted at that time, and used the specific name of *bufo* instead of *vulgaris*, the name widely been used for the European common toad (The type species of the genus *Bufo* was changed from *Bufo vulgaris* Laurenti, 1768 into *Rana bufo* Linné, 1758, but some authors debated whether to regard *bufo* as type species of the genus (Levition and Anderson, 1970: 174; Mertens, 1971)).

Among the three forms, the outline of *Bufo bufo japonicus*, the only one Japanese subspecies of the European common toad, was most unclear to him, and with some reservation, he considered that the name was to be tentatively applied to the specimens from Kobe and Nagasaki. The sole specimen he could actually examine was the one from "Miyakoshima (?)" (Stejneger, 1907: 69). He also stated that both *formosus* and true *japonicus* seemed to be included in the type series of *Bufo vulgaris* var. *japonicus* reserved in RMNH (its exact locality is unknown as stated previously). I was able to examine the series and reached a different opinion from Stejneger (Matsui, 1980c),

Table 1. Summary of the taxonomic history of Japanese toads. Abbreviations for the name of forms: b.=*bufo*, f.=*formosus*, g.=*gargarizans*, h.=*hokkaidoensis*, j.=*japonicus*, m.=*montanus*, mi.=*miyakonis*, p.=*praetextatus*, s.=*mithi*, t.=*torrenticola*, v.=*vulgaris*.

	"Japan"	Hokkaido	Honshu		Shikoku	Kyushu	Miyakojima
			NE	SW			
1826	p. Boie						
1827						p. Boie	
1838	v.j. Schlegel						
1858	v.j. Ghunter v. Bleeker						
1866	v.j. Martens						
1876			v.p. Martens	v. Martens			
1879			j. Camerano				
1880	v. Boulenger v.p. Hilgendorf						
1882	v. Boulenger						
1883			f. Boulenger				
1891	f. Okada v. Okada	v. Fritze					
1892			f. Boettger				
1898				v. Boulenger			
1900	p. Camerano						
1903	v. Namiye						
1907			f. Stejneger	(b.j.) Stejneger	s. Stejneger	(b.j.) Stejneger	(b.j.) Stejneger
1928		v.h. Okada				v.y. Okada	
1930		v.h. Okada	v.f. Okada	v.j. Okada	v.j. Okada	v.j. Okada v.y.	b.j. Okada
	b.j. Schmidt & Liu	p. Slevin					

(cont'd.)

(Table 1. cont'd.)

	"Japan"	Hokkaido	Honshu		Shikoku	Kyushu	Miyakojima
			NE	SW			
1931		v.h. Okada	v.f. Okada	v.j. Okada	v.j. Okada	v.j. Okada v.y.	b.mi. Okada
1937			v.m. Okada				
1963		b.j. Nakamura & Uéno	b.j. Nakamura & Uéno	b.j. Nakamura & Uéno	b.j. Nakamura & Uéno	b.j. Nakamura & Uéno	b.g. Nakamura & Uéno
1966		b.h. Okada	b.f. Okada b.m.	b.j. Okada	b.j. Okada	b.j. Okada b.y.	b.mi. Okada
1976			b.f. Matsui b.m. t.	b.j. Matsui t.			
1979		b.f. Matsui	b.f. Matsui t.	b.j. Matsui t.	b.j. Matsui	b.j. Matsui	b.mi. Matsui
1980				j.j. Kawamura et al. j.t.		j.y. Kawamura et al.	j.mi. Kawamura et al.

and I will report the results in detail in the latter pages of the present paper.

b) *1908–1942*

No essential changes occurred in the classification of the Japanese toads during the 20 years after Stejneger's treatment.

In 1927, Okada published a paper on the distribution of the Japanese frogs in which he listed the name of *Bufo bufo miyakoensis* (Schlegel) distributed in the Ryukyu Archipelago, but no description was made of this apparently "new" form. In the next year he described two new subspecies: *Bufo vulgaris hokkaidoensis* and *B. v. yakushimensis* (Okada, 1928). Attention must be paid to the Okada's use of "*vulgaris*" for a specific name; this point can be reviewed by examining his treatment of the toads from the Far East in his famous monograph published two years later (Okada, 1930). He recognized four subspecies of *Bufo* "*vulgaris*", i.e., *formosus*, *japonicus*, *hokkaidoensis*, and *yakushimensis*, from the islands of Japan, and eliminated Stejneger's (1907) *Bufo smithi* as a synonym of *B. v. japonicus*. He gave the name *Bufo* "*bufo japonicus*" "(Stejneger)" to the toad from Miyakojima Isl. of the Ryukyu Archipelago. What we should notice is his way of applying scientific names and his recognition of "species". According to Okada's classification, there existed two toad species named *Bufo vulgaris* and *B. bufo* in Japan, but as already shown by Stejneger (1907), the former name is nothing but a synonym of the latter.

That he did not precisely differentiate subspecies from species is evident from his description in the chapter on the distribution of Japanese toads: "...in the Japanese territory, ...the following nine 'species' occur..." (Okada, 1930: 20). It is highly probable that lack of species recognition with him resulted in a misunderstanding of meanings of Stejneger's taxonomic treatment.

He stated in the description of *B.* "*bufo japonicus*": "the subspecies was described on the basis of the specimen collected by Stejneger from Miyako Island."; but this statement is incorrect, since, as already mentioned, "*japonicus*" was described not by Stejneger but by Schlegel and the former author only assigned the name *japonicus* to a specimen deposited in the Tokyo Imperial University from an uncertain locality, "Miyakoshima?".

In the English monograph published in the next year (Okada, 1931), his treatment of the specific names of the Japanese toads was unchanged and both "*bufo*" and "*vulgaris*" were still retained. However, the toad from Miyakojima Isl. (*Bufo bufo japonicus* in 1930's monograph) was newly described under the name of *Bufo bufo miyakonis* in this monograph.

However, if it is taken into account that the concept of biological species was undeveloped in those days, Okada should be praised in spite of this taxonomic confusion, because he contributed much to the knowledge that the Japanese toads are morphologically heterogeneous and, especially, that the Miyako toad is fairly remote from the remaining members.

Even after the publication of these monographs, Okada long continued to use the species names *vulgaris* and *bufo*, and described an additional new subspecies *B. v. montanus* in 1937. Furukawa and Takashima (1942), on the contrary, proposed that the name of the Japanese toads, *Bufo vulgaris* Laurenti was only a junior synonym of *Bufo bufo* (Linné), but their opinion was not widely accepted.

c) *1943–1966*

In 1947 Inger published a review of the herpetofauna of the Ryukyu Archipelago, and in his paper he stated that Okada's original description of the Miyako toad (Okada, 1931) was incomplete, because it showed no tangible differences from the Chinese common toad. Thus he relegated *miyakonis* as a synonym of the Chinese *Bufo bufo gargarizans* Cantor (Inger, 1947). He considered that the Miyako toad had been recently introduced into Miyakojima Is., since its distribution range is restricted to this island, which is thought to have been under water through many geohistoric ages. In another paper on the distribution and speciation of the herpetofauna in the Ryukyu Archipelago, he emphasized again that there was not even a slight difference between the Miyako toad and Chinese toads except the peculiar distribution of the former (Inger, 1950).

Nakamura and Uéno (1963) contributed much to put the confusion since Okada (1930) in order. They relegated all the five subspecies recognized by Okada, which are distributed in the Japanese islands north of Yakushima, to the synonymy of *Bufo bufo japonicus* and considered it enough to recognize only *formosus* and *japonicus* as valid, if indeed there was any necessity to divide them into subspecies. They treated the Miyako toad in the same way as Inger (1947, 1950).

Okada (1966) strongly opposed Nakamura and Uéno's view by insisting on the validity of five subspecies, but his description for each subspecies was almost identical to that made 30 years ago except for the use of *bufo*, instead of *vulgaris*, for the species name.

d) *1967—*

In the years reviewed above, classification of the Japanese toads was made mainly on the basis of morphological characters, and most of the authors invariably believed that the Japanese toads were conspecific with the European common toad.

In the 1970s, detailed analyses of morphological as well as non-morphological characters began to appear and resulted in a great change in taxonomic position of the Japanese toads. Guttman (1967) showed between the European and the Japanese common toads, the existence of a great difference at more than subspecies level in the electrophoretic patterns of blood proteins. Martin (1972) supported Guttman's view from the observation of skull morphology.

I quoted the idea of these authors and suggested that the systematic relationships of the Japanese and European toads would require reexamination and, in order to pursue this, it would be necessary to make analyses on biochemicals like parotoid gland secretion as well as morphological variation analyses (Matsui, 1974a). I analyzed ontogenetic and sexual variations of external characters of the Miyako toad and have suggested that this form is different from the Chinese *gargarizans* in several characters (Matsui, 1974b). I found a new toad from Ohdaigahara, Nara Pref. and Neo, Gifu Pref., whose larvae inhabit mountain torrents—a habit up to that time known only for the larvae of *Bufo bufo andrewsi* from western South China (Matsui, 1975c)—and I described this stream toad as *Bufo torrenticola* based on the peculiar larval ecology and morphology, and adult morphology (Matsui, 1976a). The Japanese stream toad was described as a full species because I have found that this species is distributed sympatrically with *B. bufo formosus* and ecologically isolated from the latter in Neo Valley, Gifu Pref. (Matsui, 1976a).

I (Matsui, 1975d, 1976b) also made cross experiments to get better understanding of the taxonomic relations between continental and Japanese toads; I found that the hybrids of female *japonicus* × male *miyakonis* are fertile, whereas those of female *japonicus* × male *spinosus* are sterile. Further, I discussed the situation of the Eurasian anurans as a fauna complex, paying special attention to the tendencies found in the degree of specific differentiation of these animals, and from these results, suggested that the Japanese and European common toads could be separated from each other as two distinct species.

From the results of further cross tests, I showed that the Japanese toads warrant separation from the European common toad, and in addition, I found that there is almost no postmating isolating mechanism between Japanese stream toad and still-water type *formosus* (Matsui, 1977a, b). Matsui and Satow (1977), on the basis of the electrophoretic properties of hemoglobin, thought that the Japanese still-water type toads, *formosus* and *japonicus*, form a unique group with the Japanese stream toad and that they are remote from the European common toad. Moreover, Matsui and Wakana (1978) and Matsui (1980a) proposed systematic relations within the *Bufo bufo* complex from the results of a karyological study and showed that the Asiatic toads were remote from European *Bufo bufo*.

Nishioka et al. (1978), based on cross experiments, reached the same conclusion as Matsui (1977a, b) about the relations of the Japanese common toad with the European common toad and the Japanese stream toad. Kawamura et al. (1980) published the results of cross tests and made taxonomic conclusions about Japanese toads and the European common toad. Their conclusion, based purely on the results of laboratory crosses, was that all the Japanese toads may have been differentiated from the European *Bufo bufo* and could be grouped into *Bufo japonicus*.

2. *Taxomic Problems and Characters to be Chosen*

a) *Taxonomic Problems*

In view of the taxonomic history stated above, forms of toads hitherto described from Japan can be summarized as follows:

Bufo vulgaris var. *japonicus* Schlegel, 1838. Fauna Japonica, Rept. 106, 139. Japon.

Bufo formosus Boulenger, 1883. P.Z.S.L. 140. Yokohama.

Bufo smithi Steineger, 1907. Bull. U.S.N.M. 58: 64. Toza, Shikoku.

Bufo vulgaris hokkaidoensis Okada, 1928. Annot. Zool. Japon. 11: 269. Hakodate, Hokkaido.

Bufo vulgaris yakushimensis Okada, 1928. Annot. Zool. Japon. 11: 269. Yakushima.

Bufo bufo miyakonis Okada, 1931. Tailless Batr. Jap. Empire 47. Miyakojima, Riukiu Isl.

Bufo vulgaris montanus Okada, 1937. Saitô Ho-on Kai Mus. Res. Bull. 12: 189.

Chôkaizan, Yamagata Pref.

Bufo torrenticola M. Matsui, 1976. Contrib. Biol. Lab. Kyoto Univ. 25: 1. Ohdaigahara, Nara Pref.

It is certain from the recent information (Matsui, 1976b, 1977a, b; Kawamura et al., 1980) that the Japanese toads can be separated from European *Bufo bufo* at the species level. However, relationships between the toads of Japan and those of the continental Far East have not yet been clarified, and these are most important problems which need to be investigated hereafter.

Among the toads of Japan, the Miyako toad seems, even from its peculiar distribution alone, to be taxonomically different at least above subspecies level from the forms of the main islands. Although Inger (1947, 1950) regarded the Miyako toad as consubspecific with the Chinese common toad, his conclusion was derived only from literature and not from actual observations on specimens of the Miyako toad. Kawamura et al. (1980) separated the Miyako toad as a subspecies of the Japanese toad (including the Japanese stream toad), but the results of cross experiments they made between this subspecies and the Japanese stream toad clearly indicate that their taxonomic treatment is unreasonble; this indicates the difficulty in classifying toads only on the basis of cross tests in the laboratory.

More difficult problems are involved in the taxonomic relations among forms of the Japanese main islands. Of the seven forms hitherto described from Japan other than Ryukyu Archipelago, only the larvae of *Bufo torrenticola* are known to be stream types, and all the remaining forms are regarded as still-water types (*hokkaidoensis*- Muramatsu et al., 1963; *montanus*- Matsui, 1976e; *formosus*- Okada, 1938, Matsui, 1976a; *japonicus*- Nakamura, 1934, Matsui, 1976a; *smithi*- Matsui, unpublished data; *yakushimensis*- Matsui, 1979a). *Bufo torrenticola* clearly differs from the other forms ecologically, and also has peculiar morphology. Therefore, even Kawamura et al. (1980), who considered *Bufo torrenticola* to be conspecific with still-water type *japonicus* and *yakushimensis*, recognized the morphological and ecological peculiarity of *torrenticola* and were forced to separate it as a "subspecies" from *japaonicus*.

Opinions differ among authors as to the application of the results of cross tests. Even if the artificially produced hybrid of any two forms proved to be fertile, it would be dangerous to consider these two forms conspecific on the basis of such tests alone (see Simpson, 1961; Packard, 1971; Kuramoto, 1979). The different standpoint between Matsui (1976a) and Kawamura et al. (1980) is based on the difference in the recognition of species actually living in natural conditions.

Half of the forms of the still-water type (*hokkaidoensis*, *montanus* and *yakushimensis*) were described by Okada (1928, 1937), but there are instances in which his description does not agree with his measurement data (e.g., Okada, 1931: 40), and most of his forms have vague outlines partly because of his insufficient variation analyses.

On the other hand, Matsui (1976a) separated the Japanese stream toad from the still-water forms on the basis of the fact that, where they occur sympatrically, morphological difference is evident and no intermediate form occurs. By contrast, Kawamura et al. (1980) "believed" the occurrence of morphologically intermediate natural hybrids of still-water and stream types in view of the high morphological variation among the still-water forms.

Consequently, clarification of the taxonomic position of the Japanese stream toad itself would require, first of all, studies on the morphological variations.

b) *Characters to be Chosen*

The original description of *Bufo vulgaris* var. *japonicus* was rather incomplete; the basis on which Schlegel separated the Japanese toad as a variety of the European common toad were: (1) more vivid coloration, (2) conical head wider at its base, (3) more protruded snout at the level of the nostrils, and (4) more evident dark blotches on the belly. He thus recognized the differences in the coloration and the shape of the head, but he did not metrically analyze the second and third characters.

Boulenger (1883), who accepted *Bufo formosus* as a close relative of *Bufo vulgaris*, pointed out that the former could be separated from the latter by the following characters: (1) larger tympanum, (2) longer hindlimb, (3) longer toes, (4) deeper incision of the foot web, and (5) shorter first finger.

Stejneger (1907), in dividing Japanese toads into three forms, i.e. *formosus*, *smithi*, and *bufo japonicus*, paid attention to such characters as (1) the size of tympanum, (2) length of limbs, (3) length relation of first and second fingers, (4) length and thickness of parotoid, and (5) degree of web incision of the foot. Of these characters, he listed the measurements of tympanum diameter and the tympanum-eye distance for *formosus* and *smithi*.

The characters utilized by Okada (1928, 1930, 1931, 1937, 1966) in differentiating the six Japanese forms are shown in Table 2. Most of the characters employed by him were in the head region and special attention was paid to their relative sizes: the most important characters were (1) size of tympanum, especially with relation to its distance from eye, (2) snout length, (3) parotoid length, (4) relation of internarial to interorbital distance, and (5) relation of internarial or interorbital distance to tympanic diameter. In addition, degree of web extention and coloration were in some cases regarded as diagnostic characteristics.

Nakamura and Uéno (1963) pointed out the differences in body size and degree of web extention between the Japanese and the Miyako toads.

I split the Japanese stream toad from the other Japanese toads because of (1) the smaller and indistinct tympanum, (2) the shorter and less divergent parotoid, (3) the larger hand and foot, and (4) the peculiar body coloration in life, and I tabulated morphometric values (Matsui, 1976a: 4).

In short, most of the distinguishing characters differentiating either Japanese toads from the European common toad, or forms in Japan are morphometric ones and more than half of them are in the head. Only the coloration and webbing are enumerated as non-metric characters. Among the morphometric characters, authors most often mentioned tympanum size and next hindlimb length and parotoid shape.

As already stated above, most of the taxonomic problems still unsolved are concerned with relationships among forms of still-water type toads of the Japanese main islands (the Japanese common toad). Characters hitherto given importance in

Table 2. Diagnostic characters employed by Okada (1928, 1930, 1931, 1937, 1966) to differentiate six forms in Japanese toads. Abbrebiations for the forms: *for*=*formosus*, *jap*=*japonicus*, *hokk*=*hokkaidoensis*, *mon*=*montanus*, *yaku*=*yakushimensis*, *miya*=*miyakonis*.

	jap	*hokk*	*mon*	*yaku*	*miya*
for	size of tympanum position of nostril snout length	size of tympanum hindlimb length	parotoid length	size of tympanum	development of toe web
jap		size of tympanum	size of tympanum development of toe web	hindlimb length size of tympanum internarial/orbital w.	development of toe web
hokk			development of toe web	size of tympanum	development of toe web
mon				development of toe web	size of tympanum/interorbital or internarial
yaku					development of toe web

classifying the still-water type toads from the Japanese main islands are mostly morphometric characters: (1) size of tympanum, particularly in relation to its distance from eye, (2) length and width of parotoid, (3) snout length, (4) relation of internarial and interorbital widths, (5) length of limbs, and (6) web extention; this last was the only nonmetric character. Thus, morphometric characters alone sufficiently, if not completely, make it possible to reexamine the validity of taxonomic status of each form.

II

General Descriptions of Materials and Methods of Observation

1. Materials

a) Population

The main object of this study is to revise taxonomic relations of the Japanese toads chiefly from the results of variation analyses of external morphology. For this purpose, I tried to randomly collect as many specimens of toads from as wide a range as possible. Most of the specimens examined were collected by myself, and their habitats were observed at the time of collection. In addition, I was able to examine specimens presented by many people or borrowed from museums and research institutions. As a result, I could investigate holotypes or topotypes of all the eight forms of Japanese

Table 3. Number of Japanese common toads examined.

	Population	Number of specimens			
		young	adult male	adult female	Total
1	Hakodate	3	11	3	17
2	Shimokita	1	1		2
3	Tsugaru	2		1	3
4	Aomori		20	2	22
5	Hakkoda	1	6	3	10
6	Iwaizumi	1	9	1	11
7	Hayachine		1	1	2
8	Moriyoshiyama	32	16	15	63
9	Sugawa spa	4	1	1	6
10	Chokaizan	13	8	8	29
11	Yusa	1			1
12	Sendai	1	1	4	6
13	Oguni		3		3
14	Fukushima	2	1	2	5
15	Takine			1	1
16	Niigata	65	64	13	142
17	Kase		5		5
18	Shiobara	12	34	24	70
19	Tatebayashi		25	16	41
20	Mito		20	20	40
21	Tsukuba	1	10	9	20
22	Kiyosumi	10	67	18	95
23	Tokorozawa	2	22	21	45
24	Togane		15	6	21
25	Tokyo	8	39	12	59
26	Yokohama	8	6	3	17
27	Okutama	2	41	17	60
28	Hotakayama	14	1	3	18
29	Shiga Kogen	6	3	2	11
30	Asamayama	1	10	7	18
31	Ueda	2	13	3	18
32	Enzan	6	51	30	87
33	Fuji	3	2	1	6
34	Izu		29	10	39
35	Amagi	1	1		2
36	Myoko	2	1		3
37	Omachi	5	5		10
38	Matsumoto	2	70	25	97
39	Ikawa	6	14		20
40	Shizuoka		3	1	4
41	Kurobe		2		2
42	Tateyama		1	1	2
43	Kamikochi		39	6	45
44	Kiso	1	1	6	8
45	Ohkuwa		1		1
46	Ontake	3			3
47	Takayama	1	3	5	9
48	Gujyo Yahata	1	2	1	4

(cont'd.)

(Table 3 cont'd.)

Population		Number of specimens			
		young	adult male	adult female	Total
49	Horai		3	5	8
50	Nagoya		21	5	26
51	Yatsuo	2	12	3	17
52	Kanazawa	3	6	2	11
53	Hakusan	2	3		5
54	Shiramine		10	1	11
55	Nogo Hakusan	2	25	7	34
56	Mihama	1	21	14	36
57	Kohoku	5		2	7
58	Kyoto Ashu	23	8	12	43
59	Hirasan	10	57	12	79
60	Kuramayama	4	24	9	37
61	Kyoto Iwakura	1	28	11	40
62	Daimonjiyama	47	10	4	61
63	Kyoto Momoyama	65	46	36	147
64	Settsu	2	1	1	4
65	Kobe	2	5	1	8
66	Nara	24	3		27
67	Tsu	2			2
68	Ise	2		2	4
69	Yoshino	1	1	1	3
70	Izumi	23			23
71	Ryujin	2	1	3	6
72	Kumano		2	2	4
73	Kinan	95	12	12	119
74	Awaji			1	1
75	Mikata	2		2	4
76	Daisen	3			3
77	Matsue			1	1
78	Hiba	10	1	9	20
79	Kammuriyama		27	15	42
80	Hagi	91	22	10	123
81	Takamatsu	3	50	23	76
82	Sanuki	3			3
83	Tsurugisan	4	1	2	7
84	Ishizuchisan	11	3	7	21
85	Oda	3	6	3	12
86	Kochi	9	27	14	50
87	Ashizuri		3	3	6
88	Usuki	55	31	8	94
89	Hikosan	2	2	4	8
90	Iki	3			3
91	Satsumafuke		7	22	29
92	Kirishima	7		1	8
93	Hyuga		1	1	2
94	Kagoshima	1	4	1	6
95	Koshiki			1	1
96	Yakushima	13	16	11	40

Table 4. Geographic parameters for populations of the Japanese common toad.

Population	Longitude (°E)		Latitude (°N)		Altitude (m)	
	range	X̄	range	X̄	range	X̄
1		140.43		41.45	20– 280	30
2	141.14–141.28	141.21	41.18–41.25	41.22	0– 20	20
3	140.24–140.25	140.25	41.00–41.01	41.01	0– 5	5
4	140.37–140.52	140.45	40.33–40.49	40.41	40– 200	110
5	140.51–140.57	140.54	40.36–40.39	40.38	450– 920	690
6	141.50–141.59	141.54	39.39–39.48	39.42	40– 220	150
7		141.30		39.33		1350
8		140.37		39.59	630– 870	750
9		140.46		38.59		1120
10	140.00–140.01	140.01	39.06–39.07	39.07	1150–1700	1450
11		140.02		39.01		440
12		140.51		38.15		100
13	139.45–139.48	139.47	38.04–38.25	38.15	130– 400	270
14	140.13–140.23	140.21	37.36–38.09	37.53	580–1500	730
15		140.41		37.26		780
16	138.49–139.20	139.02	37.42–37.57	37.50	15– 120	50
17		139.37		37.45		300
18	139.47–139.51	139.49	36.54–37.07	36.59	960–1700	1220
19	139.33–139.52	139.43	36.14–36.20	36.17	20– 40	30
20	140.25–140.31	140.28	36.23–36.32	36.28	40– 60	50
21	140.06–140.18	140.11	35.58–36.12	36.05	20– 30	30
22		140.10	35.07–35.09	35.08	20– 228	120
23	139.19–139.26	139.23	35.50–35.51	35.50	70– 110	70
24	139.56–140.20	140.08	35.33–35.48	35.41	30– 40	35
25	139.28–139.42	139.35		35.42	30– 80	60
26	139.29–139.34	139.32	35.22–35.33	35.28	40– 60	50
27	139.10–139.13	139.11	35.28–35.48	35.42	150– 550	380
28	138.57–139.09	139.03	36.43–36.48	36.46	700–2000	1270
29	138.31–138.43	138.34	36.38–36.49	36.43	1100–2300	1810
30	138.21–138.38	138.27	36.21–36.31	36.26	1070–1700	1310
31	137.31–138.17	138.03	36.00–36.33	36.21	360–1130	730
32	138.40–139.02	139.52	35.43–35.52	35.49	800–1450	1080
33	138.42–138.58	138.49	35.18–35.25	35.21	550–1685	1280
34	138.55–139.10	139.00	34.40–35.08	35.59	5– 280	90
35		138.57		34.51		1000
36		138.05	36.52–36.53	36.53	1300–1800	1600
37	137.52–137.58	137.56	36.32–36.57	36.47	800–1300	970
38	137.59–138.16	138.05	36.11–36.15	36.14	620–1080	870
39	138.11–138.24	138.17	35.13–35.34	35.20	680–1700	1085
40	138.19–138.31	138.24	35.09–35.12	35.10	220– 600	370
41		137.28		36.35		900
42	137.31–137.35	137.33	36.26–36.27	36.27	2080–2300	2200
43	137.36–137.40	137.38	36.07–36.15	36.10	1500–1850	1630
44	137.37–137.46	137.41	35.36–35.51	35.46	440–1000	750
45		137.46		35.44		1550
46	137.24–137.30	137.27	35.49–35.52	35.51	1300–2180	1740
47	137.15–137.16	137.16	35.48–36.08	35.58	380– 580	480
48		137.00		35.45		800

(cont'd.)

(Table 4. cont'd.)

Population	Longitude (°E)		Latitude (°N)		Altitude (m)	
	range	X̄	range	X̄	range	X̄
49	137.25–137.35	137.32	34.54–35.11	35.02	400–1100	720
50		136.59		35.08	40– 80	60
51	136.31–137.06	136.50	36.15–36.30	36.27	180– 830	400
52		136.40		36.34		50
53	136.43–136.55	136.48	36.13–36.18	36.16	500–1100	820
54		136.45		36.07		850
55	136.35–136.43	136.39	35.42–35.45	35.44	400– 550	480
56	136.00–136.01	136.01	35.31–36.01	35.46	20– 200	110
57	136.07–136.24	136.18	35.15–35.36	35.23	140– 890	530
58	135.43–135.46	135.45	35.16–35.21	35.18	350– 850	580
59	135.50–135.57	135.52	35.07–35.17	35.12	280– 580	380
60	135.39–135.47	135.44	35.03–35.09	35.07	300– 650	420
61		135.48		35.05		180
62		135.48	35.01–35.03	35.02	100– 300	200
63		135.47		34.56	70– 90	80
64	135.29–135.37	135.33	34.51–34.55	34.53	140– 380	290
65	135.16–135.18	135.17	34.44–34.47	34.46	40– 650	350
66	135.40–135.52	135.46	34.40–34.41	34.41	150– 400	250
67	136.27–136.30	136.29	34.36–34.42	34.39	15– 250	130
68	136.42–136.46	136.44	34.25–34.27	34.26	30– 110	80
69	135.52–136.03	135.56	34.16–34.30	34.23	260– 860	540
70	135.23–135.40	135.33	34.20–34.26	34.23	140–1050	590
71	135.20–135.44	135.33	33.56–34.05	33.59	200– 800	470
72	135.46–135.59	135.53	33.39–33.57	33.49	70– 200	160
73	135.20–135.50	135.35	33.27–33.41	33.35	10– 100	50
74		134.52		34.14		50
75	134.32–135.00	134.46	35.31–35.35	35.33	120– 300	210
76	133.33–133.47	133.40	35.16–35.23	35.20	500– 900	700
77		133.10		35.30		20
78	132.55–133.05	133.01	35.02–35.04	35.03	560–1290	900
79		132.05		34.26		795
80	131.09–131.23	131.17	34.14–34.46	34.28	10– 150	80
81	133.49–134.04	133.59	34.23–34.29	34.25	20– 70	30
82		134.02		34.07		700
83		134.04		33.53	650–1450	1050
84	133.06–133.10	133.08	33.43–33.46	33.44	700–1700	1270
85	132.54–133.02	132.59	33.30–33.32	33.32	840– 980	890
86	133.18–133.33	133.26	33.23–33.34	33.28	10– 250	110
87	132.48–133.01	132.55	32.43–32.48	32.46	10– 200	150
88		131.48		33.07		20
89	130.56–131.26	131.10	32.51–33.29	33.12	500–1100	770
90	128.41–129.28	129.05	32.40–33.20	33.00	100– 500	300
91	130.36–130.37	130.37	32.17–33.07	32.42	200– 465	330
92		130.51		31.57	1250–1450	1350
93	131.07–131.24	131.16	31.29–31.48	31.39	20– 80	50
94	130.33–130.45	130.39	31.35–31.48	31.38	50– 70	60
95		129.52		31.51		20
96	130.21–130.39	130.30	30.16–30.27	30.22	10– 60	40

toads hitherto described. The specimens available for this study were 2,966 individuals from 283 points in various localities of Japan. As will be mentioned later, I excluded very young specimens of less than about 20 mm SVL, since analyses of external morphology were very difficult in these samples because of the poor development of some characters.

Specimens from each point are regarded to form a deme (Gilmour and Gregor, 1939; Mayr, 1978) there, but, for the convenience of comparisons, I grouped specimens of the Japanese common toad from 241 demes into 96 populations according to the geographic location and climatic conditions under which each deme exists, and in analyzing the variation, I regarded each population as a basic unit. The name of the locality, number of specimens, geographic location, and climatic environment for each deme and/or population are shown in Tables 3–5. Likewise, the data for the Miyako toad and for the Japanese stream toad are shown in Tables 6–9.

The geographical and climatological parameters for each population are the means of parametric values of all the demes included. The methods for calculating these values are described elsewhere (chapter V).

Since little is known about the dispersal range and barriers for the distribution of the Japanese toads, I chose the splitting method in grouping demes into population: if both two demes have ample number of samples, they were not grouped into one population even if their geographic locations were situated close to each other. As a result, the distributional range for each population is not necessarily the same (Fig. 2).

b) *Determination of Sex and Maturity*

In the majority of hitherto reported studies on variations in frogs, analyses were made either only on adults (e.g., Moriya, 1954; Church, 1960; Karlstrom, 1962; Berger, 1966; Inger, 1966; Nevo, 1973; De Lange, 1973; Trueb, 1977), or on samples without discrimination of sex (e.g., Cochran, 1955; Shannon and Lowe, 1955; McAlister, 1962; Schaaf and Smith, 1970). In some cases, only one sex was analyzed (Rogers, 1972).

In the present study, sex and maturity of the specimens except for a few (mostly borrowed ones), were distinguished, and analyses were basically made on four age/sex groups (young male, young female, adult male, and adult female). Since exact age determination was not made for most of the specimens, the term "age groups" is incorrect in a strict sense. The term, however, is used simply to indicate the division of relatively younger and older individuals, with the boader line drawn at sexual maturation. Adult males were identified by secondary sex characters (Liu, 1936): in sexually mature males, the base of the first finger is slightly swollen and the inside of the first, second, and third fingers is equipped with dark, horny nuptial asperities. These asperities develop most prominently during the breeding season, but most males retain rather clear asperities even in the nonbreeding seasons.

The remaining three age/sex groups are not always easily distinguished by the external features, and discrimination was made by the results of dissection. Maturity in females was determined by the degree of development of the ovary and oviduct: females with pigmented ova in ovaries, or those having ovaries with corpora lutea and enlarged and convoluted oviducts were regarded as adults (Inger, 1954: 203; Karlstrom, 1962:

Table 5. Climatic parameters for well-represented populations of the Japanese common toad.

Population	Temperature (°C)	Precipitation (mm)	Population	Temperature (°C)	Precipitation (mm)
1	8.8	1232	51	12.6	3259
3	9.7	1597	52	14.4	2931
4	9.7	1392	53	8.6	3912
5	8.1	1961	54	9.5	3663
6	10.3	993	55	12.1	3362
8	6.7	2540	56	13.9	2610
9	5.1	2081	57	11.3	2279
10	3.4	2621	58	12.1	2001
12	11.7	1232	59	12.7	2240
13	10.3	3246	60	13.0	2001
14	9.1	1525	61	14.1	1675
16	13.6	1971	62	14.5	1646
17	11.1	2913	63	15.5	1625
18	8.5	1435	64	13.7	1414
19	14.7	1105	65	12.5	1936
20	14.0	1379	66	15.0	1379
21	14.2	1245	67	14.8	1576
22	15.5	1992	68	15.7	1945
23	14.3	1333	69	12.3	2179
24	14.8	1279	70	12.7	1276
25	15.1	1274	71	12.4	2982
26	15.6	1503	72	15.0	3101
27	13.3	1450	73	17.2	2505
28	5.7	1893	75	13.5	2390
29	4.2	1825	76	11.2	2574
30	6.6	1212	78	9.4	2459
31	10.8	878	79	10.8	2307
32	8.5	1500	80	15.6	1781
33	8.3	2170	81	15.5	1230
34	15.5	1798	82	11.8	1480
36	5.1	2393	83	10.4	1549
37	8.6	2514	84	12.2	2100
38	9.8	1197	85	11.7	2100
39	9.7	2003	86	16.7	2738
40	11.9	2549	87	17.1	2804
43	5.2	2899	88	16.3	2207
44	11.9	2549	89	11.8	2743
46	5.1	2213	90	16.3	2562
47	13.5	2609	91	14.0	2674
48	10.8	2793	92	9.6	2596
49	9.6	2410	94	17.9	2214
50	15.3	1450	96	19.6	3658

Table 6. Number of Miyako toads examined.

Population		Number of specimens			
		young	adult male	adult female	Total
97	Miyakojima	32	43	56	131
98	Irabujima		5	5	10
99	Daitojima	1	21	7	29
100	Okinawajima	1	2	3	6

Table 7. Geographic and climatic parameters for populations of the Miyako toad.

Population	Longitude (°E)		Latitude (°N)		Altitude (m)		Temperature (C°)	Precipitation (mm)
	range	X̄	range	X̄	range	X̄		
97	125.16–125.20	125.18	24.45–24.50	24.48	0– 50	25	23.3	2349
98		125.11		24.50	0– 60	30		
99	131.14–131.19	131.16	25.50–25.57	25.54	20– 50	35	23.2	1711
100		125.18		24.50	0– 100	50	22.2	2143

Table 8. Number of Japanese stream toads examined.

	Population	Corresponding sympatric population of the Japanese common toad	Number of specimens			
			young	adult male	adult female	Total
101	Yatsuo	51	6	3		9
102	Shiramine	54		1	1	2
103	Nogo Hakusan	55	4	10	4	18
104	Kohoku	57	4	1	1	6
105	Kyoto Ashu	58	6	6	4	16
106	Hirasan	59	6	4		10
107	Ise	68	1		1	2
108	Takamiyama		5	13	5	23
109	Ohdaigahara		55	42	46	143
110	Ohminesan		2	11	3	16
111	Ryujin	71	2			2
112	Kumano	72	6	1	2	9
113	Owase		4	3	2	9

Table 9. Geographic and climatic parameters for populations of the Japanese stream toad.

Population	Longitude (°E)		Latitude (°N)		Altitude (m)		Temperature (°C)	Precipitation (mm)
	range	X̄	range	X̄	range	X̄		
101	136.27–137.07	136.47	36.12–36.32	36.25	550–1500	550	12.6	3259
102		136.41		36.05		920	9.5	3663
103	136.35–136.43	136.39	35.42–35.48	35.45	400– 800	590	12.1	3362
104	136.11–136.29	136.20	35.09–35.40	35.24	200–1099	580	11.3	2279
105	135.43–135.45	135.44	35.20–35.22	35.21	274– 780	480	12.1	2001
106	135.50–135.53	135.51	35.11–35.14	35.13	650– 850	750	12.7	2240
107		136.42		34.25		220	15.7	1945
108	136.03–136.14	136.08	34.11–34.27	34.19	450– 900	710	12.2	3371
109		136.06		34.11	1400–1600	1500	6.5	4510
110	135.50–135.56	135.54	34.07–34.14	34.11	440–1500	1000	10.5	2179
111		135.34		34.03	–1300	?	12.4	2982
112	135.40–136.01	135.53	33.39–33.57	33.49	200– 580	430	13.5	3101
113	136.10–136.16	136.12	34.01–34.05	34.03	80– 300	150	15.4	3820

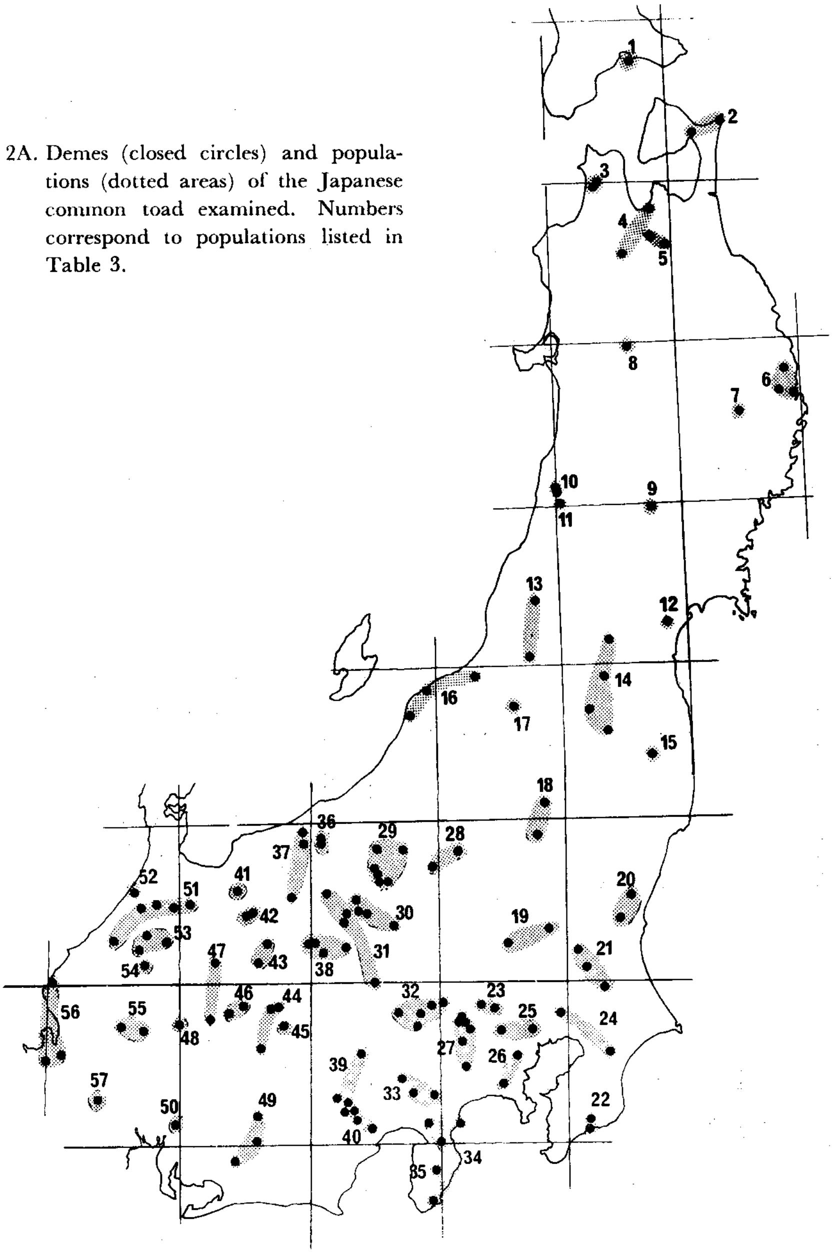

Fig. 2A. Demes (closed circles) and populations (dotted areas) of the Japanese common toad examined. Numbers correspond to populations listed in Table 3.

58, 63).

De Lange (1973) determined sex by the results of mere observations of external features, but I eschewed this method, and specimens not sexed by dissection were discarded on most occasions.

2. *Observation Methods*

a) *Measurements*

Measurements and observations were made on preserved specimens, and obviously

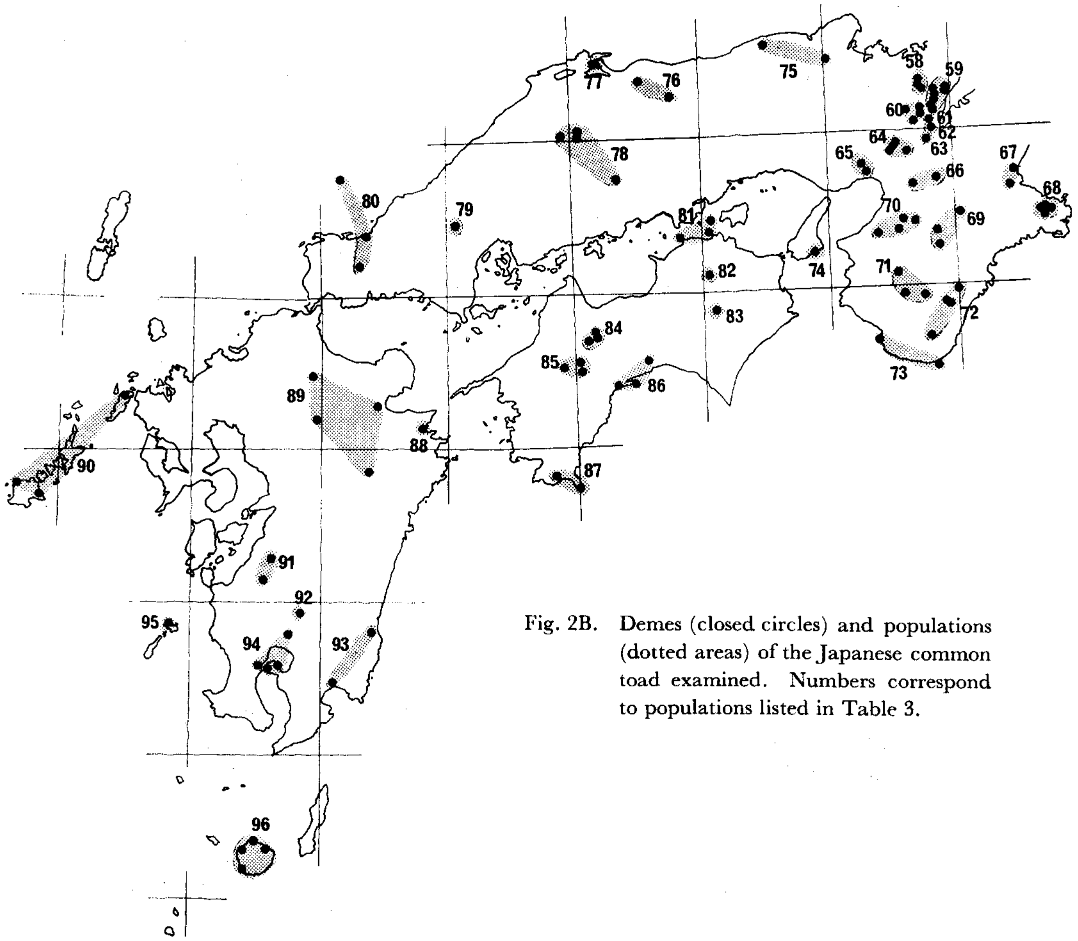

Fig. 2B. Demes (closed circles) and populations (dotted areas) of the Japanese common toad examined. Numbers correspond to populations listed in Table 3.

abnormal individuals such as those showing vertebral anomalies were excluded from the anlyses.

Measurements were taken with a divider and a vernier caliper, to an accuracy of 0.1 mm. For smaller specimens, a binocular dissecting microscope equipped with an ocular micrometer was utilized. To minimize the measurement error, I myself made all the measurements for all the specimens.

In anurans, measurements taken after fixation somewhat differ from those taken from fresh specimens; shrinkage occurs in fixed and preserved specimens, as will be mentioned later. It is, however, actually impossible to make measurements for various body parts on many fresh specimens at a time. Further, specimens kept in museums and institutions are always preserved ones, and measurement data in the literature are mostly for preserved specimens. Consequently, I chose to make measurements on preserved specimens.

Most of the specimens measured were fixed for one night in 10% commercial formalin, washed in tap water, and later transferred to and preserved in 70% ethanol (the method recommended by Pisani, 1973). Most of specimens borrowed from museums and institutions were preserved in 60–70% ethanol, except a few specimens which have been fixed and preserved long in formalin or whose method of fixation was unknown.

b) *Dimensions Measured*

The reference points for 31 chief character dimensions and comments on them are described below (see also Fig. 3). These include most of the lengths hitherto frequently measured in the taxonomy of anurans, but many of the reports so far inadequately indicate the reference points for measurements (e.g., Boulenger, 1880, 1897; Okada, 1931), and, therefore, some character dimensions treated herein do not necessarily coincide with those reported by the previous authors in regard to reference points. Usually, paired structures were measured on the left side of the body unless there was a defect or anomaly on that side. Direct line distance was measured for each dimension, unless otherwise noted.

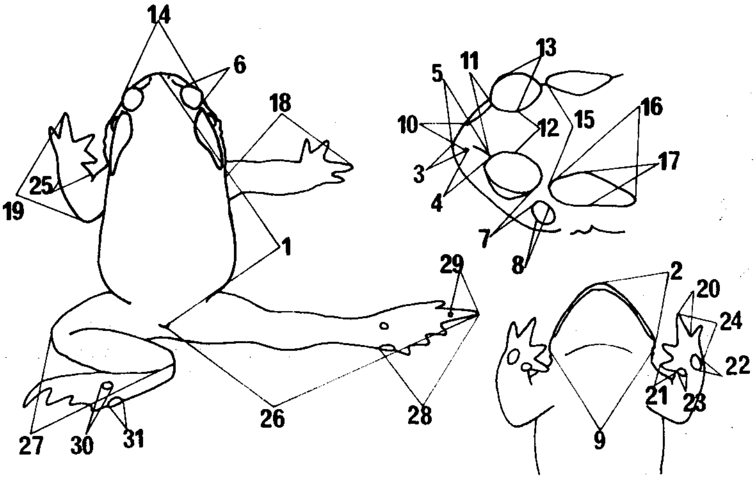

Fig. 3. Character dimensions. 1: snout-vent length (SVL); 2: head length (HL); 3: snout-nostril length (S-NL); 4: nostril-eyelid length (N-EL); 5: snout length (SL); 6: eye length (EL); 7: tympanum-eye length (T-EL); 8: tympanum diameter (TD); 9: head width (HW); 10: internarial distance (IND); 11: intercanthal distance (ICD); 12: interorbital distance (IOD); 13: upper eyelid width (UEW); 14: upper eyelid margin distance (UEMD); 15: interparotoid-tip distance (IPTD); 16: parotoid length (PL); 17: parotoid width (PW); 18: forelimb length (FLL); 19: lower arm length (LAL); 20: third finger length (TFL); 21: first finger length (FFL); 22: outer palmar tubercle length (OPTL); 23: inner palmar tubercle length (IPTL); 24: hand length (HAL); 25: forearm width (FAW); 26: hindlimb length (HLL); 27: tibia length (TL); 28: foot length (FL); 29: fourth toe length (FTL); 30: outer metatarsal tubercle length (OMTL); 31: inner metatarsal tubercle length (IMTL).

i) *Standard Character Dimension*

1) Snout-vent length (SVL=Body length): distance from the tip of the snout (=most anterior point on upper jaw in the Japanese toads) to the anterior margin of the vent, measured dorsally on flattened

body. This is the standard of body size, and the reference points are the same as those taken by most previous authors.

ii) *Character Dimensions of Head Region*

2) Head length (HL): fistance from the tip of the snout to hind border of the angle of the jaw (not parallel with the median line), measured ventrally. This is a standard of head size and the reference points are the same as those taken by Liu (1950) and Duellman (1970). For preserved toads, in contrast to frogs, it was in most instances difficult or impossible to assess accurately the length of the head measured parallel with the body axis.

3) Snout-nostril length (S-NL): distance from the center of an external naris to the tip of snout (not parallel with body axis). Previous workers seem to have measured the minimum distance between a nostril and the tip of the snout.

4) Nostril-eyelid length (N-EL): distance from the corner of the external naris to the anterior margin of the upper eyelid (not parallel with body axis).

5) Snout length (SL): distance from the tip of the snout to the angle formed by snout and upper eyelid (not parallel with body axis). The values are smaller than those measured between the tip of snout and the eye itself.

6) Eye length (EL): the greatest diameter of the eye, including upper eyelid; i.e., distance between anterior and posterior ends of upper eyelid. Consequently, in a strict sense, the measured values are larger than the actual eye diameter. I took measurements for the above dimensions because it is impossible to measure eye diameter excluding the upper eyelid (Duellman, 1970) for specimens fixed with eyes closed.

7) Tympanum-eye length (T-EL): minimum distance from the posterior corner of upper eyelid to the anterior border of tympanum. Strictly, this is not a distance between eye and tympanum. The character has been given taxonomic importance in relation to TD. It is sometimes impossible to measure this length for individuals with an indistinct tympanum.

8) Tympanum diameter (TD): the greatest diameter of the tympanum. It is a vertical distance in most individuals. This has been most frequently noticed with relation to T-EL in the taxonomy of the Japanese toads. In some individuals, especially in the Japanese stream toad, it is impossible to measure this because of the vague contour of the tympanum. In addition, the tympanum is often undeveloped in young individuals of less than about 20 mm SVL.

9) Head width (HW): the width of the head measured at the angles of the jaws; measured ventrally, excluding warts at rictus. Consequently, this measurement does not necessarily represent the maximum width of head. This is one of the standards of the head size. The greatest head width is often used in frogs (e.g., Cochran, 1955; Inger, 1966; Duellman, 1970); in toads the degree of development of warts at the rictus is various, and therefore measuring the maximum width would cause greater errors.

10) Internarial distance (IND): distance between centers of the external nares. The measured value is larger than the minimum distance between the nostrils (Inger, 1966; Duellman, 1970).

11) Intercanthal distance (ICD): distance between anterior edges of canthus. The reference points were shown by Terent'ev and Chernov (1965:56).

12) Interorbital distance (IOD): the minimum distance between the paired upper eyelids, measured perpendicular to the body axis. This is regarded as an important dimension in the taxonomy of frogs and is also frequently measured in toads (e.g., Okada, 1931; Smith, 1951). In the Japanese toads, however, the outer margins of the frontoparietals elevate dorsolaterally with growth of the body, giving a vague dorsal contour to the upper eyelids. Therefore, the reference points between which the measurements are made are sometimes vague, resulting in measurement errors.

13) Upper eyelid width (UEW): the greatest width of the upper eyelid, measured perpendicular to its antero-posterior axis. This width is noticed with relation to IOD (e.g., Smith, 1951), but measurement errors are easily encountered for the same reason as in IOD in normal specimens, as well as in specimens with closed eyes.

14) Upper eyelid margin distance (UEMD): the greatest distance between outer margins of right and left upper eyelids, measured perpendicular to the body axis. This dimension is not measurable for specimens with closed eyes.

15) Inter-parotoid-tip distance (IPTD): distance between most anterior points of right and left parotoids, measured perpendicular to body axis. The reference points are the same as those used by

Rogers (1972) and were referred to as "interparotoid space" by Matsui (1976a). If the anterior ends of the parotoids are not protruded, the median points of their anterior end were regarded as the most anterior point.

16) Parotoid length (PL): the greatest length of the parotoid gland, exclusive of the warts just behind it (Matsui, 1979b). If the right and left parotoids differed extremely in length, the larger was measured. Just as for dimension 8, this length was unmeasurable in extremely young individuals of less than ca. 20 mm SVL, since the parotoid gland is not developed in them. This length is often regarded as important in relation to dimension 17 (Okada, 1937; Porter, 1964b).

17) Parotoid width (PW): the greatest width of the parotoid gland. If the right and left parotoids were different in width, the wider was measured. This width is often used as a diagnostic character to differentiate toad species (e.g., Porter, 1964a) but is unmeasurable in young individuals for the same reason as for dimension 16.

iii) Character Dimensions of Forelimb

18) Forelimb length (FLL): distance from the axilla to the tip of the longest finger (the 3rd finger), measured with the forelimb stretched perpendicular to the body axis. This length is one of the standard measures to show sizes of toads; but in fixed materials, particularly in males, this length is often unmeasurable since the forelimbs can hardly be stretched fully as indicated by Schuster (1950) and De Lange (1973). Measurement errors may be great because the exact point at the axilla is often not determinable.

19) Lower arm length (LAL): distance from the elbow joint to the tip of the longest finger (the 3rd finger), measured with the forearm stretched straight and flexed perpendicular to the upper arm. This is a standard measure of forelimb, and measurement points are the same as those shown by Liu (1950). It is easily measurable even in firmly fixed specimens. This dimension was referred to as "radial-ulnar length" by Matsui (1976a).

20) Third finger length (TFL): distance from the base point between third and fourth fingers to the tip of the third finger, measured dorsally with the fingers stretched straight (this length equals the outer length of the third finger). In a few samples, this dimension was unmeasurable because the tip of the third finger was damaged or missing.

21) First finger length (FFL): distance from the distal end of the inner metatarsal tubercle to the tip of the first finger, measured with the finger fully stretched (this length is equal to the inner length of the first finger).

22) Outer palmar tubercle length (OPTL): the maximum length of the outer palmar tubercle, measured parallel to the forearm axis. In toads, there are numerous warts and wrinkles on the palmar surface, and therefore, the outer palmar tubercle is sometimes united with the warts near its distal end. Consequently, the reference points are sometimes obscured. This is one of the diagnostic characters given by Okada (1930) for the Miyako toad.

23) Inner palmar tubercle length (IPTL): the maximum length of the inner palmar tubercle; the reference points are not clear if the tubercle is feeble.

24) Hand length (HAL): distance from the proximal edge of the outer palmer tubercle to the tip of the longest (third) finger, measured with the hand fully stretched. The reference points are different from those shown by Liu (1950).

25) Forearm width (FAW): The greatest width of the forearm flexed perpendicular to the upper arm. The reference points are the same as those shown by Liu (1950) and Bell (1978). The measurements, however, are somewhat unreliable, because this width may vary with the method of fixation and physiological condition of each individual.

iv) Character Dimensions of Hindlimb

26) Hindlimb length (HLL): distance from the center of anus to the tip of the longest (fourth) toe, measured dorsally with the hindlimb fully stretched perpendicular to the body axis. In the specimens fixed too firmly, the character is sometimes unmeasurable because the knee joint can hardly be extended as stated by Schuster (1950). This has been frequently measured as one of the standard dimensions of the hindlimb.

27) Tibia length (TL): the greatest length of the tibia, measured with the hindlimb positioned in a Z pattern. The reference points correspond to those shown by Peters (1964: Fig. 30B-1).

28) Foot length (FL): distance from the proximal end of the inner metatarsal tubercle to the tip of the longest (fourth) toe (not parallel with hindlimb axis). This length is not measurable when the toe

tips are missing or damaged. If the right and left feet were extremely different in length, measurement was taken of the longer foot. The reference points are the same as those given by previous workers (e.g., Okada, 1931; Duellman, 1970).

29) Fourth toe length (FTL): distance from the center of the third subarticular tubercle to the tip of the fourth toe. The measurement, therefore, is shorter than the actual length of the fourth toe.

30) Outer metatarsal tubercle length (OMTL): the greatest length of the outer metatarsal tubercle, measured parallel to the hindlimb axis. This dimension may be unmeasurable, or measurement errors may be great because the base of the tubercle is often obscured.

31) Inner metatarsal tubercle length (IMTL): the greatest length of the inner metatarsal tubercle, measured parallel to its long axis. This dimension is taxonomically noted in frogs of the genus *Rana* (e.g., Berger, 1964, 1966; Borkin et al., 1979) and is also suggested to have special relation with age (Kauri, 1959).

c) *Shrinkage in Fixed Specimens*

In the mollusca, copepoda, fishes, reptiles, and mammals, all or part of the body of a preserved specimen shrinks considerably and the degree of shrinkage is precisely known (Kubo and Yoshihara, 1972; Klauber, 1937; Maeda, 1977), but information is scarce on amphibians (Inger, 1954).

Body sizes described in taxonomic works of anurans have been generally based on preserved specimens; in ecological and ethological research, on the contrary, measurements are usually taken in life chiefly because the frogs and toads are marked and released. Therefore, it is necessary to elucidate the shrinkage relation between fresh and fixed specimens so as to make it possible to compare data from both sources. Further, the degree of shrinkage changes in accordance with length of period of preservation in some fishes (Stobo, 1972), and this tendency might also occur in amphibians. Consequently it is also necessary to check whether it is possible to compare the data for long-preserved museum specimens directly with the data for recently fixed and preserved materials.

1) Shrinkage caused by formalin fixation

Inger (1954) has shown in the Philippinese anurans that measurement errors are greater in body length than in head width or tibia length. His observation seem to suggest a greater shrinkage rate by fixation in the body length than in the other measurements. Therefore, I examined the degree of shrinkage by formalin fixation for the body length.

1-a) Shrinkage in toads fixed alive

During the course of field research, toads are often directly thrown into formalin and fixed alive, and they are usually fixed with the body somewhat bent. In order to determine the shrinkage rate under these conditions, 27 male and 15 female adult toads from Kammuriyama (Pop. 79) were utilized. First, each toad was anesthetized with chloreton and then the body was fully stretched. The SVL measurement was taken in this condition. Second, after recovering from anesthesia, the toad was put into 10% formalin solution and fixed alive. The following day, measurement was taken again after the fixed toad was washed in tap water and transferred to 70% ethanol.

The percentages of SVL in the preserved condition to that in fresh state ranged from 89.5 to 93.9% ($\bar{X}=92.2\pm0.47$ (2SE)) and from 91.3 to 96.1% ($\bar{X}=93.3\pm0.74$) in males and females, respectively. The value was significantly larger in females than

Table 10. Difference between Stejneger's (1907: A) and my measurements (taken in 1978: B).

Character	Specimen									mean of 100B/A
	USNM23540 (*B. formosus*)			USNM31951 (*B. smithi*)			USNM17516 (*B. b. asiaticus*)			
	A	B	100B/A	A	B	100B/A	A	B	100B/A	
SVL	110	113.0	102.7	110	111.0	100.9	84	84.8	101.0	101.5
snout-tympanum	24	23.8	99.2	28	27.7	98.9	19	18.8	98.9	99.0
nostril-tympanum	18	18.2	101.1	21	21.2	101.0	14	14.6	104.3	102.1
IND	6	7.4	123.3	7	8.2	117.1	4	5.3	132.5	124.3
IOD	10	9.9	99.0	9.5	8.7	91.6	7	6.6	94.3	95.0
TD	8	7.8	97.5	6	6.1	101.7	3	3.8	126.7	108.6
T-EL	3	2.6	86.7	6	5.0	83.3	2.5	1.8	72.0	80.7
HW	46	43.0	93.5	43	42.3	98.4	30	29.8	99.3	97.1
FLL	66	69.0	104.5	74	79.2	107.0	52	52.4	100.8	104.1
HLL	147	149.0	101.4	154	153.0	99.4	110	107.8	98.0	99.6
TL	42	43.2	102.9	44	43.3	98.4	30	31.2	104.0	101.8
FL	52	53.2	102.3	54	53.2	98.5	39	37.6	96.4	99.1
PL	21	25.0	119.0	25	25.7	102.8	16	16.8	105.0	108.9
PW	8	8.6	107.5	8	8.2	102.5	9	9.8	108.9	106.3

Table 11. Difference between Stejneger's (1907: A) measurements of TD and T-EL and mine (taken in 1978: B). Specimens are from USNM collections.

Specimen	TD			T-EL			Specimen	DT			T-EL		
	A	B	100B/A	A	B	100B/A		A	B	100B/A	A	B	100B/A
11348	5	5.3	106.0	2.5	2.6	104.0	34325	9	9.2	102.2	3.5	4.3	122.9
34309	9	8.8	97.8	4	4.1	102.5	34326	9	9.6	106.7	3	3.0	100.0
34310	8.5	7.8	91.8	3	2.7	90.0	34327	8	7.3	91.3	3.5	3.2	91.4
34311	9	9.2	102.2	3.5	4.1	117.1	34328	6	6.3	105.0	3	2.7	90.0
34312	9	10.2	113.3	4	4.5	112.5	31851	3.5	3.9	111.4	3.5	3.2	91.4
34313	8.5	12.0	141.2	3	2.8	93.3	31929	2	2.1	105.0	2	1.4	70.0
34314	9.5	9.3	97.9	3.5	1.8	51.4	31943	5	6.2	124.0	4	3.8	95.0
34315	8.5	9.0	105.9	3	2.8	93.3	31945	3.5	3.6	102.9	3.5	3.2	91.4
34317	9	9.8	108.9	3.5	3.3	94.3	31946	2.5	2.8	112.0	2.5	2.8	112.0
34318	8.5	8.4	98.8	4	3.6	90.0	31947	2.5	2.9	116.0	2.5	2.2	88.0
34319	8.5	7.3	85.9	3	2.8	93.3	31948	2	2.4	120.0	2	2.2	110.0
34320	9.5	9.2	96.8	3.5	2.3	65.7	31949	2	1.9	95.0	2	1.9	95.0
34321	8	8.1	101.3	4	3.0	75.0	31951	6.1	6.1	100.0	6	5	83.3
34322	8	7.8	97.5	3	2.7	90.0				$\bar{X}$=106.1± 4.3 (2SE)			$\bar{X}$=94.1± 6.0 (2SE)
34323	10	12.2	122.0	3	3.8	126.7							
34324	7.5	8.8	117.3	2.5	2.2	88.0							

in males ($t=2.58$, dF=40, $.01>p>.02$). Thus, the SVL measured in toads fixed alive was 7–8% smaller than that measured in fresh specimens, and the shrinkage rate was greater in males.

1-b) Shrinkage in toads fixed dead

If enough equipment was available for preparing specimens, such as in the laboratory process, toads were killed with chloretone and fixed on a board with the body fully stretched.

To obtain data for shrinkage rate in this condition, 22 male and 4 female adults from Matsumoto (Pop. 37) were used. After having been killed with chloreton, each toad was measured for SVL with the body fully stretched, fixed in formalin for 24 hours, and then remeasured. Then, the specimens were washed in tap water and transferred to 70% ethanol, and measurements were taken once again two days after fixation.

The results thus obtained showed that the SVL after formalin fixation was 95.8–100.9% (males; $\bar{X}=98.2\pm0.62$ (2SE)) and 99.0–99.8% (females; $\bar{X}=99.4\pm0.34$) of the values before fixation. There was no significant difference between the sexes ($t=1.65$, dF=24, $.2>p>.1$). The SVL after washing and preservation in ethanol was 96.4–100.2% (males; $\bar{X}=98.6\pm0.41$) and 97.9–101.0% (females; $\bar{X}=99.4\pm1.27$) of the original SVL. Sexual difference in shrinkage rate was not detected ($t=1.55$, dF=24, $.2>p>.1$). Thus, shrinkage from the original body length was only 0.6–1.4%; there is a slight change caused by washing and preserving specimens in ethanol.

2) Shrinkage in toads long preserved in ethanol

In order to estimate the degree of shrinkage caused by long preservation, several character dimensions were measured for the specimens of the United States National Museum (USNM) collection and the obtained data values were compared with those shown by Stejneger (1907).

In this examination, the reference points adopted were not always identical and measurements were taken by different persons, and therefore, it was expected that there would be large measurement errors. The results, however, were contrary to this supposition, as shown in Tables 10–11. Although the available data were meager, these data indicate that the shrinkage rates were very small even after preservation extending over about 70 years.

III

Intrapopulation Allomorphosis in the Japanese Common Toad from Momoyama, Kyoto

As pointed out above, morphometric characters such as limb length, parotoid length, tympanum diameter and tympanum-eye length, often expressed as ratios between two dimensions, have been regarded as diagnostic in the taxonomy of the Japanese toads (e.g., Stejneger, 1907; Okada, 1931). Some of the characters, however, were used for distinguishing forms notwithstanding the presence of sexual dimorphism within a form (e.g., limb length: Okada, 1931). Sexual dimorphism in some morphometric characters is known in some toads (Cei, 1960), and further, the proportions among these characters change with growth in ranid frogs (March, 1937; Shimizu, 1940; Mecham, 1954; Kauri, 1957; Martof and Humphries, 1959 etc.).

As to the Japanese toads, such problems have hitherto been almost totally neglected, and no detailed studies have been made on sexual dimorphism and ontogenetic changes in these characters. Consequently, to analyze geographic variation of main characters and taxonomically revise the Japanese toads, the problems of sexual and ontogenetic variations must be examined. It seems of value to study first the variations of these characters in detail within a deme.

On the other hand, a proper method of age determination for the Japanese toads has not been established, and individual difference in growth rates in a given period is enormous in toads: some individuals may be sexually mature and others immature even if they are similar in body size, or conversely, animals of the same age often show great difference in body size from one individual to another, especially in immature stages.

For the metrical analyses of the character variations in animals like the Japanese toads, in which no accurate age-grouping is possible, and even if it is possible, variation in growth rates is extremely great, analyses on relative growth or allomorphic (this terminology adopted from Suzuki, 1973) relations among morphometric characters are of great value (Lundelius, 1957; Dodson, 1975).

It has also been indicated by Atchley et al. (1976) that there are statistical problems in determining the presence or absence of difference among any animal groups by comparing simple ratios between morphometric characters (e.g., Porter, 1968). Whether this idea holds true or not is still a debated problem (Corruccini, 1977; Heyer, 1978), but it is highly probable that in some morphometric characters the ratio to the standard dimension would change with growth (e.g., eye length to SVL). From this point of view, too, examinations of allometry or allomorphosis will have some value in the analyses of variations in toads.

In this paper, I will examine the allomorphic relations (in the sense of Needham and Lerner, 1940; often treated as part of allometry: Gould, 1977; see Suzuki, 1973 for terminology) of morphometric characters of body parts, including characters hitherto regarded as taxonomically diagnostic, for the toads from Momoyama, Kyoto. In addition, I will determine the validity of the method of allomorphic analyses by examining the patterns of differences related to age and sex, which are estimated by this method.

MATERIALS AND METHODS

A total of 147 toads collected during July 1972 and March 1977 from Momoyama, Fushimi-ku, in the city of Kyoto (Population 63) were used for this study. The number of individuals and body size of four groups, divided by age and sex, are shown in Table 12. Sex and maturity determinations were made by the method described above. As mentioned there, most of the young individuals ranging from just after metamorphosis to the size of ca. 20 mm in SVL had a indistinct, undeveloped tympanum and parotoid gland, and it was difficult to take correct measurements on them. Therefore, extremely

Table 12. Number and body size (SVL) for each age/sex group of the Japanese common toad from Momoyama, Kyoto.

Age/sex group	N	SVL			
		range	X̄±SD	SE	CV
♂ young	31	32.5– 90.3	68.4±14.2	2.56	20.80
♀ young	34	24.0– 99.2	64.0±19.7	3.37	30.73
♂ adults	46	79.8–116.6	98.5± 7.9	1.18	8.06
♀ adults	36	84.8–135.0	109.6±11.5	1.95	10.51

young individuals were excluded from the materials. All the specimens were first fixed in 10% formalin and later washed in tap water and preserved in 70% ethanol. The 31 measured dimensions are shown in Fig. 3. These include most of the characters hitherto given taxonomic importance. For each of the four age/sex groups (young male, young female, adult male, and adult female), SVL (X) was taken as the standard dimension and the values of the remaining 30 dimensions (Y_j) were plotted against X on a logarithmic scale. The relations of Y_j to X were expressed by the power function $Y=bX^{\alpha}$ (Huxley, 1932; Emerson, 1978; Sweet, 1980) estimated by the least square method. Variance analyses were run to examine the fitness of applying this formula to the raw data by testing the significance of regression. Since some characters showed low correlation with SVL, a significance level of 99% was set in order to eliminate possible misinterpretation. Whether each character is isomorphic or not to SVL was tested by the same method. The presence of difference in slopes and positions of any pair of lines was detected after the method of Reeve (1940). The terminology used in this chapter is adopted from Suzuki (1973).

RESULTS

a) Regression to Allomorphic Formulae

The allomorphic relationships of the 30 characters to SVL are shown in Fig. 4 and Table 13. The relation of each dimension (log Y_j) to SVL (log X) was linear on the double logarithmic axes, but the departure of the points from the calculated regression line was rather large in some characters. In order to know whether it was appropriate to correlate the relation of such variable characters to SVL, the value of correlation coefficient (*r*) between them was first examined (Inagaki, 1971).

In young females, all the 30 characters are correlated to SVL with the *r*'s greater than 0.9, and even the lowest correlation coefficient was 0.935 (TD to SVL). In young males, correlation coefficients were slightly smaller than in young females: in the three characters *r* was smaller than 0.9, and the smallest *r* was 0.883 in HAL to SVL.

In adults, *r*'s were far smaller than in the young. In the males, *r* is greater than 0.9 only in four characters and the largest *r* was 0.927 in S-NL to SVL. By contrast, in as many as 11 characters, *r*'s were smaller than 0.7 and the *r* was only 0.465 in T-EL to SVL. The lowest correlation coefficient ($r=0.347$) was found in IOD, and the correlation between this character and SVL was statistically insignificant ($F_{1,43}=5.89$,

.05 $>$ p $>$ .01). The correlation coefficients were generally greater in adult females than in adult males. In only seven characters *r* was smaller than 0.7, and the smallest *r* was 0.572 in T-EL to SVL.

Although the correlation coefficients were rather small in some characters in adults, statistically significant correlations were ascertained between such characters and SVL with only one exception (IOD in adult males), and almost all the characters could regress to SVL (Table 13). Therefore, the adult male IOD will be excluded from the description henceforth.

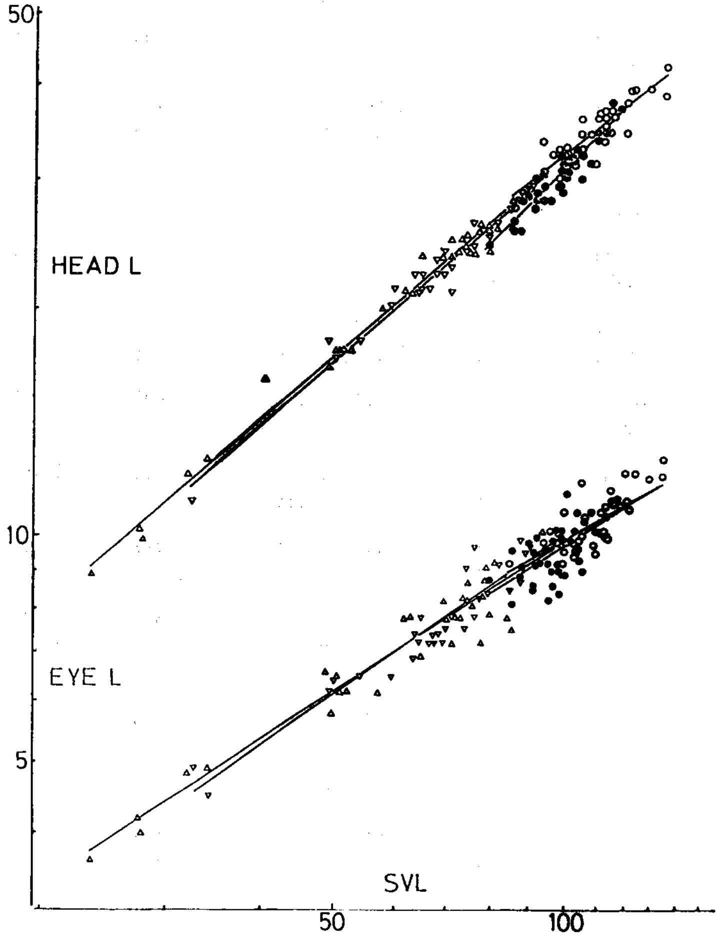

Fig. 4. Allomorphic relationships of HL (Top) and EL (Bottom) to SVL in the four age/sex groups (inverted triangles=young males, triangles=young females, closed circles =adult males, open circles=adult females) of the Japanese common toad from Momoyama, Kyoto.

There was no clear tendency for the characters highly correlated to SVL to be concentrated in any of the body regions, if the 30 characters were divided into three groups according to the regions where they lay (head, forelimb, and hindlimb). In the characters of the head region, high correlation to SVL was found in HL, HW, SL,

Table 13a. Allomorphic constants (α) and initial growth indices (B) for regression lines of each morphometric character—SVL in the Japanese common toad from Momoyama, Kyoto. Males. Growth type abbreviations are: I=isomorphosis, B=bradymorphosis, T=tachymorphosis.

Character	Maturation	N	$\alpha\pm$SD	log B	r	Growth type
HL	young	30	0.893±0.033	−0.280	0.981	B
	adults	43	1.033±0.067	−0.573	0.923	I
S-NL	young	29	0.767±0.049	−0.673	0.948	B
	adults	45	1.008±0.062	−1.132	0.927	I
N-EL	young	29	0.631±0.056	−0.505	0.901	B
	adults	45	0.999±0.155	−1.232	0.701	I
SL	young	29	0.761±0.052	−0.428	0.943	B
	adults	45	1.011±0.106	−0.929	0.825	I
EL	young	30	0.707±0.046	−0.413	0.945	B
	adults	45	0.656±0.125	−0.326	0.624	B
T-EL	young	28	1.193±0.102	−1.741	0.917	I
	adults	44	0.926±0.272	−1.286	0.465	I
TD	young	31	1.373±0.111	−2.020	0.917	T
	adults	45	1.001±0.194	−1.335	0.617	I
HW	young	31	1.034±0.031	−0.482	0.987	I
	adults	46	1.029±0.082	−0.515	0.883	I
IND	young	29	0.815±0.041	−0.808	0.968	B
	adults	45	0.762±0.086	−0.705	0.803	B
ICD	young	29	0.840±0.043	−0.619	0.966	B
	adults	41	0.920±0.176	−0.805	0.642	I
IOD	young	29	0.889±0.073	−0.813	0.920	I
	adults	45	0.583±0.240	−0.258	0.347	–
UEW	young	28	0.832±0.048	−0.756	0.960	B
	adults	44	0.853±0.130	−0.828	0.711	I
UEMD	young	29	0.863±0.032	−0.311	0.982	B
	adults	42	0.850±0.106	−0.322	0.785	I
IPTD	young	29	0.915±0.037	−0.425	0.979	I
	adults	44	0.841±0.091	−0.318	0.818	I
PL	young	31	1.101±0.068	−0.839	0.948	I
	adults	45	1.093±0.136	−0.854	0.776	I
PW	young	29	1.226±0.076	−1.507	0.952	T
	adults	45	0.952±0.180	−1.046	0.627	I
FLL	young	30	0.966±0.032	−0.123	0.985	I
	adults	46	1.123±0.097	−0.423	0.868	I
LAL	young	29	0.997±0.038	−0.286	0.981	I
	adults	45	0.920±0.083	−0.142	0.860	I

(cont'd.)

(Table 13a. cont'd.)

Character	Maturation	N	$\alpha \pm$SD	log B	r	Growth type
TFL	young	29	0.879±0.048	−0.644	0.962	I
	adults	44	0.810±0.128	−0.559	0.699	I
FFL	young	29	1.080±0.078	−1.127	0.937	I
	adults	43	1.363±0.181	−1.636	0.762	I
OPTL	young	29	1.211±0.073	−1.575	0.954	T
	adults	43	1.140±0.209	−1.444	0.648	I
IPTL	young	30	1.123±0.097	−1.579	0.910	I
	adults	43	0.731±0.163	−0.801	0.575	I
HAL	young	30	0.926±0.093	−0.443	0.883	I
	adults	43	0.905±0.083	−0.426	0.862	I
FAW	young	29	1.198±0.113	−1.406	0.898	I
	adults	43	1.363±0.181	−1.636	0.762	I
HLL	young	31	0.997±0.040	0.112	0.977	I
	adults	45	1.069±0.077	−0.008	0.904	I
TL	young	31	0.975±0.036	−0.393	0.981	I
	adults	45	1.076±0.092	−0.569	0.873	I
FL	young	31	1.053±0.043	−0.480	0.977	I
	adults	44	1.102±0.075	−0.543	0.916	I
FTL	young	29	1.096±0.066	−1.066	0.954	I
	adults	42	1.115±0.110	−1.078	0.849	I
OMTL	young	29	1.212±0.120	−1.742	0.889	I
	adults	43	1.189±0.209	−1.728	0.665	I
IMTL	young	29	0.999±0.060	−1.258	0.955	I
	adults	44	0.835±0.173	−0.923	0.597	I

Table 13b. Allomorphic constants (α) and initial growth indices (B) for regression lines of each morphometric character—SVL in the Japanese common toad from Momoyama, Kyoto. Females.

Character	Maturation	N	$\alpha \pm$SD	log B	r	Growth type
HL	young	34	0.879±0.018	−0.249	0.993	B
	adults	34	0.793±0.071	−0.075	0.891	B
S-NL	young	34	0.858±0.033	−0.833	0.978	B
	adults	34	0.835±0.078	−0.783	0.884	I
N-EL	young	33	0.750±0.034	−0.721	0.970	B
	adults	34	0.716±0.133	−0.643	0.688	I
SL	young	33	0.843±0.023	−0.582	0.989	B
	adults	34	0.717±0.083	−0.321	0.835	B
EL	young	33	0.659±0.033	−0.329	0.963	B
	adults	34	0.588±0.103	−0.178	0.711	B

(cont'd.)

(Table 13b. cont'd.)

Character	Maturation	N	$\alpha \pm SD$	log B	r	Growth type
T-EL	young	33	1.238±0.042	−1.803	0.983	T
	adults	33	0.858±0.221	−1.126	0.572	I
TD	young	34	1.063±0.071	−1.436	0.935	I
	adults	34	0.859±0.153	−1.038	0.705	I
HW	young	34	1.015±0.019	−0.437	0.994	I
	adults	35	0.825±0.074	−0.070	0.889	I
IND	young	33	0.792±0.025	−0.746	0.985	B
	adults	34	0.664±0.085	−0.479	0.810	B
ICD	young	33	0.834±0.032	−0.589	0.978	B
	adults	33	0.716±0.126	−0.353	0.714	I
IOD	young	33	0.884±0.040	−0.791	0.970	B
	adults	34	0.687±0.158	−0.415	0.608	I
UEW	young	33	0.843±0.029	−0.773	0.982	B
	adults	34	0.608±0.118	−0.307	0.673	B
UEMD	young	33	0.807±0.020	−0.201	0.990	B
	adults	33	0.624±0.082	0.162	0.806	B
IPTD	young	33	0.921±0.021	−0.431	0.992	B
	adults	34	0.670±0.084	0.053	0.814	B
PL	young	34	1.056±0.037	−0.755	0.981	I
	adults	35	0.972±0.090	−0.595	0.884	I
PW	young	33	1.002±0.043	−1.091	0.972	I
	adults	34	0.810±0.144	−0.742	0.705	I
FLL	young	34	0.965±0.024	−0.124	0.990	I
	adults	34	0.877±0.064	0.060	0.925	I
LAL	young	33	1.029±0.023	−0.346	0.993	I
	adults	34	0.852±0.067	0.001	0.914	I
TFL	young	33	0.918±0.033	−0.714	0.981	B
	adults	34	0.707±0.124	−0.294	0.710	B
FFL	young	31	1.066±0.034	−1.085	0.986	I
	adults	33	0.768±0.104	−0.489	0.797	B
OPTL	young	33	1.276±0.041	−1.676	0.984	T
	adults	34	1.065±0.161	−1.279	0.760	I
IPTL	young	33	1.154±0.059	−1.624	0.961	I
	adults	34	1.015±0.164	−1.373	0.737	I
HAL	young	34	1.010±0.022	−0.594	0.993	I
	adults	34	0.804±0.076	−0.187	0.882	I
FAW	young	32	1.165±0.052	−1.336	0.971	T
	adults	33	1.032±0.246	−1.074	0.603	I
HLL	young	34	1.003±0.019	0.092	0.995	I
	adults	33	0.880±0.061	0.344	0.934	I

(cont'd.)

(Table 13b. cont'd.)

Character	Maturation	N	$\alpha \pm$SD	log B	r	Growth type
TL	young	34	0.981±0.018	−0.406	0.994	I
	adults	34	0.910±0.056	−0.258	0.945	I
FL	young	34	1.025±0.023	−0.439	0.992	I
	adults	36	0.840±0.075	−0.067	0.887	I
FTL	young	33	1.028±0.044	−0.959	0.972	I
	adults	33	0.632±0.134	−0.161	0.647	B
OMTL	young	33	1.201±0.050	−1.710	0.974	T
	adults	34	0.894±0.189	−1.136	0.641	I
IMTL	young	33	1.178±0.054	−1.565	0.969	T
	adults	34	1.037±0.159	−1.307	0.755	I

IND, and IPTD, but the *r*'s of T-EL and IOD were small in all the four age/sex groups. As to the characters of the forelimb, FLL and LAL showed a high correlation with SVL, and the correlations of IPTL and OPTL with SVL were low. In the same manner, among the hindlimb characters the correlations of HLL, FL, and TL with SVL were high but those of IMTL and OMTL were low.

b) *Types of Allomorphosis in Each Age/Sex Group*

Except for adult male IOD, all the characters could regress to SVL as stated above. The pattern in allomorphic relation of each character to SVL was examined in each age/sex group with reference to the allomorphic constant (α in $Y = bX^{\alpha}$).

As shown in Fig. 5, the allomorphic constant (α) varies with characters. The values of α were statistically compared with the case of $\alpha = 1$ in each character for each age/sex group ($p < .01$) and were divided into three types: tachymorphosis ($\alpha > 1$, henceforth expressed as T), isomorphosis ($\alpha = 1$, I), and bradymorphosis ($\alpha < 1$, B).

In the young, 18 characters in males and 14 in females belonged to type I, but in adults, as many as 27 characters in males and 22 in females are type I. The type T was found only in the characters of the young (Table 14).

If each of the 30 characters, other than IOD, was grouped by the sequence of allomorphic types in the order of young males, young females, adult males, and adult females, nine types could be discriminated (Table 14). As many as 11 characters fall within type IIII, four characters each within types BBIB and ITII, three characters within BBII, and two characters each within TIII and BBBB. Each of the remaining three characters represented one type.

As to the location in the body, only two characters in the head region were of type IIII (i.e., isomorphic in all the four age/sex groups), and this number accounted for 12.5% of the total number of characters in the head region. By contrast, six characters (75%) in the forelimb and three characters (50%) in the hindlimb were regarded as type IIII. Conversely, all the characters of types BBIB and BBII were characters of the head region. Type ITII was found in characters of the head, forelimb, and hindlimb.

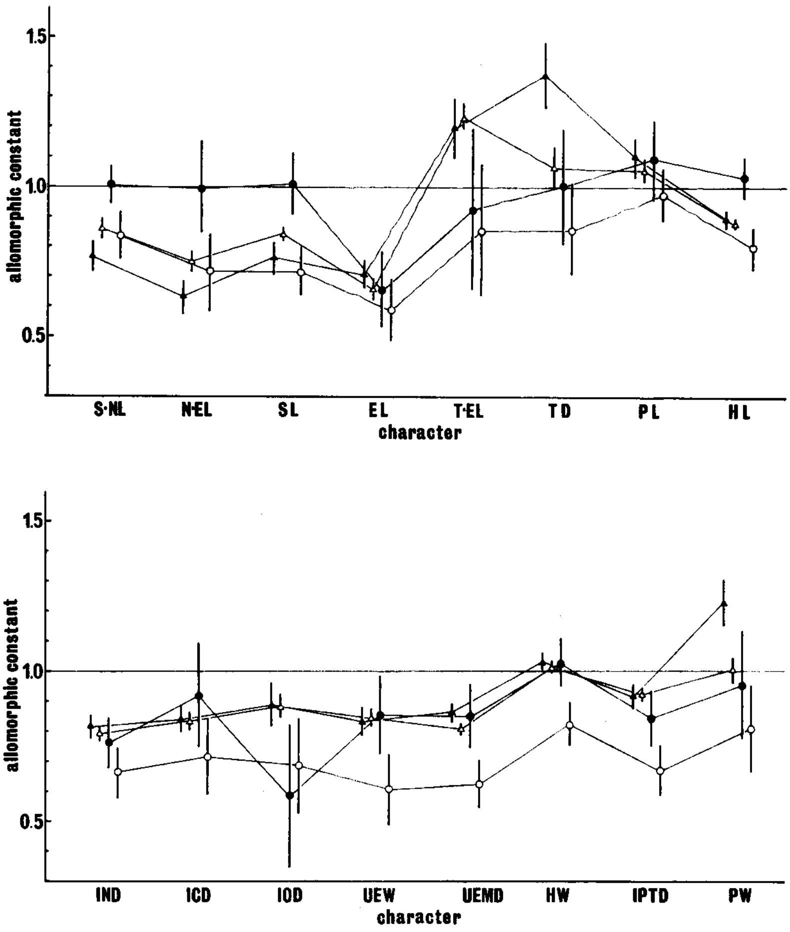

Fig. 5A. Variation in the allomorphic constant for each character. Closed triangles: young males; open triangles: young females; closed circles: adult males; open circles: adult females. Symbols indicate mean and vertical bars standard deviation.

c) *Comparison of Allomorphic Relations among Age/Sex Groups*

In some of the nine types differentiated as above, one age group was different from other groups in the allomorphic relations; e.g., when one character was of type ITII, young females were different in allomorphic relation (tachymorphic) from the remaining three groups (isomorphic). In order to know whether such a difference was statistically significant or not, slope and positional differences of the regression lines (Reeve, 1940) were examined for the four combinations of these age/sex groups: young males and young feamles; young males and adult males; young females and adult females; adult males and adult females (Table 15).

Statistically significant difference in slope was found in only a few of a total of 116 combinations, notwithstanding the great intergroup differences which were found when α (=slope of the regression line) of each group was separately compared with

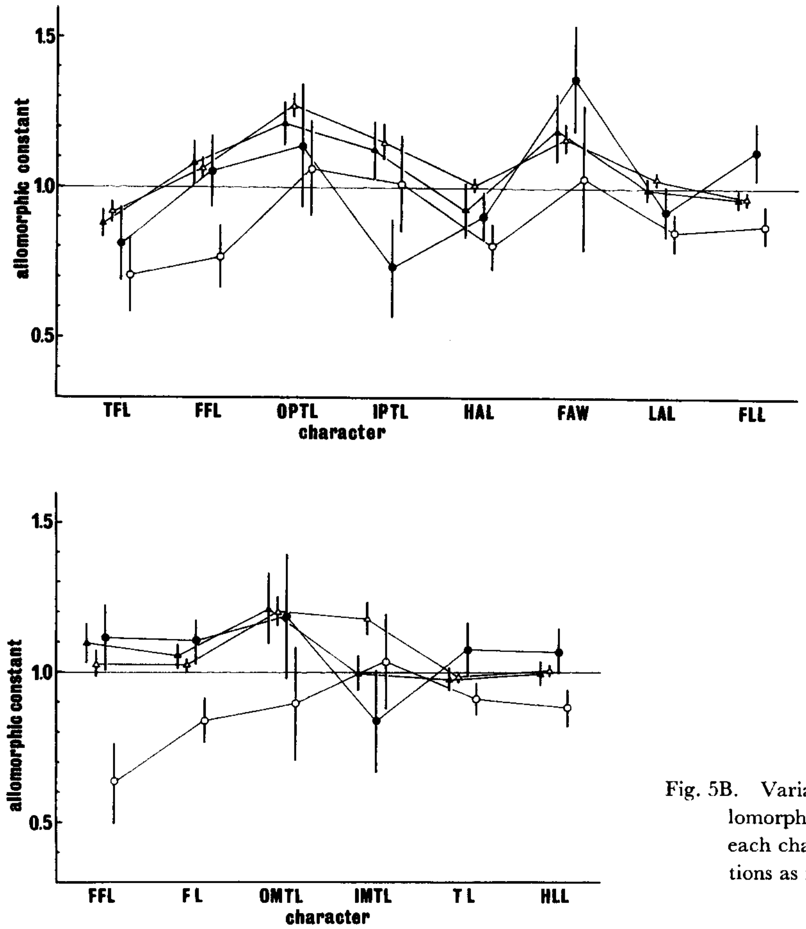

Fig. 5B. Variation in the allomorphic constant for each character. Notations as in Fig. 5A.

the case of $\alpha=1$ and expressed as I, T, or B. Namely, no significant difference in slope was found among the age/sex groups in the 26 characters (over 90% of a total of 29 characters). Only two characters of the head region and one of the hindlimb region showed significant differences in slope. Of the three significantly different characters, difference with growth was found in the male S-NL and female IPTD, and sexual difference was found in the FTL in adults.

In contrast to such uniformity in the slopes, the positions of the regression lines varied more among the age/sex groups, and there were significantly different combinations in 16 characters (over 50% of the 29 characters) (Table 15). The percentage of the characters that showed difference in some combinations was smaller in the forelimb region than in the head and hindlimb regions. This tendency coincided with that found in the slopes. In males, 12 characters were positionally different, but in females only four were different. On the other hand, only two characters were positionally different in young, but in adults 13 were different. There were clearly many positional differences in the combinations including adult males, and the adult males

Table 14. Growth type for each morphometric character in the four age/sex groups, grouped by the location on the body. Abbreviations for the growth types are as in Table 13.

Head										Forelimb					Hindlimb				
anteroposterior					lateral														
Character	young		adults		Character	young		adults		Character	young		adults		Character	young		adults	
	♂	♀	♂	♀		♂	♀	♂	♀		♂	♀	♂	♀		♂	♀	♂	♀
HL	B	B	I	B	HW	I	I	I	I	FLL	I	I	I	I	HLL	I	I	I	I
S-NL	B	B	I	I	IND	B	B	B	B	LAL	I	I	I	I	TL	I	I	I	I
N-EL	B	B	I	I	ICD	B	B	I	I	TFL	I	I	I	I	FL	I	I	I	I
SL	B	B	I	B	IOD	I	B	—	I	FFL	I	I	I	I	FTL	I	I	I	B
EL	B	B	B	B	UEW	B	B	I	B	OPTL	T	T	I	I	OMTL	I	T	I	I
T-EL	I	T	I	I	UEMD	B	B	I	B	IPTL	I	I	I	I	IMTL	I	T	I	I
TD	T	I	I	I	IPTD	I	B	I	B	HAL	I	I	I	I					
PL	I	I	I	I	PW	T	I	I	I	FAW	I	T	I	I					

Table 15. Age and sexual differences in the slope (α=allomorphic constant) and position (b) for regression lines of each morphometric character—SVL in the Japanese common toad from Momoyama, Kyoto. ++=difference at 99% level. +=difference at 95% level. —=no difference.

Character	Age				Sexual				Character	Age				Sexual			
	Male		Female		Young		Adult			Male		Female		Young		Adult	
	α	b	α	b	α	b	α	b		α	b	α	b	α	b	α	b
HL	—	++	—	—	—	—	+	++	PW	—	++	—	++	+	—	—	—
S-NL	++	—	—	—	—	—	—	—	FLL	—	—	—	—	—	—	+	+
N-EL	+	—	—	—	—	—	—	+	LAL	—	—	+	—	—	—	—	—
SL	+	—	—	—	—	—	+	+	TFL	—	++	—	—	—	—	—	++
EL	—	—	—	—	—	—	—	—	FFL	—	—	+	—	—	—	—	++
T-EL	—	++	—	++	—	—	—	—	OPTL	—	—	—	—	—	—	—	—
TD	—	+	—	+	+	—	—	—	IPTL	—	—	—	—	—	—	—	—
HW	—	++	+	+	—	+	—	++	HAL	—	++	+	—	—	—	—	++
IND	—	—	—	—	—	++	—	++	FAW	—	+	—	—	—	—	—	+
ICD	—	+	—	—	—	++	—	++	HLL	—	++	—	—	—	—	—	++
IOD	—	—	—	—	—	—	—		TL	—	++	—	—	—	—	—	++
UEW	—	++	+	—	—	—	—	++	FL	—	++	+	—	—	—	+	++
UEMD	—	++	+	—	—	—	—	++	FTL	—	+	+	++	—	—	++	—
IPTD	—	++	++	++	—	—	—	++	OMTL	—	—	—	+	—	—	—	—
PL	—	+	—	—	—	—	—	—	IMTL	—	—	—	—	—	—	—	+

were distinct from the remaining three age/sex groups.

Neither slope nor positional difference was found in the 12 characters among the four age/sex groups. This number accounted for 41.3% of the total number of the character, five characters in the head region (SL, N-EL, PL, EL, TD), five in the forelimb (OPTL, IPTL, FAW, LAL, FLL), and two in the hindlimb (IMTL, OMTL). In these characters, allomorphic relation to SVL did not change with growth, and the relation was not sexually different.

The intergroup relations for each character based on allomorphic characteristics are shown in Fig. 6. In only one character (IPTD in females), significant difference was found both in slope and position of the regression lines, but in most cases significant differences were related to position.

d) Characteristics of Allomorphic Coefficients in the Combined Groups

Of the 30 characters, only three were found to be significantly different in the

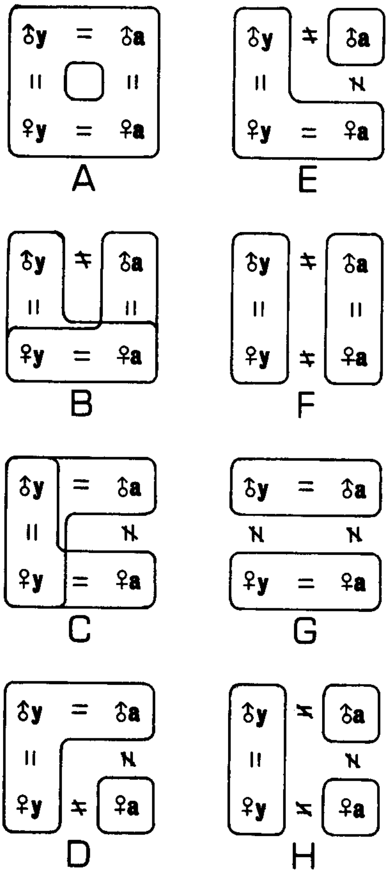

Fig. 6. Allomorphic relationships among four age/sex groups. Groups without difference in either or both slope and position of regression line are connected. A: N-EL, SL, EL, TD, (IOD), PL, FLL, LAL, OPTL, IPTL, FAW, OMTL, IMTL; B: S-NL; C: FFL; D: FTL; E: HL, HW, UEW, UEMD, TFL, HAL, HLL, TL, FL; F: T-EL, PW; G: IND, ICD; H: IPTD.

slope of the regression lines, whereas there were many significant differences in the position among the four age/sex groups. For each of the 26 characters with no significant slope differences among the four groups, and for IOD, which was omitted from the above descriptions, the four groups were combined and the allomorphic constant (=slope) was newly calculated as an average slope for each character to SVL for the toad specimens of the Momoyama deme (Table 16).

The newly obtained slopes were statistically compared with the case of $\alpha=1$. Nine cases were regarded as isomorphic (no difference from $\alpha=1$), five as tachymorphic ($\alpha>1$), and 13 as bradymorphic ($\alpha<1$). There were large differences before and after combining age groups: e.g., before combining the groups, each of the four groups had an isomorphic relation in HW, HAL, and FL to SVL, but bradymorphic and tachymorphic relations emerged in these characters after combining the groups.

In the head region, 11 characters were bradymorphic and three isomorphic to SVL, and no tachymorphic character was found. All of the seven head characters which were measured perpendicular to the body axis were bradymorphic to SVL (Fig.

Table 16. Characters showing no differences in the allomorphic constants among four age/sex groups. A summary of allomorphic relations to SVL. Four age/sex groups combined.

Character	N	$\alpha\pm$SD	log B	r	Comparson with $\alpha=1$	p	Growth type
HL	141	0.866±0.011	−0.230	0.989	F 1,139=150.18	$<.01$	B
N-EL	141	0.739±0.021	−0.704	0.949	F 1,139=156.07	$<.01$	B
SL	141	0.823±0.015	−0.545	0.978	F 1,139=144.28	$<.01$	B
EL	142	0.665±0.017	−0.339	0.959	F 1,140=402.18	$<.01$	B
T-EL	138	0.975±0.037	−1.359	0.913	F 1,136= 0.44	$>.05$	I
TD	144	1.059±0.033	−1.443	0.939	F 1,142= 3.25	$>.05$	I
HW	146	0.937±0.015	−0.310	0.983	F 1,144= 18.83	$<.01$	B
IND	141	0.795±0.014	−0.762	0.978	F 1,139=201.61	$<.01$	B
ICD	136	0.794±0.022	−0.531	0.953	F 1,134= 88.67	$<.01$	B
IOD	141	0.771±0.030	−0.603	0.909	F 1,139= 58.36	$<.01$	B
UEW	139	0.782±0.019	−0.671	0.963	F 1,137=135.60	$<.01$	B
UEMD	137	0.761±0.014	−0.126	0.976	F 1,135=273.83	$<.01$	B
PL	145	1.019±0.019	−0.694	0.976	F 1,143= 0.94	$>.05$	I
PW	141	0.898±0.027	−0.920	0.943	F 1,139= 14.30	$<.01$	B
FLL	144	0.987±0.012	−0.159	0.989	F 1,142= 1.18	$>.05$	I
LAL	141	0.982±0.012	−0.263	0.990	F 1,139= 2.36	$>.05$	I
TFL	140	0.823±0.023	−0.553	0.951	F 1,138= 60.83	$<.01$	B
FFL	134	1.017±0.020	−1.008	0.975	F 1,132= 0.72	$>.05$	I
OPTL	139	1.186±0.026	−1.528	0.969	F 1,137= 51.96	$<.01$	T
IPTL	140	1.079±0.028	−1.495	0.957	F 1,138= 8.01	$<.01$	T
HAL	141	0.933±0.018	−0.462	0.974	F 1,139= 13.44	$<.01$	B
FAW	137	1.273±0.042	−1.518	0.935	F 1,135= 43.08	$<.01$	T
HLL	143	1.032±0.013	0.049	0.989	F 1,141= 5.79	$.01<<.05$	I
TL	144	1.016±0.012	−0.463	0.990	F 1,142= 1.60	$>.05$	I
FL	145	1.063±0.018	−0.495	0.981	F 1,143= 12.91	$<.01$	T
OMTL	139	1.080±0.031	−1.505	0.947	F 1,137= 6.46	$.01<<.05$	I
IMTL	140	1.081±0.025	−1.404	0.965	F 1,138= 10.48	$<.01$	T

7). Of the characters measured parallel to the body axis, those situated anteriorly had small allomorphic coefficients and were bradymorphic; EL was particularly bradymorphic. In general, the characters posteriorly situated in the head were isomorphic. In the forelimb region, two characters were bradymorphic, three tachymorphic, and three isomorphic. Both the two bradymorphic characters, i.e., HAL and TFL, were

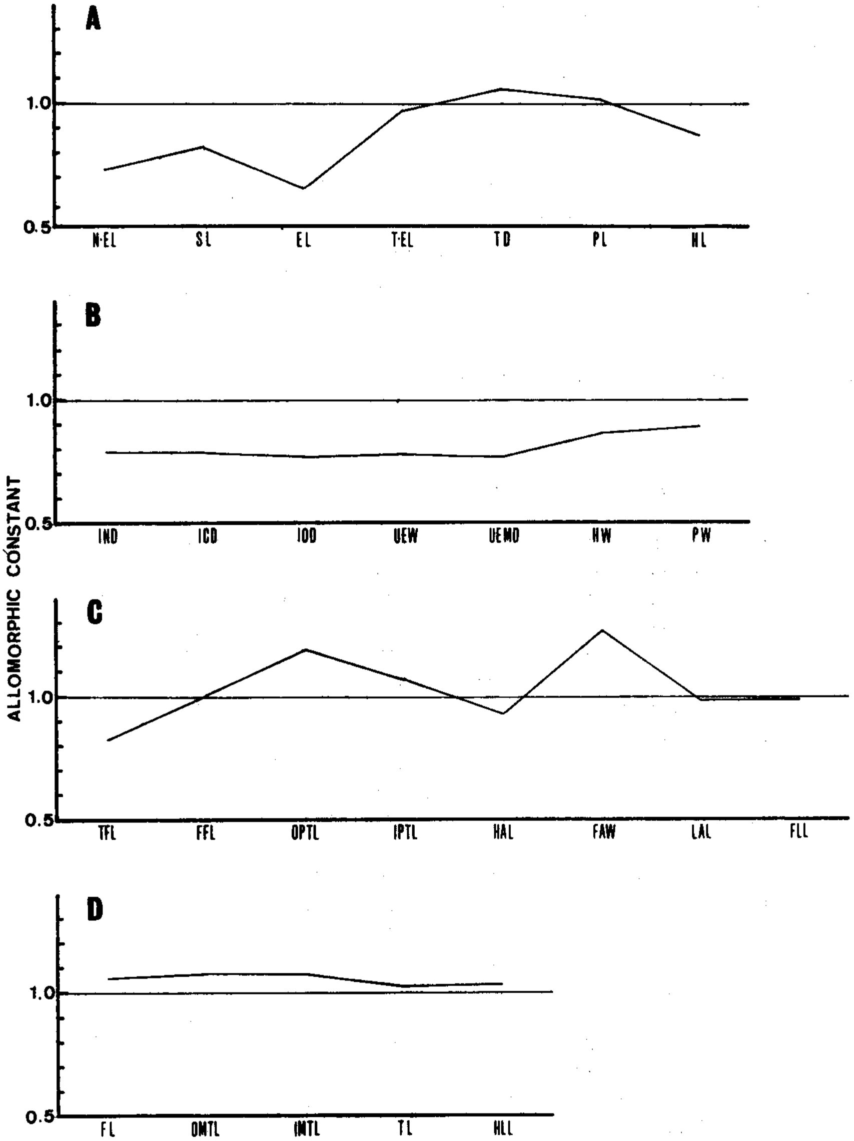

Fig. 7. Growth gradients in the characters showing no difference among four age/sex groups. Means for the combined four age groups are connected by the lines. A: characters on the head measured along body axis; B: characters on the head measured perpendicular to body axis; C: characters on the forelimb; D: characters on the hindlimb.

situated distally on the forelimb, and two tachymorphic characters were two tubercles on the palm (OPTL and IPTL). Though the allomorphic constant of FAW was great, this character could not be regarded as tachymorphic since the range of variation was too wide. In the hindlimb, three characters were isomorphic, two tachymorphic, and no bradymorphic character was found. The tachymorphic characters were FL and IMTL, both of which were situated near the distal end of the hindlimb.

DISCUSSION

Regression formula and correlation coefficients: It was March (1937) who made detailed allometric analyses on amphibians for the first time. He applied a simple regression equation $Y=aX+b$ to express the relation of hindlimb length (Y) to the body length (X) in the European grass frog (*Rana temporaria*). Several authors also applied this formula to the relations of body parts (Y) to body length (X) for the anurans including toad species (e.g., Underhill, 1961; De Lange, 1973).

However, application of this simple equation to the size relations of body parts was cautioned against by Dodson (1975). He reexamined the data obtained by Lundelius (1957) on the lizard body proportions and pointed out that it was dangerous to determine the linearity of a cloud of spots on the X-Y plane by visual inspection. He strongly recommended the use of the power function $Y=bX^{\alpha}$ for analyses of body proportions. The simple equation $Y=aX+b$, adopted by March (1937), is nothing but an isomorphic relation of X and Y (when $\alpha=1$ in $Y=bX^{\alpha}$). In applying the $Y=bX^{\alpha}$ formula, however, both variables, X and Y, are usually plotted on double logarithmic axes, and are line-fitted in the $\log Y=\alpha\log X+\log b$ formula. In this case, consequently, the range of the variables X and Y strongly affects results such as the correlation coefficient (Dodson, 1975).

As seen in the above results, the correlation coefficient of each character to SVL was in many cases rather small, and this tendency was particularly evident in adult toads. Several reasons can be assumed for this. First, it is presumed that this might be caused by narrow SVL ranges in adults on double logarithmic axes. The coefficients of variation (CV) of the SVL of young toads here treated were rather large (20.8 for males and 30.7 for females). In contrast to this, the CVs for adults were less than half of those of the young (8.1 in males and 10.5 in females). As the second reason for the small correlation coefficients in many characters, it can be supposed that there might be greater measurement errors in some characters than in others. In fact, it is evident that small correlation coefficients were obtained in those characters in which the measured reference points were often indistinct (e.g., UEW and IOD).

It is also expected that in the characters with small absolute dimensions, e.g., IPTL of the forelimb and IMTL of the hindlimb, measurement errors would be greater than in the characters with larger absolute dimensions. But this assumption is not always correct because higher correlation coefficients were obtained in some smaller characters than in those with larger absolute dimensions; in the adult male, for instance, absolutely small S-NL showed a high correlation with SVL. Further, small correlation coefficients were found more frequently in adults, despite their decidedly larger absolute dimensions than in the young. Consequently, the actual high variability in the dimensions of some characters could be adduced as the third reason for the small correlation coefficients in those characters.

Inagaki (1971) proposed regarding the correlation coefficient as a standard criterion to determine the possibility of line-fitting on the double logarithmic axes. He considered it impossible to fit the two variables on a single line if they had a correlation coefficient smaller than 0.95, and in order to obtain a 'higher correlation', he divided the set of raw data into small groups and obtained a regression line from the sequence of average values of these groups. Suzuki (1973) at first supported Inagaki's idea of utilizing correlation coefficients. But later, dealing with data obtained by the method employed in the present study and not by Inagaki's method of division, he reached the conclusion that studies of allomorphosis could not be made if the correlation coefficient value alone was too much emphasized (Suzuki and Teranishi, 1977). Just as pointed out by Shimizu (1959), paying too much attention to the linearity would make us overlook the nature of actual variation expressed as bias from the regression line. Thus, in the present study, too much stress was not put on the magnitude of correlation coefficients. Instead the statistical comparisons were run to examine whether it was appropriate to correlate each character to SVL. It became clear that all but one character were significantly correlated to SVL, and the allomorphic formula could be properly applied between these characters and SVL.

Slope and position of the regression lines: In analysing allomorphic relations of given characters, more stress has been put on the allomorphic constant (α=slope of the regression line) than on initial growth index (b in $Y=bX^{\alpha}$) (Shimizu, 1959; Kaneko, 1978; Aimi, 1980). In the present study, therefore, allomorphic patterns of the characters in each age/sex group were first analyzed with reference to the property of α. More isomorphic characters were found in adults than in young. This result seems to have been biased in relation to the small correlation coefficient value in each character in adults, and is considered to be chiefly due to the greater magnitude of character variation in adults than in young.

Therefore, allomorphic types derived from the comparisons of allomorphic constants of given characters of each group with the case of $\alpha=1$ do not seem to reflect the real allomorphic relation of such characters to SVL among groups. Thus, a definite conclusion cannot be drawn on the allomorphic patterns by examining the values of α from separate groups, and it was necessary to detect the presence of actual difference in allomorphic constants among the groups by statistical comparisons. Most of the inter-group differences in allomorphic constants of characters were not statistically significant, when the significance level was set at 99%. The three characters with significant intergroup difference (S-NL, IPTD, FTL) are considered to actually change growth rate with sexual maturity, or to be actually sexually different in growth rate. The other 27 characters seemed to have a constant allomorphic constant in the Momoyama deme, though the range of variation was wide in some of them.

When the four age/sex groups were combined, two-thirds of these 27 characters were not strictly isomorphic. This suggests that using simple ratios between two dimensions should be avoided in many cases in dealing with the morphometric characters for the taxonomic purpose, at least for the toad.

Contrary to the properties of allomorphic constants discussed above, there are inter-group positional differences in the regression lines for many characters. The biological significance of the positional difference of regression lines seems to have not been discussed sufficiently, and, some authors have paid less attention to this difference than to slope difference (e.g., Aimi, 1980). However, the tendency toward positional differences in the allomorphosis of toads from the Momoyama deme suggests that the positional difference in regression lines has even greater biological significance than the slope difference, because of the following two results obtained: (1) sexual difference was found in many characters in adults, whereas only a few characters were sexually different in the young, and (2) difference with growth was found more frequently in the characters of males than in those of females. These seem to agree well with the trend in differentiation which is generally accepted to occur in the process of morphological change in animals (Tokuda, 1957).

This seems to suggest that it is of dubious value to pay more attention to the slope difference than to the positional difference in allomorphically examining morphometric characters in the field of taxonomy. Rather, it seems necessary to find a better way to express the inter-group character difference which is expressed by the positional difference of the regression lines, yet whose biological significance has not been well established.

Intrapopulation variation: From such a viewpoint, intergroup difference in each character will be discussed here, attaching importance equally to the positional and slope differences. In the young, only two characters, ICD and IND, showed positional difference in regression lines, whereas the other 28 characters did not exhibit such a difference. Therefore, both sexes may be combined as to these 28 characters in morphometric analyses. On the contrary the 14 characters (HL, HW, IND, ICD, UEW, UEMD, IPTD, TFL, FFL, HAL, HLL, TL, FL, FTL) were sexually different in position or even in slope of regression lines in adults, and therefore, males and females should not be combined for these characters.

In the male, one characte (S-NL) had a slope difference, and 12 characters (HL, T-EL, HW, UEW, UEMD, IPTD, PW, TFL, HAL, HLL, TL, FL) had positional differences between the young and adults. Accordingly, young and adult males should not be combined for these characters. By contrast, in the female, only four characters (FTL, PW, T-EL, IPTD) showed positional difference and one (IPTD) showed slope difference between the young and adults. Though the number of characters showing difference with growth in allomorphic parameters in female was only about one-third of the male characters having such difference, the young and adults should also be treated separately for these four characters.

Inter-group difference was found neither in slope nor in position of 12 characters. Of these, three (SL, FLL, LAL) regressed to SVL with high correlations ($r>0.8$), and it is considered that they have neither sexual difference nor difference with growth in allomorphosis against SVL. On the other hand, the remaining nine characters are more variable with rather small coefficient values when correlated to SVL. Therefore, there is a possibility that sexual difference or difference with growth might be masked in these characters.

In conclusion, in dealing with each of 30 morphometric characters as a diagnostic character in taxonomy, the three groups (young, adult males, and adult females) should be treated separately for most of the characters, and males and females should be separately treated for several of them even within the young.

Growth gradient and function: Though the aim of this study is not to analyze growth-gradients in body parts and the treated characters are not always suitable for such analyses, some interesting allomorphic tendencies were observed. When the allomorphic constants of the 27 characters which have no slope difference among the groups were calculated in the combined four groups, the number of bradymorphic characters decreased, and conversely, the number of tachymorphic characters increased in the following order: head characters measured parallel with the body axis—head characters measured parallel with the body axis—forelimb characters—hindlimb characters. The tendency for the number of characters with a greater α value to increase in the sequence from the more anterior head region through mid forelimb region to more posterior hindlimb, suggests the presence of a postero-anterior gradient in body parts of the toad. This kind of gradient has been known to occur in birds (Huggins, 1940). In the hindlimb characters, TL had a larger α value than FL, suggesting the presence of a proximo-distal gradient. This tendency coincides with the result obtained by the simple equation in the European common toad (De Lange, 1973) and is also similar to the observations made in fetal mammals (Shimizu, 1947).

Generally speaking, the characters showing overall size or shape, such as HL, FLL, and HLL, were found to be isomorphic to SVL. Exceptionally, HW was bradymorphic to SVL, but this character has a greater α value than the other head characters that were measured perpendicular to the body axis. Further, the α values of the characters attached to the main body parts, such as the parotoid (both in length and width) in the head region, the lengths of two palmar tubercles in the forelimb, and IMTL in the hindlimb, were relatively large and some of these characters were even tachymorphic to SVL. Dodson (1975), who examined the allometry (=allomorphosis in the present work) of the alligator skull, concluded that the characters with negative allometry (=bradymorphic characters in the present study) decrease functional importance with growth, and conversely, the characters with positive allometry (=tachymorphic characters) increase functional importance with the increase of the standard size. The parotoid gland, as well as other skin glands, of the toad is regarded as a defense organ against predators (Lutz, 1970; Szarski, 1972), and the metatarsal tubercle is considered to be important as a fossorial organ for hiding or hibernation (Smith, 1951). Therefore, Dodson's idea (op. cit.) may apply to these organs and the weak bradymorphosis in the head width can be explained in relation to food uptake. However, sufficient understanding has not yet been obtained as to functional significance of the two palmar tubercles, and the relationships of allomorphosis and function in such characters require further investigation. Problems concerning growth gradient should also be solved by further investigation, including osteometry.

IV

Morphometric Variation in the Japanese Common Toad

As reviewed in the history of classification of the Japanese toads, many problems are involved in the taxonomy of the group whose members spend their larval life in still water (still-water type). The so-called Japanese common toad and the Miyako toad are the members in question.

Regarding classification of the Japanese common toad, there are different opinions among taxonomists, and it is in some cases divided into several forms (Okada, 1930, 1931, 1966; Matsui, 1979a), and in others treated as a single form (Nakamura and Uéno, 1963). The taxonomic position of the Miyako toad is sometimes discussed in relation to the forms of China and the nature of the basic problem is different from that involved in the Japanese common toad.

In this chapter, I will present the results of analyses of morphometric variation of the external characters of this frequently disputed Japanese common toad. In the process of analysis, I did not employ hitherto recommended ratios among characters, but used the adjusted character value (ACV) of each character at a unit body size. By separately analyzing intra- and interpopulation variation, I tried to elucidate the pattern of variation specific to each of them.

On the basis of the results thus obtained, it became clear how many forms could be differentiated for the Japanese common toad.

MATERIALS AND METHODS

a) Materials

As shown in Table 3, the materials examined for the geographic variation in the morphometric characters comprised 2,525 specimens. Determination of sexual maturity and sex identification were made by the method described in the foregoing chapter. From the results described in the previous chapter, it was evident that in young toads, there was little sexual dimorphism in the allomorphic relation of each character dimension to SVL, and therefore, both sexes were treated together for young toads. As a result, three age/sex groups, young, adult males, and adult females, were treated separately.

b) Characters Chosen and Methods for Comparisons

1) Characters

The 11 morphometric characters selected for the analyses on geographic variation were: (1) SVL, (2) head length (HL), (3) snout length (SL), (4) tympanum-eye length (T-EL), (5) tympanum diameter (TD), (6) head width (HW), (7) parotoid length (PL), (8) parotoid width (PW), (9) lower arm length (LAL), (10) tibia length (TL), and (11) foot length (FL).

2) Geographic variation in the allomorphic constant

Allomorphic relations of ten characters to SVL were examined with reference to the allomorphic constant (α) in eight populations of the Japanese common toad: Pops. 8, 16, 18, 22, 73, 80, 88, and 96. The result on Pop. 63 reported previously was also included. Each of these populations included a moderate number of specimens for each of the three age/sex groups, and the SVL range of each age/sex group was adequately wide (Table 17). In addition, the geographic distribution of these populations covers most of the known range of the Japanese common toad (Fig. 8).

In calculating allomorphic constant values, the three age/sex groups were combined, since the results obtained for Pop. 63 indicated the lack of inter-group difference in the allomorphic constants for the ten selected characters. The methods for calculation and statistical comparisons on allomorphic relations were same as those described in another chapter.

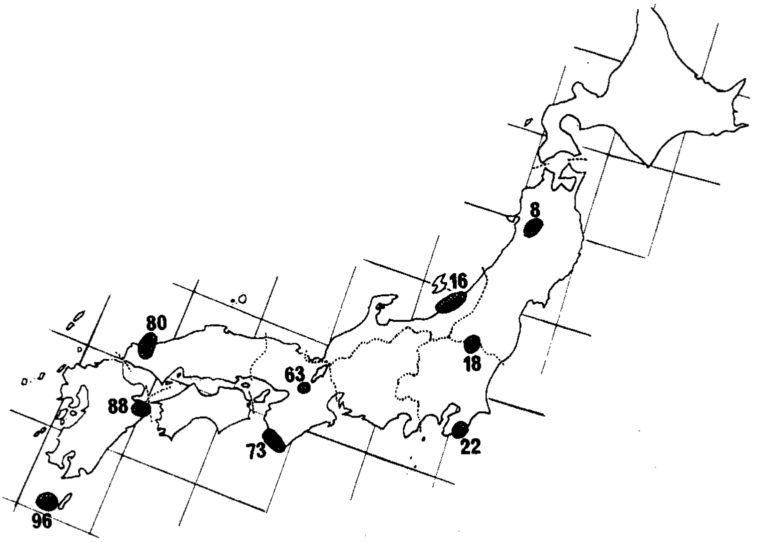

Fig. 8. Geographic locations of the nine populations of the Japanese common toad analyzed for interpopulation allomorphosis.

In order to analyze the geographic variation of the allomorphic constant, the correlation between latitude of the locality where each population lived (X) to the allomorphic constant (Y) was calculated, and the statistical significance was examined ($p < .05$) for the nine populations.

3) Calculation of ACV

The adjusted character value (ACV) described by Thorpe (1975) was calculated for each individual toad using the representative allomorphic constant for each character. In this method, the allomorphic relation of a given character dimension to a standard character dimension was obtained first for a group of animals, and next, the relative size of that character for a unit size of standard character was calculated on the basis of the assumption that the allomorphic constant first obtained represents the ontogenetic growth rate for each individual in the group. Namely, ACV ($\hat{Y}_i$), the estimate of character Y_i for an individual having standard character dimension X_i, is calculated

Table 17. Range of SVL for the nine populations of the Japanese common toad analyzed for interpopulation allomorphosis.

Population	young			adult males			adult females			Total	
	N	range	X̄	N	range	X̄	N	range	X̄	N	range
8	32	23.5– 79.0	36.1	16	66.8–111.0	88.2	15	74.3–120.5	100.1	63	23.5–120.5
16	65	24.8– 93.5	58.1	64	60.8–148.2	120.2	13	103.2–149.8	126.3	142	24.8–149.8
18	12	20.5– 91.8	45.2	34	80.4–113.2	99.0	24	87.6–119.6	102.1	70	20.5–119.6
22	10	22.8– 94.2	73.7	67	90.0–156.5	129.8	18	106.5–147.2	125.6	95	22.8–156.5
63	65	24.0– 99.2	66.1	46	79.8–116.5	98.5	36	84.0–135.0	109.6	147	24.0–135.0
73	95	24.5–105.2	70.9	12	107.2–145.0	128.3	12	120.2–155.8	137.8	119	24.5–155.8
80	91	49.5– 98.8	68.9	22	80.0–108.0	92.5	10	87.3–123.0	103.7	123	49.5–123.0
88	55	21.2– 72.8	56.5	31	62.7–102.3	82.9	8	93.6–122.0	107.6	94	21.2–122.0
96	13	23.0–137.7	74.2	16	95.2–119.8	110.1	11	131.2–176.0	160.1	40	23.0–176.0

by the formula:

$$\log \hat{Y}_1 = \alpha \log X_0 + (\log Y_1 - \alpha \log X_1)$$

where X_0 is the unit size of the standard character, and α is the representative allomorphic constant for the group including the individual in question.

The standard character treated here is SVL. The results, reported in the previous chapter, indicated the presence of sexual and/or age differences in the position of the regression lines of some characters against SVL. For such characters, three age/sex groups were treated separately in calculating ACV. For the unit size of the standard character (SVL), 100 mm was arbitrarily chosen for computing ACV, since this value was intermediate between young and adult actual mean SVLs, and, with only a few exceptions, toads of most populations pass this size in the course of growth.

For each of the nine populations mentioned above, ACVs were calculated using the α values specific to each population, and for the remaining populations of the Japanese common toad, the α values calculated by combining the data for nine populations were used. If the variation in α values for any one character against SVL proved to be significantly correlated to geographical parameter (latitude of the sampled location) in the above nine populations, the linear equation between the two variables was obtained and α values were newly calculated from the equation for all populations except for the above mentioned nine.

For either intra- or interpopulational comparison of SVL and ACVs, populations with sample size three or larger were considered. For SVL, Student's *t* tests were run at the significance level of 95%, and the means were expressed by $\bar{X} \pm 2SE$, unless otherwise noted. However, two-tailed Mann Whitney's U tests were run at the rejection level of 5% for ACVs, since the normality in the distribution of ACVs has not been ascertained, and therefore, the routine method of Student's *t* tests was not applicable. Thus, the magnitude of ACVs for any character representing a population was expressed by a median.

RESULTS

1. *SVL*

Young toads were excluded from the SVL variation analyses, since they were collected at various stages of growth, which might cause far greater size variations than in adults due to their extremely heterogeneous growth stages.

1) Interpopulation variation in the population mean SVL

The mean of the mean SVLs for 58 populations of adult males was 116.29±4.40 mm. Population 10 had the smallest mean SVL (70.9 mm), and Pop. 88 (82.9 mm) and Pop. 8 (88.2 mm) ranked next and third. The largest mean SVL (143.3 mm) was found in Pop. 56, and Pop. 61 (140.7 mm), Pop. 34 (140.6 mm), and Pop. 50 (140.6 mm) were among the populations with large mean SVL. The largest mean SVL was 2.02 times larger than the smallest.

Interpopulation variation in mean SVL (Table 18) was great, and each of 58 populations showed more or less significant differences from each other. Among them, Pop. 10 was most conspicuous, showing differences in all of the 57 possible combinations, i.e., Pop. 10 was regarded as having a mean SVL completely different from the other populations of the Japanese common toad. All the other populations had overlapping mean SVLs. Among them, Pop. 88 was remarkable, being different from other 55 populations (96.5% of total 57 populations). Population 8 (different from 87.7% of other populations), Pop. 56 (84.2%), and Pop. 61 (80.7%) were conspicuous populations frequently different from other populations in mean SVL.

In 50 female populations, the mean of the mean SVLs was 126.70±5.11 mm. The smallest population mean SVL (68.9 mm) was exhibited by Pop. 10, and Pop. 43 (98.2 mm) and Pop. 8 (100.1 mm) had also small population mean SVLs. Population 96 had the largest mean SVL (160.1 mm), and Pop. 87 (158.5 mm) and Pop. 61 (150.7 mm) ranked next and third largest. The largest value was 2.32 times larger than the smallest.

In adult female populations, the same tendency as in adult male populations was observed in interpopulation variation in mean SVL. As in males, Pop. 10 was different from all other 49 populations, and was regarded as having a distinct mean SVL among the populations of the Japanese common toad. The remaining 49 populations had more or less overlapping mean SVLs, but among them, Pop. 96 was conspicuous with 43 differences in 48 possible combinations (89.6%). Population 87 was also remarkable in having differences from other 42 populations (87.5% of total number of 48 combinations).

Of 44 well represented populations (the sample size of both males and females larger than three), 14 (31.8%) exhibited sexual dimorphism in mean SVL. In the remaining 30 populations, females tended to be larger than males, but the differences were statistically insignificant ($p > .05$). When population means were combined for each sex and the values obtained were compared, sexual dimorphism was evident ($t = 3.11$, $dF = 106$, $.005 > p > .001$), and females were generally regarded as larger in SVL than males.

For a comparison of variability in the mean SVL between males and females, mean SVL values were logarithmically transformed and variance was computed for each sex (the method proposed by Lewontin, 1966 and Moriarty, 1977). The result indicated no sexual dimorphism in the mean SVL variability ($F_{43,49} = 1.03$, $p > .05$).

2) Variation in the minimum SVL

Among 1,179 individuals of 81 populations, the smallest adult male was found in Pop. 2 (Shimokita) and was 43.2 mm in SVL. The smallest adult female among 585 individuals of 78 populations was in Pop. 3 (Tsugaru), and had an SVL of 53.5 mm (Table 18).

The means of the minimum SVLs among populations were 97.6±4.4 mm for males, and 112.2±5.6 mm for females, and these values were significantly different ($t = 4.15$, $dF = 106$, $p < .001$). Thus, females were regarded as larger than males in minimum SVL.

3) Variation in the maximum SVL

Among 1,179 individuals of 81 populations, the largest adult male was found in Pop. 79 (Kammuriyama) and was 162.5 mm in SVL. The largest adult female among

Table 18. SVL (in mm) variation in Japanese common toad adults.

Population	adult males						adult females					
	N	SVL					N	SVL				
		range	$\bar{X}$	SD	2SE	CV		range	$\bar{X}$	SD	2SE	CV
1	11	79.2–110.8	92.7	9.2	5.5	9.9	3	101.3–109.2	106.6	4.6	5.3	4.3
2	1		43.2									
3							1		53.5			
4	20	78.3–116.2	96.6	7.9	3.6	8.2	2	108.6–111.8	110.2			
5	6	96.5–108.0	102.7	4.1	3.4	4.0	3	96.2–121.8	106.7	13.4	15.5	12.5
6	9	67.2–107.8	93.9	14.2	9.5	15.1	1		109.8			
7	1		76.8				1		78.8			
8	16	66.8–111.0	88.2	11.4	5.7	12.9	15	74.3–120.5	100.1	13.0	6.7	13.0
9	1		90.4				1		94.2			
10	8	61.2–79.2	70.9	6.8	4.8	9.6	8	59.5–76.2	68.9	5.9	4.1	8.5
12	1		120.2				4	110.0–130.5	124.4	9.7	9.7	7.8
13	3	92.2–112.8	100.5	10.9	12.5	10.8						
14	1		81.7				2	100.0–109.1	104.6			
15							1		100.5			
16	64	60.8–148.2	120.2	19.3	4.8	16.1	13	103.2–149.8	126.3	13.7	7.6	11.0
17	5	108.0–134.0	124.6	9.8	8.8	7.9						
18	34	80.4–113.2	99.0	9.7	3.3	9.8	24	87.6–119.6	102.1	9.8	4.0	9.6
19	25	99.5–146.0	125.2	11.7	4.7	9.4	16	115.3–142.2	133.4	7.5	3.7	5.6
20	20	106.8–147.2	134.7	9.1	4.1	6.7	20	126.2–152.8	137.2	7.9	3.5	5.8
21	10	122.8–141.2	132.0	6.3	4.0	4.7	9	108.4–135.0	128.5	8.3	5.5	6.4
22	67	90.0–156.5	129.8	10.1	2.5	7.8	18	106.5–147.2	125.6	8.0	3.8	6.4
23	22	81.1–126.2	100.7	13.0	5.5	12.9	21	78.6–129.0	105.5	13.2	5.8	12.5

(cont'd.)

(Table 18. cont'd.)

Population	adult males						adult females					
	N	SVL					N	SVL				
		range	X̄	SD	2SE	CV		range	X̄	SD	2SE	CV
24	15	118.0–148.2	135.1	9.5	4.9	7.0	6	117.8–137.5	130.3	7.0	5.7	5.4
25	39	82.8–137.2	109.1	11.7	3.8	10.8	12	100.3–136.2	115.0	9.6	5.3	8.3
26	6	109.5–135.2	124.1	10.8	8.8	8.7	3	102.2–115.8	109.4	6.8	7.9	6.3
27	41	105.0–144.0	125.8	10.4	3.2	8.3	17	121.8–155.0	137.4	11.2	5.4	8.1
28	1		94.4				3	104.5–112.0	108.2	3.8	4.3	3.5
29	3	98.6–111.2	105.3	6.3	7.3	6.0	2	94.4–101.2	97.8			
30	10	95.0–110.4	105.0	4.9	3.1	4.7	7	97.5–116.0	106.7	6.2	4.7	5.8
31	13	91.0–143.5	116.7	14.0	7.7	12.0	3	111.0–135.0	126.8	13.7	15.8	10.8
32	51	83.2–134.5	108.2	11.1	3.1	10.3	30	97.2–131.3	114.0	8.8	3.2	7.7
33	2	104.0–106.6	105.3				1		128.2			
34	29	115.5–155.5	140.6	11.1	4.1	7.9	10	91.0–154.5	129.6	21.0	13.3	16.2
35	1		154.5									
36	1		80.0									
37	5	94.5–117.2	104.6	9.7	8.7	9.3						
38	70	95.0–135.2	115.6	9.9	2.4	8.6	25	105.6–131.2	120.4	5.9	2.4	4.9
39	14	107.8–140.0	120.3	7.6	4.1	6.3						
40	3	119.2–143.2	129.6	12.3	14.2	9.5	1		122.4			
41	2	84.6– 90.2	87.4									
42	1		81.0				1		79.2			
43	39	82.8–107.7	95.8	6.1	1.9	6.4	6	90.5–109.3	98.2	8.7	7.1	8.9
44	1		124.0				6	108.2–141.2	130.4	11.7	9.5	9.0
45	1		102.0									

(cont'd.)

(Table 18. cont'd.)

Population	adult males						adult females					
	N	SVL					N	SVL				
		range	$\bar{X}$	SD	2SE	CV		range	$\bar{X}$	SD	2SE	CV
47	3	111.0–120.0	115.8	4.5	5.2	3.9	5	121.5–134.8	129.0	5.1	4.5	3.9
48	2	137.8–140.2	139.0				1		138.5			
49	3	104.8–155.0	129.4	25.1	29.0	19.4	5	102.4–141.0	122.8	16.9	15.2	13.9
50	21	116.2–160.5	140.6	11.6	5.1	8.2	5	137.2–146.2	142.4	3.6	3.2	2.5
51	12	104.8–144.0	129.9	12.6	7.3	9.7	3	130.0–148.0	141.6	10.1	11.6	7.1
52	6	96.0–111.0	101.7	5.5	4.5	5.4	2	103.0–122.0	112.5			
53	3	98.4–108.4	102.8	5.1	5.9	5.0						
54	10	119.2–142.0	132.4	8.6	5.5	6.5	1		145.2			
55	25	110.0–158.0	139.4	12.3	4.9	8.9	7	140.8–159.2	147.5	6.8	5.1	4.6
56	21	131.0–157.0	143.3	6.3	3.8	4.4	14	125.5–145.8	139.1	6.0	3.2	4.3
57							2	114.0–119.2	116.6			
58	8	108.2–143.0	129.3	9.9	7.0	7.7	12	108.0–153.0	132.8	11.5	6.7	8.7
59	57	106.0–158.2	137.7	9.9	2.6	7.2	12	121.5–147.2	136.6	7.8	4.5	5.7
60	26	126.2–149.0	134.9	6.2	2.4	4.6	9	128.2–155.0	142.0	8.6	5.7	6.1
61	28	120.0–151.2	140.7	8.3	3.1	5.9	11	141.2–162.2	150.7	5.9	3.5	3.9
62	10	101.8–139.5	119.6	11.2	7.1	9.3	4	112.2–125.0	120.3	5.6	5.6	4.7
63	45	79.8–116.5	98.5	7.9	2.4	8.1	35	84.0–135.0	109.6	11.5	3.9	10.5
64	1		106.4				1		108.4			
65	5	102.3–129.0	112.8	10.4	9.3	9.2	1		127.5			
66	3	103.2–121.5	110.2	9.9	11.4	8.9						
68							2	123.4–146.2	134.8			
69	1		132.5				1		161.5			

(cont'd.)

(Table 18. cont'd.)

Population	adult males						adult females					
	N	SVL					N	SVL				
		range	X̄	SD	2SE	CV		range	X̄	SD	2SE	CV
71	1		149.2				3	140.8–150.4	146.1	4.9	5.6	3.3
72	2	126.2–134.2	130.2	5.7	8.0	4.3	2	126.2–135.6	130.9			
73	12	107.2–145.0	128.3	13.2	7.6	10.3	12	120.2–155.8	137.8	11.2	6.5	8.1
74							1		151.0			
75							2	117.4–129.2	123.3			
77							1		98.2			
78	1		109.6				9	108.6–144.8	126.1	11.2	7.5	8.9
79	27	95.4–162.5	129.5	11.4	4.4	8.8	15	129.5–154.2	141.1	8.1	4.2	5.7
80	22	80.0–108.0	92.5	7.1	3.0	7.7	10	87.3–123.0	103.7	12.2	7.7	11.8
81	50	103.4–148.2	128.3	9.4	2.7	7.4	23	108.0–151.0	128.8	11.2	4.7	8.7
83	1		132.6				2	115.0–129.0	122.0			
84	3	98.2–124.2	113.4	13.5	15.6	11.9	7	136.6–157.5	145.9	7.1	5.4	4.9
85	6	103.2–138.2	125.2	12.8	10.4	10.2	3	145.5–154.5	149.7	4.5	5.2	3.0
86	27	80.2–141.5	122.4	11.8	4.5	9.6	14	128.2–146.0	138.7	5.3	2.8	3.8
87	3	119.2–152.2	134.2	16.7	19.3	12.4	3	149.0–164.5	158.5	8.3	9.6	5.3
88	31	62.7–102.3	82.9	11.5	4.1	13.9	8	93.6–122.0	107.6	10.5	7.4	9.7
89	2	100.6–107.0	103.8				4	140.0–143.5	142.4	1.6	1.6	1.1
91	7	94.2–118.8	105.3	9.1	6.9	8.7	22	124.8–160.2	141.8	7.6	3.3	5.3
92							1		118.4			
93	1		116.8				1		151.0			
94	4	97.0–121.0	109.0	13.6	13.6	12.5	1		115.0			
95							1		145.0			
96	16	95.2–119.8	110.1	8.2	4.1	7.5	11	131.2–176.0	160.1	12.7	7.7	8.0

585 individuals of 78 populations was found in Pop. 96 (Yakushima), and had an SVL of 176.0 mm (Table 18).

The mean of the maximum SVLs among populations was 132.19±4.92 mm for males, and 139.29±5.13 mm for females. These values differed significantly ($t=1.99$, $dF=106$, $.01<p<.05$) and males were judged to have a smaller maximum SVL than females.

4) Geographic variation of SVL

The variation range of mean SVLs (X) among 58 adult male populations was divided into six size classes by the method presented by Yamagishi (1977:102), and the number of populations included in each size class was examined (Fig. 9). The figure showed inconspicuous bimodal distribution with peaks in the size classes $95.1 \leqq X < 107.2$, and $119.3 \leqq X < 131.4$. In adult females, 50 populations had unimodal distribution with a peak in size class $129.7 \leqq X < 144.9$ (Fig. 9).

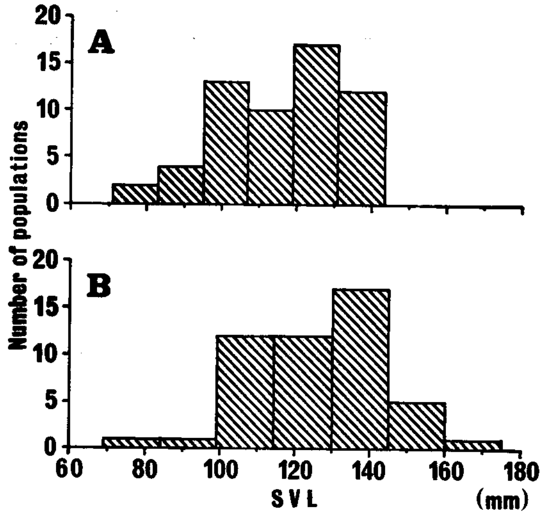

Fig. 9. Number of populations tabulated by 12.1 mm (A: adult males) or by 15.2 mm (B: adult females) intervals of population mean SVL.

These results indicated that it is difficult to divide populations in females, but in males it was possible to recognize two groups. Thus, male populations were divided into two types (I: small body size; III: large body size) by the border at SVL=113.25 mm, and female populations were arbitrarily divided into three types (I: small body size; II: moderate body size; III: large body size).

Geographic distribution of each type was examined (Fig. 10). In males, type I populations were distributed over the whole range, except for Shikoku. By contrast, type III populations were distributed in a narrower range, from Kanto to Chugoku and Shikoku, and were never found in Tohoku and Kyushu. In the areas from Hokuriku and Kanto to Kinki, where both types occurred, the number of type III populations was about twice of that of type I. Thus, populations with small body size were judged to predominate in the extremely eastern and western areas, and conversely, those with large body size occupied the area around the center of the distributional range of the Japanese common toad.

In females, type II populations showed wide distribution from Southern Tohoku to Kyushu. Type I populations were predominant from Chubu eastwards, but were sporadically found in Kinki, Chugoku, and Kyushu. A more limited range, from Chubu westwards, was occupied by type III populations. Thus, it can be roughly stated that populations with small body size decrease and, conversely, those with large body size increase from north to south in the distributional range of the Japanese common toad.

These sexually different tendencies in geographic variation of mean SVL resulted in larger female/male SVL difference in the southwestern localities, and details of this subject are stated later.

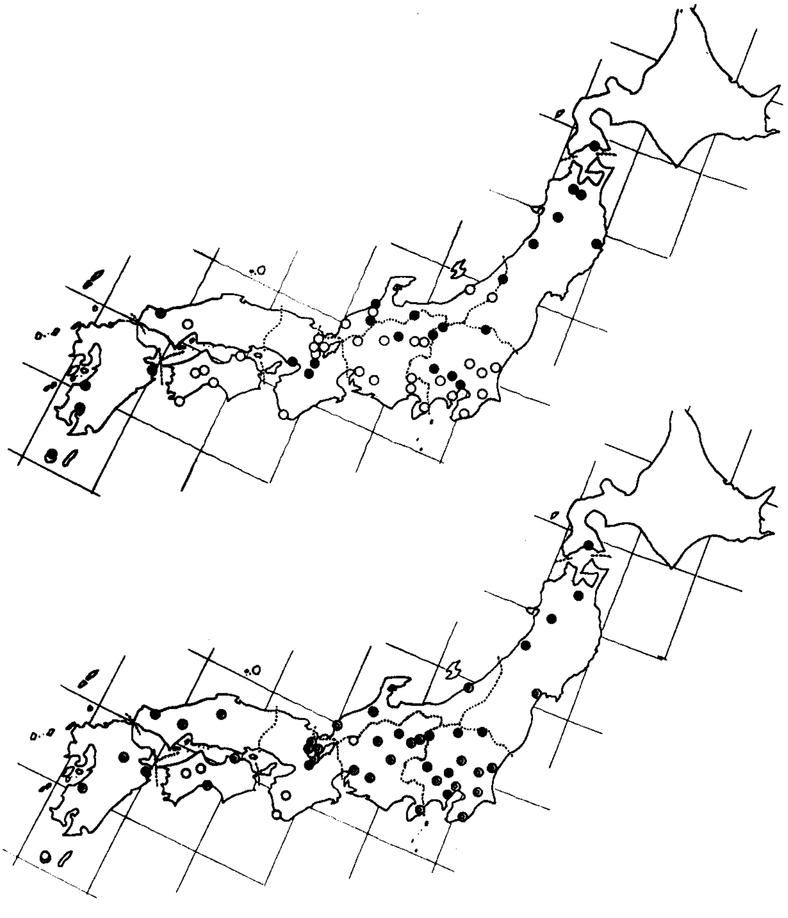

Fig. 10. Geographic distribution of type I (small-sized: closed circles), type II (medium-sized: double circles), and type III (large-sized: open circles) populations of the Japanese common toad. Top: adult males; bottom: adult females.

As evident from Fig. 10, some populations greatly differed from the surrounding populations in SVL. In adult males, the following combinations were regarded as having considerably different SVL: Pop. 10 vs. Pops. 8, 13; Pop. 13 vs. Pops. 16, 17; Pop. 18 vs. Pops. 17, 19; Pop. 43 vs. Pops. 38, 47; Pop. 23 vs. Pops. 19, 27; Pop. 25 vs. Pops. 21, 24; Pop. 52 vs. Pop. 51; Pop. 53 vs. Pops. 51, 54; Pop. 63 vs. Pops. 61, 62; Pop. 80 vs. Pop. 79. In these populations, the mean SVL of the former was more than 1.2 times smaller than that of the latter(s). The most extreme combination was Pop. 63 vs. Pop. 61; the latter had mean SVL 1.43 times larger than the former, in spite of their geographically close distribution.

In the same manner, the following combinations were obtained for adult females: Pop. 10 vs. Pop. 8; Pop. 23 vs. Pops. 19, 27; Pop. 26 vs. Pop. 27; Pop. 43 vs. Pops. 38, 47; Pop. 62 vs. Pop. 61; Pop. 63 vs. Pop. 61; Pop. 80 vs. Pop. 79; Pop. 88 vs. Pop. 89. The former population had mean SVL more than 1.2 times smaller than the latter in these combinations. In the combinations Pop. 10 vs. Pop. 8 and Pop. 63 vs. Pop. 61, the differences were particularly large (1.45 and 1.38 times, respectively). Thus, as in males, some populations of adult females were regarded as very different from the neighbouring populations in SVL.

2. *Allomorphic Variation*

a) *Variation in Allomorphic Constant*

Allomorphic relations of each character to SVL are summarized in Table 19.

1) HL: The nine populations could be arranged in the following order by the magnitude of α values: Pop. 63 ($\alpha=0.866$)—Pop. 80—Pop. 16—Pop. 8—Pop. 73—Pop. 22—Pop. 88—Pop. 18—Pop. 96 ($\alpha=0.997$). No correlation was found between the magnitude of α values and geographical parameters (represented by latitude of the locality; Fig. 11A; dF=7, $r=-0.383$, $p>.1$). There were significant differences in slope and position between the regressions of two populations having largest and smallest α values (Pop. 96 vs. Pop. 63: slope: $F_{1,175}=28.28$, $p<.01$; position: $F_{1,176}=57.52$, $p<.01$). However, the variation in α values within a population was so great that the interpopulation difference in slope was insignificant between two neighbouring populations arranged by the magnitude of α values (e.g., Pop. 63 vs. Pop. 80: slope: $F_{1,225}=5.81$, $.05>p>.01$). By contrast, positional difference was occasionally significant even between two neighbouring populations (e.g., Pop. 16 vs. Pop. 8: position: $F_{1,107}=29.38$, $p<.01$). This result indicated that there was no evident geographic trend in the variation of allomorphic constants of HL against SVL in nine populations. The combined allomorphic constant was 0.939 ± 0.004 (3SE, N=671), and showed a bradymorphic relation of HL to SVL (comparison with the case of $\alpha=1$: $F_{1,669}=206.67$, $p>.01$).

2) SL: The nine populations could be arranged as follows by the magnitude of α values: Pop. 63 ($\alpha=0.823$)—Pop. 80—Pop. 16—Pop. 8—Pop. 73—Pop. 88—Pop. 18—Pop. 22—Pop. 96 ($\alpha=0.942$). No significant correlation was found between α values and geographical parameters (Fig. 11B; dF=7, $r=-0.489$, $p>.1$). The largest α value was significantly different from the smallest (Pop. 96 vs. Pop. 63: slope: $F_{1,175}=13.14$, $p<.01$; position: $F_{1,176}=19.92$, $p<.01$), but these two extremes were

Table 19. Variation in the allomorphic constant of each character vs. SVL in the nine populations of the Japanese common toad. Means are followed by standard deviation.

Population	Character									
	HL	SL	T-EL	TD	HW	PL	PW	LAL	TL	FL
8	0.939±.008	0.859±.013	1.088±.076	1.149±.025	1.015±.020	0.960±.020	0.807±.022	1.009±.011	1.029±.011	1.095±.015
16	0.917±.015	0.859±.018	0.945±.085	1.167±.029	0.959±.021	0.975±.022	0.726±.037	0.992±.016	1.000±.014	1.005±.024
18	0.970±.011	0.910±.022	0.987±.076	1.185±.042	0.987±.018	0.987±.023	0.812±.026	0.980±.015	1.022±.015	1.086±.027
22	0.965±.018	0.924±.021	1.038±.090	1.165±.046	1.004±.023	0.979±.031	0.885±.047	0.979±.017	1.018±.019	1.072±.030
63	0.866±.011	0.823±.015	0.975±.037	1.059±.033	0.937±.015	1.019±.019	0.898±.027	0.982±.012	1.016±.012	1.063±.018
73	0.960±.010	0.892±.012	1.115±.030	1.015±.043	1.025±.013	1.043±.022	0.870±.035	0.972±.015	1.017±.011	1.073±.018
80	0.916±.016	0.849±.021	1.016±.053	1.096±.057	0.943±.023	0.991±.037	0.848±.049	0.906±.017	1.022±.022	1.026±.038
88	0.968±.016	0.903±.017	1.121±.061	0.977±.041	1.007±.021	1.046±.029	0.792±.051	1.017±.014	1.032±.018	1.134±.029
96	0.997±.019	0.942±.026	1.120±.087	0.998±.046	1.089±.039	1.016±.039	0.934±.055	0.953±.017	0.948±.017	0.947±.041

bridged over by the intermediate values. The α value obtained by combining nine populations was 0.877±0.005 (3SE, N=675), showing bradymorphic relation of SL to SVL (comparison with the case of $\alpha=1$: $F_{1,\,673}=573.64$, $p<.01$).

3) T-EL: The nine populations could be arranged as follows: Pop. 16

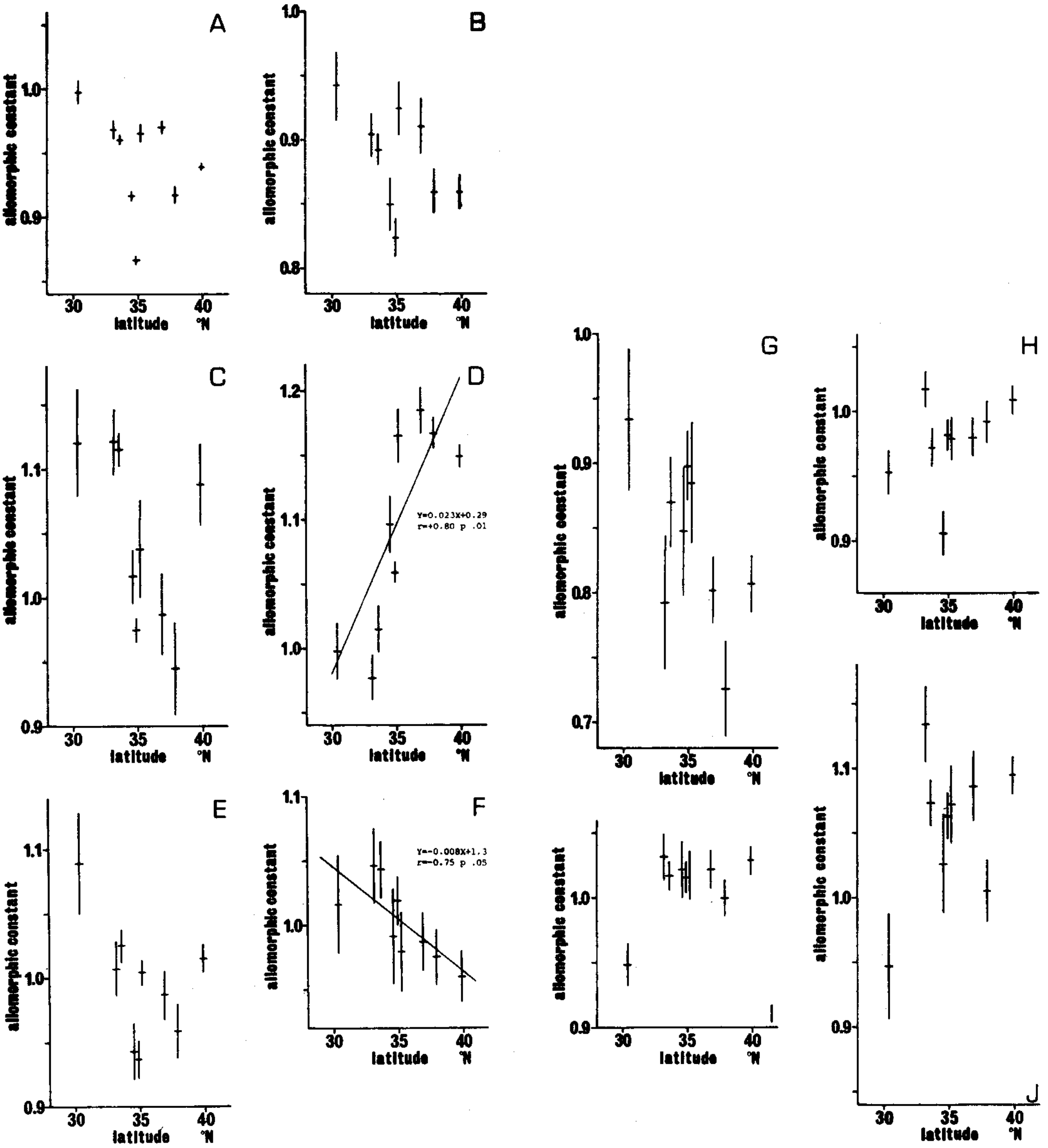

Fig. 11. Correlation between latitude of locality and allomorphic constant in the nine populations of the Japanese common toad. Horizontal bar indicates mean and vertical bar indicates standard deviation of allomorphic constant. A: HL; B: SL; C: T-EL; D: TD; E: HW; F: PL; G: PW; H: LAL; I: TL; J: FL. Significant correlations were found only in D and F.

($\alpha=0.945$)—Pop. 63—Pop. 18—Pop. 80—Pop. 22—Pop. 8—Pop. 73—Pop. 96—Pop. 88 ($\alpha=1.121$). The variation range of α value for this character was so great within each population that there was no significant slope difference between the regressions of two extreme populations, although the positional difference was significant (Pop. 88 vs. Pop. 16: slope: $F_{1,95}=2.10$, $p>.1$; position: $F_{1,95}=94.31$, $p<.01$). The α values were not significantly correlated with geographical parameters (Fig. 11C; dF=7, $r=-0.488$, $p>.1$), and the α obtained by combining nine populations was 1.052 ± 0.031 (3SE, N=536), indicating the isomorphic relation of this character to SVL (comparison with the case of $\alpha=1$: $F_{1,534}=2.79$, $p>.1$).

4) TD: Although the allomorphic constant of TD to SVL varied considerably within each population, it (Y) decreased towards the south in correlation with latitude (X) and the equation $Y=0.023X+0.290$ ($r=0.799$, $p<.01$) was obtained (Fig. 11D). The nine populations could be arranged according to the magnitude of allomorphic constants in the following manner: Pop. 88 ($\alpha=0.977$)—Pop. 96—Pop. 73—Pop. 63—Pop. 80—Pop. 8—Pop. 22—Pop. 16—Pop. 18 ($\alpha=1.185$). There were significant slope and positional differences between the populations with maximum and minimum α values (Pop. 18 vs. Pop. 88: slope: $F_{1,96}=10.90$, $p<.01$; position: $F_{1,97}=195.57$, $p<.01$), but these values were connected by values of intermediate populations. The α value obtained by combining nine populations was 1.043 ± 0.021 (3SE, N=555), indicating that this character was isomorphic to SVL (comparison with $\alpha=1$; $F_{1,553}=4.10$, $.05>p>.01$).

5) HW: The nine populations could be arranged as follows: Pop. 63 ($\alpha=0.937$)—Pop. 80—Pop. 16—Pop. 18—Pop. 22—Pop. 88—Pop. 8—Pop. 73—Pop. 96 ($\alpha=1.089$). No correlation was found between α values and latitudes (Fig. 11E; dF=7, $r=-0.458$, $p>.1$). Significant differences were found in slope and position of regression lines between two extreme populations (Pop. 96 vs. Pop. 63: slope: $F_{1,180}=17.46$, $p<.01$; position: $F_{1,181}=23.20$, $p<.01$), but the two populations were bridged over by intermediate populations (e.g., Pop. 96 vs. Pop. 73: slope: $F_{1,146}=3.37$, $p>.05$). The combined α value was 1.004 ± 0.007 (3SE, N=673) and the character was regarded as isomorphic to SVL (comparison with the case of $\alpha=1$: $F_{1,671}=0.31$, $p>.05$).

6) PL: The nine populations could be arranged as follows: Pop. 8 ($\alpha=0.960$)—Pop. 16—Pop. 22—Pop. 18—Pop. 80—Pop. 96—Pop. 63—Pop. 73—Pop. 88 ($\alpha=1.046$). The α values (Y) and latitudes (X) correlated significantly with the equation $Y=-0.0081X+1.288$ ($r=-0.752$, $.02>p>.01$; Fig. 11F). Thus the allomorphic constant of PL to SVL was regarded as decreasing from south to north. The variation range of allomorphic constant within a population was so great that there were insignificant differences in slope and position of the regressions of the two extreme populations (Pop. 88 vs. Pop. 8; slope: $F_{1,110}=5.39$, $.05>p>.01$; position: $F_{1,111}=3.29$, $p>.05$). The combined allomorphic constant was 0.997 ± 0.008 (3SE, N=555) and the character was regarded as isomorphic to SVL (comparison with $\alpha=1$: $F_{1,553}=0.11$, $p>.1$).

7) PW: The populations could be arranged by the magnitude of the allomorphic

constants in the following way: Pop. 16 ($\alpha=0.726$)—Pop. 88—Pop. 18—Pop. 8—Pop. 80—Pop. 73—Pop. 22—Pop. 63—Pop. 96 ($\alpha=0.934$). The correlation of α values to latitudes was insignificant (Fig. 11G; $r=-0.650$, dF=7, .1>p>.05). The maximum and minimum α values differed from each other (Pop. 96 vs. Pop. 16; slope: $F_{1,83}=8.852$, p<.01; position: $F_{1,84}=0.15$, p>.1), but were bridged over by the values of intermediate populations. The α value obtained by combining nine populations was 0.628 ± 0.032 (3SE, N=551) and this character proved to be bradymorphic to SVL (comparison with $\alpha=1$: $F_{1,549}=132.59$, p<.01).

8) LAL: The populations were arranged as follows: Pop. 80 ($\alpha=0.906$)—Pop. 96—Pop. 73—Pop. 22—Pop. 18—Pop. 63—Pop. 16—Pop. 8—Pop. 88 ($\alpha=1.017$), and no correlation was found between α values and latitudes (Fig. 11H; $r=0.392$, dF=7, p>.1). Intrapopulation variation range of α value was not wide and the neighbouring populations had insignificant differences in α values (e.g. Pop. 80 vs. Pop. 96; slope: $F_{1,94}=3.76$, p>.05; position: $F_{1,95}=110.94$, p<.01), although they differed greatly in the position of the regression lines. The α value of the combined nine populations was 0.999 ± 0.005 (3SE, N=554) and was regarded as isomorphic to SVL (comparison with $\alpha=1$: $F_{1,552}=0.061$, p>.1).

9) TL: The nine populations could be arranged by the magnitude of the allomorphic constant in the following way: Pop. 96 ($\alpha=0.948$)—Pop. 16—Pop. 63—Pop. 73—Pop. 22—Pop. 80—Pop. 8—Pop. 63—Pop. 88 ($\alpha=1.032$). There was no correlation between α values and latitudes (Fig. 11I; $r=0.564$, dF=7, p>.1). The α value for Pop. 96 was somewhat smaller than rather uniform values of the remaining populations, but the difference was not significant between Pop. 96 and Pop. 16, which had the second smallest value, (slope: $F_{1,84}=6.43$, .05>p>.01; position: $F_{1,85}=2.76$, p>.05). Therefore, the significant difference in α values between Pop. 96 and Pop. 88, which had the largest α value (slope: $F_{1,85}=12.22$, p<.01; position: $F_{1,86}=1.02$, p>.05), became continuous by the values of the intermediate populations. The combined α value, $\alpha=1.019\pm0.005$ (3SE, N=555), proved this character tachymorphic to SVL (comparison with the case of $\alpha=1$: $F_{1,553}=14.32$, p<.01).

10) FL: As TL, Pop. 96 had a small α value. The nine populations could be arranged as: Pop. 96 ($\alpha=0.946$)—Pop. 16—Pop. 80—Pop. 63—Pop. 22—Pop. 73—Pop 18—Pop. 8—Pop. 88 ($\alpha=1.134$). No significant correlation was detected between α values and latitudes (Fig. 11J; $r=0.454$, dF=7, p>.1). The smallest α values were significantly different from the largest (slope: $F_{1,85}=22.60$, p<.01; position: $F_{1,86}=0.52$, p>.1), but were bridged over by values of the intermediate populations (e.g., Pop. 96 vs. Pop. 16; slope: $F_{1,84}=5.22$, .05>p>.01; position: $F_{1,85}=10.29$, p<.01). The α value obtained by combining nine populations, $\alpha=1.058\pm0.007$ (3SE, N=556) indicated that FL was tachymorphic to SVL (comparison with $\alpha=1$: $F_{1,554}=64.02$, p<.01).

b) *Growth Gradient Variation*

Although the allomorphic constants of most characters against SVL varied somewhat within a population, general trends in growth gradient relations were analyzed by the use of allomorphic constants obtained by combining all age/sex groups in each population (Table 19).

The lines formed by connecting the combined α values of ten characters (bold lines in Fig. 12) were similar in shape among nine populations, with a few exceptions in some characters. The α values for TD varied somewhat among populations and populations could be divided into two groups: (a) α value for TD smaller than those for T-EL and PL (Pops. 73, 88, 96), and (b) α values for TD larger than those for T-EL and PL (Pops. 8, 16, 18, 22, 63, 80). The relation in the magnitude of α value between PW and FL showed a slight deviation in Pop. 96 from other populations: the α value for FL ($\alpha=0.947$) was almost equal to that for PW ($\alpha=0.934$) in Pop. 96, whereas the former value was somewhat larger than the latter in the remaining populations.

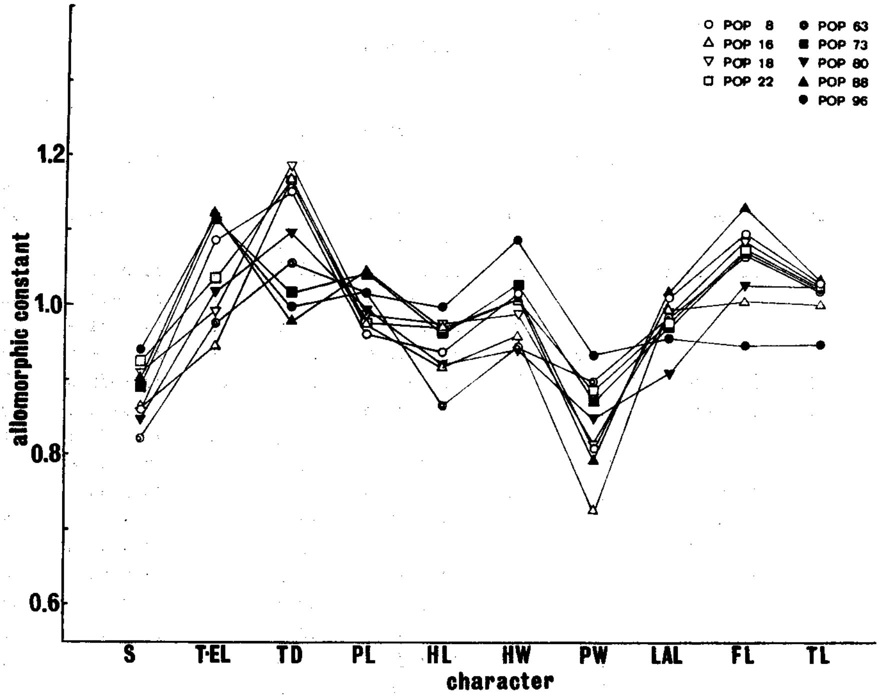

Fig. 12. Growth gradients in the nine populations of the Japanese common toad.

3. *Variation in ACV for Each Character*

a) *Variation in ACV for Each Character*

1) HL: The presence of differences in the allomorphic relation of HL and SVL among age/sex groups has been suggested in the previous chapter. Therefore, the three age/sex groups were treated separately in the analyses of ACV for this character (Table 20).

Of 552 young, the smallest ACV, 26.9, was possessed by an individual from Pop. 62, and the largest, 37.7, by one from Pop. 70. The latter value was 1.40 times larger than the former. The smallest ACV median for 39 populations of young toads was 31.0 for Pop. 31, and Pop. 1 (median=31.2) and Pop. 57 (31.3) ranked next and third.

Table 20. Variation in the HL ACV of the Japanese common toad.

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
1	3	30.8–31.5	31.2	11	29.2–34.8	31.5	3	29.3–31.8	30.9
2	1		31.2	1		32.5			
3	2	32.2–33.2	32.7				1		32.7
4				19	29.7–35.5	32.7	2	32.3–34.1	33.2
5	1		35.9	6	30.9–32.4	31.5	3	30.1–32.6	31.2
6	1		32.8	10	28.2–32.5	30.6	1		29.5
7				1		29.5	1		32.3
8	30	31.3–35.2	33.1	15	29.4–35.3	32.5	16	31.7–36.2	33.6
9	4	31.1–35.2	32.9	1		32.7	1		34.7
10	13	32.6–35.7	34.1	8	32.4–36.6	34.6	8	33.2–34.4	33.6
11	1		33.9						
12	1		32.3	1		33.1	4	32.1–33.3	32.7
13				3	31.5–35.4	33.1			
14	2	30.9–33.7	32.3	1		31.7	2	30.6–32.5	31.5
15							1		34.6
16	26	28.9–33.5	31.8	30	28.7–33.2	31.1	13	28.5–33.5	31.6
17				5	29.7–35.2	32.6			
18	11	31.1–34.6	33.1	30	31.1–34.9	32.9	24	30.8–36.3	33.2
19				25	30.2–34.4	32.4	16	31.0–34.7	32.7
20				20	30.4–33.2	31.6	20	30.7–34.4	32.4
21	1		29.3	10	30.2–32.8	31.3	9	31.5–34.5	33.0
22	11	30.0–34.9	32.7	30	30.5–33.7	32.1	18	30.9–35.6	33.2
23	2	31.7–32.7	32.2	22	28.3–33.4	30.7	21	28.9–33.4	30.8
24				15	29.7–34.1	31.2	6	31.1–32.4	31.8
25	8	31.7–35.1	33.1	30	28.8–34.4	31.2	12	28.2–33.6	32.2
26	8	31.8–35.1	33.5	6	30.9–33.9	31.9	4	30.6–33.3	31.9
27	2	31.0–36.5	33.8	30	30.9–35.7	33.4	17	31.4–35.9	33.8
28	14	29.7–35.5	33.1	1		32.5	3	33.3–34.5	33.8
29	6	31.4–35.3	32.7	3	30.6–32.4	31.8	2	33.8–34.2	34.0
30	1		32.2	4	29.4–31.0	30.2	6	30.8–35.0	32.2
31	3	29.7–31.7	31.0	12	30.7–33.5	32.0	3	31.8–33.6	32.5
32	6	30.9–34.7	32.2	30	30.2–34.8	32.8	30	30.5–36.0	33.5
33	4	30.7–35.7	33.5	2	32.5–36.0	34.2	1		31.1
34				29	28.7–35.6	32.5	10	29.9–34.4	32.0
35	1		36.9	1		33.4			
36	2	31.4–33.5	32.4	1		35.8			
37	5	33.1–36.2	33.6	5	30.8–34.6	32.8			
38	2	31.2–34.2	32.7	30	29.9–33.9	32.1	25	28.7–34.4	32.0
39	6	31.6–36.1	34.0	14	31.7–37.1	34.5			
40				3	31.3–35.9	33.9	1		36.6
41				2	32.5–32.8	32.7			
42				1		32.9	1		32.9
43				30	28.7–33.7	32.1	5	30.9–32.2	31.6
44	1		32.6				6	31.2–34.6	33.1
45				1		34.4			
46	3	31.1–35.5	34.0						
47	1		35.3	3	33.9–36.2	35.0	5	33.1–35.6	34.2
48	1		33.4	2	31.8–32.4	32.1	1		34.8

(cont'd.)

(Table 20. cont'd.)

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
49				3	32.1–34.2	33.0	5	26.9–35.8	33.5
50				16	30.1–34.8	32.6	3	29.9–32.8	31.2
51	2	32.6–34.1	33.3	12	30.8–35.2	32.6	3	32.0–34.5	32.9
52	3	29.4–33.3	31.5	6	31.0–32.4	31.9	2	32.5–32.5	32.5
53	2	34.4–36.4	35.4	3	31.7–33.4	32.4			
54				10	31.8–36.6	34.3	1		33.8
55	2	32.6–35.2	33.9	25	30.9–34.3	32.7	6	33.7–35.6	34.4
56	1		32.3	21	31.9–35.3	33.2	14	32.1–36.4	34.1
57	5	30.3–32.8	31.2				2	32.0–33.7	32.9
58	23	32.7–36.5	34.2	7	32.3–35.6	34.0	12	33.3–37.2	34.5
59	10	31.5–34.3	33.0	30	30.6–37.0	33.2	12	31.9–36.1	34.0
60	4	34.0–34.6	34.4	26	27.6–36.3	33.7	9	33.2–36.4	34.8
61	1		32.1	28	30.0–35.4	33.1	11	32.9–37.9	34.4
62	30	26.8–35.6	32.6	11	29.9–34.9	32.1	4	26.9–34.7	32.0
63	66	28.3–35.7	31.9	43	28.8–33.6	31.1	34	29.0–35.6	32.3
64	2	31.6–35.0	33.3	1		32.9	1		34.8
65	2	33.6–34.7	34.1	5	30.5–33.5	32.7	1		32.6
66	22	29.5–36.3	32.9	3	31.1–33.9	32.6			
67	1		32.8						
68	2	31.7–32.6	32.1				2	32.3–33.5	32.9
69	1		33.9	1		35.2	1		31.1
70	23	30.7–37.7	33.6						
71	1		35.2	1		34.9	3	34.7–35.0	34.8
72				2	32.1–34.4	33.3	2	32.2–33.1	32.6
73	30	30.9–36.4	33.3	13	28.9–33.8	31.9	11	31.7–36.1	33.5
74							1		32.3
75	2	30.1–32.9	31.5				2	35.1–37.3	36.2
76	3	32.9–34.2	33.4						
77							1		32.9
78	10	31.8–36.9	34.4	1		33.2	9	32.5–37.1	34.7
79				27	33.2–37.2	35.0	15	30.8–37.0	34.5
80	30	30.3–34.7	32.3	22	29.2–34.1	31.2	10	32.3–35.3	33.6
81	2	33.3–33.8	33.6	30	29.6–35.2	32.2	23	30.2–35.2	32.5
82	3	33.1–35.4	34.5						
83	4	35.3–36.9	36.0	1		35.4	2	33.8–34.2	34.0
84	11	30.4–38.5	34.0	3	32.8–35.6	34.2	7	32.4–35.1	33.5
85	3	32.8–35.1	34.2	6	30.9–36.7	34.3	3	33.9–34.6	34.3
86	9	32.4–36.4	34.1	27	30.1–36.9	34.1	14	32.3–37.3	34.7
87				3	32.5–34.1	33.3	3	33.5–35.1	34.3
88	31	30.7–36.0	32.8	30	29.2–34.4	31.7	8	29.5–35.7	32.8
89	2	32.4–33.5	32.9	2	32.7–34.6	33.6	4	33.6–34.3	33.9
90	3	31.7–34.8	33.6						
91				7	32.0–35.4	33.3	22	32.5–35.6	34.3
92	7	31.6–35.6	32.8				1		34.3
93				1		32.2	1		35.9
94	1		34.9	4	31.8–34.2	32.9	1		32.6
95							1		32.5
96	14	32.4–35.5	34.2	16	31.7–35.2	33.0	11	32.4–36.8	34.0

The largest value was 36.0 for Pop. 83, and Pop. 60 and Pop. 78 (median =34.4) followed. The largest median was 1.16 times larger than the smallest.

Of 951 adult males, the smallest ACV, 27.6, was exhibited by an individual from Pop. 60, and the largest value, 37.2, by one from Pop. 79. The largest value was 1.35 times larger than the smallest. The smallest median of 58 populations of adult males was 30.2 for Pop. 30, and the value 30.6 for Pop. 6 and 30.7 for Pop. 23 ranked next and third. Populations 47 and 79 had the largest median, 35.0, and Pop. 10 (ACV median=34.6) followed them. The largest value was 1.16 times larger than the smallest.

For 580 adult females, the smallest ACV, 26.9 was found for an individual from Pop. 49, and the largest, 37.9, was for one from Pop. 61; the latter value was 1.41 times larger than the former. The smallest median, 30.8, among 50 populations, was found in Pop. 23. Population 1 (median=30.9) and Pop. 5 (31.2) also had a small median. The largest was 34.8 for Pop. 60 and Pop. 71, and Pop. 78 (median=34.7) followed. The largest median was 1.13 times larger than the smallest. Thus, among the total of 2,804 individuals, the largest value was 1.41 times larger than the smallest.

Difference with age between young and adult males was found in five out of 27 comparable populations (18.5%; Pops. 25, 63, 73, 88, 96). Out of 24 combinations between young and adult females, the difference was significant only in Pop. 80 ($U_{20,10}=31$, $p<.05$). The median of ACV in adult males was smaller than that in young in every population having age difference, but adult females showed a larger value than young in Pop. 80. Age difference between young and adult males was more frequently observed in southwestern populations.

Sexual dimorphism was found in five out of 44 combinations (11.4%; Pops. 20, 22, 55, 63, 80), and males had smaller medians than females in all these populations.

Although all populations more or less overlapped in ACV medians, somewhat distinct populations were observed. In young, Pops. 1 and 83 were most distinct, being different from 76.3% of the remaining populations. Among the populations of adult males, Pop. 30 was most remarkable differing from 84.2% of other populations, and Pop. 79 was also distinct (differed from 82.5%). Among adult females, Pop. 23 was most conspicuous with difference from 75.5% of the remaining populations.

The variation range of ACV medians was divided into size classes for each age/sex group, and the distribution pattern of the populations for each size class was examined (Fig. 13). In young, the median (X) of most populations fell within the range of $32.3 \leq X < 34.9$, resulting in unimodal distribution with an ill-defined mode at the size class $32.3 \leq X < 33.6$. Adult males also exhibited unimodal distribution and the largest number of populations concentrated in the size class $32.6 \leq X < 33.4$. In adult females, the mode was found to deviate extremely towards the larger size classes, and a larger number of populations were found in the size class $33.6 \leq X < 35.0$.

From these results, the range of ACV medians for each age/sex group was divided arbitrarily into three, and populations were grouped into three types (I: short head; II: moderate head; III: long head) by the magnitude of the ACV median. The geographic distribution of these three types was examined for each age/sex group (Fig.

14). In all three age/sex groups, the distributional range of type II populations was wide, ranging from the Tohoku District to Kyushu, and type III populations were scattered among type II populations. Though the distribution patterns of the three types were not discrete, the range of type I populations was characteristically restricted to regions from Kinki District northwards in each age/sex group.

2) SL: From the results for Pop. 63 (see the previous chapter), three age/sex groups were combined for analysis (Table 21). Among 2,204 specimens, the smallest ACV, 10.5, was exhibited by an individual from Pop. 62, and the largest value, 15.4, by one from Pop. 39. The largest value was 1.47 times larger than the smallest. The smallest population median, 12.1, was exhibited by Pop. 30 among 83 populations, and Pop. 6 (median = 12.2), Pop. 1 (12.4), and Pop. 31 (12.4) followed. The largest median was 13.8 for Pop. 86, and Pops. 64 and 71 (ACV = 13.7) followed. The largest median was 1.14 times larger than the smallest. Interpopulation variation in medians was not evident, and one population differed from at most 69.5% of the remaining populations (Pop. 6).

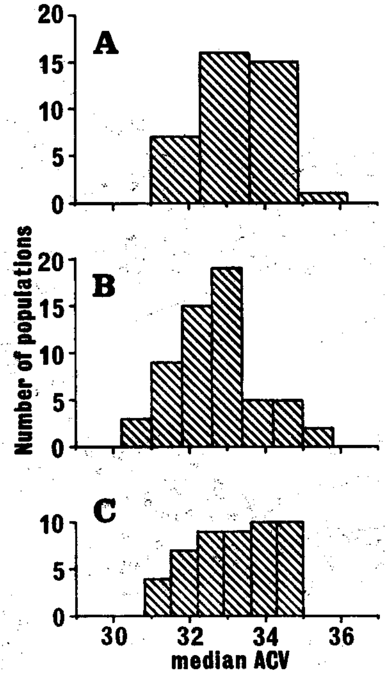

Fig. 13. Number of populations tabulated by 1.3 mm (A: young), 0.8 mm (B: adult males), and 0.7 mm (C: adult females) intervals of population ACV median of HL.

The variation range of medians for 83 populations was divided into nine size classes as shown in Fig. 15. A mode was recognized at the size class $13.1 \leqq X < 13.3$, and another lower peak was found at $12.7 \leqq X < 12.9$.

From this observation, populations were divided into two types for convenience: I, short snout, and II, long snout. The geographic distribution of the each type was far from discrete and populations of both types were found over wide ranges (Fig. 16). The number of type I populations, however, was greater in the areas from central Japan eastwards than in western areas.

3) T-EL: The three age/sex groups were separately analyzed, since the allomorphic variation was thought to affect the ACV (Table 22). Of 725 young, an individual from Pop. 16 had the smallest ACV (0.8), and one from Pop. 73 had the largest value

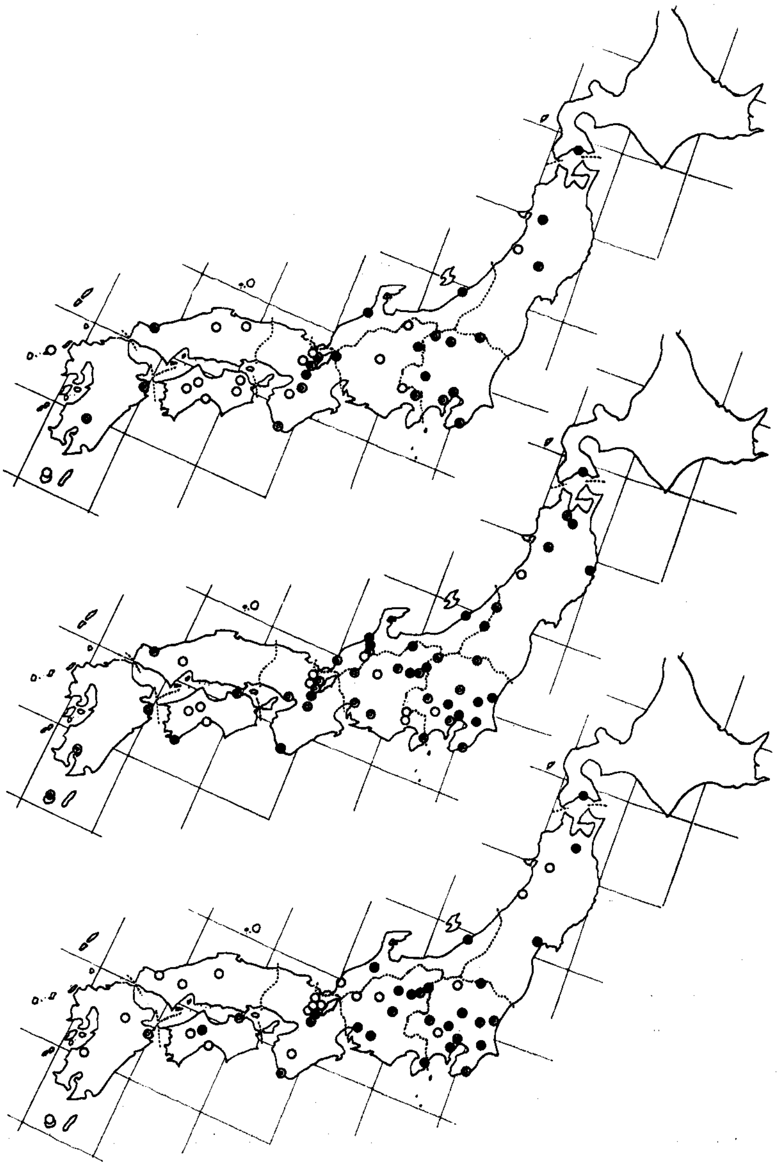

Fig. 14. Geographic distribution of type I (short head: closed circles), type II (medium head: double circles) and type III (long head: open circles) populations of the Japanese common toad. Top: young; middle: adult males; bottom: adult females.

Table 21. Variation in the SL ACV of the Japanese common toad.

Population	N	ACV		Population	N	ACV	
		range	median			range	median
1	17	10.7–13.7	12.4	49	8	12.5–14.8	13.7
2	2	12.0–12.9	12.5	50	22	11.1–14.2	12.5
3	3	12.5–13.5	12.9	51	17	12.0–14.3	13.1
4	20	11.7–13.9	12.7	52	11	11.3–13.3	12.5
5	10	11.1–13.7	12.4	53	5	12.6–13.7	13.1
6	12	11.3–13.2	12.2	54	11	12.1–14.1	13.1
7	2	11.0–12.9	12.0	55	33	11.8–14.2	13.0
8	50	10.7–14.6	12.9	56	36	12.1–14.6	13.3
9	6	12.2–13.8	12.8	57	7	12.2–13.5	12.6
10	29	12.5–15.2	13.6	58	42	12.3–14.8	13.3
11	1		12.5	59	50	11.7–15.0	13.4
12	6	12.8–13.8	13.2	60	39	12.5–14.9	13.7
13	3	12.4–13.6	13.1	61	39	11.8–15.2	13.3
14	5	11.8–13.6	12.7	62	50	10.5–14.3	12.5
15	1		13.1	63	50	11.3–14.0	12.7
16	50	10.6–14.6	12.6	64	4	13.1–14.2	13.7
17	5	11.7–13.5	13.0	65	8	11.8–14.4	13.2
18	69	11.5–14.7	13.1	66	25	11.1–14.5	12.4
19	41	11.9–14.3	13.1	67	1		14.4
20	40	11.3–14.0	12.6	68	4	12.8–14.0	13.4
21	20	12.1–14.0	13.0	69	3	12.8–13.7	13.3
22	94	11.3–13.9	12.7	70	23	12.4–14.1	13.1
23	45	11.0–13.8	12.6	71	5	13.3–14.1	13.7
24	21	11.3–14.3	12.7	72	4	12.9–14.1	13.3
25	55	11.1–14.5	12.8	73	120	11.5–14.4	13.0
26	18	12.5–13.7	13.1	74	1		13.4
27	50	12.0–14.5	13.1	75	4	12.2–13.7	13.3
28	18	11.8–14.0	13.0	76	3	12.3–13.4	13.0
29	9	12.1–14.2	13.2	77	1		11.9
30	8	11.0–13.8	12.1	78	20	12.6–14.6	13.5
31	18	10.6–13.0	12.4	79	42	12.3–15.0	13.6
32	50	11.8–14.3	13.1	80	123	11.0–14.4	12.8
33	5	12.1–13.9	13.2	81	76	11.4–14.2	13.0
34	39	11.9–15.1	13.1	82	3	13.0–13.2	13.1
35	2	13.2–13.8	13.5	83	6	12.6–14.3	13.5
36	3	12.9–13.6	13.3	84	21	11.9–14.9	13.2
37	4	12.2–13.3	12.7	85	12	13.0–14.5	13.5
38	50	11.2–14.0	12.7	86	50	12.3–15.0	13.7
39	20	11.9–15.4	13.5	87	5	13.0–14.3	13.6
40	4	12.5–15.2	13.5	88	94	11.4–13.8	12.7
41	2	12.6–13.2	12.9	89	8	12.6–14.2	13.5
42	2	12.5–13.7	13.1	90	3	11.7–14.6	13.1
43	44	11.4–14.8	13.2	91	29	11.0–14.0	12.8
44	8	12.7–14.5	13.5	92	8	12.7–13.8	13.1
45	1		14.0	93	2	13.8–14.6	14.2
46	3	12.8–13.8	13.4	94	6	12.5–13.6	13.1
47	9	12.4–14.4	13.3	95	1		12.1
48	4	12.6–14.1	13.2	96	41	11.7–15.2	13.3

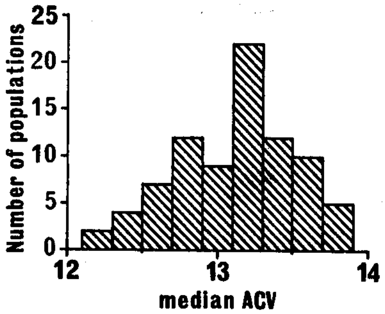

Fig. 15. Number of populations tabulated by 0.2 mm intervals of population ACV median of SL.

(5.8); the largest value was 7.25 times larger than the smallest. The smallest population median of the 39 populations of young was 2.2 shown by Pop. 10, and Pops. 18 (median=2.5) and 57 (2.6) had also small medians. Population 82 had the largest median (4.4) and the value for Pop. 84 and Pop. 70 (4.3) followed. The largest median was 2.03 times larger than the smallest.

An individual in Pop. 27 had the smallest ACV (1.0) among 1,168 adult males, and one in Pop. 80 had the largest value (ACV =5.3). The largest value was 5.38 times larger than the smallest. The smallest median for 58 adult male populations was 1.9 found in Pop. 10, and Populations 4, 5, and 28 (median=2.0) also had small medians. The largest median was 4.5 in Pop. 84, and Pop. 85 (4.3), Pop. 80 (4.2), and Pop. 62 (3.9) were among the populations with large medians. The largest median was 2.35 times larger than the smallest.

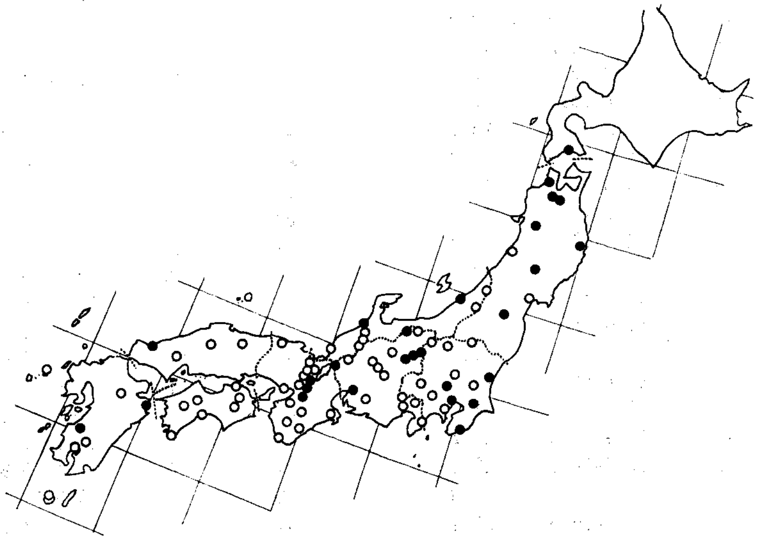

Fig. 16. Geographic distribution of type I (short snout: closed circles) and type II (long snout: open circles) populations of the Japanese common toad.

The female with smallest ACV (1.2) was found in Pop. 5 among 576 individuals. The largest ACV was shown by an individual from Pop. 86 and was 5.6, 4.62 times larger than the smallest. Among 50 adult female populations, the smallest ACV median (2.3) was shown by Pop. 31, and the populations 5 (median=2.4), 20, 16 (median=2.5) had also small medians. The largest median (4.5) was found in Pop. 62, and Pop. 80 (median=4.4), Pop. 89 (4.2), and Pop. 88 (4.2) were populations with second to fourth largest medians. The largest median was 1.95 times larger than the smallest.

There were age differences between young and adult males in nine out of 27 available populations (33.3%; Pops. 8, 16, 22, 25, 31, 39, 63, 73, 88). Significant difference was found between young and adult females only in Pops. 10 and 62. In these populations, medians of adult males were invariably smaller than those of young, and conversely, medians of adult females were larger than those of young.

Sexual dimorphism in adults was found in eight out of 44 available populations (18.2%; Pops. 10, 21, 22, 59, 62, 79, 81, 91), and females had a larger median than males in all these populations. The presence of dimorphism was more frequent in the populations from southwestern Japan.

In young, Pop. 10 was most distinct, having differences from 89.5% of the remaining populations. Among populations of adult males, Pop. 80 differed from 89.5% of the remaining populations, and Pop. 85 was also distinct, having differences from 80.7% of the remainings. Adult females had slightly lower number of differences than young and adult males, and both Pop. 62 and Pop. 80 had differences from 75.5% of the other populations.

For each age/sex group, range of medians was divided into size classes and distribution of populations in these size classes was examined (Fig. 17). In the young, two evident peaks were found in the smaller and larger extremes of size classes ($2.2 \leqq X < 2.8$, and $4.0 \leqq X < 4.6$). Similarly in adult males, two evident peaks were found and the smallest number of populations were distributed in the size class $2.9 \leqq X < 3.4$. Adult females showed a pattern similar to young and adult males with two peaks in the both sides of the size class $3.5 \leqq X < 3.9$.

These observations indicated that the populations could be divided into two types (I: short tympanum-eye; II: long tympanum-eye) by the magnitude of ACV medians in each of the three age/sex groups. In young, type I populations were distributed from the Kinki District eastwards, and type II populations were found from the Chubu District wastwards (Fig. 18). In the larger part of the Chubu district, populations of both types were found, but the number of type II populations was much smaller. A similar distribution pattern was observed in adult males, but the overlapping range was narrower than in the young. Adult females also showed a pattern similar to that found in young and adult males, but a single type II population was found in the Tohoku District remote from all other populations of that type.

4) TD: Three age/sex groups were combined for variation analyses (Table 23). Of 2,501 individuals, the smallest ACV, 3.2, was possessed by an individual from Pop. 66, and the largest, 9.8, by one from Pop. 8. The largest value was 3.03 times larger

Table 22. Variation in the T-EL ACV of the Japanese common toad.

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
1	3	2.0– 3.3	2.6	11	1.7– 2.8	2.3	3	2.2– 3.1	2.7
2	1		3.3	1		1.9			
3	2	2.4– 2.8	2.6				1		2.7
4				20	1.4– 2.8	2.0	2	2.0– 2.5	2.2
5	1		2.5	6	1.7– 2.5	2.0	3	1.2– 3.3	2.4
6	1		2.2	10	1.2– 3.0	2.2	1		2.9
7				1		2.9	1		2.4
8	15	1.8– 4.0	3.0	14	1.5– 2.9	2.4	16	1.3– 3.4	2.6
9	4	2.7– 3.2	3.0	1		2.4	1		2.0
10	13	2.0– 2.4	2.2	8	1.4– 2.6	1.9	8	2.2– 3.2	2.6
11	1		2.5						
12	1		3.2	1		3.9	4	3.9– 4.4	4.1
13				3	2.0– 2.6	2.3			
14	2	3.0– 3.1	3.0	1		2.2	2	2.2– 2.6	2.4
15							1		3.6
16	64	0.7– 3.6	2.6	63	1.2– 3.0	2.1	13	1.3– 3.6	2.5
17				5	1.4– 2.9	2.3			
18	11	1.3– 3.4	2.5	33	1.5– 3.4	2.3	24	1.9– 3.3	2.6
19				25	1.3– 2.9	2.3	16	1.5– 3.7	2.5
20				20	1.4– 3.1	2.3	20	1.4– 3.3	2.5
21	1		2.8	10	1.4– 2.9	2.3	9	2.2– 3.8	2.9
22	10	2.1– 3.4	2.7	67	1.3– 3.1	2.4	18	1.9– 3.6	2.9
23	2	3.0– 3.2	3.1	22	1.3– 3.2	2.4	21	1.8– 3.4	2.7
24				15	1.7– 3.3	2.5	6	1.9– 3.7	3.0
25	8	2.7– 4.4	3.3	38	1.8– 3.8	2.8	12	2.0– 3.2	2.8
26	8	2.0– 3.2	2.8	6	2.2– 3.1	2.6	4	2.2– 2.9	2.7
27	2	1.4– 3.2	2.3	41	1.0– 4.2	2.6	16	1.8– 3.6	2.9
28	14	2.1– 3.6	2.6	1		2.3	3	1.8– 3.5	2.6
29	5	2.4– 3.1	2.7	3	1.7– 2.4	2.1	2	2.3– 3.4	2.8
30	1		3.0	6	1.7– 2.7	2.1	5	2.0– 2.9	2.5
31	3	3.0– 3.9	3.4	12	1.2– 3.0	1.9	3	1.6– 2.8	2.3
32	6	1.6– 3.6	2.7	51	1.9– 3.6	2.8	30	2.0– 4.0	3.1
33	4	3.3– 3.9	3.4	2	3.6– 4.5	4.1	1		3.6
34				29	1.7– 3.5	2.6	10	2.3– 3.4	2.8
35	1		3.3	1		3.0			
36	2	3.3– 3.3	3.3	1		1.9			
37	5	2.2– 3.4	2.7	5	2.7– 3.1	2.9			
38	2	1.6– 2.6	2.1	69	1.8– 3.8	2.6	25	1.9– 3.9	2.8
39	5	3.8– 4.7	4.2	14	2.2– 4.0	3.2			
40				3	2.9– 3.8	3.3	1		4.7
41				2	1.9– 2.1	2.0			
42				1		2.2	1		2.4
43				38	1.4– 2.9	2.3	6	2.0– 3.8	2.9
44	1		3.5	1		2.5	6	2.4– 3.4	2.8
45				1		1.9			
46	3	2.9– 3.6	3.2						
47	1		3.9	3	2.0– 2.7	2.3	5	2.2– 3.1	2.8
48	1		3.3	2	2.7– 3.4	3.0	1		3.4

(cont'd.)

(Table 22. cont'd.)

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
49				3	2.6– 3.6	3.1	5	3.1– 3.5	3.3
50				21	2.0– 3.7	2.7	5	2.7– 3.3	3.0
51	2	2.4– 3.3	2.8	12	1.9– 3.1	2.5	3	2.3– 3.4	3.0
52	3	3.2– 3.6	3.4	6	2.6– 3.9	3.3	2	3.6– 3.9	3.7
53	2	2.2– 2.6	2.4	3	2.0– 2.8	2.3			
54				10	1.1– 3.3	2.2	1		2.3
55	2	3.0– 3.1	3.0	25	1.8– 3.8	2.7	5	2.7– 3.6	3.1
56	1		3.3	21	2.0– 3.6	2.8	14	2.0– 4.0	2.9
57	5	1.6– 3.0	2.6				2	3.3– 3.5	3.4
58	23	2.5– 4.1	3.3	6	3.2– 3.7	3.5	12	2.7– 3.9	3.3
59	10	2.3– 3.8	3.1	59	1.4– 3.7	2.7	10	2.3– 3.5	3.1
60	4	2.7– 3.9	3.4	25	2.2– 3.7	3.0	9	2.0– 3.9	3.2
61	1		3.0	28	1.9– 3.9	2.7	11	2.1– 4.7	3.2
62	43	2.2– 4.5	3.5	11	2.6– 4.7	3.6	3	4.1– 4.7	4.5
63	63	2.3– 5.3	4.1	44	2.4– 4.6	3.7	33	3.0– 4.8	3.9
64	2	2.4– 4.7	3.5	1		3.2	1		4.8
65	2	3.4– 4.7	4.1	5	2.3– 4.1	3.0	1		3.8
66	22	2.9– 4.9	4.1	3	3.4– 4.0	3.7			
67	1		3.8						
68	2	2.9– 3.2	3.1				2	3.5– 4.0	3.7
69	1		4.0	1		3.1	1		3.0
70	23	3.6– 5.0	4.3						
71	1		3.1	1		3.6	3	2.9– 3.8	3.4
72				2	3.3– 3.8	3.6	2	3.8– 4.1	4.0
73	95	3.2– 5.8	4.2	13	2.4– 4.5	3.7	11	3.7– 4.3	4.0
74							1		4.1
75	1		3.2				2	4.4– 4.8	4.6
76	3	3.5– 4.0	3.7						
77							1		2.9
78	10	3.4– 5.3	4.3	1		4.6	9	3.4– 4.7	4.1
79				27	3.0– 4.3	3.7	15	3.4– 4.7	4.1
80	91	3.0– 5.3	4.3	21	3.4– 5.3	4.2	10	4.0– 5.0	4.4
81	2	3.7– 3.8	3.7	51	2.0– 4.6	3.3	23	3.2– 4.8	3.9
82	3	4.0– 4.7	4.4						
83	4	3.4– 5.2	4.3	1		4.3	2	4.5– 5.5	5.0
84	11	3.5– 4.9	4.3	3	3.7– 5.1	4.5	7	3.4– 5.0	4.1
85	3	3.7– 4.5	4.1	6	3.4– 5.1	4.3	3	3.9– 4.4	4.1
86	9	3.3– 4.9	4.1	27	3.0– 4.6	3.8	14	3.2– 5.6	4.1
87				3	2.3– 4.4	3.4	3	3.3– 4.3	3.7
88	54	3.2– 4.9	4.1	31	2.9– 4.5	3.7	8	3.3– 5.4	4.2
89	2	4.5– 4.9	4.7	2	3.1– 3.8	3.4	4	3.4– 5.1	4.2
90	3	3.5– 4.3	3.8						
91				7	3.0– 4.1	3.8	22	3.6– 5.6	4.4
92	5	3.2– 4.4	3.7				1		4.4
93				1		3.2	1		4.7
94	1		4.1	4	2.6– 4.0	3.3	1		3.6
95							1		4.2
96	11	3.1– 5.7	4.2	16	2.8– 4.2	3.6	11	3.0– 4.5	3.9

than the smallest.

When the medians of 83 populations were examined, Pops. 90 and 92 had the smallest value, 4.4, and Pop. 73 (median=4.7) was the third. The largest median was 8.3 for Pop. 3, and the next largest value was 8.0 for Pop. 10. The largest value was 1.86 times larger than the smallest.

Interpopulation comparisons revealed overlap in ACVs among populations, and all populations had ACVs insignificantly different from at least several other populations. There were, however, many differences and Pops. 10, 40, and 80 differed from 85.4% of the remaining populations. Populations 8 and 92 were also distinct, with differences from 82.9% of the other populations.

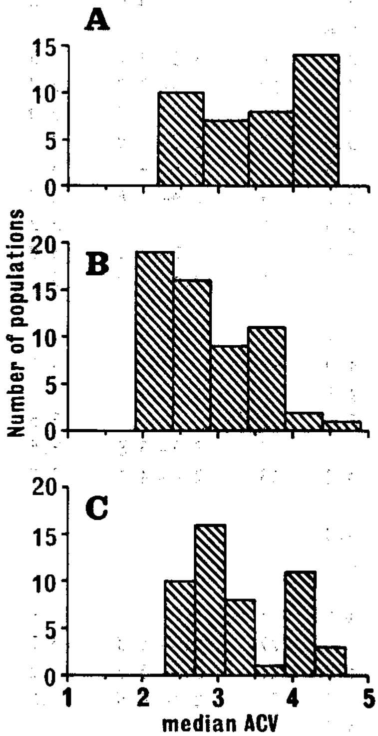

Fig. 17. Number of populations tabulated by 0.6 mm (A: young), 0.5 mm (B: adult males) and 0.4 mm (C: adult females) intervals of population ACV median of T-EL.

The range of medians was divided into ten size classes and the number of populations belonging to each size class was examined (Fig. 19). The figure showed an evident bimodal distribution of populations: two evident modes were found in the size classes, $4.9 \leqq X < 5.3$, and $6.5 \leqq X < 6.9$, and there was an evident decrease of number of populations at the size class $5.7 \leqq X < 6.1$.

From this observation, populations were divided into two types: I and II. Type I included populations with medians larger than 5.9, and type II included ones with medians smaller than 5.9. The geographic distribution of these two types was examined

(Fig. 20). As clearly seen in Fig. 20, the two types were rather clearly separated at the Kinki District; type I populations were found from there eastwards and type II populations, with one exception each in the Tohoku, Kanto, and Hokuriku districts, were distributed from Kinki westwards.

5) HW: ACV was separately analyzed for each of the three age/sex groups (Table 24). Of 554 young individuals, the smallest ACV, 31.2, was found for an

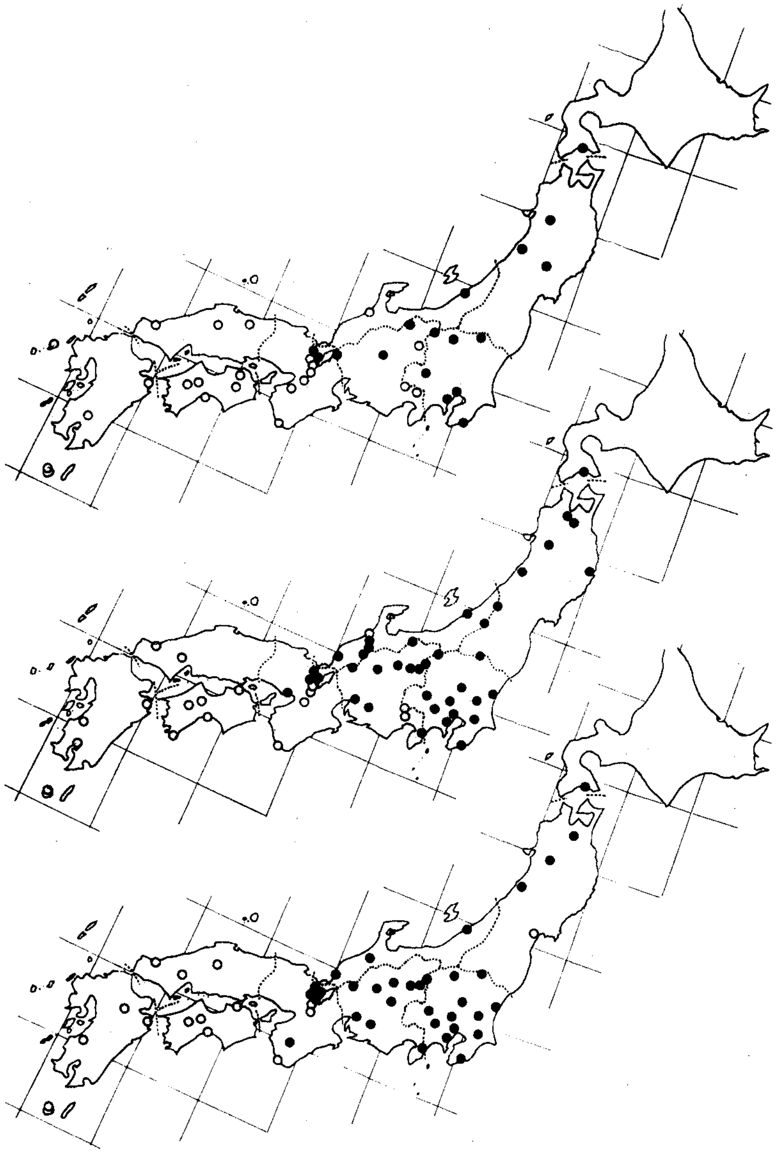

Fig. 18. Geographic distribution of type I (short T-E: closed circles) and type II (long T-E: open circles) populations of the Japanese common toad. Top: young; middle: adult males; bottom: adult females.

Table 23. Variation in the TD ACV of the Japanese common toad.

Population	N	ACV		Population	N	ACV	
		range	median			range	median
1	17	5.1– 7.1	5.9	49	8	6.0– 7.1	6.6
2	2	6.4– 8.4	7.4	50	26	5.4– 7.4	6.2
3	3	7.4– 9.0	8.3	51	17	4.9– 8.3	6.8
4	22	6.3– 8.9	7.6	52	11	4.4– 5.9	5.2
5	10	5.7– 8.1	7.1	53	5	6.9– 8.1	7.6
6	12	5.8– 7.5	6.8	54	11	5.5– 8.3	6.8
7	2	6.6– 7.1	6.9	55	33	4.9– 7.9	6.7
8	62	5.9– 9.8	7.9	56	36	5.5– 7.6	6.7
9	6	5.5– 8.4	7.3	57	7	5.4– 7.2	6.3
10	28	6.8– 9.6	8.0	58	41	5.2– 8.4	6.6
11	1		6.5	59	81	5.1– 8.4	6.7
12	6	4.7– 5.5	5.2	60	39	5.2– 8.3	6.7
13	3	6.0– 7.1	6.5	61	40	5.0– 8.1	6.7
14	5	6.1– 8.3	7.1	62	59	3.7– 7.2	5.2
15	1		7.7	63	142	3.7– 6.6	4.8
16	141	5.2– 8.1	6.7	64	4	3.7– 5.1	4.6
17	5	6.2– 7.5	7.1	65	8	3.9– 5.9	5.0
18	69	4.5– 8.7	7.2	66	25	3.2– 6.4	5.0
19	40	4.6– 8.4	6.5	67	2	4.6– 4.8	4.7
20	40	4.8– 7.5	6.0	68	4	5.7– 7.8	6.8
21	20	4.9– 7.5	6.4	69	3	6.1– 7.0	6.5
22	95	4.5– 8.5	6.6	70	23	4.3– 6.5	5.2
23	45	4.7– 8.2	6.5	71	5	5.6– 6.2	6.0
24	21	5.1– 8.1	6.6	72	4	4.7– 6.5	5.6
25	58	4.4– 7.5	5.5	73	119	3.4– 6.4	4.7
26	18	4.8– 7.3	6.2	74	1		4.6
27	60	5.1– 8.6	6.9	75	4	5.7– 7.7	6.7
28	18	5.5– 8.5	6.8	76	3	4.5– 5.4	5.0
29	11	5.6– 7.9	6.8	77	1		7.9
30	13	5.3– 7.2	6.3	78	20	4.4– 6.1	5.5
31	18	5.5– 8.6	6.7	79	42	3.6– 6.9	5.5
32	86	4.4– 8.5	7.1	80	123	3.6– 6.0	4.8
33	7	6.3– 7.5	6.7	81	76	3.6– 6.3	5.0
34	39	5.0– 8.5	6.6	82	3	4.5– 5.4	4.8
35	2	7.2– 8.9	8.0	83	7	3.7– 5.9	5.1
36	3	5.1– 7.5	6.1	84	21	4.1– 5.9	5.0
37	10	6.1– 7.9	6.9	85	12	4.3– 6.2	5.3
38	97	4.9– 8.0	6.5	86	50	4.0– 6.8	5.3
39	19	5.1– 8.5	6.8	87	5	4.1– 6.3	5.4
40	4	6.8– 9.1	7.9	88	93	3.5– 6.1	5.0
41	2	7.0– 8.0	7.5	89	8	4.4– 5.6	5.0
42	2	6.6– 8.0	7.3	90	3	4.0– 6.8	4.5
43	44	5.6– 9.6	7.7	91	29	4.1– 6.0	5.0
44	8	5.4– 7.8	6.6	92	6	3.8– 4.9	4.5
45	1		8.1	93	2	5.3– 5.5	5.4
46	3	6.9– 8.0	7.4	94	6	4.5– 6.1	5.2
47	9	6.0– 8.3	7.1	95	1		4.0
48	4	5.3– 7.6	6.6	96	40	4.1– 5.7	5.0

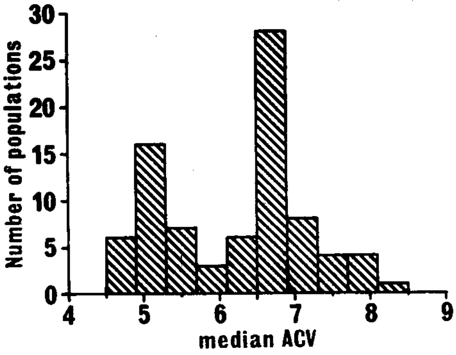

Fig. 19. Number of populations tabulated by 0.4 mm intervals of population ACV median of TD.

individual in Pop. 39, and the largest, 45.8, for one from Pop. 58; the largest was 1.47 times larger than the smallest. The smallest median of 39 populations was 35.8 for Pops. 1 and 52, and Pop. 57 (36.5) had the third smallest median. The largest median was 41.0 for Pop. 46, and Pop. 58 (median=40.8) and Pop. 83 (40.7) followed. The largest median was 1.15 times larger than the smallest.

The smallest ACV among 950 adult males was 30.8 for an individual of Pop. 21, and the largest was 44.0 for one in Pop. 84; the largest was 1.43 times the smallest. The smallest median of 58 populations was 33.7 for Pop. 1, and Pop. 21 (33.8) and Pop. 24 (34.0) showed the next and third smallest value. The largest median was 40.5 for Pop. 84, and Pop. 47 (median=40.2) and Pop. 13 (39.2) followed. The largest value was 1.20 times larger than the smallest.

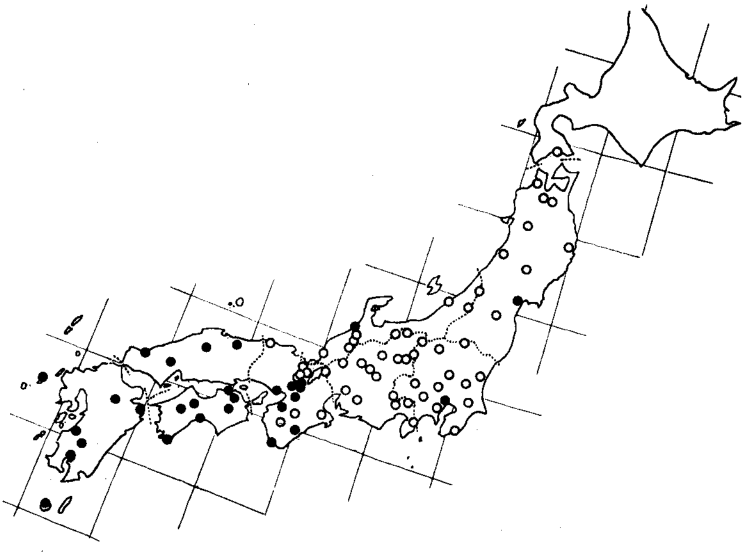

Fig. 20. Geographic distribution of type I (large-TD: open circles) and type II (small-TD: closed circles) populations of the Japanese common toad.

Table 24. Variation in the HW ACV of the Japanese common toad.

Population	young			adult males			adult females		
	N	ACV range	ACV median	N	ACV range	ACV median	N	ACV range	ACV median
1	3	34.8–37.2	35.8	11	31.1–36.2	33.7	3	35.7–36.4	36.2
2	1		34.8	1		37.9			
3	2	38.0–38.1	38.0				1		36.0
4				19	34.0–38.0	35.8	2	36.8–40.3	38.6
5	1		41.0	6	32.9–38.1	36.2	3	35.9–38.7	37.3
6	1		36.2	10	31.1–38.3	34.6	1		35.8
7				1		34.9	1		37.1
8	30	35.3–40.9	38.7	15	33.6–38.8	36.7	15	37.8–40.9	39.1
9	4	36.4–41.3	38.9	1		36.7	1		41.2
10	13	37.3–41.6	38.5	8	33.3–41.0	38.1	7	38.0–39.4	38.6
11	1		40.6						
12	1		39.6	1		38.0	4	38.3–40.0	39.0
13				3	36.1–41.7	39.1			
14	2	33.8–37.6	35.7	1		38.1	2	37.5–37.8	37.6
15							1		38.0
16	30	33.1–40.5	36.9	30	31.0–38.5	34.9	13	34.2–39.2	36.9
17				5	32.6–39.6	35.6			
18	8	32.6–39.7	37.3	30	32.7–38.6	35.2	24	34.7–39.6	37.6
19				25	31.0–38.0	35.1	16	36.1–41.2	38.2
20				20	32.2–36.6	34.4	20	35.4–40.6	37.6
21	1		34.1	10	30.8–35.6	33.8	9	36.8–40.0	38.1
22	10	35.6–38.8	37.2	30	32.5–39.3	36.4	18	36.1–42.1	39.0
23	2	37.2–38.2	37.7	22	31.1–36.9	34.1	21	33.0–39.6	36.0
24				15	32.5–36.0	34.0	6	34.9–37.5	35.9
25	8	36.8–42.3	39.4	30	31.3–40.2	34.9	10	33.5–39.7	37.0
26	8	36.4–42.8	39.8	6	35.5–38.3	37.4	4	36.0–41.5	38.2
27	2	39.1–41.7	40.4	30	31.1–42.2	37.2	17	34.9–42.7	39.0
28	14	34.4–41.2	38.8	1		37.5	3	40.5–40.7	40.7
29	6	36.0–41.0	37.7	3	35.1–37.5	36.1	2	39.7–40.3	40.0
30	1		35.7	3	32.9–36.8	34.7	5	35.0–46.0	38.6
31	3	36.5–37.2	36.9	12	32.2–37.6	34.6	3	36.2–39.2	37.8
32	6	35.3–40.8	37.2	30	34.2–40.9	36.5	29	34.5–41.5	38.5
33	4	36.0–42.8	40.7	2	40.1–43.2	41.6	1		37.2
34				29	32.1–39.2	36.1	10	35.9–40.3	37.9
35	1		42.9	1		38.3			
36	2	34.4–40.7	37.6	1		32.8			
37	5	35.2–39.7	38.0	5	35.1–39.9	37.8			
38	2	35.5–39.2	37.4	30	32.6–40.5	35.8	25	32.8–39.8	36.8
39	6	31.2–41.5	37.9	14	33.6–41.0	36.9			
40				3	35.0–39.6	37.5	1		43.4
41				2	36.4–37.2	36.8			
42				1		37.3	1		39.6
43				30	33.0–37.7	35.1	6	34.0–39.2	36.2
44	1		39.6	1		38.7	6	35.8–41.0	39.0
45				1		37.4			
46	3	37.5–43.6	41.0						
47	1		41.9	3	39.3–41.9	40.2	5	40.2–44.0	41.4
48	1		38.8	2	37.1–39.3	38.2	1		40.5

(cont'd.)

(Table 24. cont'd.)

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
49				3	36.8–39.9	38.0	5	38.6–40.9	40.3
50				14	34.4–39.4	36.8	2	37.3–38.9	38.1
51	2	37.2–38.9	38.1	12	34.2–40.3	36.7	3	36.3–41.1	38.3
52	3	34.2–37.1	35.8	6	34.3–36.2	35.1	2	36.2–39.4	37.8
53	2	40.7–41.8	41.3	3	34.3–35.8	35.1			
54				10	32.0–38.8	36.2	1		36.8
55	2	38.5–40.4	39.5	25	34.0–39.5	36.5	7	35.5–42.4	39.6
56	1		36.9	21	34.8–39.3	37.0	14	36.0–41.7	38.4
57	5	33.8–39.9	36.5				2	37.9–38.0	37.9
58	23	38.1–45.8	40.8	7	37.3–41.4	38.0	12	38.8–43.1	40.4
59	10	35.8–42.2	38.6	30	31.8–39.6	35.6	12	36.9–41.9	38.8
60	4	39.4–41.4	40.2	26	34.1–40.6	37.2	9	35.7–41.2	39.3
61	1		38.3	28	33.8–40.6	36.8	11	38.2–41.1	39.7
62	30	33.6–44.1	39.4	10	33.7–39.7	37.1	4	36.9–41.8	39.0
63	66	32.7–40.3	37.4	46	31.6–37.9	34.9	35	34.8–41.3	37.7
64	2	39.6–41.8	40.7	1		38.7	1		40.6
65	2	38.5–39.6	39.1	5	33.5–36.6	35.0	1		37.8
66	23	36.0–44.5	39.2	3	33.1–43.2	39.1			
67	2	38.3–39.4	38.8						
68	2	35.6–38.5	37.0				2	39.5–42.5	41.0
69	1		40.5	1		40.3	1		38.2
70	23	36.6–42.0	39.7						
71	2	34.3–41.2	37.7	1		39.1	3	40.0–41.8	40.8
72				2	37.1–38.2	37.6	2	37.4–38.6	38.0
73	30	35.5–43.9	39.6	13	34.2–38.3	36.2	11	36.2–42.7	39.0
74							1		38.1
75	2	35.5–38.4	37.0				2	42.7–43.5	43.1
76	3	36.9–38.6	37.9						
77							1		40.6
78	10	36.5–45.4	40.6	1		38.4	9	36.8–42.1	39.8
79				27	36.2–40.6	37.6	15	34.4–42.2	39.3
80	30	35.3–42.1	38.0	22	34.4–40.6	36.6	10	37.7–41.9	39.8
81	2	38.5–39.4	39.0	30	35.0–41.9	36.6	23	35.1–43.2	39.0
82	3	37.8–42.6	40.7						
83	4	39.0–42.2	40.7	1		40.5	2	38.9–43.1	41.0
84	11	37.2–44.8	40.0	3	37.2–44.0	40.5	7	36.9–40.4	38.9
85	3	35.7–41.5	39.4	6	36.0–41.9	38.1	3	37.2–39.7	38.6
86	9	36.9–41.0	39.1	26	36.1–41.2	38.4	14	36.6–44.4	39.5
87				3	37.1–38.7	37.8	3	38.1–39.7	39.1
88	30	35.2–41.5	38.2	30	32.5–38.2	35.2	8	35.1–40.9	38.8
89	2	38.5–42.5	40.5	2	37.0–37.2	37.1	4	37.2–41.9	39.0
90	3	37.4–41.7	40.2						
91				7	35.6–40.8	37.5	21	37.1–45.2	40.8
92	7	36.6–40.5	37.8				1		42.4
93				1		36.6	1		40.5
94	1		41.7	4	34.8–37.7	36.1	1		36.5
95									
96	14	36.5–43.4	40.6	16	34.0–38.8	36.2	11	38.2–44.8	40.1

Among 574 adult females, the smallest ACV, 32.8, was possessed by an individual from Pop. 38, and the largest, 46.0, by one from Pop. 30; the latter was 1.40 times the former. The smallest median for 49 populations was 35.9 for Pop. 24, and the values for Pop. 23 (36.0) and Pop. 1 (36.2) ranked next and third. The largest value was 41.4 for Pop. 47, and Pops. 71 and 91 (ACV=40.8) followed. The largest value was 1.15 times the smallest. Thus, among 2,078 individuals, the magnitude of difference between the largest and the smallest ACVs was 1.47 times.

Age differences were found between young and adult males in 12 out of 27 available populations (44.4%; Pops. 8, 16, 25, 31, 58, 59, 60, 63, 73, 80, 88, 96), and between young and adult females in four out of 24 available populations (16.7%; Pops. 22, 25, 28, 80). The medians of adult males were invariably smaller than those of young. In adult females, medians were larger than in young in Pops. 22, 28, and 80, whereas in Pop. 25, young had a larger median than adult females.

Sexual dimorphisms in medians were found in 28 out of 43 available populations (65.1%), and adult females always had a larger value than males. There was no particular trend in the occurrence of intrapopulation ACV variation in relation to geographic distribution.

In young, one population (Pop. 1) had differences from only 60.5% of the remaining populations. By contrast, in adult males, Pop. 47 differed from 78.9% of the remaining populations, and Pop. 24 also had many differences (77.2%). In adult females, Pops. 1, 23, and 24 each had differences from 77.1% of other populations.

The variation range of medians was divided into size classes, and the number of populations included was examined for each age/sex group (Fig. 21). In young, a clear peak was not found and most of the populations fell within the range of $37.1 \leqq X < 41.0$. By contrast, adults showed marked unimodal distributions. There was a clear peak at $36.1 \leqq X < 37.3$ in males and at $38.6 \leqq X > 39.5$ in females. Thus, it was impossible to divide the populations by the magnitude of ACV medians.

Populations were arbitrarily divided into three types (I: narrow head; II: moderate head; III wide head), by the magnitudes of the medians, and the geographic distribution of each type was examined (Fig. 22). In young, type II populations showed wide distribution from Tohoku to Kyushu, type I populations were limited to areas east of Kinki, and type III populations were found from Kanto westwards. In adult males, type I populations were limited to east of Chubu as in young, but the distributional range of type III was wider than in young, extending from Tohoku to Kyushu. Again in adult females, type I populations were distributed from Chubu eastwards; the range of type II extended from Tohoku to Kyushu, and type III exhibited scattered distribution from northern Kanto to Kyushu.

6) PL: Three age/sex groups were treated together in the analyses of ACV (Table 25). Of 1,789 individuals, the smallest ACV, 17.1, was found for one from Pop. 87, and the largest, 28.7, was for one from Pop. 54. The latter value was 1.68 times larger than the former.

When the medians of 83 populations were compared, Pop. 83 had the smallest value, 19.1, and Pops. 76 and 87 (median=20.1) ranked next. The largest median, 24.6, was for Pop. 46, and Pop. 54 (ACV=23.6), Pop. 52 (23.3) and Pop. 70 (23.1) followed. The largest value was 1.24 times the smallest.

Interpopulation comparisons revealed that no population could be completely separated from all other populations by ACVs. Some populations, however, were found to be distinct. Among them, Pop. 46 was most conspicuous, differing from 95.1% of the remaining populations, and Pop. 83 was also marked with differences from 86.6% of the remainings.

The range of medians (X) was divided into ten size classes, and the number of populations included in each size class was examined (Fig. 23). As seen in the figure, there was an evident unimodal distribution, and the mode was observed at the size class $20.9 \leq X < 22.1$.

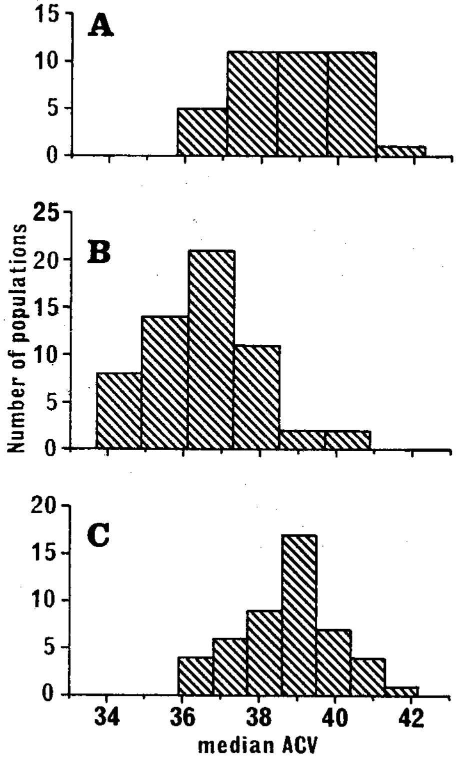

Fig. 21. Number of populations tabulated by 1.3 mm (A: young), 1.2 mm (B: adult males), and 0.9 mm (C: adult females) intervals of population ACV median of HW.

From this observation, populations were arbitrarily grouped into three types (I: short parotoid; II: medium parotoid; III: long parotoid) to examine geographic variation. Figure 24 indicates wide distribution of these three types: type I populations were found from Tohoku to Chugoku and Shikoku, and types II and III were distributed over nearly the entire range of the Japanese common toad.

7) PW: The three age/sex groups were separately analyzed (Table 26). Of 536 young, an individual from Pop. 75 had the smallest ACV (4.4), and one from Pop.

73 had the largest value (10.8); the latter value was 2.45 times larger than the former. The smallest median of 39 populations of young was 5.1 for Pop. 1, and Pop. 9 (median =5.8) and Pop. 85 (5.9) ranked next and third. Population 73 exhibited the largest median, 8.3, and Pop. 63 (7.8) and Pop. 31 (7.7) followed. The largest median was 1.63 times larger than the smallest.

Among 945 adult males, one from Pop. 43 showed the smallest ACV (5.3), and

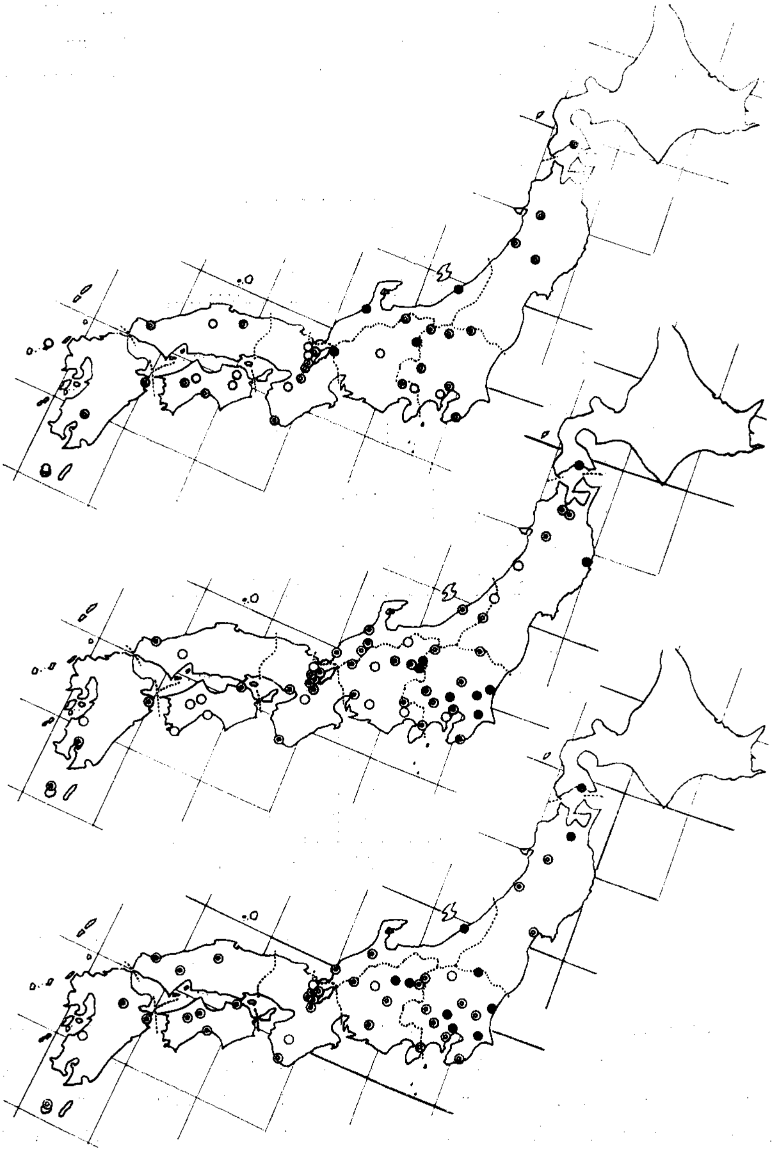

Fig. 22. Geographic distribution of type I (narrow head: closed circles), type II (medium head: double circles), and type III (wide head: open circles) populations of the Japanese common toad. Top: young; middle: adult males; bottom: adult females.

Table 25. Variation in the PL ACV of the Japanese common toad.

Population	N	ACV		Population	N	ACV	
		range	median			range	median
1	17	18.5–23.9	21.3	49	8	19.5–23.7	21.9
2	2	21.8–22.0	21.9	50	22	18.8–23.7	20.4
3	3	19.7–22.2	20.2	51	17	18.1–24.8	21.3
4	22	19.8–25.2	22.7	52	11	21.6–25.3	23.3
5	10	19.2–22.6	21.1	53	5	19.9–22.1	21.0
6	12	19.7–23.1	21.8	54	11	19.9–28.7	23.6
7	2	20.3–20.5	20.4	55	33	17.7–25.0	21.5
8	40	17.6–25.6	21.6	56	35	19.0–24.0	21.3
9	6	19.5–22.5	21.0	57	7	18.3–24.4	21.8
10	29	20.1–26.4	22.6	58	40	17.6–23.9	21.0
11	1		24.0	59	40	17.5–24.2	21.6
12	6	20.2–24.1	22.2	60	39	18.2–26.6	21.9
13	3	18.5–23.1	21.2	61	40	17.2–24.0	21.0
14	5	18.3–22.8	20.3	62	40	18.7–26.0	21.5
15	1		22.6	63	112	18.5–27.0	22.0
16	40	20.2–26.2	22.7	64	4	20.9–22.3	21.6
17	5	18.6–22.7	20.9	65	8	18.0–22.8	21.1
18	40	17.5–24.5	21.8	66	25	18.0–25.2	21.7
19	41	18.0–24.5	21.5	67	1		21.4
20	40	17.5–23.8	21.0	68	4	19.0–22.4	20.4
21	20	19.4–23.7	21.8	69	3	20.5–22.2	21.6
22	40	18.2–25.0	22.2	70	23	19.7–25.8	23.1
23	40	18.6–23.7	21.7	71	5	20.0–24.2	22.0
24	21	18.1–23.4	20.8	72	4	19.4.22.5	21.3
25	40	17.7–23.5	20.7	73	40	18.3–25.3	21.9
26	18	19.9–26.4	22.1	74	1		21.0
27	40	17.6–25.9	22.6	75	4	20.0–22.4	21.2
28	18	18.2–24.9	21.3	76	3	19.8–20.4	20.1
29	11	19.0–25.9	21.4	77	1		20.6
30	13	18.1–24.5	21.1	78	20	17.1–26.8	21.5
31	18	18.4–24.4	21.2	79	40	18.9–24.7	22.1
32	40	18.4–25.9	21.9	80	40	17.3–22.6	20.4
33	7	20.4–25.0	22.4	81	40	18.6–24.3	21.3
34	39	18.7–25.6	22.2	82	3	18.0–21.5	20.3
35	2	19.5–22.3	20.9	83	7	17.7–20.2	19.1
36	3	21.4–24.7	23.1	84	21	18.5–22.6	20.9
37	10	17.8–25.1	21.9	85	12	19.3–23.4	21.7
38	40	18.8–24.8	22.2	86	40	17.8–24.8	21.3
39	20	18.7–23.1	21.1	87	5	17.1–21.6	20.1
40	4	19.2–26.1	22.3	88	40	19.2–26.2	22.6
41	2	20.8–23.4	22.1	89	8	20.1–24.7	22.7
42	2	23.7–24.2	23.9	90	3	20.9–24.3	22.6
43	40	18.0–24.6	21.6	91	29	18.0–25.8	22.7
44	8	18.6–24.2	21.6	92	8	20.5–24.0	22.4
45	1		18.8	93	2	18.6–23.7	21.2
46	3	24.3–25.1	24.6	94	6	19.7–23.8	21.3
47	9	18.5–24.2	21.2	95	1		18.6
48	4	19.7–22.8	21.1	96	40	19.1–26.6	21.9

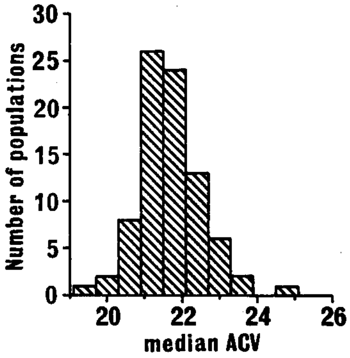

Fig. 23. Number of populations tabulated by 0.6 mm intervals of Population ACV median of PL.

another from Pop. 34 showed the largest (10.3); the latter was 1.94 times larger than the former. The smallest median among 58 adult male populations was 6.5 for Pops. 40 and 58, and Pop. 47 (ACV=6.6) had also small median. The largest median was 8.4 for Pop. 19, and Pop. 21 (8.3) and Pop. 34 (8.2) followed. The largest median was 1.30 times larger than the smallest.

The smallest ACV among 577 adult females was 5.0 exhibited by an individual from Pop. 18, and the largest was 10.5 for one in Pop. 86; the largest was 2.12 times the smallest. Among 50 populations, Pop. 43 had the smallest median (6.6), and Pops. 18, 61, and 88 (6.9) followed. The largest median (8.8) was found for Pop. 81, and Pop. 71 (median=8.6) and Pop. 12 (8.5) ranked next and third. The largest value

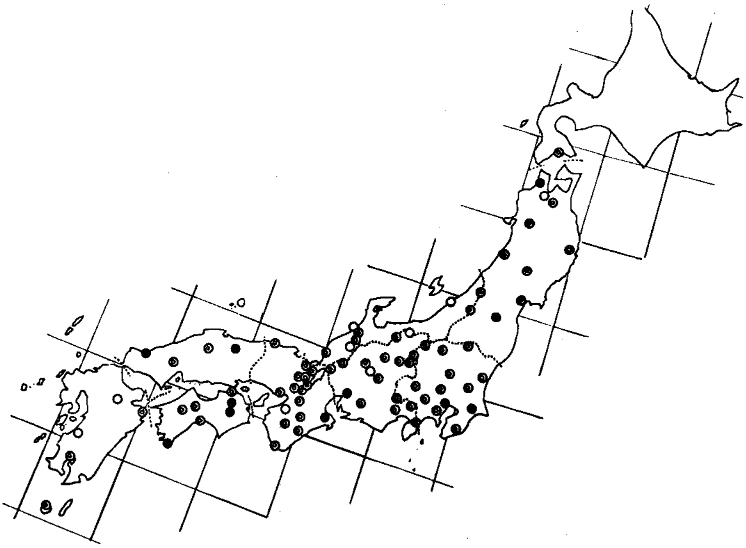

Fig. 24. Geographic distribution of type I (short parotoid: closed circles), type II (medium parotoid: double circles) and type III (long parotoid: open circles) populations of the Japanese common toad.

was 1.33 times larger than the smallest.

Age differences were found between young and adult males in five out of 27 available populations (18.5%; Pops. 1, 32, 39, 59, 88), and between young and adult females in four out of 24 available populations (16.7%, Pops. 26, 32, 58, 73). The medians of young were in most cases smaller and in only two cases larger (Pops. 73 and 88) than those of adults. Sexual dimorphism was found only in three out of 44 available populations (6.8%; Pops. 10, 19, 81), and females had larger medians than males in two of these three populations. Difference with age between young and adult males was more frequently observed in the populations from northeastern Japan.

There were some distinct populations: in young, Pop. 1 differed from 89.5% of the remaining populations, and Pop. 73 differed from 81.6% of other populations. In adult males, Pop. 40 was most distinct, differing from 77.2% of the remaining populations. Among populations of adult females, Pop. 81 differed from 83.7% of other populations.

The variation range of medians was divided into size classes, and the number of populations included was examined for each age/sex group (Fig. 25). In young,

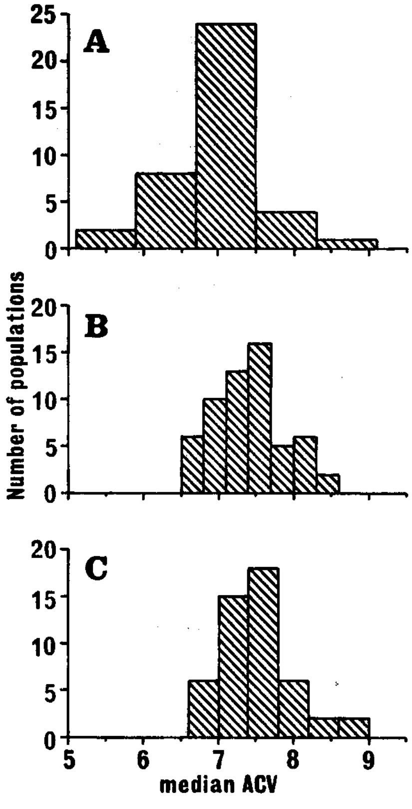

Fig. 25. Number of populations tabulated by 0.8 mm (A: young), 0.3 mm (B: adult males), and 0.4 mm (C: adult females) intervals of population ACV median of PW.

Table 26. Variation in the PW ACV of the Japanese common toad.

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
1	3	4.9– 5.4	5.1	11	5.9– 8.1	7.1	3	7.2– 7.8	7.5
2	1		5.1	1		7.1			
3	2	5.8– 6.3	6.0				1		5.8
4				20	5.9– 7.6	6.9	2	5.7– 6.7	6.2
5	1		5.6	6	6.9– 8.0	7.3	3	7.0– 8.1	7.4
6				10	6.5– 8.1	6.9	1		6.9
7				1		5.8	1		6.0
8	30	5.5– 8.3	7.0	15	5.9– 8.7	7.1	16	6.4– 8.1	7.0
9	4	5.2– 6.1	5.8	1		6.2	1		6.0
10	13	5.8– 8.0	6.9	8	6.2– 7.3	6.7	8	6.7– 7.8	7.3
11	1		6.7						
12	1		6.9	1		6.2	4	7.8– 9.3	8.5
13				3	5.6– 7.5	6.8			
14	2	5.0– 7.5	6.2	1		5.9	2	6.2– 6.5	6.4
15							1		6.2
16	30	6.0– 8.5	7.3	30	5.5– 9.3	7.3	13	5.7– 8.2	6.9
17				5	6.3– 8.5	7.0			
18	11	6.2– 7.9	7.1	30	5.9– 8.1	7.1	24	5.0– 8.3	6.9
19				25	6.9–10.1	8.4	16	6.8– 8.7	7.8
20				20	7.5– 9.9	8.1	20	6.4– 9.9	7.8
21	1		5.0	10	6.6– 9.8	8.3	9	6.8– 8.2	7.7
22	10	5.8– 8.6	7.3	30	6.4– 8.7	7.5	18	5.9– 8.7	7.2
23	2	6.6– 7.2	6.9	22	6.1– 9.0	7.5	21	6.5– 8.9	7.7
24				15	6.1– 8.9	7.8	6	6.5– 8.0	7.4
25	8	6.5– 7.7	7.1	30	6.4– 9.3	7.7	12	6.2– 9.2	7.5
26	8	5.6– 8.5	6.8	6	6.6– 8.2	7.5	4	7.8– 8.4	8.1
27	2	5.4– 6.4	5.9	30	6.2– 8.9	7.8	17	5.8– 8.6	7.5
28	14	5.5– 8.6	7.0	1		7.5	3	7.2– 7.3	7.3
29	6	5.2– 7.8	6.5	3	6.3– 8.4	7.4	2	6.2– 8.5	7.3
30	1		6.0	7	6.0– 8.4	7.5	6	6.9– 8.7	7.8
31	3	6.5– 9.8	7.7	12	6.4– 9.0	7.6	3	6.5– 7.9	7.3
32	6	5.3– 7.2	6.2	30	6.1– 8.4	7.2	30	6.3– 8.5	7.3
33	4	7.3– 8.5	7.7	2	6.9– 8.3	7.6	1		7.9
34				29	6.6–10.3	8.2	10	7.3–10.2	8.0
35	1		8.2	1		6.5			
36	2	6.8– 7.5	7.1	1		6.7			
37	5	6.2– 7.5	6.8	5	5.5– 8.3	7.2			
38	2	6.4– 6.7	6.5	30	6.2– 8.5	7.4	25	6.0– 9.0	7.4
39	6	5.2– 7.5	6.2	14	6.3– 8.1	7.4			
40				3	5.6– 7.6	6.5	1		7.2
41				2	7.3– 8.0	7.6			
42				1		7.2	1		6.1
43				30	5.3– 8.2	6.6	6	5.6– 7.2	6.6
44	1		6.1	1		5.7	6	6.7– 9.4	7.7
45				1		6.1			
46	3	6.9– 7.4	7.4						
47	1		6.5	3	5.5– 7.1	6.5	5	6.3– 7.5	7.1
48	1		6.4	2	7.2– 7.3	7.2	1		6.0

(cont'd.)

(Table 26. cont'd.)

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
49				3	6.0– 8.1	6.9	5	6.4– 7.7	7.0
50				19	6.6– 8.0	7.1	4	6.7– 8.1	7.6
51	2	5.8– 7.5	6.6	12	5.8– 8.0	6.9	3	7.0– 8.4	7.5
52	3	6.1– 7.8	7.0	6	6.7– 8.6	7.6	2	7.8– 8.0	7.9
53	2	6.9– 7.0	7.0	3	6.3– 7.7	7.2			
54				10	6.3– 8.9	7.7	1		8.3
55	2	6.6– 7.4	7.0	25	5.5– 9.3	7.4	6	7.2– 9.4	8.1
56	1		8.7	21	5.9– 8.1	7.0	13	6.3– 8.2	7.0
57	5	5.0– 7.3	6.7				2	6.4– 7.1	6.8
58	23	5.3– 7.5	6.5	7	4.7– 7.6	6.5	12	6.2– 9.1	7.4
59	10	4.8– 7.7	6.6	30	6.1– 8.5	7.3	12	5.9– 8.1	6.9
60	4	6.4– 7.2	7.0	26	5.8– 9.0	7.4	9	6.3– 8.1	7.5
61	1		5.8	28	6.0– 8.4	6.9	11	5.8– 7.9	6.9
62	30	4.5– 8.9	6.9	11	6.1– 8.8	7.5	4	6.6– 8.9	7.6
63	30	6.0– 9.2	7.8	30	6.1– 8.8	7.4	30	6.6– 9.0	7.6
64	2	5.8– 7.6	6.7	1		7.6	1		6.8
65	2	6.9– 8.1	7.5	5	7.7– 8.4	8.0	1		8.7
66	22	5.9– 8.3	7.0	3	6.9– 7.9	7.3			
67	1		9.6						
68	2	4.9– 6.9	5.9				2	7.7– 8.1	7.9
69	1		7.0	1		8.4	1		7.4
70	23	5.1– 8.0	6.9						
71	1		7.2	1		7.9	3	8.0– 9.1	8.6
72				2	7.9– 8.5	8.2	2	9.3– 9.9	9.6
73	30	6.1–10.8	8.3	13	5.4– 8.9	7.5	11	6.6– 8.6	7.3
74							1		9.4
75	2	4.4– 6.1	5.3				2	7.5– 7.9	7.7
76	3	4.7– 8.3	6.8						
77							1		7.0
78	10	5.8– 8.7	7.3	1		8.3	9	6.8– 8.3	7.7
79				27	5.7– 9.2	7.6	15	6.0– 8.3	7.1
80	30	5.5– 9.2	7.2	22	6.3– 8.1	7.1	10	6.5– 7.8	7.2
81	2	7.7– 8.6	8.2	30	6.6– 9.1	8.0	23	6.6–10.1	8.8
82	3	6.4– 7.6	7.0						
83	4	6.1– 7.8	7.2	1		7.4	2	7.1– 8.1	7.6
84	11	6.4– 8.3	7.3	3	6.1– 8.3	7.4	7	5.9– 8.4	7.2
85	3	4.9– 6.6	5.9	6	6.1– 7.6	6.8	3	7.0– 7.9	7.5
86	9	4.6–10.2	6.8	27	6.4– 9.6	7.7	14	6.4–10.5	7.8
87				3	7.8– 8.2	8.0	3	6.1– 8.0	6.8
88	30	5.1– 9.1	7.5	30	5.7– 7.5	6.7	8	5.9– 8.2	6.9
89	2	6.4– 6.5	6.4	2	5.9– 6.0	6.0	4	6.2– 8.0	7.3
90	3	5.6– 7.4	6.9						
91				7	7.3– 9.0	7.7	22	6.0– 8.5	7.4
92	6	5.6– 7.1	6.1				1		9.2
93				1		7.4	1		6.0
94	1		9.4	4	7.3– 8.8	8.2	1		8.1
95							1		8.9
96	14	5.1– 8.4	7.1	15	6.1– 8.1	7.0	11	5.6– 8.4	7.2

marked unimodal distribution was observed and a large number of populations was concentrated in the size class $6.7 \leqq X < 7.5$. By contrast, in adult males, one moderate peak and another faint peak were found in the size classes $7.4 \leqq X < 7.7$ and $8.0 \leqq X < 8.3$, respectively. Adult females exhibited unimodal distribution with a peak in the size class $7.4 \leqq X < 7.8$.

These results made it difficult to recognize particular groups and populations were arbitrarily divided into two types (I: narrow parotoid; III: wide parotoid) for young and adult males, and a third type, type II (medium parotoid), was added to the adult female populations. The geographic distribution of these two or three types was examined (Fig. 26). In young, type I populations were found over a wide range from Hokkaido to Kyushu, and type III also showed a wide distribution from Hokuriku westwards. In adult males, the distribution range of type I populations was wide as in young, but that of type III populations was limited to the southern part of Honshu, Shikoku, and Kyushu. In adult females, populations of types I and II were distributed over almost the whole range, whereas type III populations were found scattered among the other two types from Tohoku to Shikoku.

8) LAL: Three age/sex groups were combined for ACV variation analyses (Table 27). Among 1,888 individuals, the smallest ACV, 41.5, was possessed by one from Pop. 34, and the largest value, 57.9, by one from Pop. 13. The largest value was 1.40 times larger than the smallest. The smallest median for 83 populations was 45.6 for Pop. 20, and Pop. 24 (median=46.0), Pop. 50, and Pop. 65 (46.1) followed. The largest median, 52.9, was found for Pop. 85, and Pop. 90 (52.7) and Pop. 46 (52.5) ranked next and third. The largest value was 1.16 times larger than the smallest.

Interpopulation comparisons in medians revealed that each population could not be separated from at least several other populations. Population 20 was most conspicuous, having differences from 92.7% of all other populations. Pop. 50 differed from 86.6% and Pop. 24 from 84.1% of the remaining populations.

The variation range of medians for 83 populations was divided into ten size classes, and the number of populations included was examined (Fig. 27). The figure showed a distribution with three peaks; one strong peak in the size class $48.8 \leqq X < 49.6$ and another in $50.4 \leqq X < 51.2$, plus an weak peak in $45.6 \leqq X < 46.4$.

From this observation, three types (I: short arm; II: medium arm; III: long arm) were discriminated, and the geographic distribution of each type was examined (Fig. 28). As seen in Fig. 28, type II populations were found everywhere except Kyushu, and type III also had a wide distributional range from southern Tohoku to Kyushu. Type I populations, however, were more confined, with scattered distribution from Kanto to Kinki.

9) TL: The three age/sex groups were separately analyzed for ACV (Table 28). Of 759 young, the smallest ACV, 30.3, was exhibited by an individual from Pop. 80, and the largest, 42.8, by one from Pop. 32; the largest value was 1.41 times of the smallest. The smallest median of 39 populations was 34.0 for Pop. 66, and Pop. 29 (ACV=34.2) and Pop. 9 (34.4) ranked next and third. The largest median was 38.0 for Pop. 85, and Pop. 46 (ACV=37.7), Pop. 92 and Pop. 88 (37.5) were second, third,

and fourth. The largest value was 1.12 times larger than the smallest.

Of 1,175 adult males, the smallest ACV, 30.2, was possessed by an individual from Pop. 80, and the largest, 42.6, by one from Pop. 84. The latter value was 1.41 times the former. The smallest median of 58 adult male populations was 34.7 for Pop. 65, and the values 35.1 (Pop. 24) and 35.3 (Pop. 50) ranked next and third. The largest

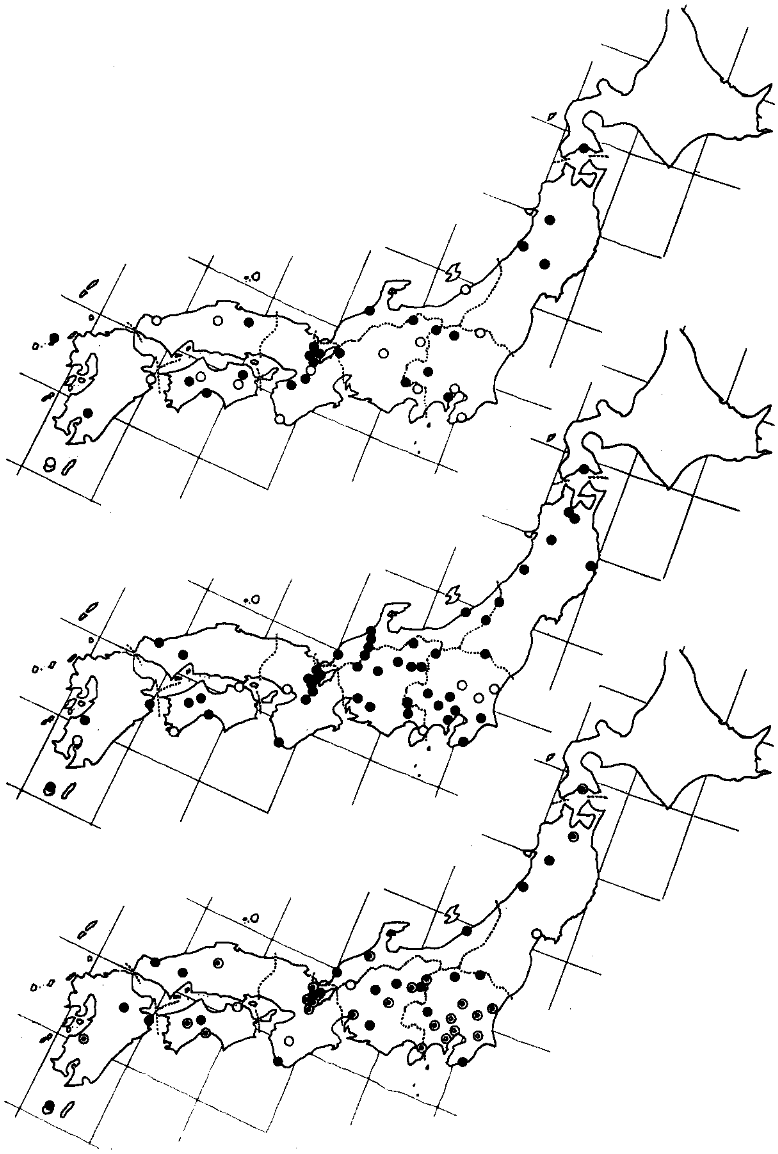

Fig. 26. Geographic distribution of type I (narrow parotoid: closed circles), type II (medium parotoid: double circles) and type III (wide parotoid: open circles) populations of the Japanese common toad. Top: young; middle: adult males; bottom: adult females.

Table 27. Variation in the LAL ACV of the Japanese common toad.

Population	N	ACV		Population	N	ACV	
		range	median			range	median
1	17	45.2–51.0	48.4	49	8	47.4–54.2	51.1
2	2	43.4–51.3	47.4	50	21	43.5–49.0	46.1
3	3	47.1–51.5	49.5	51	17	44.4–53.9	48.0
4	22	45.1–50.9	48.1	52	10	47.7–51.6	49.0
5	10	44.3–52.3	48.8	53	5	47.8–53.4	50.0
6	12	44.4–50.8	47.4	54	11	46.1–51.6	49.0
7	2	47.1–47.2	47.2	55	34	46.0–56.3	50.4
8	50	43.8–55.5	48.9	56	36	44.2–51.3	48.6
9	6	46.7–52.0	49.0	57	7	45.2–50.8	48.8
10	29	45.9–54.1	49.4	58	41	46.7–55.8	51.5
11	1		47.9	59	50	43.1–51.3	47.5
12	6	48.2–51.8	49.4	60	39	43.3–51.8	49.0
13	3	45.8–57.9	51.2	61	40	44.8–51.5	48.5
14	5	44.8–50.2	48.0	62	59	46.2–54.6	50.5
15	1		49.0	63	50	46.6–55.5	50.6
16	50	44.0–53.0	48.3	64	4	49.1–53.4	50.8
17	5	47.0–54.2	50.1	65	8	44.4–50.1	46.1
18	50	44.3–54.1	49.3	66	25	47.7–53.8	50.8
19	41	43.2–50.9	47.4	67	1		50.6
20	39	42.5–49.0	45.6	68	4	47.0–52.6	49.5
21	20	44.3–50.5	47.2	69	3	45.3–52.7	49.2
22	50	45.2–54.7	49.8	70	23	47.4–53.8	51.3
23	45	43.5–51.3	47.1	71	5	46.4–54.3	49.6
24	20	42.5–51.0	46.0	72	4	48.7–50.1	49.5
25	50	44.3–54.1	48.8	73	50	43.3–57.3	49.4
26	18	45.8–52.7	49.1	74	1		49.2
27	50	45.3–55.4	50.2	75	4	46.7–50.9	49.8
28	18	45.7–52.0	49.1	76	3	51.0–51.7	51.3
29	11	45.7–52.7	48.3	77	1		53.2
30	18	44.1–54.4	47.6	78	20	47.4–54.0	50.8
31	18	43.8–53.2	48.6	79	42	46.1–53.6	49.5
32	50	44.4–56.7	51.1	80	50	45.1–51.7	48.4
33	7	48.3–56.8	51.1	81	50	44.2–54.7	48.1
34	39	41.5–52.7	47.9	82	3	50.4–53.4	52.1
35	2	48.4–56.1	52.3	83	7	47.3–57.0	51.6
36	3	48.5–51.4	49.6	84	21	48.4–56.6	52.9
37	10	47.4–56.0	50.6	85	12	48.2–57.4	52.5
38	50	44.5–53.6	49.6	86	50	47.1–55.4	51.2
39	20	46.3–53.7	51.6	87	5	46.1–52.1	49.5
40	4	47.6–54.8	52.5	88	50	47.6–55.6	51.3
41	2	48.7–49.0	48.8	89	8	47.9–55.3	52.3
42	2	49.5–49.6	49.6	90	3	51.1–54.9	52.7
43	45	43.9–53.7	49.3	91	24	47.5–55.3	51.9
44	8	46.6–52.4	50.5	92	8	50.7–54.0	52.2
45	1		49.2	93	2	46.8–50.5	48.7
46	3	46.8–57.8	52.5	94	6	48.9–52.2	50.5
47	9	45.8–54.5	50.5	95			
48	4	48.2–51.0	49.4	96	41	47.9–56.2	52.2

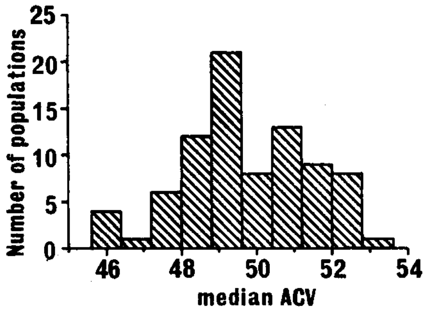

Fig. 27. Number of populations tabulated by 0.8 mm intervals of population ACV median of LAL.

median was 39.0 for Pop. 84 and Pop. 85, and Pop. 66 (38.9) followed. The largest value was 1.12 times larger than the smallest.

Of 581 adult females, the smallest ACV, 30.0, was exhibited by an individual from Pop. 60, and the largest, 40.2, by one from Pop. 83; the latter was 1.34 times the former. Among 50 populations of adult females, the smallest median, 33.0, was shown by Pop. 5, and Pop. 23 (median=33.2) and Pop. 24 (33.5) also showed small medians. The largest value was found for Pop. 84 (median=36.9), and Pop. 96 (36.6) and Pop. 1 (36.5) ranked next and third. The largest value was 1.12 times larger than the smallest. Thus, among a total of 2,515 individuals, the smallest ACV was 1.42 times smaller than the largest.

Differences with age were found between young and adult males in 11 out of 27

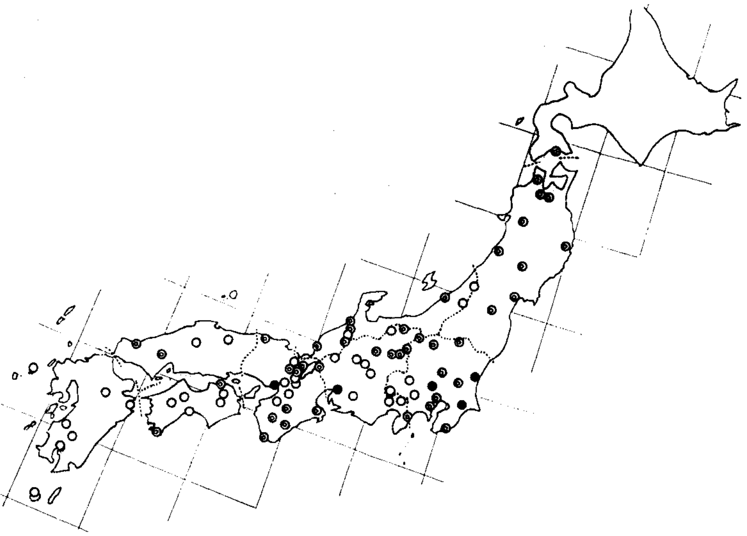

Fig. 28. Geographic distribution of type I (short arm: closed circles), type II (medium arm: double circles) and type III (long arm: open circles) populations of the Japanese common toad.

Table 28. Variation in the TL ACV of the Japanese common toad.

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
1	3	32.8–37.5	36.3	11	36.0–39.8	37.9	3	34.6–38.1	36.5
2	1		32.9	1		38.3			
3		32.7–35.8	34.3				1		35.4
4				20	35.2–39.9	37.9	2	34.7–34.8	34.7
5	1		35.3	6	37.0–39.8	38.3	3	31.2–34.5	32.9
6	1		34.2	10	33.8–37.4	35.6	1		35.6
7				1		33.0	1		33.4
8	31	32.1–38.5	35.7	15	32.0–39.0	36.3	16	32.7–38.7	35.4
9	4	33.8–35.5	34.4	1		36.6	1		34.9
10	13	34.1–37.1	35.6	8	35.5–41.4	37.6	8	31.4–36.7	34.2
11	1		35.5						
12	1		35.9	1		38.1	4	34.3–36.1	35.3
13				3	35.5–39.3	37.0			
14	2	32.4–34.5	33.4	1		37.1	2	33.7–36.8	35.2
15							1		35.0
16	65	31.3–39.2	35.5	63	34.0–39.9	37.1	13	33.0–37.9	35.3
17				5	36.7–41.6	38.6			
18	12	33.4–37.7	35.9	34	34.2–40.2	37.2	24	31.5–36.9	34.9
19				25	33.5–39.1	36.5	16	32.0–37.6	34.8
20				20	32.3–37.8	35.6	20	31.4–34.7	33.6
21	1		33.7	10	34.4–36.9	36.0	9	33.5–36.7	34.9
22	11	34.8–39.2	35.9	67	33.6–40.1	36.6	17	33.6–38.5	35.8
23	2	36.8–36.8	36.8	22	34.2–38.2	35.8	21	31.0–36.5	33.2
24				15	32.7–37.0	35.1	6	32.7–34.5	33.5
25	8	33.5–37.8	35.7	39	33.6–40.3	36.7	12	31.0–36.1	34.2
26	8	33.1–37.9	36.0	6	35.3–38.2	36.9	4	32.8–35.0	34.0
27	2	33.9–36.7	35.3	41	34.2–40.7	37.6	16	32.1–37.7	35.5
28	14	32.5–38.0	34.9	1		36.3	3	32.3–36.3	34.8
29	6	30.0–38.3	34.2	3	35.7–38.4	37.0	2	33.3–36.5	34.9
30	1		33.8	10	34.6–39.0	36.7	7	32.2–36.7	34.3
31	3	34.3–37.0	35.9	12	35.7–39.0	37.0	3	32.8–37.8	35.6
32	6	34.4–42.8	36.6	51	34.3–41.7	37.6	30	33.2–38.3	35.4
33	4	34.3–37.0	35.7	2	36.3–41.3	38.8	1		33.2
34				29	32.6–39.0	35.6	10	31.9–35.6	33.9
35	1		38.1	1		35.8			
36	2	33.9–36.7	35.3	1		38.0			
37	5	34.2–38.3	35.9	5	35.2–38.9	37.2			
38	2	36.4–37.7	37.1	70	33.9–40.9	36.9	25	31.7–38.0	34.7
39	6	32.7–38.7	36.0	14	36.8–40.0	38.4			
40				3	35.2–40.3	37.3	1		39.2
41				2	35.8–36.4	36.1			
42				1		38.3	1		35.3
43				39	33.0–39.5	36.5	6	32.7–37.4	35.4
44	1		37.0	1		34.9	6	33.5–38.2	35.4
45				1		36.0			
46	3	33.9–40.2	37.7						
47	1		37.0	3	36.1–39.4	37.2	5	32.6–36.4	35.0
48	1		32.5	2	36.3–37.7	37.0	1		33.6

(cont'd.)

(Table 28. cont'd.)

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
49				3	36.3–39.1	37.7	5	33.6–37.0	35.3
50				18	32.8–37.0	35.3	4	33.4–36.8	35.2
51	2	36.0–36.3	36.2	12	32.7–39.5	36.3	3	33.8–35.1	34.6
52	3	34.8–35.6	35.2	6	35.4–40.1	37.6	2	35.1–35.3	35.2
53	2	38.7–41.9	40.3	3	34.8–37.4	35.7			
54				10	35.6–39.9	37.8	1		36.6
55	2	33.9–37.5	35.7	25	34.2–41.1	37.5	7	34.9–38.3	36.4
56	1		32.7	21	34.4–38.2	36.4	14	33.5–37.6	35.7
57	5	31.3–36.8	35.2				2	34.5–35.2	34.9
58	23	31.8–38.9	36.0	7	35.6–38.8	36.7	12	32.6–37.9	35.3
59	10	32.9–37.3	34.7	57	33.1–39.0	36.6	12	30.8–37.1	34.6
60	4	34.7–36.6	35.8	26	33.8–39.4	37.1	9	30.0–38.4	35.5
61	1		34.6	28	33.8–39.3	36.7	11	33.1–36.7	35.0
62	44	32.0–39.4	34.7	10	36.1–39.9	37.6	4	34.6–37.2	35.8
63	67	31.5–41.5	36.7	45	34.3–42.2	38.3	34	34.1–38.9	36.2
64	2	34.4–37.9	36.1	1		36.8	1		35.2
65	2	34.7–35.8	35.2	5	33.3–35.8	34.7	1		33.4
66	23	31.2–37.0	34.0	3	37.1–41.8	38.9			
67	2	35.2–35.2	35.2						
68	2	33.6–35.4	34.5				2	31.2–33.8	32.5
69	1		36.1	1		37.2	1		30.4
70	23	33.8–38.3	35.7						
71	2	33.8–35.2	34.5	1		34.7	3	33.1–36.1	35.0
72				2	34.9–36.9	35.9	2	33.6–35.2	34.4
73	95	32.5–38.1	34.8	13	33.6–37.3	35.5	11	32.3–39.0	34.4
74							1		33.8
75	2	34.0–35.2	34.6				2	35.8–38.1	37.0
76	3	34.2–39.0	36.7						
77							1		36.4
78	10	33.3–37.3	35.7	1		36.3	9	32.1–38.1	35.5
79				27	35.4–39.3	37.2	15	33.3–37.0	35.2
80	91	30.3–39.1	34.7	22	30.2–39.7	36.3	10	33.4–37.7	34.7
81	2	34.2–39.2	36.7	51	32.5–39.5	35.8	23	32.1–37.4	34.7
82	3	34.7–37.2	35.9						
83	4	36.1–37.6	36.6	1		38.3	2	36.6–40.2	38.4
84	11	34.1–42.4	36.8	3	36.2–42.6	39.0	7	34.7–38.2	36.9
85	3	37.5–38.4	38.0	6	36.9–40.5	38.9	3	33.7–37.4	35.7
86	9	34.7–39.1	36.9	27	34.7–40.4	37.8	14	33.9–37.6	36.0
87				3	37.5–39.2	38.4	3	33.9–36.0	35.2
88	56	34.2–39.6	37.5	31	34.3–40.9	38.8	8	34.8–37.8	36.3
89	2	36.1–37.9	37.0	2	38.6–39.4	39.0	4	33.5–36.8	35.8
90	3	33.5–36.9	35.4						
91				7	36.9–39.8	38.5	22	33.6–37.1	35.6
92	7	35.6–40.0	37.5				1		37.2
93				1		34.8	1		34.7
94	1		37.5	4	36.3–37.3	36.7	1		33.3
95									
96	11	35.7–37.2	36.3	16	36.1–38.9	37.7	11	35.0–37.5	36.5

available populations (40.7%; Pops. 10, 16, 18, 52, 59, 62, 63, 66, 80, 88, 96), and adult males had invariably larger medians than young. By contrast, only one out of 24 populations (Pop. 88) showed significant age difference with age between young and adult females. Sexual dimorphism was found in 24 out of 44 available populations (54.5%), and males had larger ACV than females in all these populations. The occurrence of intrapopulation variation in the median was found more frequently in the populations from southwestern Japan.

There were some interpopulation differences in each age/sex group. In young, Pop. 85 was most distinct, with differences from 71.1% of the other populations. In adult males, Pop. 24 differed from 68.4% of the other populations. Populations of adult females had less variable medians: the most marked Pop. 84 differed from only 44.9% of the other populations.

The variation range of ACV medians was divided into size classes, and the number of populations included was examined for each age/sex group (Fig. 29). In young, a unimodal distribution was found and the peak was in the size class 35.0≦X<36.0. Adult males exhibited a less distinct mode, and larger number of populations were found in the three size classes between 36.1 and 38.2. In adult females, the histogram showed a marked unimodal distribution, and the peak was in the size class 35.1≦X<35.8.

From these results it was difficult to divide the populations according to their

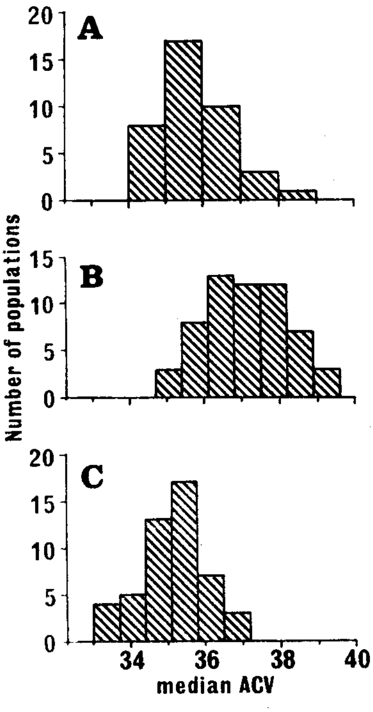

Fig. 29. Number of populations tabulated by 1.0 mm (A: young), males), 0.7 mm (B: adult and 0.7 mm (C: adult females) intervals of population ACV median of TL.

medians, and three types were arbitrarily set (I: short tibia; II: moderate tibia; III: long tibia) to examine geographic variation (Fig. 30). In young, type II populations were distributed over almost the whole range. Type I populations were found in several localities in Honshu, and type III populations showed scattered distribution in Kyushu and Chubu. In adult males, type II populations showed a wide distribution and type III populations also ranged widely from Tohoku to Kyushu. Type I popu-

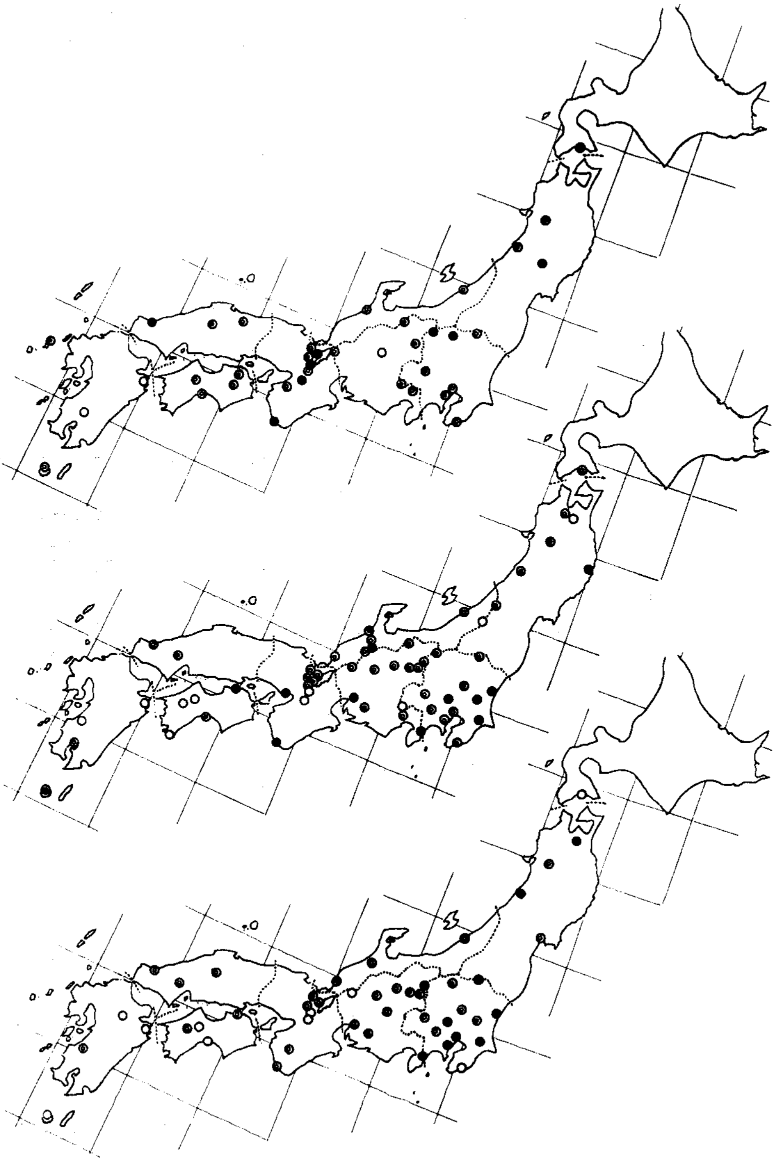

Fig. 30. Geographic distribution of type I (short tibia: closed circles), type II (medium tibia: double circles), and type III (long tibia: open circles) populations of the Japanese common toad. Top: young; middle: adult males; bottom: adult females.

Table 29. Variation in the FL ACV of the Japanese common toad.

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
1	3	39.4–42.1	41.1	11	42.0–48.4	46.6	3	39.2–41.6	41.2
2	1		39.3	1		46.7			
3	2	43.5–44.8	44.2				1		43.0
4				20	42.9–50.3	47.0	2	40.3–40.3	40.3
5	1		42.4	6	45.1–48.7	47.2	3	34.7–42.4	39.1
6	1		42.0	10	42.7–48.3	45.2	1		40.9
7				1		41.9	1		42.7
8	32	40.7–49.1	44.3	15	39.4–52.1	47.1	16	38.3–47.9	42.5
9	4	41.0–46.4	43.2	1		47.8	1		39.6
10	13	42.9–50.0	46.3	8	45.0–53.5	50.1	8	42.7–47.7	44.6
11	1		40.0						
12	1		45.7	1		44.4	4	37.4–41.0	38.5
13				3	42.7–45.8	44.1			
14	2	40.2–40.8	40.5	1		49.3	2	42.7–44.0	43.3
15							1		40.6
16	64	33.3–46.2	40.8	63	36.7–47.8	44.0	13	35.6–42.7	39.2
17				5	44.3–52.5	47.4			
18	11	40.5–53.1	44.8	34	43.2–51.6	47.0	24	38.0–44.5	41.5
19				25	39.7–50.6	42.8	16	34.3–42.4	37.4
20				20	38.2–45.0	40.8	20	34.7–39.0	36.5
21	1		40.6	9	39.5–46.8	42.0	9	34.8–41.3	37.7
22	11	39.5–45.0	42.1	66	38.3–48.7	43.8	17	36.5–42.5	40.1
23	2	40.9–45.2	43.0	22	40.9–49.0	44.9	21	34.5–40.3	37.5
24				15	37.3–43.5	40.6	6	33.1–38.1	35.9
25	8	37.7–47.6	41.3	38	41.6–51.5	44.9	12	37.5–43.4	39.3
26	8	39.0–44.9	42.6	6	40.9–46.7	44.0	4	38.4–40.3	39.2
27	2	41.2–43.0	42.1	41	40.5–53.1	46.2	16	39.0–44.5	40.5
28	14	38.1–46.3	42.2	1		44.4	3	36.9–42.3	40.3
29	6	40.0–43.5	41.7	3	44.0–46.9	45.0	2	38.7–43.7	41.2
30	1		45.2	9	39.9–48.2	43.8	7	37.0–42.1	39.5
31	3	39.0–45.7	42.6	12	40.4–47.0	43.4	3	38.4–40.5	39.7
32	6	39.7–50.5	42.4	51	42.3–50.9	47.2	30	38.7–45.6	41.7
33	4	40.9–43.1	42.2	2	45.3–53.3	49.3	1		42.1
34				29	37.1–48.0	42.8	10	32.7–41.8	38.4
35	1		44.9	1		43.7			
36	2	39.9–42.4	41.1	1		47.1			
37	5	40.9–44.9	42.4	5	42.4–47.3	44.8			
38	2	44.2–44.9	44.6	70	39.0–51.1	45.3	25	36.5–43.4	39.7
39	6	38.6–47.4	42.9	14	44.7–51.5	47.5			
40				3	42.0–48.6	45.7	1		44.2
41				2	43.9–50.2	47.1			
42				1		48.5	1		42.1
43				39	39.9–51.2	46.2	6	39.3–45.5	42.5
44	1		50.6	1		46.4	6	38.0–42.6	40.5
45				1		47.8			
46	3	38.2–49.6	45.1						
47	1		42.5	3	43.6–49.1	46.2	5	37.0–40.4	39.1
48	1		40.8	2	42.2–46.3	44.3	1		36.7

(cont'd.)

(Table 29. cont'd.)

Population	young			adult males			adult females		
	N	ACV		N	ACV		N	ACV	
		range	median		range	median		range	median
49				3	40.6–46.8	44.1	5	38.5–42.7	41.4
50				20	36.0–45.8	39.8	5	36.1–39.7	37.5
51	2	41.7–43.8	42.7	12	40.1–48.0	44.0	3	36.8–40.3	38.8
52	3	37.1–40.3	38.4	6	40.4–47.2	43.9	1		38.8
53	2	44.2–48.0	46.1	3	45.5–48.5	47.4			
54				10	42.3–48.2	45.2	1		35.6
55	2	41.1–44.3	42.7	25	37.5–48.6	44.3	7	38.3–41.4	40.4
56	1		38.6	21	38.0–46.6	42.2	14	36.4–40.3	38.9
57	5	37.0–42.6	40.1				2	39.3–39.4	39.4
58	23	38.1–45.5	42.9	7	41.2–46.0	43.8	12	37.5–44.7	41.6
59	10	38.0–44.7	41.8	58	37.7–48.2	43.3	10	35.6–40.4	38.1
60	4	42.8–44.7	43.6	26	37.3–47.3	43.4	9	34.2–40.6	37.9
61	1		40.7	28	40.4–48.7	43.2	11	35.8–39.3	37.8
62	47	37.6–45.9	41.3	10	44.0–47.2	45.4	4	40.9–46.4	43.2
63	65	35.7–47.8	42.1	44	42.5–50.6	45.9	34	37.1–44.6	40.3
64	2	40.1–46.5	43.3	1		45.1	1		39.9
65	2	36.9–41.5	39.2	5	41.1–46.4	43.4	1		35.7
66	22	38.5–45.3	41.3	3	43.5–46.8	44.9			
67	1		40.9						
68	2	37.5–43.9	40.7				2	36.0–38.3	37.1
69	1		39.9	1		45.4	1		33.7
70	23	38.2–45.2	42.1						
71	1		41.2	1		45.3	3	39.0–41.2	39.8
72				2	42.2–43.8	43.0	2	39.9–42.2	41.0
73	95	38.4–47.0	42.1	13	38.5–49.5	43.8	11	35.0–46.8	40.6
74							1		38.9
75	2	39.6–42.6	41.1				2	40.7–44.0	42.3
76	3	41.8–44.9	42.9						
77							1		43.1
78	10	40.6–44.4	42.3	1		45.6	9	38.1–44.2	40.3
79				27	41.6–48.7	45.3	15	37.0–42.5	39.9
80	91	37.8–49.6	42.7	22	43.3–49.5	46.3	10	38.6–42.8	40.4
81	2	39.5–46.2	42.9	50	35.0–46.0	41.5	23	34.3–41.7	37.7
82	3	40.4–44.9	42.7						
83	4	43.5–45.5	44.4	1		46.9	2	43.3–48.0	45.6
84	11	41.9–50.5	44.4	3	43.9–49.1	46.2	7	39.4–43.7	41.4
85	3	42.9–46.6	44.4	6	42.8–51.9	47.1	3	37.1–41.5	39.3
86	9	40.2–47.6	42.9	27	42.2–48.2	45.4	14	37.1–43.7	40.7
87				3	43.5–44.2	43.9	3	35.0–39.7	37.4
88	56	40.8–50.9	45.3	31	44.2–53.9	49.7	8	40.5–44.8	41.7
89	2	42.8–44.2	43.5	2	48.7–49.2	48.9	4	36.9–42.1	39.4
90	3	38.9–43.2	40.5						
91				7	45.8–50.2	47.3	22	35.9–44.9	39.8
92	7	42.0–45.2	44.1				1		38.9
93				1		43.4	1		38.3
94	1		44.3	4	41.4–44.4	43.4	1		38.1
95									
96	11	39.6–43.8	42.0	16	45.8–52.6	48.1	11	39.2–46.3	42.6

lations occurred from Tohoku to a part of Shikoku. In adult females, type II populations showed a wide distribution as in young and adult males, but type I populations were limited from Kanto and Chubu northwards. Type III populations were found scattered in the regions from Chubu westwards, in a part of Kanto, and in Hokkaido.

10) FL: The three age/sex groups were separately analyzed for ACV variation (Table 29). Of 756 young, the smallest ACV, 33.3, was found for an individual from Pop. 16, and the largest, 53.1, was for one from Pop. 18. The largest value was 1.59 times larger than the smallest. The smallest median of 39 populations of young toads was 38.4 for Pop. 52, and Pop. 57 (median=40.1) and Pop. 90 (40.5) were populations with small medians. The largest value was 46.3 for Pop. 10, and Pop. 88 (45.3) and Pop. 46 (45.1) also had large medians. The largest median was 1.20 times larger than the smallest.

Among 1,172 adult males, the smallest ACV, 35.0, was exhibited by an individual from Pop. 81, and the largest, 53.9, by one from Pop. 88; the latter value was 1.54 times the former. The smallest median of 58 populations of adult males was 39.8 for Pop. 50, and the values 40.6 for Pop. 24 and 40.8 for Pop. 20 ranked next and third. The largest median was 50.1 for Pop. 10, and Pop. 88 (median=49.7) and Pop. 96 (48.1) followed. The largest value was 1.26 times the smallest.

Of 579 adult females, the smallest ACV was exhibited by an individual from Pop. 34 and was 32.7. The largest ACV, 47.9, was found for one from Pop. 8, and the value was 1.47 times larger than the smallest. The smallest median for 50 populations of adult females was 35.9 for Pop. 24, and Pop. 20 (median=36.5), Pop. 19 (37.4) and Pop. 87 (37.5) had also small medians. The largest median was 44.6 for Pop. 10, and Pop. 62 (median=43.2) and Pop. 96 (42.6) ranked next and third. The largest value was 1.24 times the smallest. Thus, among the total of 2,507 individuals, the largest ACV was 1.65 times larger than the smallest.

Differences with age between young and adult males were found in 18 out of 27 available populations (66.7%), and in all these populations, adult males had larger medians than young. In the comparisons of young and adult females, nine out of 24 available populations (37.5%) showed significant differences, and adult females had a larger median than young in every population.

Sexual dimorphism in adults was found in all but two (Pops. 62 and 73) populations, accounting for 95.5% of the total number of 44 populations. In every population, males had a larger median ACV than females. No clear relation was observed between geographic distribution and occurrence of variations.

In young, Pop. 52 was most marked, with differences from 73.7% of the remaining populations. More conspicuous differences were observed in adult males: Pop. 50 differed from 93.0% of the other populations, and Pop. 24 from 91.2% of the remaining populations. In adult females, Pop. 10 had the largest number of differences and 87.8% of the remaining populations differed from it.

For each age/sex group, variation range of medians was divided into size classes, and distribution of the populations in these size classes was examined (Fig. 31). In all the three age/sex groups, histograms showed marked unimodal distribution. In young, there was a peak in the siee class 40.4≦X<42.4, and adult males also showed a peak at 43.2≦X<46.6. Adult female populations exhibited an even more marked peak at 38.9≦X<40.4. Thus, the populations could not be divided by the shape of the histogram.

Three types (I: short foot; II: moderate foot; III: long foot) were arbitrarily set for analyzing geographic variation (Fig. 32). In young, type II populations were distributed over the whole range, and type I populations were restricted to a part of Hokuriku. Type III populations showed scattered distribution from Tohoku to Kyushu. In adult males, distribution pattern of type II populations was similar to that in young, but the distributional range of type III was wider than in young. Type I populations were limited to the regions from Kanto to Hokuriku, and a part of Shikoku. Adult females showed a pattern similar to young and adult males, with wider distributions of type II and III populations. Type I populations were never found at the extremities of the distributional range.

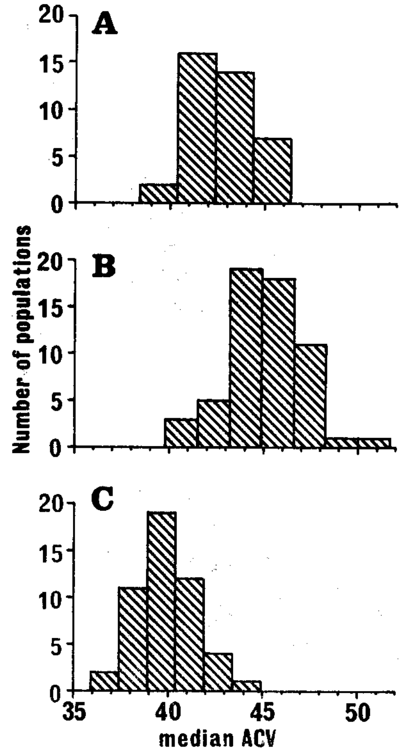

Fig. 31. Number of populations tabulated by 2.0 mm (A: young), 1.7 mm (B: adult males), and 1.5 mm (C: adult females) intervals of population ACV median of FL.

b) *Patterns of Intra- and Interpopulation Variation in ACV*

1) Intrapopulation variation in ACV

All the characters analyzed exhibited more or less marked intrapopulation variations as described above. The degree of variability for a character was estimated by the magnitude of ratio of extremes (RE=max. ACV observed/ min. ACV observed; modification of Dubois 1976: 36) within each age/sex group of each population (Table 30). The most variable character was T-EL and RE exceeded 4.0 in several populations (young: Pop. 16, RE=4.77; adult males: Pop. 28, RE=4.29). However, in the majority of the remaining populations, RE for T-EL ACV were within the range of 1.1–2.7, and the median was about 1.6 for young and adult males. In adult females, T-EL ACVs were less variable (range of RE=1.12–2.79). The next highly variable

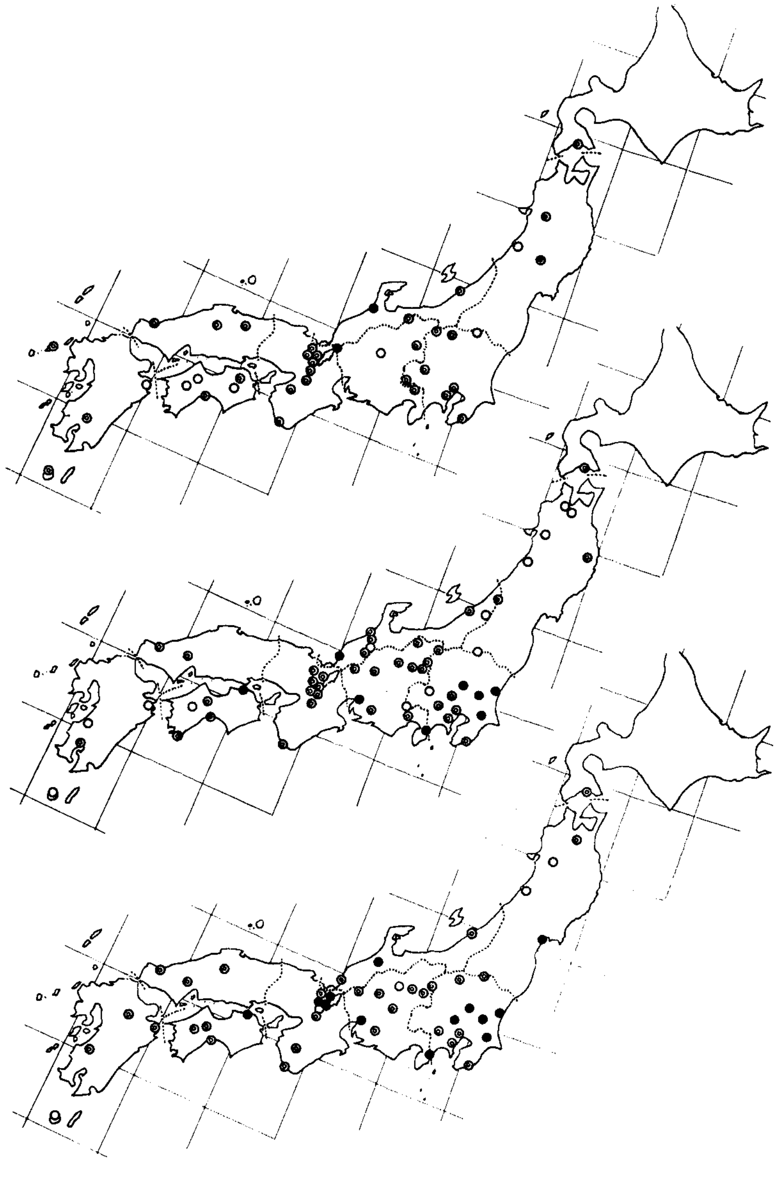

Fig. 32. Geographic distribution of type I (short foot: closed circles), type II (medium foot: double circles) and type III (long foot: open circles) populations of the Japanese common toad. Top: young; middle: adult males; bottom: adult females.

Table 30. Degree of variability in each character measured by RE (=maximum value observed/minimum value observed).

Character	Age/sex group	N	RE in all individuals	N	RE in population medians
HL	Young	552	1.40	39	1.16
	♂ Adults	951	1.35	58	1.16
	♀ Adults	580	1.41	50	1.13
	Total	2084	1.41	—	—
SL	Combined	2204	1.47	83	1.14
T-EL	Young	725	7.76	39	2.03
	♂ Adults	1168	5.38	58	2.35
	♀ Adults	576	4.62	50	1.95
	Total	2469	7.76	—	—
TD	Combined	2501	3.03	83	1.86
HW	Young	554	1.47	39	1.15
	♂ Adults	950	1.43	58	1.20
	♀ Adults	574	1.40	49	1.15
	Total	2078	1.47	—	—
PL	Combined	1789	1.68	83	1.24
PW	Young	536	2.45	39	1.63
	♂ Adults	945	1.94	58	1.30
	♀ Adults	577	2.12	50	1.33
	Total	2058	2.45	—	—
LAL	Combined	1888	1.40	83	1.16
TL	Young	759	1.41	39	1.12
	♂ Adults	1175	1.41	58	1.12
	♀ Adults	581	1.34	50	1.12
	Total	2515	1.42	—	—
FL	Young	756	1.59	39	1.20
	♂ Adults	1172	1.54	58	1.26
	♀ Adults	579	1.47	50	1.24
	Total	2507	1.65	—	—

character was TD, and RE ranged 1.1–2.0 in this character. PL and PW also showed a large RE. By contrast, HL and TL exhibited little variability; RE was at most 1.3 in these characters.

Difference with age was more conspicuous in males than in females (Table 31). When the degree of differentiation was estimated by percentages of significantly different populations to the total number of examined populations, there was a high degree of differentiation between young and adult males: in 66.7% of the examined populations they differed for FL; in 44.4% for HW, and in 40.7% for TL. When there was a difference, adult males had larger TL and FL ACV and smaller HW ACV than young. On the contrary, the largest percentage value of difference between young and adult females was 37.5% for FL; and in only 16.7% for HW and PW, the examined populations differed between these two groups. Adult females had larger FL ACV,

Table 31. Occurrence frequency of ontogenetic and sexual differences in the ACV median among populations of the Japanese common toad. For division of populations, see text. An intermediate population, Pop. 25 is included in the total.

Character	Combination	type A		type B		Total	
		N of Pops.	% of differing Pops.	N of Pops.	% of differing Pops.	N of Pops.	% of differing Pops.
HL	Y:♂Ad.	15	0	11	36.4	27	18.5
	Y:♀Ad.	13	0	10	10.0	24	4.2
	♂Ad:♀Ad.	30	10.0	13	15.4	44	11.4
T-EL	Y:♂Ad.	15	33.3	11	27.3	27	33.3
	Y:♀Ad.	13	7.7	10	10.0	24	8.3
	♂Ad:♀Ad.	30	13.3	13	30.8	44	18.2
HW	Y:♂Ad.	15	40.0	11	45.5	27	44.4
	Y:♀Ad.	13	15.4	10	10.0	24	16.7
	♂Ad:♀Ad.	29	65.5	13	61.5	43	65.1
PW	Y:♂Ad.	15	26.7	11	9.1	27	18.5
	Y:♀Ad.	13	23.1	10	10.0	24	16.7
	♂Ad:♀Ad.	30	6.7	13	7.7	44	6.8
TL	Y:♂Ad.	15	26.7	11	63.6	27	40.7
	Y:♀Ad.	13	0	10	10.0	24	4.2
	♂Ad:♀Ad.	30	50.0	13	61.5	44	54.5
FL	Y:♂Ad.	15	60.0	11	72.7	27	66.7
	Y:♀Ad.	13	38.5	10	30.0	24	37.5
	♂Ad:♀Ad.	30	100	13	84.6	44	95.5

but in HW and PW, young had a larger value than adult females in some populations and the situation was reversed in others. These results indicated a higher frequency of ontogenetic differentiation in males than in females. This tendency was especially obvious in FL and HW. In adult females, FL exhibited a much higher degree of ontogenetic differentiation than other characters.

As to sexual dimorphism in adults, three (HW, TL and FL) of the six characters showed even higher frequency of differences than in the ontogenetic comparisons between young and adult males. Among these, difference in FL was most conspicuous, and 95.5% of the examined populations showed sexual dimorphism in this character. HW and TL were sexually dimorphic in more than one half of the examined populations. From these results, it is postulated that sexual differentiation usually occurs in the characters of hindlimb and in head width: adult males are judged to have a proportionately narrower head and longer hindlimb than adult females in the Japanese common toad.

2) Interpopulation variation in ACV

In the ten characters examined, no population had an ACV median completely different from all the other populations. Even the most distinct population at most differed from less than 75% of the other populations (FL in young, TL in all the three age/sex groups). Consequently, it was impossible to divide the population of the Japanese common toad by the magnitude of ACV medians for any one character, if the geographic distribution of each population was not taken into account.

After examining geographic variation in the ACV medians of the ten characters, clear geographic distribution patterns were found only in a few characters. In the three characters on the head (HL, SL and HW) and in TL (of adult females), popu-

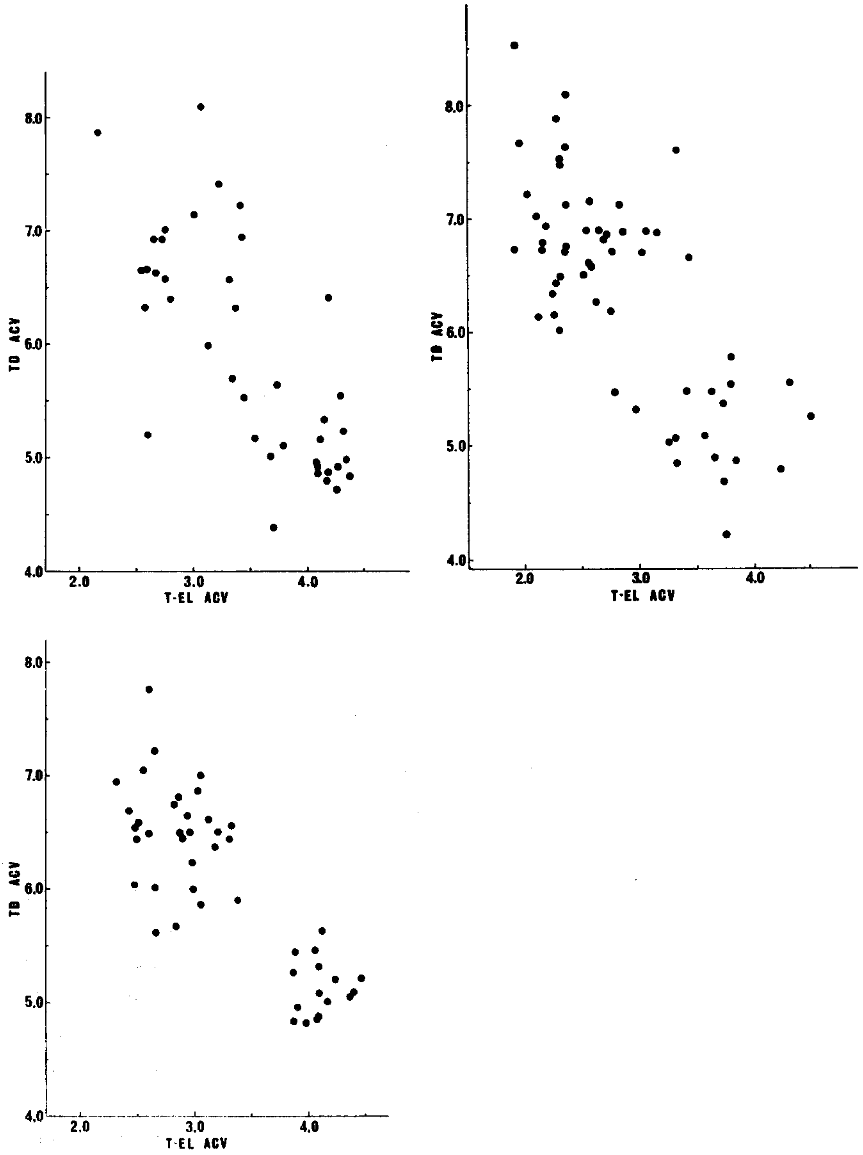

Fig. 33. Correlation between T-EL ACV and TD ACV in well represented populations of the Japanese common toad. Population ACV median plotted. Top left: young; top right: adult males; bottom: adult females.

lations with smaller ACV tended to be limited to northeastern Japan. In adult toads, populations having small ACV in FL were not found in the northern and southern extremities of the distribution range.

On the contrary, a clear geographic distribution pattern was observed in TD and T-EL. In these characters, bimodal distribution was found in the frequency distribution of populations classified by the magnitude of ACV medians, and the two groups of populations thus divided had a distributional boundary around the Chubu or Kinki District.

Fig. 34. Geographic distribution of type A (closed range), intermediate type (dotted range) and type B (open range) populations of the Japanese common toad. Broken line indicates the boundary between type A and type B populations.

From the relation between T-EL and TD (Fig. 33), two distinct types (A: with large tympanum and short tympanum-eye distance; B: with small tympanum and long tympanum-eye distance) could be distinguished. The presence of the two types could be most clearly recognized in adult females, and was obscure in young. When each population was grouped into either of the two types for each age/sex group, the results agreed well among the three age/sex groups: one population regarded as type A in young was also grouped into the same type in adults of both sexes. Thus, by synthesizing the results for each age/sex group, each population could be grouped into either of the two types.

The populations indicating a slight difficulty in grouping were Pop. 1 (Hakodate), Pop. 25 (Tokyo), and Pop. 39 (Ikawa). In Pop. 1, the young had smaller ACV in both characters than in the other populations. Both sexes of adults, however, had characteristics completely within the range of type A, and therefore, the population was classified as that type. In Pop. 25, adult males were judged to belong to type B, but adult females to type A. Young were situated in an intermediate position. Therefore, Pop. 25 was treated as an intermediate type. The young of Pop. 39 were judged to be type A by the size of the tympanum, but had larger tympanum-eye length than any other population of type A. The tendency, though much less conspicuous, was also observed in adult males. It was, however, judged that there was no serious problem in classifying the population as type A.

From these results, the distribution of each population was plotted on a map, and a clear-cut distribution pattern was observed: populations of type A were distributed from the Kinki District eastwards, and those of type B were found from there westwards. By the relation of T-EL and TD, populations which had been excluded from the foregoing analyses because of the small sample size could be divided into either of the two types. The distributional pattern of these populations agreed well with that obtained for well-represented populations. In this way, the borderline for the distribution range of the two types could be drawn (Fig. 34).

There were, however, a few exceptions, and two type B (Pop. 12 and Pop. 52) and one intermediate type (Pop. 25) populations were included in the distribution range of type A. The discrepancy in this distribution will be discussed later.

Discussion

As stated previously, morphometric characters hitherto given importance in the classification of the Japanese toads include TD, T-EL, PL, PW, SL, IND, IOD, and HLL. For these characters, intrapopulation allomorphosis against SVL has been examined for the population from Momoyama, Kyoto (Pop. 63; see the previous chapter). The result obtained in that study indicated that IOD did not correlate with SVL and was a very variable character, at least in adult males. This character is easily measured for ranid frogs and some species of true toads (especially for the broad-skulled types having bony crests on the head), whereas in the *Bufo bufo* complex, it is often very difficult to take an accurate measurement for this dimension, because of the vague reference points. For this reason, I omitted this character from analyses, and also ignored analyses based on IND, since the character has significance only when compared with IOD. Measuring HLL is very difficult for specimens which have been fixed too hard. In the present study, TL and FL were examined instead of HLL. All the other important characters were included in the analyses, and therefore, the examination of the ten characters here treated seems sufficient, if not complete, for detecting morphometric variation pattern in the Japanese common toad.

Pattern of allomorphosis and a comparison by ACV: In comparing the size of a character between two animal groups which have different standard length range, we must calculate the "relative size" of the character by certain methods. As a standard for such methods, ratios were widely employed by many authors (e.g., Mayr, Linsley, and Usinger, 1953), and were considered to be useful in every field of biology.

External meristic characters, such as scales in lizards and snakes, and costal grooves in salamanders, are generally few in anurans, and the dimensions of morphometric characters are far more important in this animal group. Many authors used ratios in expressing external morphology and in comparing different taxa (e.g., Berger, 1964; Blair, 1955; Church, 1960; Ferguson and Lowe, 1969; Inger, 1947, 1954, 1966; McAlister, 1962; Porter, 1968; Schaaf and Smith, 1970).

Atchley et al. (1976), after theoretically pursuing the variance of two character dimensions and their ratios, which are used in discriminant analysis, warned against the use of ratios for comparing taxa. Corrucini (1977) and Dodson (1978) opposed the opinion of Atchley et al. (op. cit.), and the use of ratios is still rather popular (e.g., Hemmer et al., 1978; Heyer, 1978; Dubois and Khan, 1979; Busse, 1981).

Aside from the discussion bv Atchley et al. (1976), the use of simple ratios must be made prudently, since ontogenetic change is known to occur in ratios among some characters (e.g., Kauri, 1957; Martof and Humphries, 1959). As stated in the previous chapter, some characters showed isomorphic relations to SVL, whereas others were tachymorphic or bradymorphic in the population of the Japanese common toad from Momoyama, Kyoto. Consequently, it seems more proper at first to examine allomorphic relations among characters in comparing character dimensions among groups of toads, especially when groups include animals of different ages.

On the other hand, it is far more troublesome and complex, and less easily understandable, to express size relations by allomorphic equation than by ratios. Moreover, the Y intercept of allomorphic equation (B of $Y=BX^{\alpha}$) seems to have little concrete meaning and the interpretation of that meaning is in no way easy (White and Gould, 1965).

For these reasons, I gave up trying to express size relations by ratios nor allomorphic equations, but employed ACV (Thorpe, 1975: 29) instead. By using this value, two characters having tachymorphic or bradymorphic relations to each other could be safely analyzed, and further, the significance of positional difference in allomorphic equations (see the discussion of previous chapter) seems to be well reflected (Fig. 35).

As a first step for calculating ACV, variation in allomorphic constants was examined in nine populations of the Japanese common toad. Although geographic trends were found in only two characters (TD and PL), all the other characters exhibited some minor variation in the magnitude of the allomorphic constant. The presence of geographic variation in allomorphosis of some characters elucidated in this paper is in accordance with that reported for some fish species (Kubo and Yoshihara, 1972), and by accumulating and analyzing a larger number of populations, some clear geographic pattern may be detected in all characters. It is, however, estimated that the use of combined α value for calculating ACV acted towards decreasing, and not increasing, interpopulation differences in ACV.

Variation in SVL: Since ectothermic vertebrates, including anurans, appear to continue size increase throughout their life, it has been argued that mean body size of such animals cannot be estimated (Kauri, 1959: 87; Trueb, 1977: 175).

Although reports on the growth of the Japanese toads are few, the available data indicate that the growth rates are much slower in mature adults than in immature young (Matsui, 1975a; Hisai, 1975). This tendency coincides well with those observed for other Bufonid toads or frogs of other families (e.g., Hamilton, 1934; Blair, 1953; Martof, 1956; Turner, 1960; Briggs and Storm, 1970; Oukouchi, 1978). The body size of the Japanese common toad has been found to vary more prominently within an age class than between age classes (Matsui, unpublished; Hisai, 1981). Hisai (1981) reported the body size of breeding males from Tokyo as follows: two years old = 109 ± 11 (SD) mm, three years old = 110 ± 9 mm, four years old = 109 ± 8 mm. These figures indicate almost no differences among different age groups. According to this author, breeding females had slightly larger mean body sizes, but the variation range largely overlapped that for males (Fig. 36). Further, almost no difference was found in the body siee of adult males between the individuals which matured at certain years of age and those which matured more than one year later (Matsui, unpubl.; Hisai 1981).

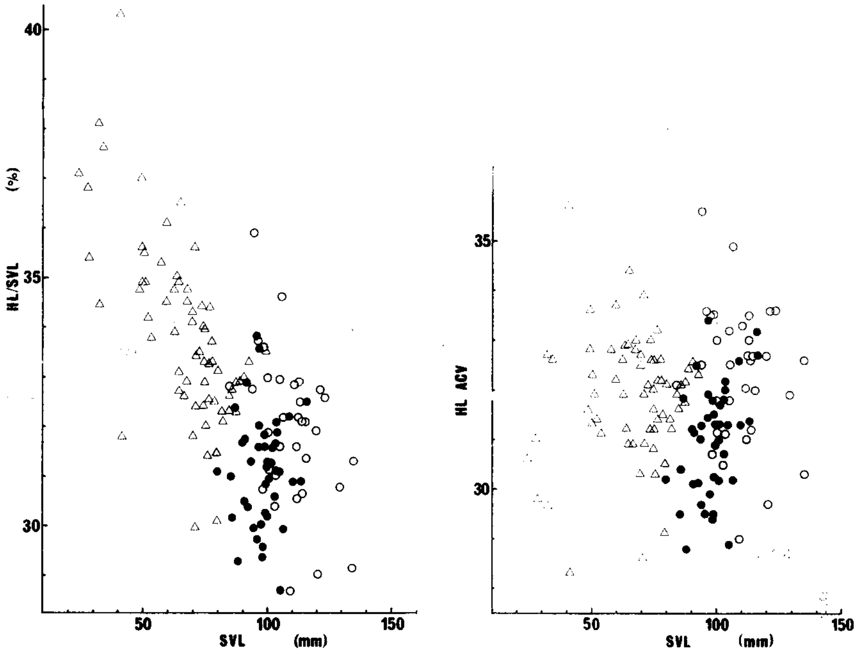

Fig. 35. Correlations between SVL and HL/SVL ratio (left) and between SVL and HL ACV (right) in the Japanese common toad from Momoyama, Kyoto. Open triangles: young; closed circles: adult males; open circles: adult females.

This information seems to permit comparing mean body sizes of adult toads in spite of the doubt expressed above, at least if we exclude individuals which have just matured sexually. The cause of the great variation in the adult body size is thus largely attributed to the great variation in the individual growth rate, but another ecological factor is also important. In the population from Momoyama, Kyoto (Pop. 63), the body sizes of breeding adults varied yearly, and there was a strong negative correlation between the number of breeding toads and the yearly mean body size (Matsui, 1981; Fig. 37). In this case, population density further affected the body sizes of yearly breeding toad populations.

In interpopulation comparisons, it was found that both sexes of some populations did not overlap adjacent populations in the mean SVLs. Among such cases, some combinations included a large altitudinal gap: e.g., 1,170 m of altitudinal difference between Pop. 16 and Pop. 18, and 760 m of difference between Pop. 38 and Pop. 43. In these combinations, the difference in mean SVL might have been related to the difference in altitude, but other combinations did not include such altitudinal gaps (e.g., Pop. 61 vs. Pop. 63, and Pop. 24 vs. Pop. 25). In these combinations the mean SVL of one

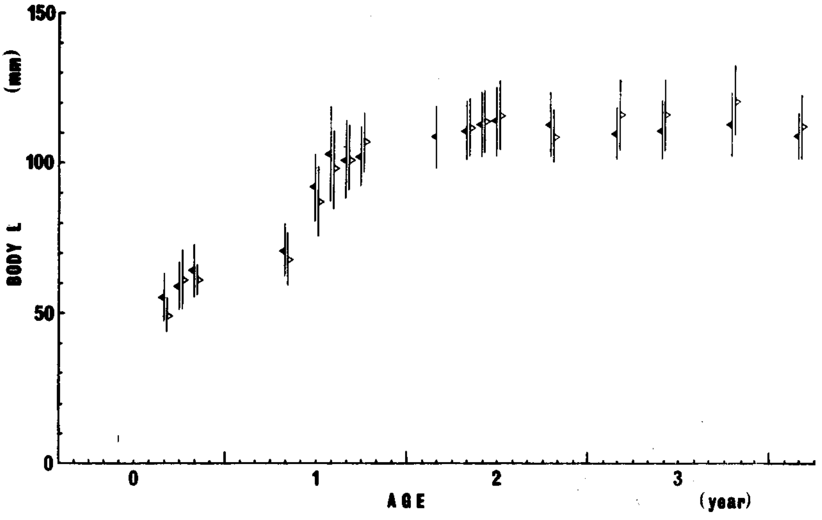

Fig. 36. Body length growth in the Japanese common toad from Tokyo, reported by Hisai (1981). Closed triangles: males; open triangles: females. Symbols indicate mean and vertical bars standard deviation.

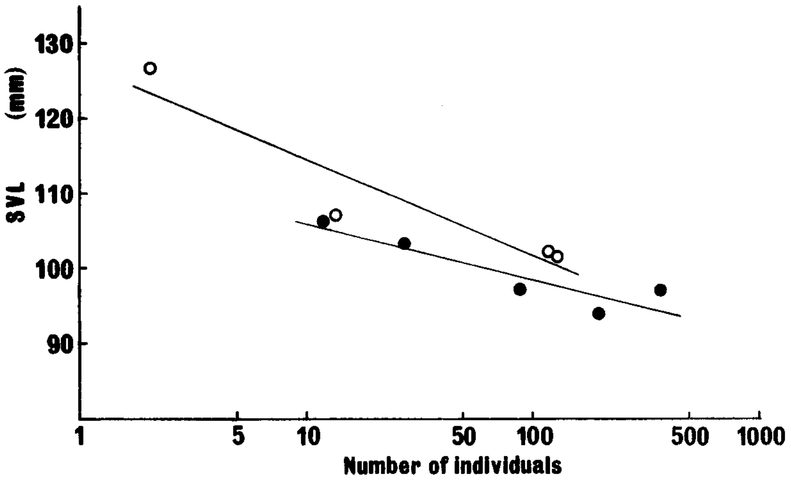

Fig. 37. Correlation between number of individuals (on a logarithmic scale) and SVL in the Japanese common toad from Momoyama, Kyoto. Field data for 1973–1977 breeding seasons. Closed circles: adult males; open circles: adult females.

population was extremely smaller than that of surrounding populations, in spite of their geographic similarities. Such a trend was obvious in Pop. 23, 25, 52 and 63, and these populations had some ecologically remarkable features. The toads of Pop. 23 were obtained from a pond where a large number of breeding toads are yearly captured by frog collectors (Ouchi, Pers. Com.). The toads of Pop. 25 lived in gardens surrounded by human habitations in the center of Tokyo, and those of Pop. 52 were from the campus of a university. Samples of Pop. 63 were also from an isolated area of a shrine in the city. All of the habitats of these populations were isolated places and the population densities were high. To date there is no accurate ecological information, but it is easily surmised that a limited area of activity, high population density, and the increased possibility of human influence will affect the body size of toads. A similar effect of human influence on toad body size has been pointed out for the Chinese common toad, which is a close relative of the Japanese common toad (Boring and Liu, 1934).

Body size (SVL in the present study) thus varied greatly intrapopulationally, but there were far greater interpopulational SVL differences among some populations. In Pop. 10, which included adults of both sexes with the smallest mean SVLs among all the examined populations, males attained sexual maturity at the SVL of 61 mm and females at 60 mm SVL, and no individuals greater than 79 mm in males and 76 mm in females were obtained. Conversely, in Pop. 96, which included the females with the largest mean SVL, males less than 95 mm SVL and females less than 130 mm SVL were all sexually immature. Therefore, the SVL of the smallest mature male in Pop. 96 was 1.2 times larger than the largest adult male in Pop. 10, and the smallest mature female in Pop. 96 had an SVL 1.7 times larger than the largest adult female of Pop. 10. These values are far greater than the ordinary range of intrapopulation SVL variation.

The trends in the geographic variation of mean SVL differed between the two sexes, i.e., populations with larger SVL tended to be distributed in more southern localities in females, but populations with smaller SVL were often found in the northern and southern extremities of the distributional range in males. Reflecting such trends, the female mean SVL of the southernmost population (Pop. 96, Yakushima: mean SVL=160 mm) was the largest among the examined populations, whereas the male mean SVL of the same population (110 mm) was smaller than that for populations from more northern localities. In the habitats of this population, the natural environment was well preserved, and therefore, it is unlikely that the small body size in males is the result of human influence or restricted habitat conditions. Even if there might be some unnoticed environmental selective pressures, effects on only one sex are not easily interpreted. Consequently, the mean SVL of each population, although it might be more or less affected by environmental pressures, is considered to have a specific genetical basis in expression.

Members of Pop. 10 had distinctly small SVLs and differed from all other populations in mean SVL in both sexes. However, populations from northernmost Honshu, though excluded from the analyses of means due to small sample size, had even smaller SVLs (one male from Pop. 2 had an SVL of only 43 mm, and one female from Pop. 3 had an SVL of 54 mm), and might not differ from Pop. 10 in mean SVL. Therefore, mean SVL alone does not seem useful in differentiating populations of the Japanese common toad.

ACV variation: In homoiothermal vertebrates, body size is specifically or subspecifically uniform, and direct comparisons in some characters can be made by absolute measurements. Even in frogs, such an analytical process is possible if the variation range in body size is extremely small (e.g., Trueb, 1977). In analyzing the morphometric character variation of the Japanese common toad, however, comparisons by absolute dimensions are impossible since there is a great intrapopulational variation in the unit length (=SVL), and the magnitude of interpopulational difference in the unit length is greater than four times.

By employing ACVs, comparisons among groups of toads having different SVLs seem to have been achieved more accurately. Within one population, highly variable characters were T-EL, TD, PL and PW, and HL and TL showed lesser degree of variability. These results coincide with those reported by Underhill (1961, a, b), who showed that adults of *Bufo woodhousei* and *B. hemiophrys* from South Dakota had higher variability (compared by the magnitude of CV for the ratios of characters to SVL) in PL and PW than in HL, SL, and TL.

All the characters showing high variability had absolutely small dimensions, and greater measurement errors might have been included than in characters with larger absolute dimensions. Two organs, the tympanum and parotoid gland, are related to the four highly variable characters, and are essentially not supported by bony elements. This might be a more important reason for the higher variability in the ACVs of related characters. Further, the tympanum apparently has the single function of a receptor of airborne sounds (Martin, 1972; Capranica, 1976) and the parotoid gland that of a defense organ against enemies (Lutz, 1970). Other organs (head, forelimb, and hindlimb), including less variable characters, have multiple functions. Therefore, higher variability in the relative size of the former two organs within a population and/or within an age/sex group seems to suggest that these organs are less vital to the individual toad than the latter organs.

In the characters analyzed by differentiating age/sex groups, adult females generally exhibited lesser degree of variability than in young and adult males. Alhough this result agreed with that obtained by Trueb (1977) in the Ecuadorian *Hyla lanciformis* skull measurements, Kellicott (1907) reported higher variability in some characters (e.g., HL, TL and FL) in females than in males in adult *Bufo lentiginosus americanus* (=*B. americanus*) from Ohio. Underhill (1961a) reported that the ratios of character dimensions to SVL were slightly more variable in females of *B. woodhousei*. He also reported, however, that males were more variable in some characters in *B. hemiophrys* (Underhill, 1961b). Moreover, in the three species of European pond frogs of the *Rana esculenta* group, the variability in the two sexes varied according to the species and the characters (Berger, 1966). Consequently, a generalized conclusion cannot be drawn about sexual dimorphism in the degree of character variability.

Ontogenetic comparisons within a population revealed greater difference in ACV between young and adult males than between young and adult females. The highest degree of differentiation was observed in FL between young and adult females, but even in this case, only less than half of the examined populations exhibited significant differences. Though the actual difference might have been masked by the small sample size in some populations, it may be concluded that adult females ontogenetically differentiate morphological characters less markedly than adult males.

Only a few papers have reported age variation in anurans. McAlister (1962) found ontogenetic change in HL/Body L ratio in *Rana pipiens* and noted that juveniles had larger heads than adults. Blair (1955) indicated no difference in HLL/SVL ratio between adult females and juveniles of *Bufo microscaphus*, although sexual dimorphism was obvious in this character. These previously reported results coincide well with the results reported here, whereas the ontogenetic change in TL/Body L ratio in *Rana esculenta* complex (Kauri, 1954, 1959) and *R. sylvatica* (Martof and Humphries, 1959) contradicted my results. There might be a generic difference between *Bufo* and *Rana* in the ontogenetic change in hindlimb proportions.

The sexual dimorphism in adults discussed above reflected the ontogenetic features. In a large number of populations, sexual dimorphism was found in HW, TL, and FL, and males had smaller HW and longer TL and FL than females.

There is a high correlation between HW and mouth width in toads (Matsui, unpubl.), and the relatively larger HW in females suggests the presence of sexual dimorphism in the feeding ability. Hisai (1981) found that, in the Japanese common toad from Tokyo, mouth width was sexually dimorphic and that females had significantly wider mouths than the males of same body size.

The observation that the characters of the hindlimb develop better in males than in females coincides well with those reported for many species of *Bufo* (*B. b. bufo*: De Lange, 1973; *B. b. gargarizans*: Fang and Chang, 1931, Boring, 1939; *B. viridis*: Opatrný, 1974, Hemmer et al., 1978; *B. hemiophrys*: Underhill, 1961b; *B. microscaphus*: Blair 1955). In other species, however, no sexual dimorphism was found in the hindlimb characters (*B. woodhousei*: Blair, 1955, Underhill, 1961b). The greater development of hindlimb characters in males suggests that they are more active than females, especially in the breeding season, for searching, pursuing females, and fighting with the same sex (Opatrný, 1974; De Lange, 1973).

Thus, the results of the intrapopulation variation analyses largely coincided with those obtained from allomorphic analyses (previous chapter), and suggested that in analyzing morphometric variation of toad populations, at least HW and hindlimb characters should be separately treated for the three age/sex groups.

Interpopulation variation: The ten morphometric characters dealt with in the present study included most of the characters hitherto considered important for classifying the Japanese toads, but no character differentiated a particular population from all the other populations. Several characters exhibited vague trends in geographic variation pattern, but none of them, except TD and T-EL, differentiated geographically sharply outlined population groups.

There was a marked geographical trend in the pattern of variation in TD and T-EL, and the relation of these two characters enabled me to divide the populations of the Japanese common toad into two groups. T-EL is the distance between posterior corner of upper eyelid and anterior corner of tympanum, and, since the shape of the head as a whole is almost uniform, is affected by the size of the tympanum (TD). The total size of T-EL and TD, however, is not necessarily constant, and therefore, the two metric characters can be treated independently.

Both T-EL and TD were not only intrapopulationally highly variable in ACV, but also variable among populations. In dealing with such variable characters, careful examination of variation patterns are at first required, since even intrapopulationally highly variable characters can be taxonomically diagnostic (e.g., PW: Underhill, 1961a). If the variation pattern of one character has no relation with geographic distribution, and similar variation pattern is only sporadically observed, the taxonomic value of that character should be regarded as low.

As a matter of fact, the distributional patterns of T-EL and TD were found to be regular, and two groups of populations were distinguished in the northeastern and southwestern parts of Japan by the magnitude of ACV medians. Further, by comparing these two characters, the distributional range of the two groups could be clearly defined throughout the three age/sex groups. Therefore, the populations of the Japanese common toad were divided into two types: one, type A, is found northeast of the Kinki District, and the other, type B, is found from the Kinki District southwestwards.

Exceptional populations were found at three localities in the area from the Hokuriku District eastwards. Both Pop. 12 (Sendai) and Pop. 52 (Kanazawa) belonged to type B, but their localities were fairly distant from the main distributional range of other type B populations. Toads of these two populations were collected on the campus of universities, and it is highly possible that they are descendants of individuals artificially introduced for laboratory purposes. Population 25 (Tokyo) was a unique intermediate of types A and B, and was collected from the center of large cities. In this region, the native population, probably having morphometric traits similar to surrounding Pop. 23, 24, and 26, seems to have been hybridized with individuals artificially introduced from other, probably southwestern, localities of Japan for laboratory, pharmacological, and other purposes. It is probable that, in the areas where samples of Pop. 12 and Pop. 52 were obtained, native toad populations might have nearly perished because of overcollecting for laboratory purposes, and later, small portions of introduced individuals might have established stable populations. Since these areas are in the city region and largely isolated from nearby montane regions, hybridization with the surrounding populations might have occurred only rarely, and formation of intermediate type populations might have been prevented.

Although seldom recorded accurately, the Japanese common toad has been artificially introduced into regions where native populations were absent (Sado Is.: Okada, 1930, Iwasawa, 1960; Tsushima Is.: Murakami, 1981; Izu Oshima Is.: Goris and Terada, 1977; Miyakejima and Hachijojima Is.: Matsui, unpubl.). Further, toads have been transported for human utilization: in the periods of Meiji and Taisho, a great number of toads seem to have been brought to large cities for making bags and other leather articles of their skin for export (Okada, 1938: 346; Tokita, 1962: 210). The abundant literature dealing with toads as experimental materials clearly indicates that toads have been extensively used for laboratory purposes, and it is highly probable that the toads from various parts of Japan were transported to large cities where there were universities and laboratories.

Artificially introduced amphibians establish stable colonies and steadly widen the distribution range (e.g., *Bufo marinus*: Honegger, 1970, Matsui, 1975b, Easteal, 1981; *Rana catesbeiana*: Matsui, 1980f; *R. tigerina*: Matsui, 1979b; *Xenopus laevis*: Bury and Luckenbach, 1976, Behler and King, 1979). Doubtlessly a portion of the Japanese common toads artificially transported for commercial and laboratory purposes will get free or be released and establish a new population if the environmental conditions are suitable. Indeed, toads have been artificially transferred much more often than is usually expected.

From these considerations, the occurrence of the three exceptional populations mentioned above is regarded as a result of artifact, and by eliminating these populations, the distribution range of the two types are more clearly defined.

In conclusion, analyses of variation in morphometric characters revealed a high morphological variability of the Japanese common toad, but the geographic variation trends in two characters, i.e., tympanum diameter and tympanum-eye length, allowed me to recognize two groups of populations: one (type A) is distributed in northeastern Japan and is characterized by large TD and small T-EL; the other (type B) is found in southwestern Japan and has small TD and large T-EL.

V

Geographic and Climatic Clines in the Morphometric Characters of the Japanese Common Toad

In the Japanese common toad the SVL and the adjusted character value (ACV: Thorpe, 1975) of each character exhibit complex geographic variation patterns. The existence of particular geographic gradients in population median ACV is suggested in some characters, but in others such obvious trends are not found. In this paper, the variation of SVL and ACV of each character will be analyzed in relation to the geographical and climatological parameters which are considered to reflect environmental conditions of the distributional ranges. In order to grasp what geographic and climatic factors may be involved in the variation of each character, morphometric clines of each character against each parameter are studied.

Geographic and climatic clines of morphometric characters exhibited by amphibians have been studied in some species (e.g., Schmidt, 1938; Schuster, 1950; Ruibal, 1957; Kauri, 1959; Terent'ev, 1962; Nevo, 1972, 1973), but only a few of these studies strictly clarified relationships among parameters and character dimensions. As to the Japanese amphibians, only vaguely outlined geographic gradients were found among roughly grouped populations (e.g., Moriya, 1954; Sawada, 1963; Wada, 1964; Kuramoto, 1968), and no strict parametric analyses have been made on the clines.

Taking these circumstances into consideration, I examined populations of the Japanese common toad, which were split as geographically small as possible, and precisely determined the geographical and climatological parameters.

MATERIALS AND METHODS

Each well-represented population of the Japanese common toad ($N \geqq 3$ for each age/sex group in Table 3) was a basic unit for the analyses. Characters (X_1, for abbreviations, see chapter II of this paper) analyzed for the elucidation of clines included: mean SVL of adult males and adult females; relative female and male mean SVL; ACV median of HL, T-EL, HW, PW, TL, and FL for adult males; ACV median of SL, TD, PL, and LAL for combined three age/sex groups. The data for these characters are to be found in the previous chapter.

For geographical parameters, latitude (X_2), longitude (X_3), and altitude (X_4) of the locality where each population was collected have been employed (Fig. 2, Table 4). These parameters were mostly represented as means of the values for demes involved in the population. Parameters for each deme were read from 1:50,000 scale maps. However, if most of the samples of a population belonged to a single deme, values for that deme were taken as representing that population.

For climatological parameters, estimated values of annual mean temperature (X_5) and annual precipitation (X_6) of the locality of populations were chosen (Table 5). In a few instances, exact climatological parameters were taken for the exact locality of the demes. Therefore, I first obtained the data from *The temperature of Japan* and *The rainfall of Japan* (Jap. Meteorological Agency, 1973a, b) for three locations nearest to a deme. Next, theoretical values for the three locations, as if they were at the same altitude with the deme, were calculated for the temperature values on the assumption of a 0.55°C temperature decrease per 100 m increase in altitude (Yoshino, 1965). The average of values estimated for the three localities were considered to represent temperature parameters for the encircled deme, and then, the averages for these demes were treated as parameters for the population. Since no simple relationship with the change in altitude has been demonstrated for precipitation (Yoshino, 1961), uncorrected values were used for analyses. Consequently, there may be greater errors in the precipitation parameter than in that of the temperature. The annual minimum temperature and average temperature for the coldest month were provisionally analyzed in relation to the mean SVL of adult females, but the results were not markedly different from those obtained for the annual mean temperature.

In the previous chapter, populations of the Japanese common toad were grouped into either A, B, or intermediate type (Fig. 34). Since only one population was included in the intermediate type, analyses were first made separately on types A and B, and if the two types had the same tendencies, overall tendency was estimated, with the two types and the intermediate type combined. Values for each morphometric character were first plotted against parametric values, and then the regression analyses were run on the basis of the distribution pattern of these plotted dots.

In most cases, morphometric values were regressed linearly with parameters, but in a few instances, the second degree polynomial regressions were applied. The significance of fitness of the regression line was judged by the value of correlation coefficient at the significance level of 95%. The multiple and partial correlations were analyzed for elucidating the interaction among parameters.

For the mean SVL and relative female and male mean SVL, relations with all the five parameters were analyzed, and from the results of these analyses, only relationships with climatological parameters were analyzed for the ACV median of each character.

RESULTS

a) *Relationships between Geographical Parameters and Mean SVL*

As shown in Fig. 38, the relation of the population mean SVL (X_1) of adult males to the latitude (X_2) was somewhat variable, but, as a whole, seemed to fit either a simple linear or second degree polynomial regression. When the plotted dots were linearly regressed, there was a significant negative correlation ($p<.001$) in the type A populations, but the regression was insignificant in type B ($p>.1$). If all the populations were combined, a significant linear regression was obtained ($.01>p>.005$). Populations of type B, however, had a rather small SVL in spite of their localities in lower latitudes, and no population with large SVL was included. To solve this discrepancy, a second degree polynomial regression model was fitted for combined populations. The obtained formula, $X_1=-0.804\ X_2^2+55.633\ X_2-841.137$, could be significantly fitted (F_{RO}, F_{VO}, F_T: $p<.01$), and had still higher correlation ($r=0.460$) than in the linear regression ($r=-0.366$). From this equation, it was estimated that the maximum SVL, 120.99 mm, was reached at 34° 35′ 18″N, and from this latitude northwards and southwards, the SVL decreased.

The correlation of adult male mean SVL with longitude (X_3) was weak (Fig. 28), and only in the type A populations, was the regression to the simple linear equation significant ($p<.001$). Regressions for type B and for combined three types were insignificant ($p>.1$).

Although SVL greatly varied in the lower altitudes (0–100 m) (Fig. 38), there was a significant negative correlation between mean SVL of adult males and altitude (X_4) in the type A populations ($.005>p>.001$). When the three types were combined, a significant negative correlation ($.05>p>.02$) was obtained. Thus, after combining all the populations, it was estimated that the SVL decreased about 1.0 mm with a 100 m increase in altitude (Table 32).

As in the adult males, mean SVL of the adult females was negatively correlated ($p<.001$) with the latitude in the type A populations, and significant negative correlation ($.05>p>.02$) was detected in type B, too. These two regressions were not different from each other in the slope and position (slope: $F_{1,45}=0.06$, $p>.25$; position: $F_{1,46}=1.01$, $p>.25$), and all the populations could be combined together with the intermediate type population, and were regarded as forming a single latitudinal cline (Fig. 39). The combined regression had a strong negative correlation ($p<.001$) and a 5.5 mm decrease in SVL per one degree increase in latitude was estimated (Table 33).

Also, as in the adult males, there was a significant negative correlation ($p<.001$)

between longitude and mean SVL of the type A populations of the adult females (Fig. 39). Although no correlation was obtained in the type B populations ($p > .1$), a strong

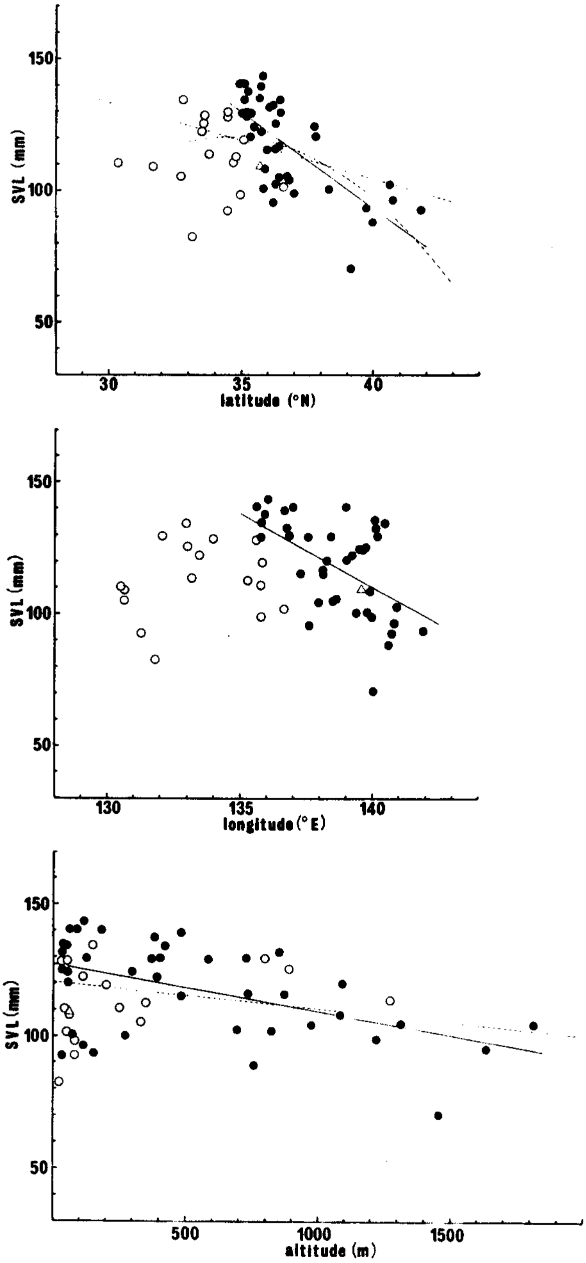

Fig. 38. Correlation between geographical parameters (Top: latitude; middle: longitude; bottom: altitude) and adult male mean SVL. Closed circles: type A population; open circles: type B population; open triangles: intermediate population. Statistically significant regression lines for each type (bold) and/or combined (dashed) populations are shown.

negative correlation was obtained when all the populations were combined ($p<.001$), and a 2.8 mm decrease in SVL with the increase of one degree in latitude was estimated.

Table 32. Correlation between geographical or climatological parameters (X_2=latitude, X_3=longitude, X_4=altitude, X_5=annual mean temperature, X_6=annual precipitation) and SVL (X_1) in the Japanese common toad. Adult males. A single population of intermediate type is included in the combined populations.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_2	A	40	−7.24680	383.4678	−0.714	<.001	**
	B	17	−0.60606	133.6411	−0.061	>.1	NS
	Combined	58	−2.90789	220.3842	−0.366	.01≫.005	**
X_3	A	40	−5.59660	893.4971	−0.528	<.001	**
	B	17	1.08415	−31.4847	0.159	>.1	NS
	Combined	58	−0.54794	191.4079	−0.098	>.1	NS
X_4	A	40	−0.01789	127.2726	−0.491	.005≫.001	**
	B	17	0.01086	110.1340	0.277	>.1	NS
	Combined	58	−0.01036	120.9312	−0.288	.05≫.02	*
X_5	A	40	4.19120	71.1894	0.760	<.001	**
	B	17	−0.91750	127.0137	−0.152	>.1	NS
	Combined	58	2.01390	91.4112	0.420	<.001	**
X_6	A	40	0.00049	116.7962	0.021	>.1	NS
	B	17	0.00119	110.5160	0.052	>.1	NS
	Combined	58	0.00045	115.3507	0.020	>.1	NS

Table 33. Correlation between geographical or climatological parameters (X_2–X_6) and SVL (X_1) in the Japanese common toad. Adult femlales. Notation as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_2	A	33	−6.44610	358.1864	−0.608	<.001	**
	B	16	−5.78990	330.0406	−0.549	.05≫.02	*
	Combined	50	−5.53450	323.6105	−0.613	<.001	**
X_3	A	33	−6.29930	995.6470	−0.601	<.001	**
	B	16	−1.89510	386.3900	−0.287	>.1	NS
	Combined	50	−2.85600	517.5243	−0.490	<.001	**
X_4	A	33	−0.02287	135.4962	−0.601	<.001	**
	B	16	0.01422	128.3601	0.339	>.1	NS
	Combined	50	−0.01374	132.9739	−0.345	.02≫.01	*
X_5	A	33	3.93230	78.2665	0.740	<.001	**
	B	16	0.40790	127.6732	0.067	>.1	NS
	Combined	50	3.04430	88.5621	0.578	<.001	**
X_6	A	33	0.00253	118.8810	0.093	>.1	NS
	B	16	0.01779	93.7210	0.661	.01≫.005	**
	Combined	50	0.00855	109.5250	0.317	.05≫.02	*

The negative correlation between altitude and mean SVL (Fig. 39) was also significant in type A, but the correlation was insignificant in type B. When all the populations were combined, a significant negative correlation (.02>p>.01) was obtained, and a 1.4 mm average decrease in SVL was estimated to occur per 100 m increase

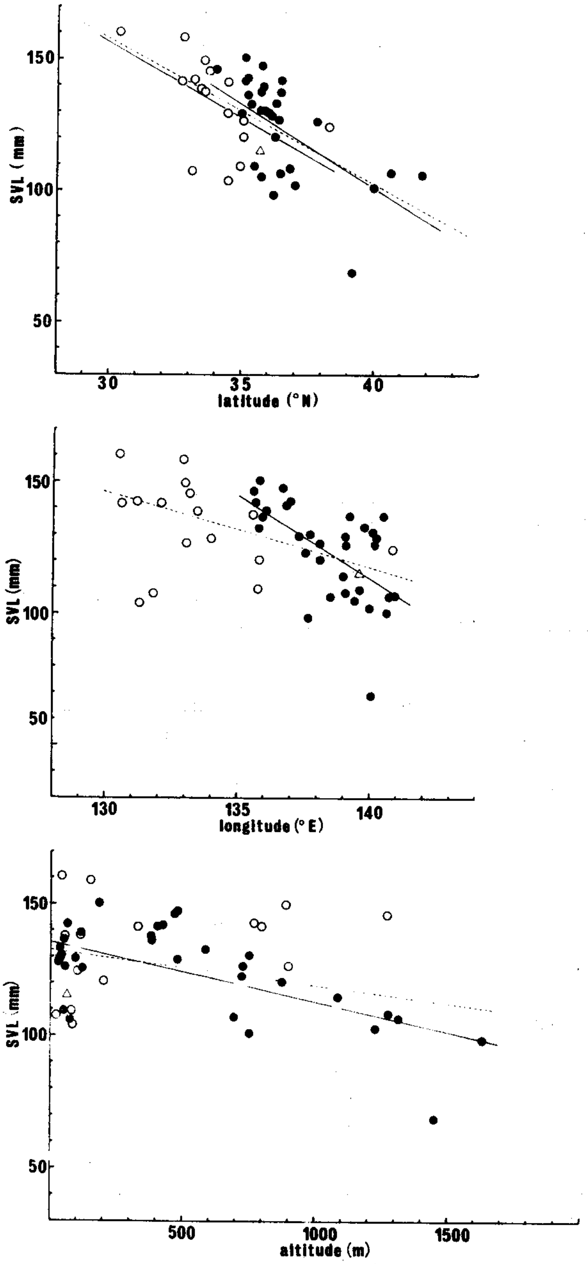

Fig. 39. Correlation between geographical parameters (Top: latitude; middle: longitude; bottom: altitude) and adult female mean SVL. Notations as in Fig. 38.

Table 34. Multiple correlation (R) and partial correlation (r) between geographic or climatological parameters (X_2–X_6) and SVL (X_1) in the Japanese common toad. Three types of populations combined. Notations as in Table 32. Multiple correlation equation for the males: $X_1 = -78.430 - 6.047X_2 + 3.025X_3 - 0.008X_4$, and for the females: $X_1 = 363.703 - 4.446X_2 - 0.543X_3 - 0.010X_4$.

Correlation	adult males			adult females		
	r	p		*r*	p	
$R_{1.234}$	0.537	.02≫.01	**	0.657	.01>	**
$R_{1.23}$	0.503	.01>	**	0.613	.01>	**
$R_{1.34}$	0.291	.05≫.02	*	0.553	.01>	**
$R_{1.42}$	0.424	.01>	**	0.651	.01>	**
$R_{1.56}$	0.421	.01>	**	0.667	.01>	**
$r_{12.3}$	−0.495	.01>	**	−0.380	.02≫.01	**
$r_{12.4}$	−0.325	.02≫.01	**	−0.590	.001>	**
$r_{13.2}$	0.370	.01>	**	−0.050	.1<	NS
$r_{13.4}$	−0.047	.1<	NS	−0.490	.001>	**
$r_{14.2}$	−0.230	.1≫.05	NS	−0.310	.05≫.02	*
$r_{14.3}$	−0.275	.05≫.02	*	−0.320	.05≫.02	*
$r_{15.6}$	0.421	.01>	**	0.621	.001>	**
$r_{16.5}$	0.034	.1>	NS	0.261	.1<	NS
$r_{12.34}$	−0.487	.01>	**	−0.370	.02≫.01	*
$r_{13.24}$	0.387	.01>	**	−0.040	.1<	NS
$r_{14.23}$	−0.257	.1≫.05	NS	−0.300	.1≫.05	NS

in altitude.

Since each of the three geographic parameters was not considered to affect the magnitude of mean SVL independently, multiple correlation analyses were run for each sex (Table 34). In the adult males, the combination of latitude and longitude had the highest correlation, that of latitude and altitude next, and that of longitude and altitude had the lowest correlation. In the adult females, the order of the first and second was reversed, but the longitude-altitude combination still had the lowest correlation. These results indicated that the complex action of latitude with the other two parameters most effectively affects the magnitude of the mean SVL.

Further, statistically "pure" action of the three parameters on mean SVL was estimated by partial correlation analyses for the combined populations. When longitude and altitude parameters were held constant, latitude had a strong negative correlation to mean SVL both in the adult males ($p < .01$) and in the adult females ($.02 > p > .01$). Only in the adult males was there a significant "positive" correlation between longitude and mean SVL under constant conditions of latitude and altitude. Significant correlation was found neither in adult males nor in adult females between altitude and mean SVL, when latitude and longitude were kept constant. This is in contrast to the results obtained by simple and multiple correlation analyses.

b) *Relationships between Climatological Parameters and Mean SVL*

As shown in Fig. 40, there was a highly significant correlation between annual mean temperature (X_5) and mean SVL of the type A populations in the adult males. Though insignificant correlation was obtained for type B populations, a significant positive correlation was obtained when the three types were combined ($p<.001$). In the combined populations, a 2.0 mm increase in SVL was estimated to occur with the increase of one degree in temperature. From Fig. 40, possibility of fitness of plotted dots on the second degree polynomial regressions might be suggested, but the estimated equation, $X_1=-0.159\ X_5^2+7.243\ X_5+57.968$, was insignificant in the second degree regression ($F_{v0}=0.806$, $dF=1,\ 38$, $p>.05$).

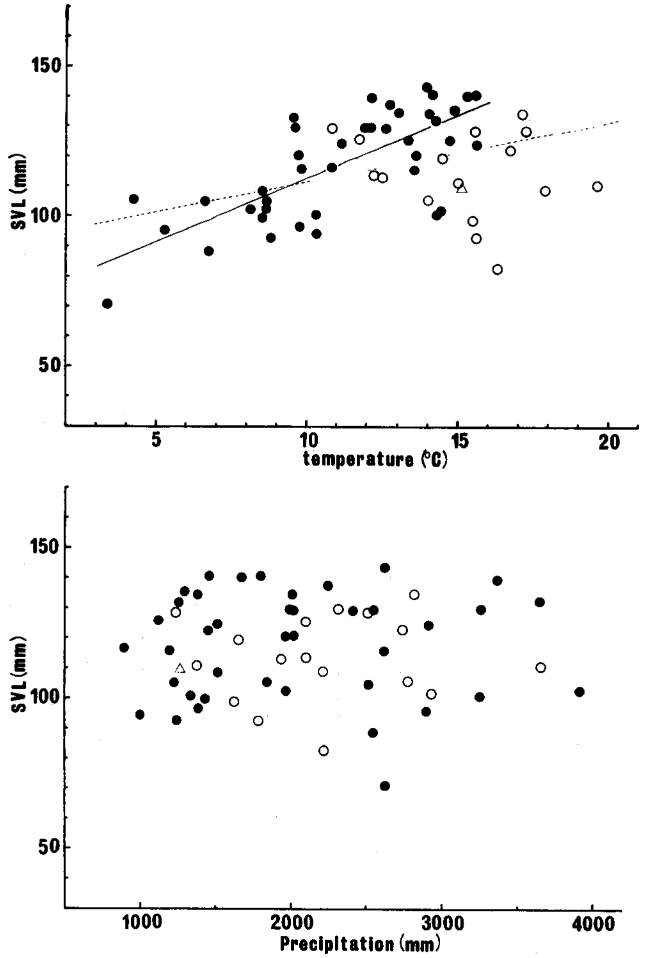

Fig. 40. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and adult male mean SVL. Notations as in Fig. 38.

No significant correlation was found in either type A or type B populations between annual precipitation (X_6) and adult male mean SVL (Fig. 40), and when all the populations were combined, there was also no significant correlation ($p>.1$, Table 32).

In the adult females (Fig. 41, Table 33), as in the adult males, there was a significant positive correlation between annual mean temperature and mean SVL in the type A populations ($p<.001$), but no correlation was detected in type B. When all the populations were combined, a highly significant positive correlation ($p<.001$) was obtained. Thus, if all the populations were combined, they would constitute a single cline, along which a 3.0 mm increase in SVL occurs with an increase of 1°C in temperature.

In contrast to the adult males, a significant positive correlation ($.01 > p > .005$) was observed between the annual precipitation and mean SVL in the type B populations (Fig. 41). When all the populations were combined, there was a significant positive correlation ($.05 > p > .02$), and a 0.86 mm SVL increase with an increase of 100 mm in precipitation was estimated (Table 33).

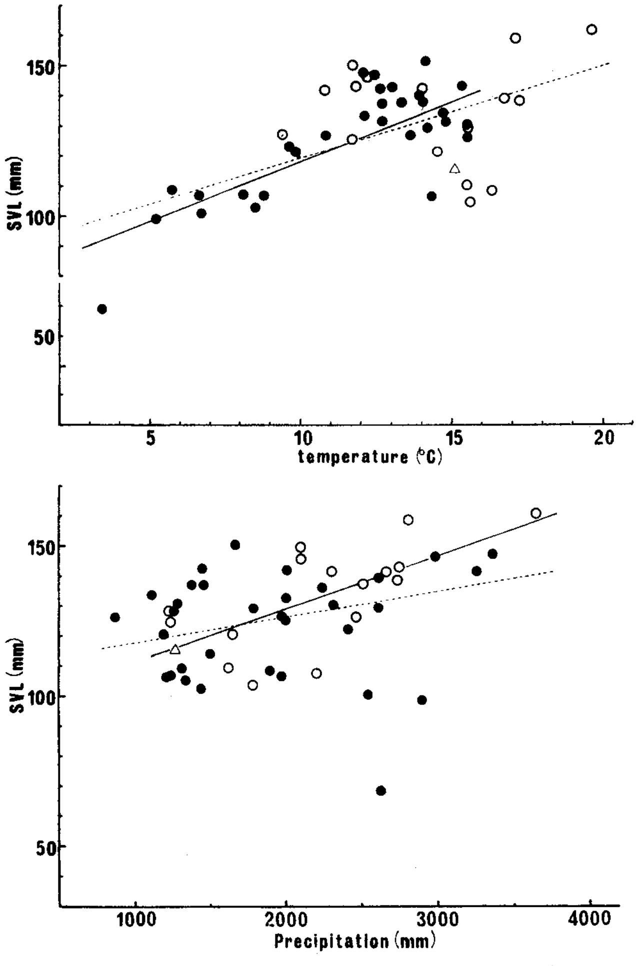

Fig. 41. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and adult female mean SVL. Notations as in Fig. 38.

When all the populations were combined and multiple correlations of the two climatological parameters with mean SVL were analyzed (Table 34), high correlation coefficient values were obtained for both sexes, and particularly in the adult females, the value thus obtained ($R_{1.56}=0.667$) was even higher than the maximum value obtained from the analyses of geographical factors ($R_{1.24}=0.651$). Therefore, the two climatological parameters were regarded as equally good or even better predictors of mean SVL than the geographical parameters.

c) Relationships between Geographical and Climatological Parameters and Relative Female and Male Mean SVL

As noted above, there was a certain geographic trend in the variation of the sexual dimorphism in the mean SVL, and the relationship of mean SVL with latitude could be expressed not only by a simple linear equation, but also by a second degree polynomial regression equation in the adult males, whereas only the former equation could be applied in the adult females. Therefore, it was naturally assumed that there might be certain relationships between the degree of sexual dimorphism and latitude, and the sexual difference in mean SVL in relation to each parameter was analyzed.

The sexual difference in mean SVL was expressed by female/male mean SVL ratio for each population, and the obtained values were correlated with each parameter. As

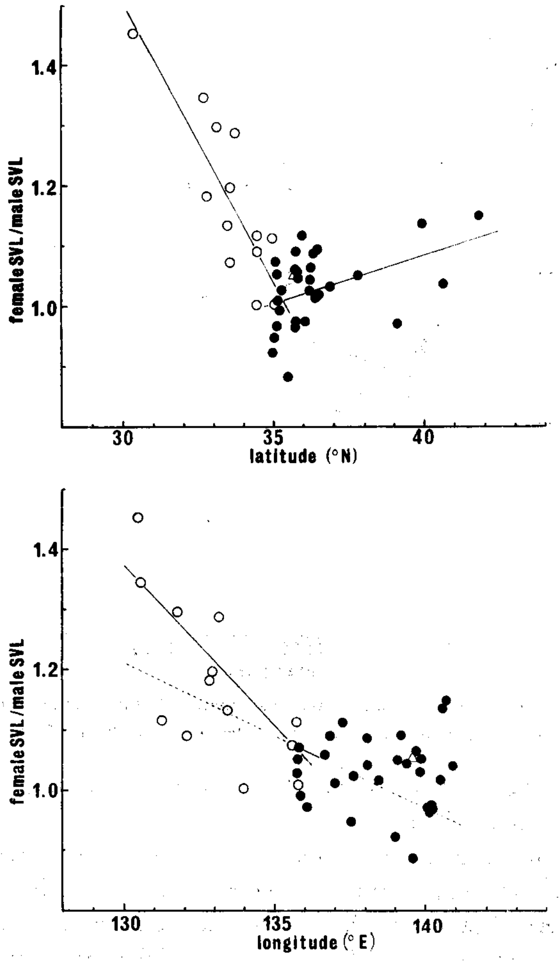

Fig. 42. Correlation between geographical parameters (Top: latitude; bottom: longitude) and relative female and male mean SVL. Notations as in Fig. 38.

shown in Fig. 42, the type A populations completely differed from those of type B in the relationship of latitude with the relative female and male mean SVL. In the type A populations, there was a significant positive correlation with latitude, whereas a significant negative correlation was found for the type B populations. Regression equations for the two types (Table 35) markedly differed from each other both in the slope and position, indicating the existence of two different clines between the two types. There was greater sexual dimorphism in the mean SVL in more northern type A populations and in more southern type B populations.

Table 35. Correlation between geographical or climatological parameters (X_2–X_6) and relative female and male mean SVL (X_1) in the Japanese common toad. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_2	A	30	0.01599	0.4460	0.448	$.02 \gg .01$	**
	B	13	−0.09291	4.2966	−0.845	$< .001$	**
	Combined	44	−0.02325	1.9006	−0.429	$.005 \gg .001$	**
X_3	A	30	−0.00074	1.1311	−0.021	$> .1$	NS
	B	13	−0.05327	8.2656	−0.724	$.01 \gg .005$	**
	Combined	44	−0.02380	4.3315	−0.657	$< .001$	**
X_4	A	30	0.00001	1.0230	0.097	$> .1$	NS
	B	13	0.00005	1.1610	0.151	$> .1$	NS
	Combined	44	−0.00001	1.0752	−0.019	$> .1$	NS
X_5	A	29	−0.00466	1.0825	−0.256	$> .1$	NS
	B	13	0.01221	0.9919	0.223	$> .1$	NS
	Combined	43	0.00766	0.9759	0.240	$> .1$	NS
X_6	A	30	0.000003	1.0228	0.036	$> .1$	NS
	B	13	0.00015	0.8326	0.714	$.01 \gg .005$	**
	Combined	44	0.00007	0.9405	0.409	$.01 \gg .005$	**

In the type B populations, relative female and male mean SVL was significantly and negatively correlated to longitude ($.01 < p < .05$), but no significant correlation was obtained for the type A populations (Fig. 42). When all the populations were combined, there was a significant negative correlation ($p < .001$). Therefore, the more western populations were judged to exhibit greater sexual dimorphism in the mean SVL. No correlation was obtained between altitude and relative female and male mean SVL.

Annual mean temperature was not significantly correlated with relative female and male mean SVL. By contrast, there was a significant positive correlation between annual precipitation and relative female and male mean SVL in the type B populations ($.01 > p > .005$; Fig. 43). When all the populations were combined, there was a significant positive correlation ($.01 > p > .005$), and it was judged that a greater sexual dimorphism in mean SVL occurred in the regions where there was a larger amount of annual precipitation.

d) Relationships between Climatological Parameters and ACV Median of Each Character

From the results of analyses on the relations of mean SVL with each parameter, it was estimated that both sexes showed in many cases similar clinal tendencies, and climatological parameters seemed to be equally good or better predictors of the mean SVL than the geographical parameters. Consequently, in the following analyses, only adult males were used for the characters which had been determined to be separately analyzed for the three age/sex groups in the foregoing chapter. Only relations between population ACV median of each character and the climatological parameters were analyzed.

1) HL: No obvious correlation was found between annual mean temperature and median of HL ACV (Fig. 44), and correlation coefficients were in no instances significant (Table 36). By contrast, there was a significant positive correlation between annual precipitation and ACV median in the type A populations (Fig. 44). When all the populations were combined, there was a highly significant positive correlation ($p<.001$), which suggested that in the populations inhabiting areas of greater precipitation, the toads had a longer head.

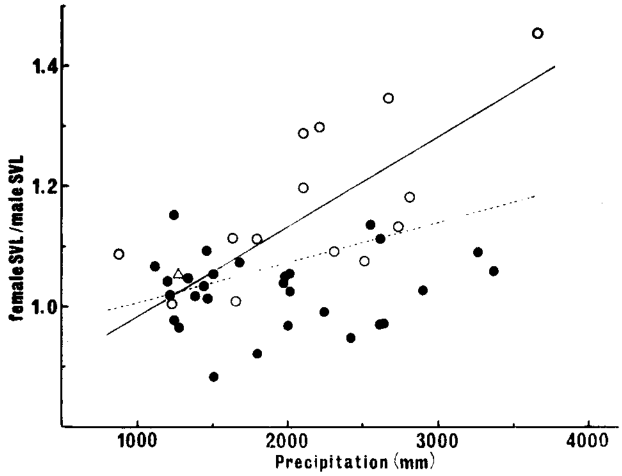

Fig. 43. Correlations between annual precipitation and relative female and male mean SVL. Notations as in Fig. 38.

2) SL: No correlation was observed between mean annual temperature and ACV median (Fig. 45). By contrast, a significant positive correlation was obtained in the type A populations between annual precipitation and SL ACV median (Fig. 45 and Table 37), and a highly significant positive correlation was obtained for the combined populations ($p<.001$). These trends were similar to those found for HL ACV median.

3) T-EL: Although the correlations between annual mean temperature and ACV median were insignificant in both the type A and type B populations (Table 38, Fig. 46), a significant positive correlation was obtained when all the populations were combined. No correlation was observed between annual precipitation and ACV median (Table 38).

4) TD: In the type A populations, a significant negative correlation was found

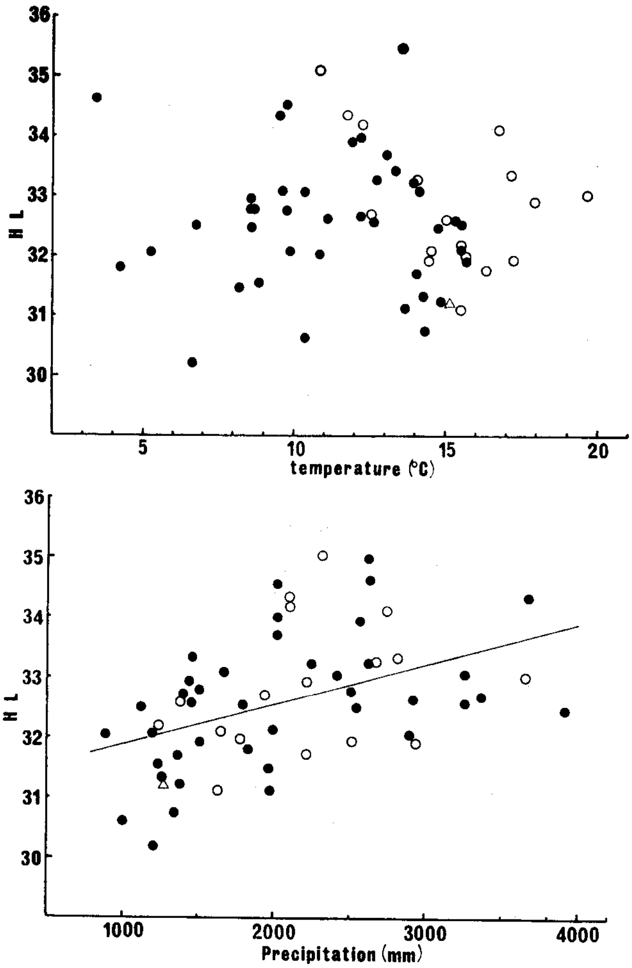

Fig. 44. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and adult male HL ACV median. Notations as in Fig. 38.

Table 36. Correlation between climatological parameters (X_5–X_6) and HL ACV median (X_1) in the Japanese common toad. Adult males. Notation as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_5	A	40	−0.01592	32.7337	−0.047	$>.1$	NS
	B	17	−0.20247	35.8972	−0.442	$.1 \gg .05$	NS
	Combined	58	−0.02128	32.8804	−0.067	$>.1$	NS
X_6	A	40	0.00068	31.1878	0.478	$.005 \gg .001$	**
	B	17	0.00050	31.7400	0.285	$>.1$	NS
	Combined	58	0.00067	31.2221	0.452	$<.001$	**

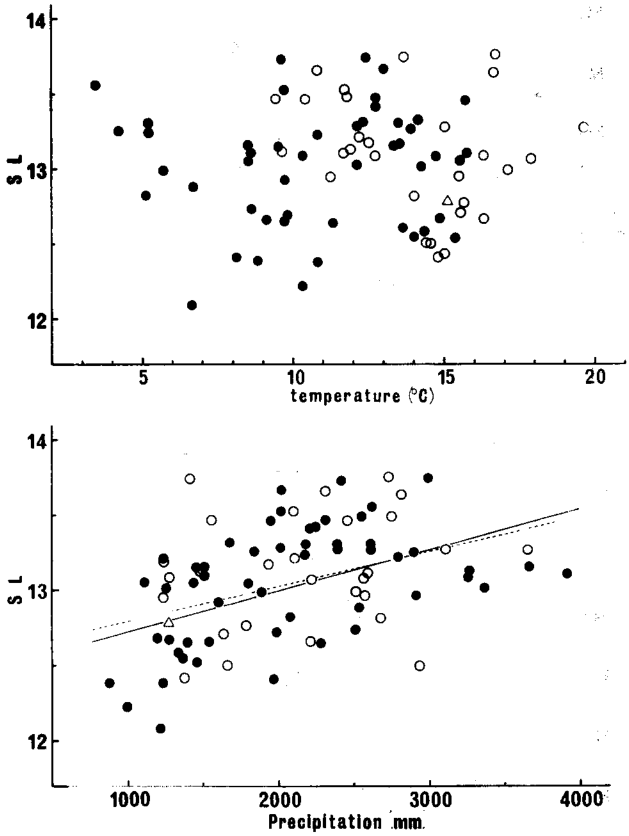

Fig. 45. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and SL ACV median. Three age/sex groups combined. Notations as in Fig. 38.

Table 37. Correlation between climatological parameters (X_5–X_6) and SL ACV median (X_1) in the Japanese common toad. Three age/sex groups combined. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$ a	b	r	p	
X_5	A	54	0.00090	13.0177	0.008	>.1	NS
	B	28	−0.03354	13.5926	−0.237	>.1	NS
	Combined	83	−0.00115	13.0712	−0.010	>.1	NS
X_6	A	54	0.00027	12.4618	0.494	<.001	**
	B	28	0.00012	12.8742	0.196	>.1	NS
	Combined	83	0.00023	12.5712	0.412	<.001	**

between annual mean temperature and ACV median, and the latter value was judged to decrease in the region where higher temperature prevailed. No significant correlation was found in the type B populations (Fig. 47). A significant negative cor-

Table 38. Correlation between climatological parameters (X_5–X_6) and T-EL ACV median (X_1) in the Japanese common toad. Adult males. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1 = aX_i + b$		r	p	
			a	b			
X_5	A	40	0.03397	2.1028	0.296	$.1 \gg .05$	NS
	B	17	−0.04991	4.4406	−0.298	$> .1$	NS
	Combined	58	0.09592	1.6551	0.503	$< .001$	**
X_6	A	40	0.00006	2.3579	0.128	$> .1$	NS
	B	17	−0.00006	3.8187	−0.093	$> .1$	NS
	Combined	58	0.00013	2.5772	0.141	$> .1$	NS

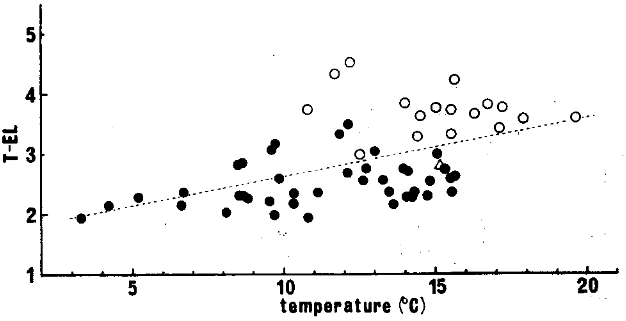

Fig. 46. Correlation between annual mean temperature and adult male T-EL ACV median. Notations as in Fig. 38.

relation ($p < .001$) was obtained when all the populations were combined (Table 39). No significant correlation was found between annual precipitation and ACV median (Fig. 47, Table 39).

5) HW: There was no correlation between annual mean temperature and HW ACV median (Fig. 48), but a significant positive correlation ($.005 > p > .001$) was found between annual precipitation and ACV median in the type A population (Table 40). Although no correlation was detected in the type B, combined populations exhibited a significant positive correlation ($.01 > p > .005$) between annual precipitation and ACV median, notwithstanding the high variance as shown in Fig. 48. These trends were the same as those found for HL and SL.

6) PL: No significant correlation was obtained between the two climatological parameters and PL ACV median (Fig. 49, Table 41).

7) PW: Between the two climatological parameters and ACV median of PW, significant correlations were found only in the type A populations (Fig. 50, Table 42). When all the populations were combined, significant correlations were found in relation to both parameters. The relationships, however, differed between the two parameters, and annual mean temperature positively, and annual precipitation negatively, correlated with ACV median. Thus, PW ACV median, in the combined populations, increased in the region where high temperature and low precipitation prevailed.

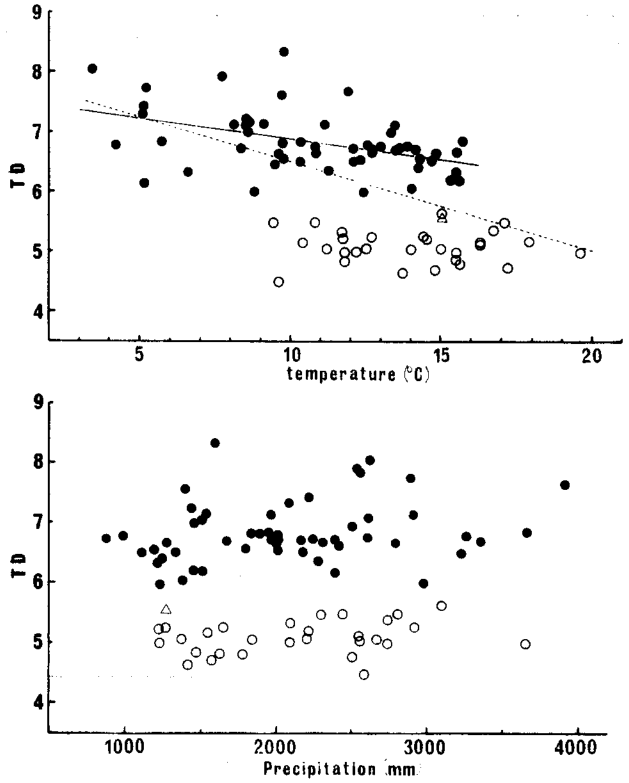

Fig. 47. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and TD ACV median. Three age/sex groups combined. Notations as in Fig. 38.

Table 39. Correlation between climatological parameters (X_5–X_6) and TD ACV median (X_1) in the Japanese common toad. Three age/sex groups combined. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_5	A	54	−0.06913	7.5634	−0.443	<.001	**
	B	28	−0.00103	5.0922	−0.010	>.1	NS
	Combined	83	−0 14825	7.9787	−0.543	<.001	**
X_6	A	54	0.00018	6.4564	0.238	.1≫.05	NS
	B	28	0.00009	4.8721	0.227	>.1	NS
	Combined	83	0.00008	6 0509	0.057	>.1	NS

8) LAL: There was a weak, but significant negative correlation between annual mean temperature and ACV (.05>p>.02) in the type A populations, but no correlation was found in the type B (Fig. 51). Further, no significant correlation was obtained for the combined populations (p>.1, Table 43). Between annual precipitation and ACV median, there was a significant positive correaltion ($p \leqq .01$) in the type A popu-

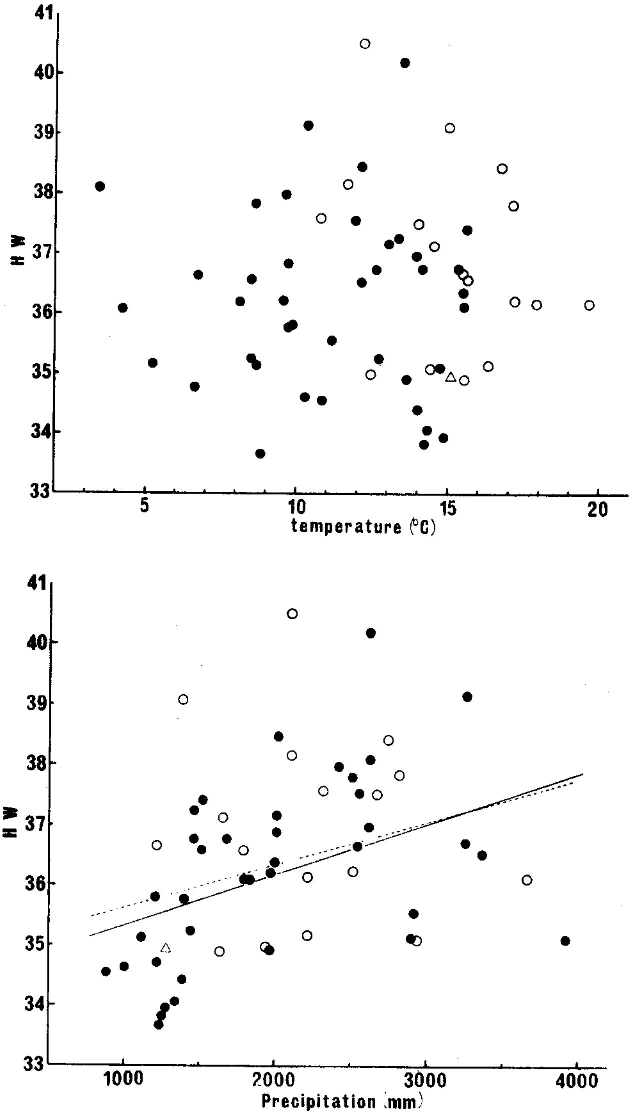

Fig. 48. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and adult male HW ACV median. Notations as in Fig. 38.

lations, and the correlation was still significant when all the populations were combined (Fig. 51).

9) TL: A significant negative correlation was found between annual mean temperature and median ACV only in the type A populations, and type B and combined populations exhibited insignificant correlations (Fig. 52, Table 44). Also, no correlation was found between annual precipitation and median ACV (Table 44).

10) FL: In the type A populations, the two climatological parameters correlated

Table 40. Correlation between climatological parameters (X_5–X_6) and HW ACV median (X_1) in the Japanese common toad. Adult males. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_5	A	40	0.00257	36.1494	0.030	>.1	NS
	B	17	−0.20469	40.0279	−0.308	>.1	NS
	Combined	58	0.00189	36.3578	0.018	>.1	NS
X_6	A	40	0.00085	34.4620	0.447	.005≫.001	**
	B	17	−0.00021	37.3989	−0.082	>.1	NS
	Combined	58	0.00071	39.9212	0.340	.01≫.005	**

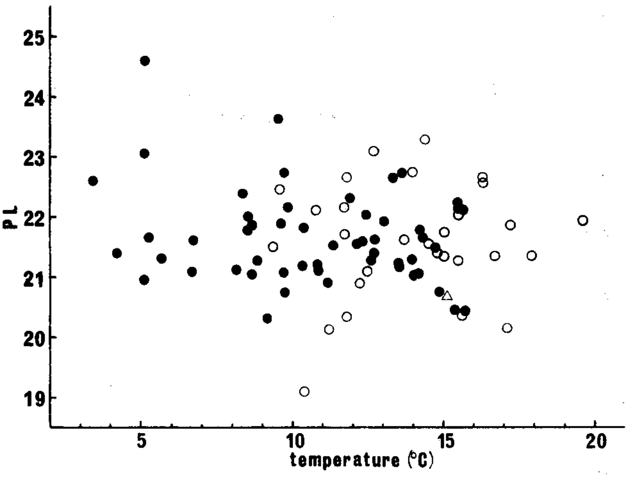

Fig. 49. Correlation between annual mean temperature and PL ACV median. Three age/sex groups combined. Notations as in Fig. 38.

Table 41. Correlation between climatological parameters (X_5–X_6) and PL ACV median (X_1) in the Japanese common toad. Three age/sex groups combined. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_5	A	54	−0.05676	22.2503	−0.238	.1≫.05	NS
	B	28	0.03383	21.1245	0.093	>.1	NS
	Combined	83	−0.03328	22.0083	−0.134	>.1	NS
X_6	A	54	0.00015	21.3334	0.131	>.1	NS
	B	28	0.00029	20.9744	0.188	>.1	NS
	Combined	83	0.00020	21.1875	0.162	>.1	NS

well with FL median ACV, but no correlation was found in the type B. When all the populations were combined, ACV median could be significantly and negatively correlated with annual mean temperature (Table 45, Fig. 53), and positively with annual

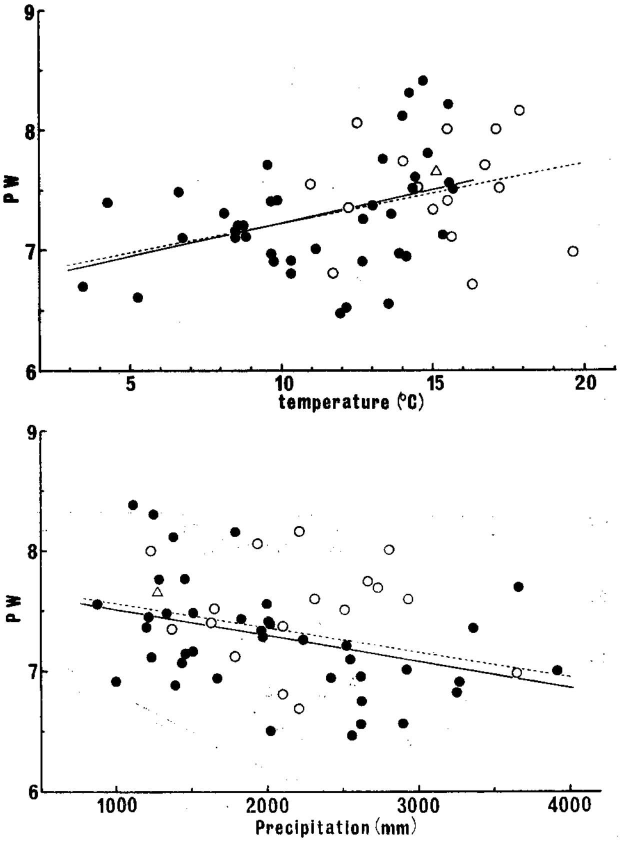

Fig. 50. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and adult male PW ACV median. Notations as in Fig. 38.

Table 42. Correlation between climatological parameters (X_5–X_6) and PW ACV median (X_1) in the Japanese common toad. Adult males. Notations as in Table 32.

Variable X_i	Type of population	N	X_1=aX_i+b a	X_1=aX_i+b b	r	p	
X_5	A	40	0.05492	6.6562	0.380	.02≫.01	*
	B	17	0.00440	7.4324	0.024	>.1	NS
	Combined	58	0.05008	6.7230	0.377	<.01	**
X_6	A	40	−0.00026	7.7827	−0.429	.005≫.001	**
	B	17	−0.00006	7.6318	−0.086	>.1	NS
	Combined	58	−0.00020	7.7512	−0.317	.002≫.001	**

precipitation (Fig. 53). These trends were the opposite of those found for PW ACV.

To sum up, the ten morphometric characters could be divided into the following four types by the relationships of ACV median to climatological parameters (annual

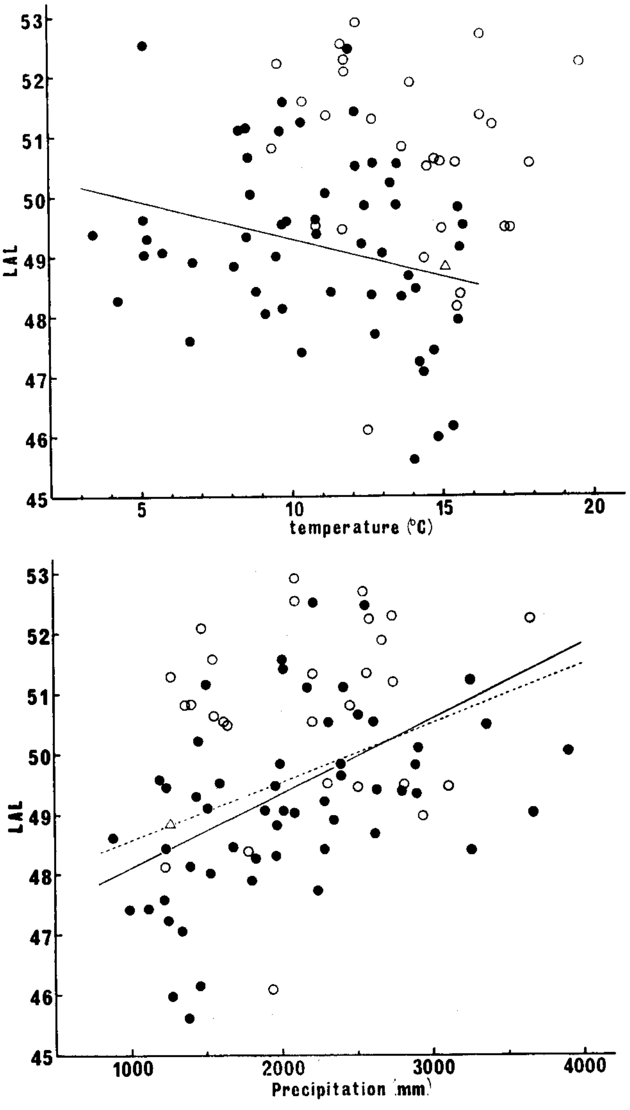

Fig. 51. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and LAL ACV median. Three age/sex groups combined. Notations as in Fig. 38.

mean temperature=X_5, annual precipitation=X_6) when both types A and B were combined:

a) PW and FL: correlated with X_5 and X_6
b) T-EL and TD: correlated with X_5
c) HL, SL, HW, and LAL: correlated with X_6
d) PL and TL: not correlated with X_5 and X_6

Table 43. Correlation between climatological parameters (X_5–X_6) and LAL ACV median (X_1) in the Japanese common toad. Three age/sex groups combined. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1 = aX_i + b$		r	p	
			a	b			
X_5	A	54	−0.12792	50.5621	−0.283	$.05 \gg .02$	*
	B	27	−0.06771	51.6359	−0.112	$> .1$	NS
	Combined	82	−0.00772	49.7705	−0.016	$> .1$	NS
X_6	A	54	0.00099	47.1275	0.465	$< .01$	**
	B	27	0.00059	49.3149	0.234	$> .1$	NS
	Combined	82	0.00096	47.6347	0.394	$< .001$	**

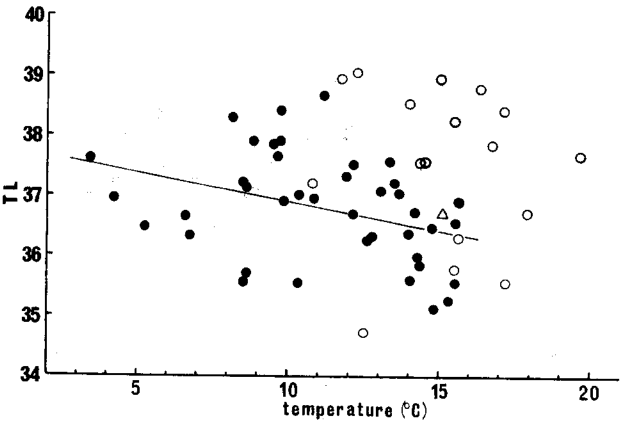

Fig. 52. Correlation between annual mean temperature and adult male TL ACV median. Notations as in Fig. 38.

Table 44. Correlation between climatological parameters (X_5–X_6) and TL ACV median (X_1) in the Japanese common toad. Adult males. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1 = aX_i + b$		r	p	
			a	b			
X_5	A	40	−0.09440	37.8703	−0.346	$.05 \gg .02$	*
	B	17	−0.05470	38.3423	−0.098	$> .1$	NS
	Combined	58	−0.01640	37.2256	−0.054	$> .1$	NS
X_6	A	40	0.00020	36.4306	0.168	$> .1$	NS
	B	17	0.00030	36.8611	0.140	$> .1$	NS
	Combined	58	0.00027	36.4799	0.178	$> .1$	NS

Table 45. Correlation between climatological parameters (X_5–X_6) and FL ACV median (X_1) in the Japanese common toad. Adult males. Notations as in Table 32.

Variable X_i	Type of population	N	$X_1=aX_i+b$		r	p	
			a	b			
X_5	A	40	−0.45970	49.8457	−0.693	<.001	**
	B	17	0.00880	45.2533	0.010	>.1	NS
	Combined	58	−0.22590	47.7186	−0.377	=.005	**
X_6	A	40	0.00082	43.0649	0.300	.05≫.02	*
	B	17	0.00096	43.2692	0.303	>.1	NS
	Combined	58	0.00087	43.1279	0.310	.02≫.01	*

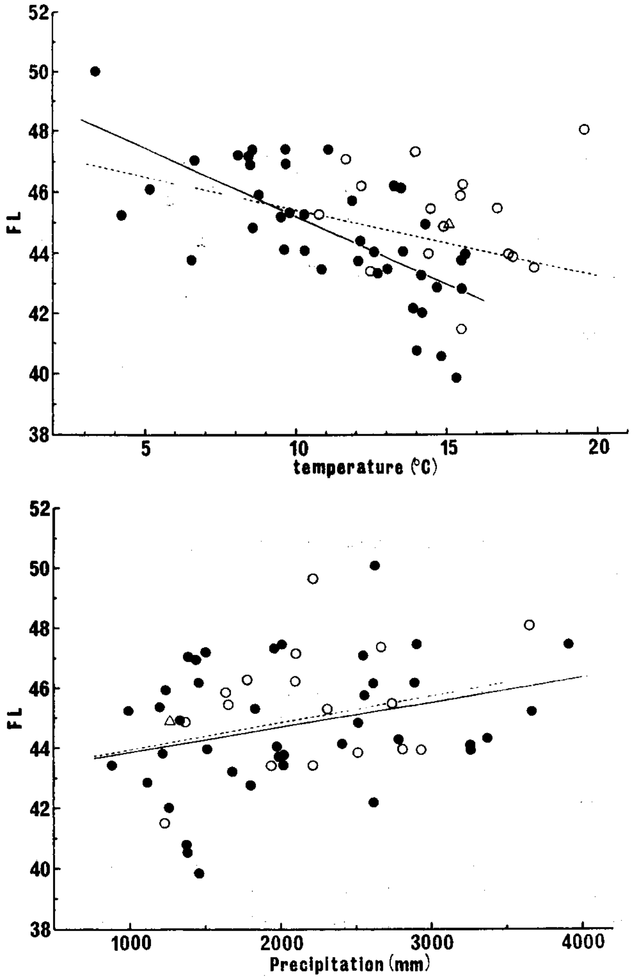

Fig. 53. Correlation between climatological parameters (Top: annual mean temperature; bottom: annual precipitation) and adult male FL ACV median. Notations as in Fig. 38.

DISCUSSION

Almost all characters correlated with at least some of the parameters in the type A populations, but only a small number of characters correlated with the parameters in the type B populations. The variation ranges of the geographic parameters were wider in type A than in type B, but the ranges of the climatological parameters were not markedly different between the two types (Fig. 54). The smaller number of type B populations might have affected the insignificant correlations of morphometric values with the parameters, but the results are so different between the two types that it is judged that there are actually different relations of morphometric values with parameters between types A and B. Therefore, the trends obtained by combining the two types are mere rough estimations for the general clinal tendencies of the Japanese common toad.

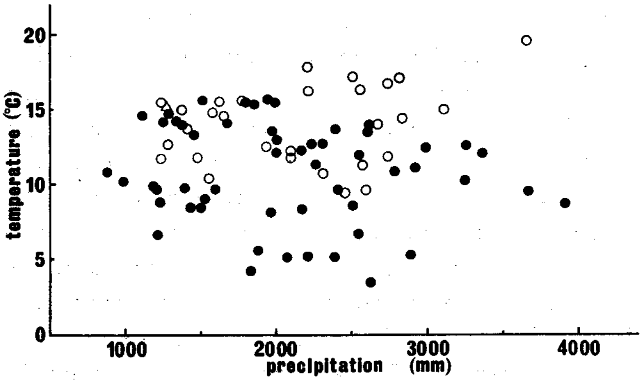

Fig. 54. Variation in the climatological parameters among populations of the Japanese common toad. Notations as in Fig. 38.

SVL: Male mean SVL correlated well with latitude and altitude, and the correlation with the former was particularly high. The relation, however, was not simple and after combining the two types, the correlation was higher in the second degree polynomial regression than in the simple linear regression. Namely, the Japanese common toad, as a whole, increased in SVL in the southern part of Japan, but in the extreme south, the SVL again decreased. Wada (1964) noted that a Japanese green frog, *Rhacophorus arboreus*, reached maximum body size at 35°N and became smaller from there southwards and northwards. Although based on rather a rough estimation, his conclusion agrees well with my results. A decrease of SVL in the regions with lower latitudes is also known for Middle American *Bufo valliceps* and *B. mazatraensis* (Porter, 1964).

In adult females, SVL correlated with all the geographic parameters and increased in more southern or western regions and in the regions of lower altitude. Schmidt (1938) and Alle et al. (1949) considered that the body size of poikilothermal animals increases as they approach to the optimum climatic conditions or to the optimum habitat. Rensch (1932) stated that the maximum size is attained in the optimum portion of the species range if factors other than the temperature affect the body size. If these theories are applied to the present results, the two sexes would seem to have different optimum climatic condition or optimum habitat. Martof and Humphries (1959) claimed that the optimum environment for increasing the body size is not always the one for increasing the number of individuals, and insisted that the optimum environment should be measured by the abundance of individuals. The sexually different geographic clines in the SVL of the Japanese common toad, thus, are not easily explained by the rather vague concept of the optimum environment.

Most of the previous authors explained body size clines in relation to temperature and/or humidity. The present report revealed that the Japanese common toad increased its body size towards lower latitudes to some extent in the male, and over the whole range in the female. Further, both sexes increased in body size at lower altitudes. These results agree well with the trends found for the European common toad, *Bufo bufo* (Schuster, 1950; De Lange, 1973), for North American *Bufo exsul* (Schuierer, 1962), and for North American *Rana sylvatica* (Martof and Humphries, 1959).

De Lange (1973) attributed the larger body size in the southern region to the longer growth period and to the growth acceleration under higher temperature. Schuierer (1962) stated that the small body size of *Bufo exsul* from the highland of California reflects adaptive selection towards a shorter growth period. The study of Martof and Humphries (1959) on *Rana sylvatica* is far more precise than the two studies on *Bufo*, but they could find only a vague cline in one part of the distribution range. They considered the small body size advantageous in the colder region because of the possibility of faster heat exchange, but they could not correlate the body size of the frog with annual mean temperature. The ambiguous results obtained by Martof and Humphries (op. cit.) may in part be due to the method they employed for elucidating the cline, i.e., splitting the wide range of distribution, a method similar to that employed for the present study. By contrast, well established clines are often found when only several points are chosen in a wide range of species distribution, or samples from several distant localities are combined to represent a sampling point (e.g., Schuster, 1950; De Lange, 1973).

There are some reports which revealed the trends opposite to the body size increase in higher temperature regions mentioned above. Kauri (1959) examined the geographic variation of the European and North African *Rana esculenta* complex, and analyzed the patterns of variation in relation to the climate. He found that the body lengths at metamorphosis and at sexual maturity are larger in the northern region or in the samples reared at lower temperatures, and thus he concluded that Bergmann's law applies to the body size cline of *Rana esculenta*. Ray (1960) experimentally examined the possibility of applying Bergmann's rule to poikilotherms, and concluded that the rule applies to the body size of amphibians, since he found that the North American *Bufo boreas* and *Rana sylvatica*, when reared at lower temperatures, become larger at metamorphosis. These two studies also indicate the prolongation of body growth at lower temperatures. Kozlowska (1971) found the body length in breeding female *Rana temporaria* from Poland larger at higher elevations, and ascribed the results to the possible higher mean age of the frogs at higher elevations.

Several studies analyzed the correlation of precipitation or humidity with body size clines. Blair and Littlejohn (1960) studied combinations of related anurans distributed in the eastern and western North America, i.e., *Pseudacris ornata*— *P. streckei*, *Acris gryllus*— *A. crepitans*, and *Bufo w. woodhousei*— *B. w. fowleri*, and found that the western representatives are larger than the eastern ones. They considered the larger body size to be adaptively advantageous for water conservation in the more xeric western region. Nevo (1972) found that the males of *Bufo viridis* from Israel increase in body length and body weight from the more humid southern coastal region towards the arid northern desert region. He considered the larger body size with relatively small evaporative body surface area to be advantageous in the arid region for enduring the longer dry season. He failed, however, to detect a significant precipitation-dependent body size cline in the female. He (Nevo, 1973) further examined the correlation of body size with ten parameters including climatic and geographic ones, in the eastern North American *Acris crepitans* and *A. gryllus*. He found that the frogs from arid regions were larger and indicated that the body length variation is best explained by the annual precipitation. He further clarified the adaptive significance of the body size increase against aridity by experimentally demonstrating higher tolerance for dessication in the larger frogs than in the smaller ones.

By contrast, Schuierer (1962) reported that in the North American *Bufo boreas*, the body size of populations from desert regions is smaller than in populations from coastal or montane regions. But he did not show the actual data.

In the present study, the SVL of both sexes of type A (more northeastern populations) exhibited highly significant positive correlation with the temperature, but no correlation was found with the precipitation. In type B (more southwestern populations), the SVL of neither sex correlated with the temperature, but the female SVL highly correlated with the precipitation. These results suggest that the body size of both sexes is directly affected by the temperature in the type A populations, but in the distribution range of type B, neither temperature nor precipitation restricts the body size. The significant correlation with precipitation in the female is a result of the influence of other unknown factors, since the trend found in the female, the body size increase with the increase of precipitation, is opposite to the trends shown by previous authors (Blair and Littlejohn, 1960; Nevo, 1972, 1973). Thus, unlike the case of North American or Israeli frogs and toads, it seems that the amount of precipitation does not so much affect the body size of the Japanese common toad as to select the larger individuals to survive. The mean annual rainfall ranges from 100 to 850 mm in the habitats of *Bufo viridis* in Israel (Nevo, 1972), and even the wettest area has less precipitation than in the range covered by the Japanese common toad (annual precipitation of more than 878 mm). The lack of correlation of male body size with precipitation in the type B populations also suggests the effect of factors other than climate on body size. The fact that the region where the male Japanese common toad reaches maximum body size approaches the overlap zone with the Japanese stream toad should be also noted. The interspecific relations of the toad body size are discussed elsewhere in the following chapter.

Relative female and male mean SVL: The sexually different clinal trends in the body size naturally affect the clines in the relative female and male mean SVL. To date, only Martof and Humphries (1959) mentioned the relative female and male body size cline in anurans. They found in *Rana sylvatica* that the relative female and male body size increased in parallel with the increase in body size of both sexes towards southern regions of the distribution range. Their results cannot be directly compared with mine since they did not give concrete data, but they are in agreement with mine at least in that the relative female and male body size increases in the southern region and regions where the female increases in body size.

The present study revealed the presence of completely different relative female and male mean SVL clines between types A and B. In the type B populations, the female/male SVL ratio became extremely greater towards the south. The known body size growth pattern in the Japanese common toad indicates a remarkable growth up to the time of sexual maturity and a subsequent decrease in the growth rate. It is also known that the females mature sexually more than one year later than the males. On the basis of this information, the uniformly small body size in the southern male toads seems to suggest that these toads mature sexually and almost cease growth when they are still small.

By contrast, the large size in the southern females seems to suggest that they become sexually mature and decrease in growth rate after they have attained a large size. Namely, a difference in the body size growth curves between the two sexes is suggested. Further, the sexually extremely different mean SVL, which is thought to approximate the body size at the time of sexual maturity, seems to suggest a difference in the time of sexual maturity between the two sexes.

In the southern distribution ranges of the Japanese common toad, the temperature and the precipitation probably do not act to inhibit growth, and the longer growth period is likely to act to increase the growth of the toad unless there are other inhibitory factors. The large size in the female would be the result of such a condition, but the male would mature sexually and cease growth at a rather early period in its life. The difference of one year in the time of maturity in the two sexes will act to strengthen the sexual difference in the body size of the southern populations more effectively than in the northern populations. Further, the breeding period tends to be longer in the southern populations (e.g., November to March in Yakushima and Nagasaki: Matsui, 1979a; Nakamura, 1934); and in such conditions, it is probable that the males tend to stay longer at the breeding sites and have more chance to be attacked by enemies than the females, which generally stay at the breeding site only a few days. Consequently, it is expected that the mortality in the breeding males would be higher in the southern populations than in the northern ones, resulting in the fact that the male breeding population is composed of younger generations (generally based the collection for the present study).

The adaptive significance of the geographic cline of the relative female and male mean SVL is to date unknown. Licht (1976) argued that the difference in optimum body size between the two sexes permits effective amplexus and fertilization in *Bufo americanus*. Davies and Halliday (1977) found that, in *Bufo bufo* from Oxford, England, the male body size differed before and during fertilization, and was larger in the latter case. They experimentally demonstrated lower fertility in the combination of smaller male and larger female and considered that a higher fertilization rate was maintained by non-random pair formation. Likewise, Gittins et al. (1980) reported pair formation by larger males in the same species from mid-Wales, although pair formation was already determined before fertilization in this population, probably due to much stronger male competition for females than in Oxford.

These reports indicate a lower fertility rate for the smaller male and larger female pair, but the sexual difference in the body size is far smaller than that found in the type B populations from Southern Japan. Therefore, if we admit the results obtained for *Bufo bufo* from England, it follows that the southern populations of the Japanese common toad would have very low fertilization rates. There are negative data for the correlation of sexual differences in body size and fertility rate (Kruce, 1981), and as far as I have observed in the field, there seem to be no remarkably unfertilized egg masses at the breeding sites of the type B populations. The marked sexual difference in the body size of the southern populations might be related to the life of the metamorphosed toads (e.g., possible sexual segregation in food uptake) rather than to reproductive strategy.

ACV clines: Compared with studies of the body size, rather few reports have correlated the size of anuran body parts with climatological parameters. Among the characters showing general shape of the head, HL, SL, and HW, increased in size with the increase of precipitation, but no correlation was found with temperature. Ruibal (1957) examined the shape of the snout in the widespread North American *Rana pipiens* (currently divided into several distinct species) and found that relative bluntness of the snout was expressed as a function of latitude and altitude and was better correlated with environmental temperature; i.e., the snout became blunter in cooler regions. According to him, similar clines were observed in some other species of *Rana* found in the same area. The results of the present study do not coincide with Ruibal's observations, and the difference might be due either to the difference in the measured reference points or to the generic difference between *Rana* and *Bufo*. Ruibal (1957) did not mention precipitation.

The results of the present work show a relatively small head in the regions of less precipitation, and this trend can be interpreted as an adaptation to diminish water loss in the more arid regions by decreasing the surface of protruding parts of the body.

Among the four characters in the posterior part of the head, PL exhibited insignificant correlation with climatological parameters. Blair (1941) could not find geographic clines for PL and PW in *Bufo fowleri* and *B. americanus* distributed in the eastern part of the U.S.A. Since the geographic sequence he studied seems to represent temperature and/or precipitation gradation to some degree, his result is thought to show the lack of climatic clines in PL and PW in the two toad species. Consequently, my results regarding PL coincided with Blair's observations. Regarding PW, however, my results contradicted those of Blair, and ACV median correlated positively to temperature and negatively to precipitation. The function of the parotoid gland is considered to be restricted to protection from enemies, and it seems difficult to functionally interpret the significant correlation of PW with climatological parameters, although PL exhibited no such correlation. Further, a larger PW in regions where lower precipitation prevails seems to contradict the adaptive significance interpreted for HL, SL, and HW. The occurrence of larger PW in the warmer and more arid regions of Japan, however, coincides well with the situation in most of the toad species of the broad-skulled type (Martin, 1972), which are distributed in hot and arid regions and possess a broad parotoid as represented by *Bufo marinus*. As discussed later, the climatic clines found in PW can be interpreted to have adaptive significance in relation to FL.

Two characters, TD and T-EL, were utilized to separate the Japanese common toad into two types, A and B. When each of the two types was separately analyeed, only TD of type A showed negative correlation with temperature, and in neither type A nor type B did T-EL exhibit climatological clines (i.e., ACV was almost constant in each group). After combining the two groups, however, both TD and T-EL could be correlated with temperature. As already stated, T-EL and TD have an antagonistic size relation from their topology. Reflecting this relation, T-EL showed a positive, and TD a negative, relation to temperature. Whether or not such clinal tendencies are general in anurans cannot be assessed, since no study has been made on the cline of the tympanum size.

In general, the absolute size of the anuran tympanum increases in proportion to the body size (see chapter III of this paper), and the larger anurans (hence with larger tympanum) are said to have higher sensitivity and, by better impedence adjustment and more efficient transmission to the mid-ear, have less cut-off for higher frequency sound than the smaller ones (with smaller tympanum) (Martin, 1972). On the other hand, Capranica (1976: 447) could find neither sexual nor age differences in sensitivity in electrophysiological recordings from the VIII nerve of *Bufo* sp. and *Rana catesbeiana* and has stated that the functional significance of tympanum size variation is unknown.

If the assumption that a larger tympanum has better sensitivity is correct, some adaptive significance could be found in the climatic cline which shows a larger tympanum in colder regions. Both sexes of the Japanese common toad have smaller body size in the colder regions. The call frequency of the Japanese common toad, as in other bufonid toads (Zweifel, 1968; Nevo and Schneider, 1976), has little correlation with the temperature, but is negatively correlated with body size (Matsui, 1980f). Consequently, in smaller toads, emitting a higher frequency sound would be more advantageous for effective aggregation at the breeding site, if they had larger tympanums. Indeed, the breeding season in the colder regions is more delayed and at the same time much shorter than in the warmer regions. Further, in extremely delayed breeding seasons, as in high mountains of the Tohoku region, several anuran species breed together at one breeding site. In such cases, it is highly probable that the role of the mating call, though usually considered to be unimportant for species recognition in lower or warmer regions, is more important, and the relatively large tympanum seems to be advantageous in this respect.

On the other hand, the cline obtained in the combined populations indicated decrease of the male mean SVL in the much warmer southern region. The combined cline for TD showed that the tympanum was relatively small in this region, and this condition may be regarded as less advantageous for effective breeding aggregation. In this warmer region, however, the breeding period is long, and aggregation at a time of a large number of individuals is supposed to be less important than in colder regions. Further, the fact that type B populations, when not combined with type A, did not exhibit the clinal tendency in TD indicates a relatively constant tympanum size in contrast to the decrease in body size. From this fact, the selection, which would be expected to act effectively in the colder regions, seems to compensate the disadvantage due to decrease in body size, though in a weaker way than in the colder regions.

The climatic cline in T-EL might be largely explained in relation to TD, but the inconstant sum of the regression lines of T-EL and TD clearly indicates that T-EL is not wholly dependent on TD.

Among the characters of the limbs, LAL and FL showed climatic clines, whereas TL exhibited significant correlation with temperature only in type A, and no climatic cline was found when the two types were combined. This is an unexpected result, since in previous works in which the applicability of Allen's rule to the anurans was tested, the length of the tibia was most thoroughly investigated, and most of the published data report that the relative tibia length becomes shorter in the regions of higher latitude and lower altitude (Schmidt, 1938; Schuster, 1950; Kauri, 1959; Martof and Humphries, 1959; Ray, 1960; Terent'ev, 1962). This trend is not limited to the Bufonidae (*Bufo boreas* and *Bufo bufo*), but is also found in the Hylidae (*Pseudacris septentrionalis*) and Ranidae (*Rana sylvatica*, *R. temporaria*, *R. arvalis*, *R. pipiens*, *R. esculenta* complex, *R. nigromaculata*). The only exception, reported by Kauri (1964) for *R. esculenta* from Sweden, indicated the shorter tibia under higher temperature, but this result was obtained for experimentally reared frogs and is regarded as an abnormal condition due to temperatures higher than the optimum limit. Schuster (1950) found a north-to-south increase of limb part proportions in European *Bufo bufo*, and reported that the trend was more prominent in the tibial than in the tarsal portion including FL. Therefore, the absence of correlation between temperature and TL in the combined Japanese common toad populations seems to indicate the presence of a subtle difference in the adaptation to the environment between types A and B. The weak negative correlation of TL with temperature observed in type A is in agreement with the experimantal case reported by Kauri (1964), and is opposite to the generally reported trend mentioned above. The trend found in type A is also in agreement with that found in FL.

Whether or not the larger LAL in the regions with more precipitation is a general phenomenon is undetermined, since no comparable data are available, but, like the characters of the head region, the trend can be regarded as adaptive for preventing evaporation in the more arid regions. At the same time, the shorter LAL would be advantageous for hiding under the ground in the more arid regions.

A similar interpretation can be made for FL. Blair and Littlejohn (1960) observed a parallel phenomenon among *Bufo, Pseudacris*, and *Acris* distributed in the U.S.A., in which each of the eastern representatives had larger foot than the corresponding western relative. They suggested that the shorter foot in the more arid western region was a surface-to-mass phenomenon in relation to water conservation. Nevo (1973) reported that the relative foot length in the eastern North American *Acris crepitans* was correlated with the complex factors of humidity, precipitation, longitude, and the number of sympatric frog species. He concluded that foot length was related to predation pressure and/or competition for food, rather than to a single climatological parameter, and that the relatively long FL was an adaptation for efficient jumping.

The present study indicated a longer FL in regions with lower temperature and greater precipitation. In such regions there is heavy snowfall, and the longer FL seems to reflect the need for more effective activity in a shorter active season. As already stated, males have more developed feet than young and females, and this may indicate that the longer foot may be particularly significant in the male reproductive activity. The Japanese common toad has few opportunities to swim during non-breeding seasons, and its locomotion depends on walking rather than hopping or jumping (Matsui, 1978a). Further, it seldom occupies the same niche with other frog species. Thus, the adaptive significance of a longer FL suggested by Nevo (1973) seems to be not always applicable in the case of the Japanese common toad.

The tendency in the climatic cline for FL was opposite to that found for PW: i.e., FL increased in the colder and wetter regions, whereas PW increased in warmer and drier regions. This seems to suggest the compensative significance of the two characters for escaping from enemies. Possibly, the toads with a longer foot will jump away, whereas those with a wider parotoid will sit still and protect themselves by gland secretion. Further, it is easily imagined that the shorter foot is advantageous for digging to prevent desiccation in regions of less precipitation. Similar considerations have been made for African toads inhabiting deserts and regions with a long dry season (Tandy and Keith, 1972).

Cline and taxonomy: In conclusion, most of the morphometric characters examined in the Japanese common toad, as a whole, exhibited geographic and/or climatic clines. This seems to indicate an adaptive significance for each character, but the degree of adaptation seems to be stronger in type A than in type B. The relation of morphological clines found in animal groups and their taxonomic relationships has long been discussed, and generally, groups of animals exhibiting a single cline cannot be divided into separate taxonomic units (Bogert, 1954; Trueb, 1968). Some authors divide such groups into different taxa by the presence of more than two clines. Imaizumi (1970: 189), for example, was of the opinion that the populations of a single species always form a single cline in some characters, and therefore, if characters of one population do not fit the well established clines of the species, the exceptional population should be regarded as belonging to another species. On the other hand, at least in the taxonomy of anurans, the system that does not recognize different species, or even subspecies, when the characters of combined populations show a single cline, often leads to unreliable taxonomic conclusions. For example, Kauri (1959) and Terent'ev (1962) lumped the formerly named taxa included in the European *Rana esculenta* complex, after confirmed a single cline in each character of examined populations. At the present, however, the complex is known to include two distinct species and their hybrids (Günther, 1979). Consequently, both the system of attributing different clines to species differences (Imaizumi, 1970) and the system of not recognizing the different taxa for an observed single cline (Kauri, 1959; Terent'ev, 1962) are two extremes. For taxonomic decision morphological clines should be treated carefully, combining all the data from every source.

In the Japanese common toad, the clinal differences found between types A and B are insufficient requisites for recognizing two distinct species, but at the same time the observed differences would indicate that it is inappropriate to regard them as a single taxon. Accordingly, it would seem reasonable to rank the two types as different taxa below the species level, i.e., races or subspecies.

VI

Morphometric Variation in the Miyado Toad

Members of the genus *Bufo* are absent in the larger part of the Southwestern Islands between Yakushima Isl. and Taiwan, and in this region, toads have long been reported only from Miyakojima Is. In addition, the occurrence of toad species in the Daitojima islands has recently been reported (Matsui, 1975b; Ikehara and Shimojana, 1975).

The toad occurring in Miyakojima Is. was named *Bufo bufo miyakonis* by Okada (1931), and has been treated as a different species from the Japanese common toad (*Bufo vulgaris* ssp.) distributed in the regions from Yakushima Is. northwards and the Bankoro toad (*Bufo bankorensis*) in Taiwan. Later authors, however, considered the occurrence of the Miyako toad in Miyakojima Is. as artificial, and regarded this form as a subspecies identical with the Chinese common toad (Inger, 1947, 1950; Nakamura and Uéno, 1963).

I provisionally analyzed morphological variation of the Miyako toad from Miyakojima with emphasis on the postmetamorphic ontogeny (Matsui, 1974b). In the present study, morphometric variation of the population from Miyakojima Is., as well as of the populations artificially introduced into other islands, are further investigated. The results thus obtained are compared with the patterns of variation found in the Japanese common toad, and the systematic relationship of the Miyako toad with the Japanese common toad is briefly discussed.

MATERIALS AND METHODS

The localities and sample sizes for four populations of a total of 176 Miyako toads are shown in Table 6. The samples composing Pop. 100 (Okinawajima) are American Museum of Natural History collections (AMNH 6329–6334) from Nago. Introductions of the Miyako toad from Miyakojima into Okinawajima, were reported to have been made between 1934 and 1937 (Yashiro, 1938), and the introduced populations are reported to have increased in number for some time (Takashima, 1954), but the establishment of further stable populations seems to have been unsuccessful.

The allomorphic relations between SVL and ten morphometric characters were examined for the pooled 63 individuals (23 young, 20 adult males, and 20 adult females) from Miyakojima (Pop. 97), and ACV of each character for each individual toad was calculated from the allomorphic constants thus obtained.

In comparing intra- and interpopulation variations, as well as in the comparison with the Japanese common toad, only age/sex groups with a sample size of three or larger were considered. Statistic procedures were the same as those utilized for the analyses of the Japanese common toad.

RESULTS

1. SVL

1) Variation in the mean SVL

The population mean SVL of the three populations ranged from 80.7 mm (Pop. 99) to 90.3 mm (Pop. 98) in adult males, and the mean of the population means was 84.71±5.76 mm. The largest population mean was 1.12 times larger than the smallest.

The mean SVL of four populations ranged from 87.7 mm (Pop. 99) to 105.0 mm (Pop. 98) in adult females; the largest was 1.20 times larger than the smallest, and the mean for population means was 96.73±7.84 mm.

Of the three comparable populations, two (66.7%) showed sexual dimorphism in mean SVL ($p<.05$), but the difference in the mean of population means was not significant between the two sexes ($t=2.30$, $dF=5$, $.1>p>.05$). Females were not regarded as being larger than the males probably due to the small number of sampled populations.

The mean SVL of adult males showed a significant difference between Pop. 98 and Pop. 99, but these two populations were linked by the intermediate value of Pop. 97.

Of the six possible combinations among four populations in adult females, three were significantly different (Pop. 97 vs. Pop. 99; Pop. 99 vs. Pop. 98; Pop. 99 vs. Pop. 100), but all the populations were bridged by the overlap of intermediate populations.

2) Variation in the minimum SVL

Among 71 adult males from four populations, the smallest individual was found in Pop. 97, and was 61.3 mm in SVL. The smallest adult female among 71 individuals of four populations was also found in Pop. 97, measuring 77.0 mm (Table 46).

The mean of the population minimum SVLs was 73.0±14.81 mm for males and 88.63±5.74 mm for females. The difference was insignificant ($t=17.60$, $dF=5$,

Table 46. SVL (in mm) variation in adult Miyako toads.

Population	adult males						adult females					
	N	SVL					N	SVL				
		range	X̄	SD	2SE	CV		range	X̄	SD	2SE	CV
97	43	61.3–113.2	83.2	10.9	3.3	13.1	56	77.0–119.0	92.9	10.4	2.8	11.2
98	5	86.7–100.7	90.3	6.0	5.4	6.7	5	99.6–110.9	105.0	5.4	4.8	5.1
99	21	71.0– 95.2	80.7	6.1	2.7	7.6	7	82.2–102.0	87.7	6.9	5.2	7.9
100	2	79.2– 81.3	80.3				3	95.7–105.2	101.3	5.0	5.7	4.9

$.2 > p > .1$), and both sexes were regarded as having the same minimum SVL.

3) Variation in the maximum SVL

Among 71 adult males from four populations, the largest individual was found in Pop. 97, and was 113.2 mm in SVL. The largest adult female among 71 specimens of four populations was also found in Pop. 97 and had an SVL of 119.0 mm (Table 46).

The mean of the population maximum SVLs was 103.03 ± 10.65 mm for males and 109.28 ± 7.46 mm for females. The difference between these means was statistically insignificant ($t = 1.00$, $dF = 5$, $.4 > p > .2$), and no sexual dimorphism in maximum SVL was detected.

4) SVL difference between the Miyako toad and Japanese common toad

In adult males, some populations of the Miyako toad were similar in mean SVL to several Japanese common toad populations which have small SVLs, and each of the three populations of the Miyako toad was not different from 2–10 of 58 Japanese common toad populations in mean SVL.

The mean of population mean SVLs, 84.71 ± 5.76 mm for the Miyako toad, however, was significantly smaller ($p < .01$) than that for the 58 populations of the Japanese common toad (116.29 ± 4.40 mm), and the means of the minimum and maximum SVLs were also significantly smaller in the Miyako toad ($p < .05$ and $p < .01$, respectively). Thus, the Miyako toad was regarded as being smaller than the Japanese common toad in the SVL of adult males.

In adult females, the mean SVL of each of the four populations of the Miyako toad was not different from that of 2–16 of 50 populations of the Japanese common toad. However, the mean of population mean SVLs (96.73 ± 7.84 mm) was significantly smaller ($p < .01$) than that of the Japanese common toad (126.70 ± 5.11 mm). The means of minimum and maximum SVLs were also significantly different between the two forms ($p < .01$). Therefore, like males, adult females of the Miyako toad were judged to have smaller SVLs than those of the Japanese common toad.

2. *Allomorphic Variation*

a) *Difference in the Allomorphic Constant between the Miyako Toad and the Japanese Common Toad*

Populations other than Pop. 97 contained an insufficient number of samples for the analysis of allomorphic variation, and the allomorphic relationship of each of the 10 characters to SVL in Pop. 97 was examined and compared with that obtained for the Japanese common toad (Table 47).

For HL, SL, LAL, TL, and FL, the allomorphic constant for Pop. 97 was within the variation range of the Japanese common toad. For T-EL, the allomorphic constant of Pop. 97 ($\alpha = 0.800$) was generally smaller than that of the Japanese common toad populations, but was insignificantly different from the smallest α value of the Japanese common toad ($\alpha = 0.945$, Pop. 16; slope: $F_{1,106} = 2.48$, $p > .05$; position: $F_{1,107} = 20.56$, $p < .01$). The allomorphic constant of TD in the Miyakojima population ($\alpha = 0.810$) was smaller than the smallest value in the Japanese common toad populations (Pop. 88, $\alpha = 0.977$), and there were significant differences in slope and position between these two populations (slope: $F_{1,105} = 8.41$, $p < .01$; position: $F_{1,106} = 12.99$, $p < .01$). Thus,

Table 47. Allomorphic constants (α) and initial growth indices (B) for regression of each morphometric character—SVL in the Miyako toad from Miyakojima. Three age/sex groups combined. Growth type abbreviations are: I=isomorphosis, B=bradymorphosis.

Character	N	$\alpha \pm$SD	log B	r	Growth type
HL	60	0.873±0.020	−0.264	0.985	B
SL	60	0.865±0.025	−0.647	0.976	B
T-EL	63	0.800±0.057	−1.157	0.875	I
TD	63	0.810±0.054	−0.983	0.887	B
HW	60	0.932±0.031	−0.305	0.970	I
PL	60	0.964±0.054	−0.687	0.919	I
PW	63	0.986±0.053	−1.155	0.921	I
LAL	60	0.934±0.038	−0.216	0.954	I
TL	60	0.954±0.031	−0.382	0.971	I
FL	60	0.972±0.042	−0.369	0.950	I

the north to south decrease in α value found in the Japanese common toad populations was further strengthened in the Miyako toad.

For HW, the allomorphic constant of Pop. 97 (α=0.932) was insignificantly different from the smallest value (α=0.937, Pop. 63) of the Japanese common toad (slope: $F_{1,202}=0.02$, $p>.05$; position: $F_{1,203}=1.43$, $p>.05$). The α value for PL in the Miyakojima population (α=0.964) was within the variation range of the Japanese common toad, but was closer to the values for northern populations of the latter form (Pop. 8: α=0.960; Pop. 16: α=0.975) than to those of southern populations, contrary to the cline found among the populations of the Japanese common toad. For PW, the α value of Pop. 97 (α=0.986) was insignificantly different from that of Pop. 96 (α=0.934), which was the largest in the Japanese common toad populations (slope: $F_{1,93}=0.21$, $p>.05$; position: $F_{1,94}=0.67$, $p<.01$).

b) Growth Gradient Variations

Marked deviation from the populations of the Japanese common toad was found in the Miyako toad. First of all, α values of T-EL (α=0.800) and TD (α=0.810) were much smaller than those of SL (α=0.865) and PL (α=0.964) in Pop. 97, strongly contrasting to the condition in the Japanese common toad. The relation in α value between T-EL and TD was similar to that of type A populations of the Japanese common toad, whereas the relation between TD and PL resembled that of type B populations. Further, the α value of PW (α=0.986) was slightly larger than those of HW (α=0.932) and LAL (α=0.934) in the Miyako toad. This is also opposite to the condition that prevails in the Japanese common toad.

3. Variation in ACV for Each Character

a) Variation in ACV for Each Character

1) HL: Among 26 young, both the smallest and the largest ACVs, 27.9 and 33.0, respectively, were exhibited by individuals from Pop. 97, and the largest value was 1.18 times larger than the smallest. Only the data for this population were adequate for the analysis, and the median for the population was 30.6 (Table 48).

Of 39 adult males, the smallest ACV, 28.3, was for an individual from Pop. 97, and

Table 48. Variation in ACV of the Miyako toad. Three age/sex groups separated.

Character	Population	young			adult males			adult females		
		N	ACV		N	ACV		N	ACV	
			range	median		range	median		range	median
HL	97	25	27.9–33.0	30.6	25	28.3–31.2	30.0	41	27.8–32.9	30.6
	98				5	29.5–31.8	30.7	5	29.0–32.1	29.9
	99				7	29.5–31.8	30.7	1		30.0
	100	1		31.3	2	29.0–29.9	29.5	3	29.9–31.0	30.6
T-EL	97	32	2.0– 3.3	2.8	31	2.0– 3.4	2.8	51	2.2– 3.8	2.8
	98				5	2.4– 3.2	2.6	5	2.2– 3.1	2.7
	99				21	2.2– 3.8	2.8	7	2.5– 3.7	3.1
	100	1		2.9	2	2.3– 2.4	2.3	3	2.3– 3.6	2.9
HW	97	32	33.2–43.2	36.3	35	30.6–38.8	35.7	53	33.3–40.5	36.6
	98				5	34.1–37.8	36.3	5	34.6–38.8	36.1
	99				8	33.7–38.1	35.1	2	33.9–34.8	34.3
	100	1		37.9	2	35.0–36.1	35.6	3	36.7–38.3	37.3
PW	97	32	4.5– 8.4	6.5	31	5.0– 7.8	6.4	54	5.5– 8.0	6.6
	98				5	6.0– 8.3	7.1	5	6.5– 7.4	6.9
	99	1		6.6	21	5.4– 7.8	6.4	7	5.6– 6.7	6.3
	100	1		7.2	2	6.5– 7.2	6.9	3	5.4– 7.8	6.9
TL	97	20	30.6–36.4	32.7	20	32.3–39.1	35.0	20	31.0–34.4	33.0
	98				5	34.9–37.7	36.8	5	31.8–33.9	33.5
	99	1		30.4	21	31.5–36.9	34.6	7	30.7–33.6	32.3
	100	1		33.2	2	32.2–34.1	33.1	3	32.1–34.8	33.4
FL	97	20	33.1–40.5	36.7	20	36.1–45.5	39.2	20	34.4–38.4	35.6
	98				5	41.0–43.8	42.3	5	34.4–38.3	35.3
	99	1		37.0	21	35.9–45.4	40.2	7	34.8–37.9	36.5
	100	1		38.1	2	38.4–39.1	38.8	3	35.4–40.0	36.3

the largest 31.8, was for ones from Pops. 98 and 99. The latter value was 1.13 times larger than the former. In the three well represented populations, the smallest median, 30.0, was shown by Pop. 97, and the largest, 30.7, by Pops. 98 and 99. The largest value was 1.03 times the smallest.

Of 50 females, both the smallest ACV, 27.8, and the largest, 32.9, were exhibited by individuals from Pop. 97. The largest value was 1.18 times larger than the smallest. Population medians varied from 29.9 (Pop. 98) to 30.6 (Pops. 97 and 100), and the latter value was 1.02 times the former. Thus, among a total number of 115 individuals, the largest ACV was 1.19 times larger than the smallest value.

Neither age nor sexual difference in ACV was found in Pop. 97. Adequate samples for ontogenetic comparisons were not available for other populations, but no sexual dimorphism was found in Pop. 98, either. Interpopulation differences in medians were detected neither in adult males nor in adult females.

2) SL: Among 135 individuals, both the smallest and the largest ACVs were exhibited by individuals from Pop. 97, and were 10.8 and 13.6, respectively (Table 49).

Table 49. Variation in ACV of the Miyako toad. Three age/sex groups combined.

Character	Population	N	ACV range	ACV median	Character	Population	N	ACV range	ACV median
SL	97	109	10.8–13.6	12.2	LAL	97	45	40.1–49.6	44.7
	98	10	11.8–12.9	12.2		98	10	44.1–49.2	45.9
	99	10	11.5–13.2	12.1		99	29	40.7–50.9	43.8
	100	6	11.8–12.9	12.5		100	6	43.6–48.6	45.5
TD	97	124	3.2– 5.5	4.3					
	98	10	3.5– 4.9	4.6					
	99	28	3.3– 5.4	4.5					
	100	6	3.8– 5.9	5.4					
PL	97	109	14.4–21.1	17.3					
	98	10	14.3–19.7	16.3					
	99	29	14.5–21.0	18.0					
	100	6	12.7–19.7	16.8					

The largest ACV was 1.26 times larger than the smallest.

Medians for four populations varied from 12.1 (Pop. 99) to 12.5 (Pop. 100). The largest median was only 1.03 times larger than the smallest. Interpopulation difference was not detected among six combinations of four populations.

3) T-EL: Thirty-two young of Pop. 97 had ACVs ranging 2.0–3.3, and an individual from Pop. 100 had the value within this range. The largest value was 1.57 times larger than the smallest. The median for the young of Pop. 97 was 2.8.

Of 59 adult males, the smallest ACV, 2.0, was for an individual from Pop. 97, and the largest value, 3.8, was for one from Pop. 99. The latter value was 1.87 times larger than the former. Medians for the three populations ranged from 2.6 (Pop. 98) to 2.8 (Pop. 99). The latter value was 1.07 times the former.

ACV for 66 adult females ranged from 2.2 to 3.8. Both of these values were found for individuals from Pop. 97, and the largest was 1.77 times larger than the smallest. Medians for the four populations ranged from 2.7 (Pop. 98) to 3.1 (Pop. 99). The largest value was 1.16 times the smallest. Thus, among 157 individuals, the largest ACV was 1.91 times larger than the smallest. Intrapopulation and interpopulation variation analyses revealed the absence of differences in all combinations.

4) TD: Among 168 individuals, the smallest ACV, 3.2, was exhibited by an individual from Pop. 97, and the largest, 5.9, by one from Pop. 100 (Table 49); the largest value was 1.83 times larger than the smallest.

The medians for the four populations ranged from 4.3 for Pop. 97 to 5.4 for Pop. 100, the largest value being 1.25 times larger than the smallest.

The result of the interpopulation comparisons of ACVs revealed only one significant difference out of six possible combinations: Pop. 100 had a significantly larger median than Pop. 97 ($U_{6,20}=20$, $p<.05$).

5) HW: Among 33 young, both the smallest and the largest ACVs, 33.2 and 43.2, respectively, were exhibited by individuals from Pop. 97 (Table 48), and the

largest value was 1.30 times larger than the smallest. The median ACV for Pop. 97 young was 36.3.

Of 50 adult males, the smallest ACV, 30.6, and the largest, 38.8, were found for individuals from Pop. 97, and the latter value was 1.27 times the former. Among the three populations, the smallest median, 35.1, was for Pop. 99, and the largest, 36.3, was for Pop. 98. The latter value was only 1.03 times the former.

Of 63 adult females, individuals from Pop. 97 exhibited the smallest (ACV=33.3) and the largest values (ACV=40.5); the latter was 1.22 times larger than the former. Medians varied from 36.1 (Pop. 98) to 37.3 (Pop. 100), and the latter value was only 1.03 times larger than the former. Thus, among 146 individuals, the largest ACV was 1.41 times larger than the smallest.

In the comparisons of interpopulation and intrapopulation difference in medians, only sexual dimorphism was detected in Pop. 97, and females had a larger median than males in this population ($U_{20,\,20}=115.5$, $p<.05$).

6) PL: Among 154 individuals, the smallest ACV, 12.7, was found for one in Pop. 100, and the largest, 21.1, for one in Pop. 97 (Table 49). The largest value was 1.66 times the smallest.

Medians for four populations varied from 16.3 (Pop. 98) to 18.0 (Pop. 99), and the latter value was 1.10 times larger than the former. Interpopulation difference in medians was observed between Pop. 98 and Pop. 99 ($p<.05$).

7) PW: Thirty-two young of Pop. 97 had ACV ranging 4.5–8.4, and an individual in Pop. 99 and another in Pop. 100 had values within this range (Table 48). The largest value was 1.86 times larger than the smallest. The median for the young of Pop. 97 was 6.5.

Of 59 adult males, the smallest ACV, 5.0, was for an individual from Pop. 97, and the largest, 8.3, was for one from Pop. 98. The latter value was 1.67 times larger than the former. Medians for the three populations ranged 6.4 (Pops. 97 and 99) to 7.1 (Pop. 98); the largest was 1.11 times the smallest.

ACVs of 69 adult females ranged from 5.4 (exhibited by one from Pop. 100) to 8.0 (by one from Pop. 97), and the largest was 1.48 times larger than the smallest. Medians for four populations ranged from 6.3 (Pop. 99) to 6.9 (Pops. 98 and 100), and the largest value was 1.10 times larger than the smallest.

Neither intrapopulation nor interpopulation difference in ACV median was found.

8) LAL: Among 90 individuals, the smallest ACV, 40.1, was shown by one in Pop. 97, and the largest, 50.9, by one in Pop. 99 (Table 49); the largest value was 1.27 times larger than the smallest.

Medians for four populations varied from 43.8 (Pop. 99) to 45.9 (Pop. 98), and the latter value was 1.05 times larger than the former.

Interpopulation comparisons revealed two significant differences (Pop. 97 vs. Pop. 98: $U_{20,\,10}=50.5$, $p<.05$; Pop. 98 vs. Pop. 99: $U_{10,\,20}=31$, $p<.05$).

9) TL: Among 22 young, the smallest ACV, 30.4, was exhibited by an individual from Pop. 99, and the largest, 36.4, by one from Pop. 97 (Table 48). The largest value was 1.19 times larger than the smallest. Only Pop. 97 had adequate sample size, and

had the median, 32.7.

Of 48 adult males, the smallest ACV, 31.5, was exhibited by one from Pop. 99, and the largest, 39.1, by another from Pop. 97; the latter value was 1.24 times larger than the former. Among the three populations, the smallest median, 34.6, was for Pop. 99, and the largest, 36.8, for Pop. 98. The largest median was 1.06 times larger than the smallest.

Of 35 adult females, the smallest ACV was exhibited by an individual from Pop. 99, and was 30.7. The largest ACV, 34.8, was shown by one from Pop. 100, and was 1.13 times larger than the smallest value. Medians for the four populations varied from 32.3 (Pop. 99) to 33.5 (Pop. 98); the latter was 1.04 times larger than the former. Thus, among 105 individuals, the largest ACV was 1.29 times larger than the smallest.

In the comparison of intrapopulation variation for medians, a significant age difference was found between young and adult males of Pop. 97 ($U_{20,20}=84$, $p<.05$), and adult males had a larger median than young. Sexual dimorphism was found in Pops. 97 ($U_{20,20}=56.5$, $p<.05$), 98 ($U_{5,5}=0$, $p=.01$), and 99 ($U_{20,7}=9$, $p<.05$), and males had a larger median than females.

Interpopulation comparisons revealed significant differences among adult males: Pop. 98 had a significantly larger median than Pop. 97 ($U_{5,20}=14$, $p<.05$) and Pop. 99 ($U_{5,20}=11$, $p<.05$).

10) FL: Among 22 young, both the smallest and the largest ACV, 33.1 and 40.5, respectively, were found in individuals from Pop. 97 (Table 48). The largest value was 1.22 times larger than the smallest. Only Pop. 97 had a large sample size, with a median of 36.7.

Among 48 adult males, the smallest ACV, 35.9, was found for an individual from Pop. 99, and the largest, 45.5, for one from Pop. 97; the largest value was 1.27 times larger than the smallest. Among the three populations, the smallest median, 39.2, was for Pop. 97, and the largest, 42.3, for Pop. 98; the largest was 1.08 times the smallest.

Of 35 adult females, the smallest ACV, 34.4, was exhibited by two individuals from Pops. 97 and 98, and the largest, 40.0, by one from Pop. 100; the latter value was 1.16 times larger than the former. The medians for the four populations ranged 35.3 (Pop. 98)–36.5 (Pop. 99); the largest value was 1.03 times larger than the smallest. Thus, among 105 individuals, the largest ACV was 1.37 times larger than the smallest.

In the comparisons of intrapopulation variation in medians, a significant age difference was found between young and adult males of Pop. 97 ($U_{20,20}=74$, $p<.05$), and adult males had larger median than young. Sexual dimorphism was found in Pops. 97 ($U_{20,20}=17$, $p<.05$), 98 ($I_{5,5}=0$, $p=.01$), 99 ($U_{20,7}=6$, $p<.05$), and adult males had a larger median than females.

In adult males, interpopulation comparisons revealed significant differences: Pop. 98 had a significantly larger median than Pop. 97 ($U_{5,20}=13$, $p<.05$) and Pop. 99 ($U_{5,20}=15$, $p<.05$).

b) *Patterns of Intrapopulation and Interpopulation Variation in ACV and Comparison with the Japanese Common Toad*

1) Intrapopulation variation

Most conspicuous intrapopulation variation was found in T-EL, and TD, PL, and PW also varied markedly. By contrast, HL, HW, and TL had rather stable ACVs within a population.

Since the sample size of young toads was inadequate, detailed analysis was impossible for age variation. In the single available population (Pop. 97), the young differed from adult males in TL and FL. Marked sexual dimorphism was observed in TL and FL, and all the three examined populations exhibited significant differences. Only one out of the three populations showed sexual dimorphism in T-EL and HW. Though the number of examined populations was limited, it can be concluded that adult males had longer hindlimbs than adult females.

2) Interpopulation variation

Generally, only slight interpopulation variation was observed (Table 50). Only

Table 50. Degree of variability in each character measured by RE (=maximum ACV/minimum ACV) in the Miyako toad.

Character	Age/sex group	N	RE in all individuals	N	RE in population medians
HL	Young	26	1.18		
	♂ Adults	39	1.13	3	1.03
	♀ Adults	50	1.18	3	1.02
	Total	115	1.19	-	—
SL	Combined	135	1.26	4	1.03
T-EL	Young	32	1.57		
	♂ Adults	59	1.87	3	1.07
	♀ Adults	66	1.77	4	1.16
	Total	157	1.91	-	—
TD	Combined	168	1.83	4	1.25
HW	Young	33	1.30		
	♂ Adults	50	1.27	3	1.03
	♁ Adults	63	1.22	3	1.03
	Total	146	1.41	-	—
PL	Combined	154	1.66	4	1.10
PW	Young	32	1.86		
	♂ Adults	59	1.67	3	1.11
	♀ Adults	69	1.48	4	1.10
	Total	162	1.86	-	—
LAL	Combined	90	1.27	4	1.05
TL	Young	22	1.19		
	♂ Adults	48	1.24	3	1.06
	♀ Adults	35	1.13	4	1.04
	Total	105	1.29	-	—
FL	Young	22	1.22		
	♂ Adults	48	1.27	3	1.08
	♀ Adults	35	1.16	4	1.03
	Total	105	1.37	-	—

two out of six combinations exhibited significant differences in LAL, adult male TL, and adult male FL. Therefore, one population differed only incompletely from another in morphometric characters.

3) Comparisons with the Japanese common toad

From the results of the interpopulation variation analyses, populations of the Japanese common toad were divided into two types (see preceding pages), and each of them was separately compared with the Miyako toad (Table 51).

When populations of the Miyako toad were combined for each age/sex group and the range of ACV medians for a character in the combined populations was compared with the ACV median for each population of the Japanese common toad, the Miyako toad did not differ from some populations of the Japanese common toad in every character. The characters showing marked differences were: PL, FL (of young), TL (of young), and HL (of young and adult females). In PL, the Miyako toad differed from

Table 51. Percentage of the Japanese common toad populations showing significant difference in ACV median from all populations of the Miyako toad (only one population available for young). A single intermediate type of the Japanese common toad is included in the total.

Character	Age/sex group	type A		type B		Total	
		N of pops.	% of differing pops.	N of pops.	% of differing pops.	N of pops.	% of differing pops.
HL	Young	20	70.0	18	94.4	39	82.1
	♂ Adults	40	62.5	17	70.6	58	63.8
	♀ Adults	33	69.7	16	93.8	50	80.0
SL	Combined	54	42.6	28	60.7	83	48.2
T-EL	Young	20	20.0	18	100	39	59.0
	♂ Adults	40	10.0	17	76.5	58	29.3
	♀ Adults	33	0	16	81.3	50	26.0
TD	Combined	54	94.4	28	0	83	61.4
HW	Young	20	45.0	18	72.2	39	59.0
	♂ Adults	40	0	17	5.9	58	1.7
	♀ Adults	32	21.9	16	31.3	49	24.5
PL	Combined	54	94.4	28	89.3	83	94.4
PW	Young	20	25.0	18	27.7	39	25.6
	♂ Adults	40	0	17	0	58	0
	♀ Adults	33	0	16	0	50	0
LAL	Combined	54	66.7	28	96.4	83	77.1
TL	Young	20	70.0	18	88.9	39	84.6
	♂ Adults	40	5.0	17	23.5	58	10.3
	♀ Adults	33	9.1	16	37.5	50	18.0
FL	Young	20	95.0	18	88.9	39	92.3
	♂ Adults	40	40.0	17	58.8	58	44.8
	♀ Adults	33	15.2	16	37.5	50	18.0

94% of the Japanese common toad populations. On the contrary, in both PW (of adult males and adult females) and HW (of adult males), only slight or even no difference was observed. Two types of the Japanese common toad differed from each other in the frequency of differences from the Miyako toad: e.g., in T-EL, only 0–20% of the type A populations differed from the Miyako toad in every age/sex group, whereas 77–100% of the type B populations differed from the Miyako toad. Conversely, the Miyako toad differed from 94% of type A populations, but did not differ from all of the type B populations in TD. As a whole, the Miyako toad more clearly differed from geographically adjacent type B populations than from distant type A. The number of characters in which more than 80% of the Japanese common toad populations differed from the Miyako toad was only three of type A, and only one half of type B.

It was possible to summarize the relation of ACV magnitudes for each character between the Miyako toad and the Japanese common toad as follows. (1) HL: The Miyako toad had generally smaller ACV than the Japanese common toad, especially type B populations. (2) SL: The Miyako toad had ACV smaller than about one half of the Japanese common toad populations. (3) T-EL: The Miyako toad usually had smaller ACV than type B populations, but had ACV similar to type A populations; (4) TD: The Miyako toad had ACV similar to type B, but had a clearly smaller ACV than type A populations. (5) HW: The Miyako toad tended to have smaller ACV than type B in young, but did not differ in other combinations. (6) PL: The Miyako toad had markedly smaller ACV than the Japanese common toad. (7) PW: No marked difference between the two forms. (8) LAL: The Miyako toad tended to have smaller ACV, especially in comparison with most of the type B populations. (9) TL: In young, the Miyako toad tended to have smaller ACV than the Japanese common toad, but in adults the difference was slight. (10) FL: In young, the Miyako toad had smaller ACV, and in adult males it had smaller ACV than about one half of the Japanese common toad populations. In adult females, the difference was slight.

Discussion

The distribution of the Miyako toad is confined to small islands like Miyakojima, Irabujima, Shimojijima, Kita and Minami Daitojima (Matsui, 1979a; Shimojana, 1976; Toyama et al., 1980). As expected from this restricted distribution, ACV of each morphometric character exhibited a low degree of variation. Characters showing large variation in the Japanese common toad were also variable in the Miyako toad, and the high variability of T-EL, TD, PL, and PW in both forms seems to suggest that these characters are variable in the entire *Bufo bufo* complex. The degree of variability in these characters, however, was much less in the Miyako toad than in the Japanese common toad. This may be due to the much smaller number of populations included in the Miyako toad, and at the same time, to the fact that each population of the Miyako toad is limited in the range of distribution.

The slight interpopulation variation in the Miyako toad is different from the condition in the Japanese common toad, and this suggests that the populations inhabiting the islands other than Miyakojima have been artificially introduced from Miyakojima relatively recently. The population from the Kita and Minami Daitojima Islands have been regarded as descendants of artificially introduced populations from Taiwan (Ikehara and Shimojana, 1975; Shimojana, 1976). In addition, the Miyako toad coexists with the Giant toad, *Bufo marinus*, in these islands (Matsui, 1975b). No morphologically marked deviation from the other populations, however, was detected in the toads from these islands. Populations from the Daitojima islands, like other island populations of the Miyako toad, are morphologically quite different from the Taiwan populations of *B. bankorensis* (Matsui, 1979a), and the close morphological similarity of the Daitojima populations with the population from Miyakojima indicates a higher possibility of introduction from the latter island than from Taiwan. The absence of morphological deviation relating to possible ecological segregation with *B. marinus* seems to suggest that the niche of the two species overlaps only narrowly in the islands partly because of their phylogenetically remote relationship and short history in the islands.

The Miyako toad differed morphometrically from the Japanese common toad in many characters, and the difference was particularly conspicuous in the length of the parotoid. ACV of PL was smaller in the Miyako toad than most populations of the Japanese common toad, whereas ACV of PW did not differ markedly. In other words, the Miyako toad had a relatively much shorter parotoid gland than the Japanese common toad. The degree of protrusion in the parotoid was not examined in the present study, but the parotoid gland in the Miyako toad usually protrudes less than in most Japanese common toad populations, and is much flatter than the Formosan *B. bankorensis*. Since the parotoid gland is a defense organ against enemies, the less developed short parotoid of the Miyako toad seems to suggest the relatively little importance of this organ, and hence, the relative lack of predators in the restricted environment of the small islands. ACV of characters in the hindlimb (TL and FL) tended to be smaller in the Miyako toad than in the Japanese common toad. The length of hindlimb is regarded as correlated to the ability to jump, and hence, to escape from enemies. Thus, the characters of the hindlimbs also support the idea that relatively few enemies occur in the habitats of the Miyako toad.

As reported in the previous chapter, the body size of the female Japanese common toad showed a cline with clear body size increase towards the south. The population from Yakushima, which had the largest SVL among populations of the Japanese common toad, is geographically nearest to the range of the Miyako toad. Females of the Miyako toad had instead small body size and their SVL equaled that of the Japanese common toad populations from distant northern Honshu. The small body size of the female Miyako toad clearly deviates from the cline obtained for the Japanese common toad. Although males of the Miyako toad seem to fit on the latitudinal cline in the Japanese common toad (as expressed by a second degree polynomial regression model), the small size of females makes the Miyako toad deviate from the relative female and male mean SVL cline found in the type B populations of the Japanese common toad.

The Miyako toad differed not only from the distant type A populations of the Japanese common toad in the ACV of TD and FL (of young), but also from the adjacent type B populations in the ACV of HL, T-EL, and LAL. These characters have been considered to have some relation with the climatic conditions of the habitats in the Japanese common toad (especially in type A populations; see previous chapter), and the differences between the Miyako toad and the type B populations of the Japanese common toad seem to suggest the presence of difference between them in the mode of adaptation to environmental conditions as represented by climate. Namely, the Miyako toad is regarded as having physiological features different from the Japanese common toad. Non-metric characters such as degree of toe webbing and body colour, though not treated in this paper, differ between the Miyako toad and the Japanese common toad. In addition, the two forms differ in skull morphology (Matsui, 1979a) and karyology (Matsui, 1980a). Therefore, the Miyako toad is thought to represent an evolutionary lineage different from the Japanese common toad. The Miyako toad is closer to the continental population around Shanghai (Matsui, 1979a) than to populations from Taiwan, Fukien, and Szechwan. I will report in detail the relation of the Miyako toad to the Formosan and Chinese representatives in future publications.

VII

Morphometric Variation in the Japanese Stream Toad, Bufo torrenticola

The Japanese stream toad, *Bufo torrenticola*, was first reported for its stream-dwelling larvae (Matsui, 1975c), and was later described as a full species by its distinct larval ecology and morphology, adult morphology, and, particularly, sympatric distribution with the Japanese common toad (Matsui, 1976a).

The species is known only from Kinki and western Chubu districts of Honshu, and about 30 localities have hitherto been recorded (Matsui, 1976a, d, 1980e; Sasaji, 1979; Miyazaki, 1979; Tomita, 1980; Nambu, 1980; Tamai, pers. comm.).

Recently, Kawamura et al. (1980) proposed to treat the Japanese stream toad as a subspecies of the Japanese common toad, and to use the name *Bufo japonicus torrenticola*. Their proposal was made purely on the basis of the results of laboratory hybridizations. The results obtained by Kawamura et al. (op. cit.) are essentially similar to my previous reports (Matsui, 1977a, b, 1979a) in that the reciprocal crosses of the Japanese stream toad and the Japanese common toad result in fertile F_1.

The most important problem is whether or not natural hybridization actually occurs as Kawamura et al. (1980) "believed", and this problem must be solved by a all-round approach. A better taxonomic conclusion can be made after the accumulation of sufficient information about the relationship of the two forms under natural conditions.

In the present chapter, I will analyze the morphometric variations of the Japanese stream toad and compare them with variations in the sympatric and allopatric populations of the Japanese common toad, and the Miyako toad.

MATERIALS AND METHODS

The localities and sample sizes for 13 populations of a total of 265 Japanese stream toads analyzed for morphometric variation are shown in tables 8 and 9. The data for the Japanese common toad and the Miyako toad used for comparison are shown in the previous chapters.

The methods for determining maturity and sex, the body parts measured, and the method of taking measurements are as described in the previous chapter.

For the morphometric characters, (1) SVL; (2) head length (HL); (3) snout length (SL); (4) tympanum-eye length (T-EL); (5) tympanum diameter (TD); (6) head width (HW); (7) parotoid length (PL); (8) parotoid width (PW); (9) lower arm length (LAL); (10) tibia length (TL); and (11) foot length (FL) were chosen. The allomorphic relations of the ten characters to SVL were first obtained for 61 pooled individuals (31 young, 15 adult males, and 15 adult females) from Ohdaigahara (Pop. 109), and ACV for each individual toad, at the SVL of 100 mm, was calculated for each character with the allomorphic constants thus obtained.

Intrapopulation and interpopulation comparisons, as well as comparisons with the Japanese common toad and the Miyako toad, were made of SVL and the calculated ACVs. Three age/sex groups (young, adult males, and adult females) were distinguished for the comparisons. In the comparison of morphometric values, populations with a sample size of three or greater for each age group were considered. As shown in Table 52 and Fig. 55, the populations of the Japanese common toad employed for comparisons were divided into three groups according to the relative distance from the sympatric zone.

Table 52. Eighty-three populations of the Japanese common toad classified by their geographic location in relation to the distributional range of the Japanese stream toad.

Sympatric zone		Allopatric zone adjacent to the zone of sympatry		Allopatric zone distant from zone of sympatry							
Population	Type	Population	Type	Population	Type	Population	Type	Population	Type	Population	Type
51	A	47	A	1	A	20	A	36	A	81	B
54	A	48	A	3	A	21	A	37	A	82	B
55	A	50	A	4	A	22	A	38	A	83	B
57	A	52	B	5	A	23	A	39	A	84	B
58	A	53	A	6	A	24	A	40	A	85	B
59	A	56	A	8	A	25	A	43	A	86	B
68	A	60	A	9	A	26	A	44	A	87	B
71	A	61	A	10	A	27	A	46	A	88	B
72	B	62	B	12	B	28	A	49	A	89	B
		63	B	13	A	29	A	65	B	90	B
		64	B	14	A	30	A	75	A	91	B
		66	B	16	A	31	A	76	B	92	B
		69	A	17	A	32	A	78	B	94	B
		70	B	18	A	33	A	79	B	96	B
		73	B	19	A	34	A	80	B		

Statistic procedures employed were the same as in the preceding chapters.

Results

1. *Variation in SVL*

Young toads were omitted from the analysis because of the greater variation than in adults due to their heterogeneous growth stages.

1) Variation in the mean SVL

The mean of the adult male mean SVLs in the eight populations was 94.98±5.47 mm. Population 110 had the smallest mean (82.9 mm), and Pop. 105 had the largest (104.2 mm: Table 53). The largest mean SVL was 1.26 times larger than the smallest.

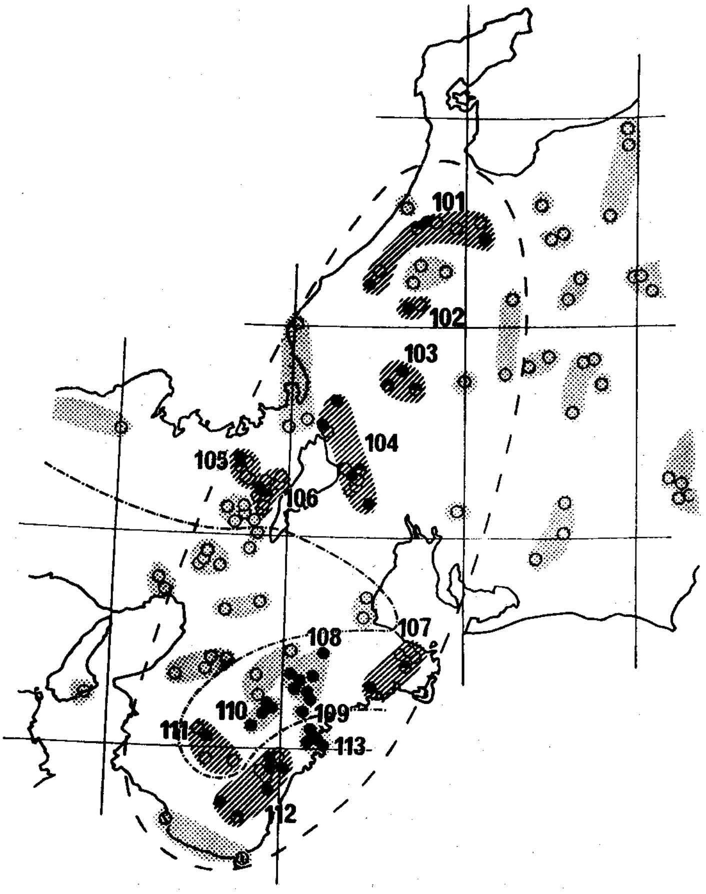

Fig. 55. A map of western Chubu and Kinki districts of Honshu, showing locations for the demes and populations of the Japanese stream toad. Closed circles = stream toad demes; open circles = common toad demes; half-filled circles = microsympatric demes of the two forms. Hatched areas = sympatric populations; dotted areas = allopatric populations. Dashed line encircles the allpoatric populations of the common toad adjacent to the sympatric zone; long-and-short dashed line indicates the boundary between type A and type B populations of the common toad.

Table 53. SVL (in mm) variation in adult Japanese stream toads.

Population	adult males						adult females					
	N	SVL					N	SVL				
		range	$\bar{X}$	SD	2SE	CV		range	$\bar{X}$	SD	2SE	CV
101	3	84.2–101.0	94.1	8.8	10.2	9.4						
102	1		108.2				1		122.8			
103	10	85.4–117.6	101.4	12.2	7.7	12.0	4	95.2–135.6	120.5	18.5	18.5	15.3
104	1		98.2				1		117.8			
105	6	95.1–116.2	104.2	7.6	6.2	7.3	4	129.2–146.0	137.8	6.9	6.9	5.0
106	4	76.2– 95.4	88.7	8.6	8.5	9.6						
107							1		106.2			
108	13	70.5–119.5	97.4	14.0	7.8	14.4	5	124.0–135.4	128.7	4.4	4.0	3.4
109	42	70.0–101.8	88.6	7.8	2.4	8.7	46	88.2–119.2	103.9	7.6	2.2	7.3
110	11	71.8– 97.5	82.9	7.9	5.2	8.9	3	110.6–127.2	116.4	9.3	10.8	8.0
112	1		117.0				2	116.4–119.8	118.1			
113	3	81.2–120.6	102.7	19.9	23.0	19.4	2	167.0–168.0	167.5			

Interpopulation variation in mean SVL was not great, and only six out of 28 combinations (21.4%) proved to be different. Thus, the mean SVL of each population overlapped the SVLs of the other populations.

For the five female populations, the mean of the population means was 121.45±11.42 mm. The smallest mean SVL, 103.9 mm, was exhibited by Pop. 109, and the largest, 137.8 mm, by Pop. 105. The latter value was 1.24 times the former.

Like males, interpopulation variation in females was not great, and only three out of 10 combinations were found to be significantly different (Pop. 105 vs. Pops. 109, 110; Pop. 108 vs Pop. 109). The two extreme populations were thus linked by the intermediate populations.

Sexual dimorphism in the mean SVL was evident, and four of five populations (80.0%) were sexually different in mean SVL ($p<.05$). Females had a larger mean of mean SVLs than males ($t=4.71$, dF$=11$, $p<.001$).

Relative female and male mean SVL ranged from 1.19 (Pop. 103) to 1.40 (Pop. 110), and averaged 1.28.

2) Variation in the minimum SVL

Among 95 individuals of 11 populations, the smallest adult male was found in Pop. 109 and was 70.0 mm in SVL. The smallest adult female among 69 individuals of 10 populations was also in Pop. 109 and had an SVL of 88.2 mm.

The means of the population minimum SVLs were 79.30±6.24 mm for males and 109.44±15.86 mm for females, and females were statistically significantly larger in minimum SVL ($p<.05$).

3) Variation in the maximum SVL

The largest adult male among 95 individuals was found in Pop. 113 and was 120.6 mm. The largest adult female among 69 individuals was also found in Pop. 113 and had an SVL of 168.0 mm.

The means of the population maximum SVLs were 108.70±7.57 mm for males and 132.68±9.00 mm for females, and females were judged to be larger in maximum SVL than males ($p<.05$).

2. *Intrapopulation Allomorphosis in the Japanese Stream Toad from Ohdaigahara*

The intrapopulation allomorphosis patterns of the Japanese stream toad from Pop. 109 are summarized in Table 54.

Table 54. Allomorphic constants (α) and initial growth indices (B) for regression of each morphometric character—SVL in the Japanese stream toad from Ohdaigahara. Three age/sex groups combined. Growth type abbreviations are: I=isomorphosis, B=bradymorphosis, T=tachymorphosis.

Character	N	$\alpha \pm$SD	log B	r	Growth type
HL	61	0.922±0.016	−0.328	0.991	B
SL	61	0.788±0.026	−0.492	0.970	B
T-EL	61	1.191±0.053	−1.714	0.946	T
TD	61	1.106±0.093	−1.779	0.839	I
HW	61	0.996±0.023	−0.424	0.984	I
PL	61	1.021±0.044	−0.809	0.950	I
PW	61	0.865±0.034	−0.909	0.957	B
LAL	60	1.013±0.017	−0.293	0.992	I
TL	61	0.948±0.017	−0.328	0.990	B
FL	61	1.107±0.025	−0.533	0.986	T

Among ten characters, four were isomorphic to SVL: TD, HW, PL, and LAL. T-EL and FL were tachymorphic, and HL, SL, PW, and TL were bradymorphic, to SVL.

When these results were compared with those obtained for the Japanese common toad described in the previous chapter, only two characters, T-EL and TL, exhibited differences. The allomorphic constant for T-EL against SVL in the Japanese stream toad ($\alpha=1.191$) was larger than the value derived from the combination of nine Japanese common toad populations ($\alpha=1.052$). However, the slopes of the regression lines for the Japanese stream toad and for the Pop. 88, which had the largest α value among the nine common toad populations, did not differ significantly (slope: $F_{1,106}=0.745$, $p>.05$; position: $F_{1,107}=40.28$, $p<.01$).

TL exhibited bradymorphic relation to SVL in the Japanese stream toad, whereas the combined Japanese common toad populations had a tachymorphic relation. In this case, however, the α value for the Japanese stream toad ($\alpha=0.948$) was within variation range of α values (0.939–1.032) for the Japanese common toad populations, and insignificant differences in α value were found between the Japanese stream toad and populations of the Japanese common toad having small α values.

The shape of the growth gradient curve in the Japanese stream toad was similar to that of the Japanese common toad except for relations among T-EL, TD, and PL.

3. *Variation in ACV for Each Character*

a) *Variation in ACV for Each Character*

1) HL: Of 87 young, the smallest ACV, 30.2, was shown by an individual from Pop. 109, and the largest, 37.9, by one from Pop. 105 (Table 55). The latter value

Table 55. Variation in ACV of the Japanese stream toad. Three age/sex groups separated.

Character	Population	young			adult males			adult females		
		N	ACV		N	ACV		N	ACV	
			range	median		range	median		range	median
HL	101	6	32.0–36.3	33.9	3	32.0–34.2	32.9			
	102				1		35.0	1		33.6
	103	4	31.2–34.1	33.0	10	30.9–35.1	33.6	4	33.7–36.1	35.6
	104	4	31.0–34.9	33.6	1		33.8	1		37.0
	105	6	32.9–37.9	34.5	6	33.3–35.8	34.2	4	35.1–36.5	36.0
	106	6	30.9–35.7	33.7	4	31.7–34.4	32.2			
	107	1		32.1				1		36.2
	108	5	31.4–36.0	33.8	13	30.7–34.9	32.7	5	33.4–35.5	35.0
	109	43	30.2–36.0	32.7	38	29.6–35.1	32.5	33	31.4–36.4	33.2
	110	2	32.2–34.0	33.1	11	31.5–34.9	33.3	3	33.2–34.2	33.9
	112	6	31.7–35.4	34.0	1		32.2	2	34.1–35.7	34.9
	113	4	33.9–35.3	34.8	3	33.7–35.2	34.9	2	33.0–35.6	34.3
T-EL	101	5	3.7– 5.6	4.7	3	4.6– 5.2	4.9			
	102				1		4.5	1		5.4
	103	4	4.3– 5.8	4.9	9	4.1– 5.3	4.4	4	4.4– 5.6	5.0
	104	4	4.2– 5.1	4.6	1		3.9	1		5.6
	105	6	4.4– 5.3	4.8	6	4.7– 5.1	4.9	4	4.7– 5.7	4.9
	106	5	4.4– 5.7	5.4	4	4.1– 5.0	4.7			
	107	1		4.1				1		5.8
	108	5	4.2– 5.1	4.5	12	3.5– 5.3	4.4	5	4.0– 5.3	5.0
	109	45	3.2– 6.3	4.5	41	3.7– 5.9	4.6	44	3.0– 6.4	4.8
	110	2	4.3– 4.7	4.5	10	3.9– 5.6	4.5	3	4.4– 6.1	5.1
	112	6	4.4– 5.2	4.7	1		3.7	2	4.2– 4.8	4.5
	113	4	4.5– 5.5	5.0	3	4.6– 5.4	4.9	2	3.9– 4.3	4.1
HW	101	6	36.2–42.9	39.6	3	37.2–38.6	37.9			
	102				1		38.6	1		40.5
	103	4	36.0–40.1	38.3	10	35.6–39.6	37.2	4	40.7–43.3	41.0
	104	4	36.7–40.7	38.9	1		39.2	1		43.9
	105	6	37.3–43.2	40.5	6	36.6–40.2	38.1	4	41.1–42.0	41.5
	106	6	35.3–41.5	38.3	4	36.4–39.1	37.2			
	107	1		37.9				1		42.7
	108	5	34.6–41.2	38.7	13	34.3–39.7	37.1	5	38.6–41.6	40.1
	109	44	34.3–41.2	37.2	38	32.4–37.8	35.3	33	35.4–41.2	38.3
	110	2	36.4–39.0	37.7	11	36.1–41.0	37.9	3	39.5–40.0	39.8
	111	2	34.1–38.9	36.5				2		
	112	6	36.0–43.3	38.8	1		38.3	2	39.3–41.1	40.2
	113	4	38.9–40.9	40.7	3	37.8–40.4	39.0	2	37.8–40.8	39.3
PW	101	6	6.4– 7.3	6.9	3	6.0– 6.7	6.6			
	102				1		7.3	1		6.5
	103	4	5.9– 7.1	6.7	10	5.8– 8.1	6.9	4	5.5– 6.9	6.1
	104	4	6.1– 7.2	6.8	1		6.3	1		7.6
	105	6	5.5– 8.6	6.5	6	5.4– 7.5	6.4	4	5.2– 6.3	5.8
	106	6	5.7– 7.3	6.3	4	5.6– 7.1	6.1			
	107	1		8.2				1		6.6

(cont'd.)

(Table 55. cont'd.)

Character	Population	young			adult males			adult females		
		N	ACV		N	ACV		N	ACV	
			range	median		range	median		range	median
	108	5	5.7– 6.7	6.3	13	5.7– 7.5	6.2	5	6.0– 6.6	6.3
	109	44	5.3– 8.1	6.7	40	5.2– 8.8	6.8	33	5.6– 7.5	6.5
	110	2	7.1– 7.7	7.4	11	5.4– 8.7	7.5	3	5.5– 6.7	6.2
	112	6	6.0– 7.5	6.7	1		7.2	2	6.6– 6.8	6.7
	113	4	5.2– 6.6	6.1	3	6.2– 7.4	6.7	2	6.3– 6.3	6.3
TL	101	6	34.0–38.6	36.0	3	39.1–41.3	40.3			
	102				1		40.1	1		39.7
	103	4	34.7–37.9	36.5	10	38.2–43.1	41.1	4	37.9–41.1	39.6
	104	4	34.9–39.6	37.5	1		40.9	1		40.9
	105	6	37.3–39.2	38.4	6	38.0–42.7	40.1	4	39.3–40.9	40.0
	106	6	36.0–38.7	37.6	4	39.6–41.6	41.0			
	107	1		36.5				1		38.0
	108	5	36.2–41.6	38.1	13	35.9–41.6	39.7	5	36.9–39.8	37.9
	109	44	34.0–39.7	36.8	40	33.7–42.1	38.5	33	33.3–40.7	36.8
	110	2	34.9–41.1	38.0	11	38.4–42.4	40.0	3	37.3–39.8	38.5
	111	2	34.5–39.2	36.9						
	112	6	31.0–40.5	37.8	1		38.1	2	39.3–39.8	39.5
	113	4	38.4–40.0	38.8	3	38.9–40.7	40.0	2	36.7–38.0	37.4
FL	101	6	44.0–49.5	46.1	3	52.3–55.2	53.9			
	102				1		52.7	1		46.8
	103	4	42.6–50.5	46.6	10	46.3–57.4	52.7	4	44.6–47.3	44.7
	104	4	46.2–52.6	48.9	1		50.2	1		48.5
	105	6	45.4–48.4	45.8	6	49.0–55.8	52.7	4	43.2–45.8	44.6
	106	6	45.8–49.4	47.6	4	51.7–55.0	52.4			
	107	1		46.8				1		49.4
	108	5	45.1–52.5	49.2	13	47.9–55.1	53.0	5	41.7–45.9	45.0
	109	44	41.0–53.1	47.7	40	46.6–59.1	52.3	33	41.8–51.2	45.8
	110	2	44.7–53.7	49.2	11	50.8–59.6	53.5	3	45.4–46.7	46.3
	111	1		44.2						
	112	6	44.5–48.8	46.1	1		48.1	2	46.8–47.1	47.0
	113	4	47.2–52.6	47.7	3	48.9–50.6	49.8	2	41.0–41.3	41.1

was 1.26 times larger than the former. Among the population medians of ACV in nine populations, the smallest was 32.7 for Pop. 109, and the largest, 34.8, for Pop. 113; the largest was 1.06 times larger than the smallest.

Of 91 adult males, the smallest ACV, 29.6, was exhibited by an individual from Pop. 109, and the largest value, 35.8, by one from Pop. 105. The largest value was 1.21 times larger than the smallest. The smallest ACV median of eight populations of adult males was 32.2 for Pop. 106, and the largest value was 34.9 for Pop. 113. The latter value was 1.08 times larger than the former.

Of 56 adult females, the smallest ACV, 31.4, was exhibited by an individual from Pop. 109, and the largest, 37.0, by one from Pop. 104; the largest was 1.18 times the smallest. The smallest ACV median for five populations was 33.2 for Pop. 109, and the largest was 36.0 for Pop. 105. The largest value was 1.08 times larger than the smallest. Thus, among a total of 234 individuals, the largest ACV was 1.28 times larger than the smallest.

Age related differences in ACV median were not detected between young and either adult males or adult females. Sexual dimorphism in ACV was found in three out of five combinations (60.0%; Pops. 103 ($U_{10,4}=5$, $p=.05$), 105 ($U_{6,4}=2$, $p=.038$), 108 ($U_{12,5}=6$, $p<.05$)), and females had larger medians than males.

As to interpopulation differences, only two out of 36 combinations in young revealed significant differences (Pop. 105 vs. Pop. 109: $U_{6,20}=26$, $p<.05$; Pop. 109 vs. Pop. 113: $U_{20,4}=13$, $p=.05$). In adult male populations, four out of 28 combinations were significantly different (Pop. 105 vs. Pop. 108: $U_{6,12}=8$, $p<.05$; Pop. 105 vs. Pop. 109: $U_{6,20}=22$, $p<.05$; Pop. 108 vs. Pop. 113: $U_{12,3}=1$, $p<.05$; Pop. 109 vs. Pop. 113: $U_{20,3}=7$, $p<.05$). Three out of ten combinations were different in adult females (Pop. 103 vs. Pop. 109: $U_{4,19}=9.5$, $p<.05$; Pop. 105 vs. Pop. 109: $U_{4,19}=13$, $p<.05$; Pop. 108 vs. Pop. 109: $U_{5,19}=19$, $p<.05$).

2) SL: Among 178 individuals, the smallest ACV, 10.7, was exhibited by one from Pop. 109 and the largest value, 14.9, by one from Pop. 112 (Table 56); the latter value was 1.40 times the former. Medians for ten populations varied from 12.1 (Pop. 109) to 13.5 (Pops. 112 and 113). The largest median was 1.11 times larger than the smallest.

Among 45 combinations, nine (20.0%) were found to be significantly different interpopulationally. Population 109 had the largest number of different combinations, and was different from the other seven populations in median.

3) T-EL: Among 87 young, the smallest ACV was exhibited by one from Pop. 109 (ACV=3.2), and the largest (6.3) also by an individual from the same population (Table 55). The largest value was 2.00 times larger than the smallest. Of the nine populations examined, the smallest median, 4.5, was for Pop. 108, and the largest, 5.4, was for Pop. 106; the largest value was 1.20 times the smallest.

Of 91 adult males, the smallest ACV, 3.5, was shown by an individual from Pop. 108, and the largest value, 5.9, by one from Pop. 109. The latter value was 1.71 times larger than the former. Medians for eight populations ranged from 4.4 (Pop. 103) to 4.9 (Pop. 101), and the largest value was 1.13 times the smallest.

ACVs of 67 adult females varied from 3.0 to 6.4. Both of the extreme values were found for individuals from Pop. 109, and the largest was 2.14 times larger than the smallest. Medians for five populations ranged from 4.8 (Pop. 109) to 5.1 (Pop. 110), and the largest median was 1.07 times the smallest.

Intrapopulation variation analyses revealed neither age nor sexual differences in any of the examined populations. Likewise, interpopulation variation was slight with only one difference out of 28 combinations in adult males (Pop. 105 vs. Pop. 108), and no significant differences were found in the combinations for young and adult females.

4) TD: Among 240 individuals, the smallest ACV, 1.7, was exhibited by an individual from Pop. 109, and the largest, 5.1, by one from Pop. 103 (Table 56); the largest was 2.95 times larger than the smallest. The median of ACVs for ten popu-

Table 56. Variation in ACV of the Japanese stream toad. Three age/sex groups combined.

Character	Population	N	ACV		Character	Population	N	ACV	
			range	median				range	median
SL	101	8	11.3–14.2	13.0	PL	101	9	14.1–19.5	17.8
	102	2	13.2–13.8	13.5		102	2	20.1–20.9	20.5
	103	18	11.6–14.3	13.0		103	18	14.5–23.0	17.8
	104	6	11.8–14.0	13.0		104	6	15.1–18.4	16.2
	105	16	12.3–14.8	13.4		105	16	14.2–20.8	16.1
	106	10	11.2–14.4	12.8		106	10	16.4–18.7	17.0
	107	2	12.4–13.2	12.8		107	2	16.7–17.4	17.1
	108	22	11.4–14.3	12.9		108	23	13.4–20.9	16.4
	109	61	10.7–13.7	12.1		109	60	13.3–22.0	17.2
	110	15	11.4–13.4	12.7		110	16	15.0–19.9	17.8
	112	9	12.3–14.9	13.5		112	9	13.1–20.2	18.3
	113	9	12.5–14.6	13.5		113	9	15.1–18.9	16.8
TD	101	8	3.3– 4.2	4.1	LAL	101	9	50.2–56.9	53.5
	102	2	3.2– 3.2	3.2		102	2	53.2–57.4	55.3
	103	17	2.1– 5.1	3.3		103	18	50.1–58.1	54.6
	104	6	3.3– 4.2	3.8		104	5	52.6–60.1	56.1
	105	16	2.4– 4.4	3.6		105	16	50.3–56.6	54.3
	106	9	3.1– 4.6	3.5		106	10	52.2–57.0	54.9
	107	2	3.6– 3.9	3.7		107	2	53.1–53.4	53.3
	108	22	2.6– 3.7	3.1		108	23	48.1–58.6	55.0
	109	126	1.7– 4.9	3.1		109	60	49.6–58.3	54.2
	110	14	3.1– 4.2	3.4		110	16	51.5–58.4	54.8
	112	9	2.6– 3.6	3.1		112	9	52.8–57.3	55.6
	113	9	2.4– 4.0	3.1		113	9	49.5–60.0	55.2

lations ranged from 3.1 for Pop. 108 and Pop. 109 to 4.1 for Pop. 101; the largest value was 1.33 times larger than the smallest.

The interpopulation comparison of medians revealed 16 significant differences out of 45 possible combinations; Pops. 108 and 109 differed from the other five populations in median.

5) HW: Among 90 young, the smallest ACV, 34.2, was exhibited by an individual from Pop. 111 and the largest, 43.3, by one from Pop. 112; the largest value was 1.27 times larger than the smallest. Among nine populations, the medians varied from 37.2 for Pop. 109 to 40.7 for Pop. 113 (Table 55). The largest median was 1.10 times larger than the smallest.

Of 91 adult males, the smallest ACV, 32.4, was found in an individual from Pop. 109, and the largest, 41.0, in one from Pop. 110. The former value was 1.27 times the latter. The medians for eight adult male populations ranged from 35.3 (Pop. 109) to 39.0 (Pop. 113), and the largest value was 1.11 times larger than the smallest.

Of 56 adult females, the smallest ACV, 35.4, was exhibited by an individual from Pop. 109, and the largest, 43.3, by one from Pop. 103; the latter value was 1.23 times the former. Among five populations, the medians ranged from 38.3 for Pop. 109 to 41.5 for Pop. 105, and the largest value was 1.08 times larger than the smallest. Thus, among 237 individuals, the largest ACV was 1.34 times larger than the smallest.

As to intrapopulation variation, age variation in HW ACV was not marked, with significant differences in only two out of 11 combinations; in Pop. 109, young had a larger median than adult males ($U_{19,19}=58$, $p<.05$), and in Pop. 103, adult females had a larger value than young ($U_{4,4}=0$, $p=.028$).

By contrast, sexual dimorphism was conspicuous, and all the five populations examined showed significant differences. Adult females were invariably larger than adult males in the median of ACVs.

In the comparisons of interpopulation variation, the following number of combinations were found to be significantly different: two out of 36 combinations in young, seven out of 28 combinations in adult males, and seven out of ten combinations in adult females. Members of Pop. 109 were most conspicuous, having a larger number of different combinations with other populations, and adult males of Pop. 109 had a smaller median than any of other populations.

6) PL: Among 180 individuals, the smallest ACV, 13.1, was found in one from Pop. 112, and the largest, 23.0, in one in Pop. 103 (Table 56). The largest value was 1.75 times larger than the smallest. Medians for ten populations varied from 16.1 (Pop. 105) to 18.3 (Pop. 112), and the latter value was 1.13 times larger than the former.

Interpopulation difference in medians was not observed among 45 possible combinations.

7) PW: Among 88 young, the smallest ACV, 5.2, was exhibited by an individual from Pop. 113, and the largest, 8.6, by one from Pop. 105 (Table 55). The latter value was 1.64 times larger than the former. Of nine populations, Pop. 113 exhibited the smallest median, 6.1, and Pop. 101 showed the largest value (6.9). The largest median was 1.12 times larger than the smallest.

Of 93 adult males, the smallest ACV, 5.2, was exhibited by an individual from Pop. 109, and the largest, 7.5, also by one from the same population. The latter value was 1.70 times the former. Medians for eight populations ranged from 6.1 (Pop. 106) to 7.5 (Pop. 110); the largest was 1.24 times the smallest.

ACVs for 56 adult females ranged from 5.2 (exhibited by one from Pop. 105) to 7.6 (by one from Pop. 104), and the largest was 1.47 times larger than the smallest. Medians for five populations ranged from 5.8 (Pop. 105) to 6.5 (Pop. 109); the largest median 1.12 times larger than the smallest.

Neither age difference nor sexual dimorphism in medians was observed in any of the populations. Interpopulation variation in medians was not great: one out of 36 combinations (Pop. 101 vs. Pop. 113: $U_{6,4}=2$, $p=.038$) in young, one out of 28 in adult males (Pop. 108 vs. Pop. 110: $U_{11,13}=20.5$, $p<.05$), and one out of ten in adult females (Pop. 105 vs. Pop. 109: $U_{4,19}=10$, $p<.05$), were significantly different.

8) LAL: Among 179 individuals, the smallest ACV, 48.1, was shown by one in Pop. 108, and the largest, 60.1, by one in Pop. 104 (Table 56); the largest value was 1.25 times larger than the smallest. Medians for ten populations varied from 53.5 (Pop. 101) to 56.1 (Pop. 104), and the latter value was 1.05 times larger than the former.

Interpopulation comparisons revealed no significant differences in medians among

45 possible combinations.

9) TL: Of 90 young, the smallest ACV, 31.1, was exhibited by an individual from Pop. 112, and the largest, 41.7, by one from Pop. 108 (Table 55); the latter value was 1.34 times larger than the former. Among nine populations, the smallest median, 36.0, was for Pop. 101, and the largest, 38.8, for Pop. 113. The largest ACV median was 1.08 times larger than the smallest.

Of 93 adult males, the smallest ACV, 33.7, was exhibited by an individual from Pop. 109, and the largest, 43.1, by one from Pop. 103; the latter value was 1.28 times larger than the former. Among eight populations, the smallest ACV median, 38.5, was for Pop. 109, and the largest, 41.1, for Pop. 103. The largest median ACV was 1.07 times larger than the smallest.

Of 56 adult females, the smallest ACV was exhibited by an individual from Pop. 109, and was 33.4. The largest ACV, 41.1, by one from Pop. 103, was 1.23 times larger than the smallest value. Medians for five populations varied from 36.8 (Pop. 109) to 40.4 (Pop. 105); the latter was 1.09 times larger than the former.

Marked differences with age in medians were observed between young and adult males: out of seven available populations, five (71.4%) differed significantly and adult males had a larger median than young in these populations. The difference between young and adult females was not so marked, and two (Pop. 103: $U_{4,4}=0$, $p=.028$; Pop. 105: $U_{6,4}=0$, $p=.01$) out of four populations resulted in significant differences. In these populations young had smaller medians than adult females. Sexual dimorphism was observed only in one (Pop. 109) out of five populations, and males exhibited a larger value than females.

Interpopulation variation in ACV medians was not great. In young, six out of 36 combinations proved to be different, and Pop. 113 differed from four of the eight other populations. In adult males, three out of 28 combinations were different, and all of these differences were exhibited by Pop. 109. Three out of ten combinations differed in adult females, and Pop. 109 differed from two of four other populations.

10) FL: Of 89 young, the smallest ACV, 41.0, was exhibited by an individual from Pop. 109, and the largest, 53.7, by one from Pop. 110 (Table 55); the latter value was 1.31 times larger than the former. Among nine populations, the smallest ACV median, 45.8, was for Pop. 105, and the largest, 49.2, for Pop. 108. The largest median was 1.08 times larger than the smallest.

Of 93 adult males, the smallest ACV, 46.3, was exhibited by an individual from Pop. 103, and the largest, 59.6, by one from Pop. 110; the latter value being 1.29 times larger than the former. Among eight populations, the smallest ACV median, 49.8, was found in Pop. 113, and the largest, 53.9, in Pop. 101. The largest median was 1.08 times larger than the smallest.

Of 56 adult females, the smallest ACV, 41.0, was exhibited by one from Pop. 113, and the largest, 51.2, by one from Pop. 109. The latter value was 1.25 times the former. The median ACV for five populations ranged from 44.6 (Pop. 105) to 46.3 (Pop. 110), and the largest value was 1.04 times the smallest. Thus, among 238 individuals, the largest ACV was 1.45 times larger than the smallest.

As in TL ACV medians, marked age differences were observed between young and adult males in medians of FL; five (71.4%) out of seven combinations differed and adult males had larger value than young. Between young and adult females, the difference was slight, and only one out of four combinations differed significantly (Pop. 108: $U_{5,5}=2$, $p=.032$). Young had a larger value than adult females in this population.

Sexual dimorphism in this character was great and all the five examined populations showed significant differences. Males invariably had larger medians than females.

In young, interpopulation variation in medians of ACV was less marked than in TL, and none of the 36 combinations resulted in significant differences. Also, in adult males, only one out of 28 combinations proved to be significantly different (Pop. 110 vs. Pop. 113: $U_{11,8}=0$, $p<.05$). None differed out of 10 combinations in the adult

Table 57. Degree of variability in each character measured by RE (=maximum ACV observed/minimum ACV observed).

Character	Age/sex group	N	RE in all individuals	N	RE in population medians
HL	Young	87	1.26	9	1.06
	♂ Adults	91	1.21	8	1.08
	♀ Adults	56	1.18	5	1.08
	Total	234	1.28	—	—
SL	Combined	178	1.40	10	1.11
T-EL	Young	87	2.00	9	1.20
	♂ Adults	91	1.71	8	1.13
	♀ Adults	67	2.14	5	1.07
	Total	245	2.14	—	—
TD	Combined	240	2.95	10	1.33
HW	Young	90	1.27	9	1.10
	♂ Adults	91	1.27	8	1.11
	♀ Adults	56	1.23	5	1.08
	Total	237	1.34	—	—
PL	Combined	180	1.75	10	1.13
PW	Young	88	1.64	9	1.12
	♂ Adults	93	1.70	8	1.24
	♀ Adults	56	1.47	5	1.12
	Total	237	1.70	—	—
LAL	Combined	179	1.25	10	1.05
TL	Young	90	1.34	9	1.08
	♂ Adults	93	1.28	8	1.07
	♀ Adults	56	1.23	5	1.09
	Total	239	1.34	5	1.09
FL	Young	89	1.31	9	1.08
	♂ Adults	93	1.29	8	1.08
	♀ Adults	56	1.25	5	1.04
	Total	238	1.45	—	—

female populations.

b) Patterns of Intrapopulation and Interpopulation Variation in ACV

1) Intrapopulation variation in ACV

When the variability of ACV was estimated by RE, TD and T-EL showed the highest variability, and PW ranked next (Table 57). The values of RE, however, were low compared with those for the Japanese common toad.

No age difference was detected for HL, T-EL and PW (Table 58). By contrast, HW, TL, and FL showed differences, and among them, the differences in TL and FL were marked between young and adult males. TL showed a distinct difference between young and adult females. Thus, in males, the characters of the hindlimb were judged to increase their relative length in the course of sexual maturity.

Table 58. Summary of intrapopulation variation in the median of ACV among populations of the Japanese stream toad.

Character	Combination	N of populations	N of differing populations	% of differing populations
HL	Y.: ♂Ad.	7	0	0
	Y.: ♀Ad.	4	0	0
	♂Ad.: ♀Ad.	5	3	60.0
T-EL	Y.: ♂Ad.	7	0	0
	Y.: ♀Ad.	4	0	0
	♂Ad.: ♀Ad.	5	0	0
HW	Y.: ♂Ad.	7	1	14.3
	Y.: ♀Ad.	4	1	25.0
	♂Ad.: ♀Ad.	5	5	100
PW	Y.: ♂Ad.	7	0	0
	Y.: ♀Ad.	4	0	0
	♂Ad.: ♀Ad.	5	0	0
TL	Y.: ♂Ad.	7	5	71.4
	Y.: ♀Ad.	4	2	50.0
	♂Ad.: ♀Ad.	5	1	20.0
FL	Y.: ♂Ad.	7	5	71.4
	Y.: ♀Ad.	4	1	25.0
	♂Ad.: ♀Ad.	5	5	100

Marked sexual dimorphism was observed in HW and FL, and all the examined populations differed in these characters between the two sexes of adults. In the 60% of the examined populations, HL showed dimorphism, whereas TL showed few sexual differences and T-EL and PW exhibited no dimorphism.

2) Interpopulation variation in ACV

The young did not exhibit marked interpopulation variation, and at most 16.7% of the examined combinations resulted in significant differences (Table 59). Likewise, adult males exhibited little variation, and they differed in HW in 25% of possible combinations. Adult females showed slightly higher variation, and differed in HW

Table 59. Summary of interpopulation variation in the median of ACV among populations of the Japanese stream toad.

Character	Age/sex group	N of combinations	N of differing combinations	% of differing combinations
HL	Young	36	2	5.6
	♂ Adults	28	4	14.3
	♀ Adults	10	3	30.0
SL	Combined	45	9	20.0
T-EL	Young	36	0	0
	♂ Adults	28	1	3.6
	♀ Adults	10	0	0
TD	Combined	45	16	35.6
HW	Young	36	2	5.6
	♂ Adults	28	7	25.0
	♀ Adults	10	7	70.0
PL	Combined	45	0	0
PW	Young	36	1	2.8
	♂ Adults	28	1	3.6
	♀ Adults	10	1	10.0
LAL	Combined	45	0	0
TL	Young	36	6	16.7
	♂ Adults	28	3	10.7
	♀ Adults	10	3	30.0
FL	Young	36	0	0
	♂ Adults	28	1	3.6
	♀ Adults	10	0	0

in 70% of the examined combinations, whereas no interpopulation difference was observed in T-EL and FL.

As to the characters examined by combining the three age/sex groups, PL and LAL showed no difference, and TD differed in about one-third of the combinations examined. From these results, interpopulation variation in the Japanese stream toad was judged to be low.

4. *Comparisons with the Japanese Common Toad and the Miyako Toad in SVL and Medians of ACV*

a) SVL

adult males.—All of the four populations of the Japanese stream toad had a mean SVL 1.24–1.55 times significantly smaller than the corresponding sympatric populations of the Japanese common toad (Pop. 101 vs. Pop. 51; Pop. 104 vs. Pop. 55; Pop. 105 vs. Pop. 58; Pop. 106 vs. Pop. 59).

Means of the mean SVLs for the four sympatric and four allopatric populations of the Japanese stream toad did not differ significantly (97.07±7.03 and 92.88±8.84 mm, respectively). Similarly, in the five sympatric and 11 adjacent allopatric populations of the Japanese common toad, means of mean SVLs did not differ (133.75±4.11 and 121.50±10.21 mm, respectively). The values for the Japanese common toad were significantly larger than those for the Japanese stream toad.

Among 58 populations of the Japanese common toad, three out of five (60.0%) sympatric and four out of 11 (36.4%) adjacent allopatric populations significantly differed from all populations of the Japanese stream toad. All of these common toad populations having different mean SVLs from the stream toad populations were type A. Out of 42 more distantly distributed allopatric populations, only six (14.3%) differed significantly from all of the stream toad populations, and in this case also, the different common toad populations were all type A. Thus, only 13 out of a total of 58 populations (22.4%) of the Japanese common toad completely differed from all populations of the Japanese stream toad in mean SVL. Among the populations of the Japanese common toad having mean SVL different from the stream toad, only Pop. 10 had a smaller mean than any of the Japanese stream toad populations, and the remaining common toad populations invariably had a larger mean SVL than the stream toad populations. None of the three available populations of the Miyako toad differed from populations of the Japanese stream toad in mean SVLs.

adult females.—Of the two available corresponding sympatric populations (Pop. 103 vs. Pop. 55, and Pop. 105 vs. Pop. 58), the two forms differed significantly in only one (Pop. 103 vs. Pop. 55), and the Japanese common toad had a mean SVL 1.22 times larger than the Japanese stream toad in these populations. The means of the mean SVLs for three allopatric populations (116.32±14.30 mm) overlapped the mean for the two sympatric populations ($\bar{X}=129.14$) in the Japanese stream toad. Similarly, in the five sympatric and seven adjacent allopatric populations of the Japanese common toad, means of the mean SVLs did not differ (140.95±5.57 and 132.66±10.60 mm, respectively). Only the values for allopatric populations of the Japanese stream toad and sympatric populations of the Japanese common toad differed significantly.

Among 50 populations of the Japanese common toad, none of the sympatric and only one out of eight (12.5%; Pop. 61) adjacent allopatric populations differed significantly from all populations of the Japanese stream toad. The single different common toad population belonged to type A. Out of the 37 remaining more distant allopatric populations, only three (8.1%) differed significantly from all of the stream toad populations. These included one type A and two type B populations. Thus, only four out of 50 (8.0%) common toad populations had mean SVLs completely different from all populations of the stream toad. Three out of four (75.0%) populations of the Miyako toad were significantly smaller in mean SVLs than all populations of the Japanese stream toad.

b) *ACV Median*

1) HL: young.—Medians of ACV for the Japanese stream toad and for the Japanese common toad did not differ between each of the three corresponding sympatric populations ($p>.05$), and in the zone of sympatry, the median of population medians for the six populations of the stream toad (33.0–34.5, median of population medians = 33.8) was not different ($U_{6,3}=5.5$, $p=.46$) from that for the three populations of the

Japanese common toad (31.3–34.2, median=33.0).

No significant difference in median of population ACV medians was obtained between the populations from the sympatric zone and those from the allopatric region (N=3, 32.7–34.8, median=32.7; $U_{6,3}=9$, $p=.10$) in the Japanese stream toad, and likewise in the Japanese common toad, sympatric and neighbouring allopatric populations (N=7, 31.5–34.4, median=33.0) did not differ in the median of population medians ($U_{3,7}=10$, $p=1.0$). All of the seven allopatric common toad populations distributed adjacent to the sympatric zone were not different from at least one population of the Japanese stream toad in the median of ACV.

Also, all of the 29 remaining distantly distributed allopatric populations of the Japanese common toad had insignificantly different ACV medians from at least one population of the Japanese stream toad. A single population of the Miyako toad (Pop. 97) had a significantly smaller median for HL ACV than in all the Japanese stream toad populations.

adult males.—Medians for the Japanese stream toad and for the Japanese common toad did not differ between each of the four corresponding sympatric populations, and in the sympatric zone, the median of population ACV medians for the four populations of the stream toad (32.2–34.2, median of population medians=33.3) and those for the five populations of the common toad (32.6–34.3, median=33.2) did not differ ($U_{4,5}=9$, $p=.90$).

In the Japanese stream toad, populations from sympatric and allopatric zones did not differ in the medians (medians for the latter populations=32.5–34.9, median of population medians=33.0; $U_{4,4}=8$, $p=1.11$), and also in the common toad, the median of population ACV medians did not differ in the sympatric and adjacent allopatric (31.1–35.0, median=32.5, N=10) populations ($U_{5,10}=14$, $p>.05$). All of the 11 allopatric populations of the Japanese common toad from neighbouring localities did not differ from at least some of the Japanese stream toad populations in medians.

Among the 42 remaining allopatric populations of the Japanese common toad from more distant localities, only two geographically isolated type A populations (4.8%; Pos. 23, 30) differed from all populations of the Japanese stream toad. Thus, only two (3.5%) of a total of 58 common toad populations differed completely from the stream toad populations. One of the three populations of the Miyako toad (Pop. 98) differed significantly from all populations of the Japanese stream toad by smaller HL ACV.

adult females.—Only two corresponding populations (Pop. 103 vs. Pop. 55, and Pop. 105 vs. Pop. 58) were available for comparison. In one of these (Pop. 105 vs. Pop. 58), stream and common toad differed significantly, and the former had a larger median than the latter ($U_{4,12}=6$, $p<.05$). In the Japanese stream toad, populations from the sympatric zone exhibited slightly larger medians (35.6 and 36.0) than those of three allopatric populations (population median=33.2–35.0, median of population medians=33.9), and some combinations among these populations resulted in significant differences as stated previously.

Each of the five populations of the common toad from the sympatric zone (population median ACV=32.9–34.8, median of population medians=34.1) did not differ from at least one of the five Japanese stream toad populations in medians.

Among eight populations of the Japanese common toad from neighbouring localities (population median ACV=31.2–34.8, median of population medians=33.8), only one (12.5%; Pop. 63=type B) differed from all populations of the stream toad. In 36 more distant allopatric populations of the Japanese common toad, only six (16.7%; Pops. 4, 16, 23, 24, 38, 43) were different from all populations of the stream toad. These different populations were all type A, and had smaller HL medians than in the stream toad. Thus, only seven (14.0%) of the total of 50 common toad populations completely differed from all populations of the stream toad.

Two of the three populations of the Miyako toad (Pops. 97, 98) also differed from all of the Japanese stream toad populations, and had smaller ACV.

The above results indicated a similar tendency through three age/sex groups: in and near the zone of sympatry, populations of the Japanese stream and common toads were similar in the median of HL ACV. A few populations of the Japanese common toad having differences from the stream toad were all in the localities distant from the sympatric zone, and had smaller medians than the stream toad. The Miyako toad was judged to have a smaller ACV median than the Japanese stream toad.

2) SL: The corresponding four populations of the Japanese stream and common toad differed insignificantly in medians.

Population medians of ACV for the six sympatric and four allopatric populations of the stream toad did not differ (12.8–13.5, median=13.0, and 12.1–13.5, median=12.8, respectively; $U_{6,4}=6.5$, $p=.31$). Likewise, nine populations of the Japanese common toad from the sympatric zone and 15 from the neighbouring allopatric range had similar medians (12.6–13.7, median=13.2 and 12.4–13.7, median=13.1).

None of the 24 Japanese common toad populations in and near the sympatric zone differed from any of the Japanese stream toad populations in medians. Similarly, all the 59 remaining allopatric populations of the common toad from more distant localities had ACV medians similar to at least one of the stream toad populations.

Populations of the Miyako toad differed from 3–7 of 10 Japanese stream toad populations, but none differed completely from the latter.

3) T-EL: young.—When the medians for the Japanese stream toad and for the common toad were compared in each of the corresponding sympatric populations, all the three combinations resulted in significant differences (Table 60). In all the sympatric populations, the Japanese stream toad had medians of T-EL ACV 1.45–1.79 times larger than those of the Japanese common toad, and in no corresponding populations did the range of ACV overlap. Thus, six populations of the stream toad and three populations of the common toad from the sympatric zone differed significantly in the medians (4.6–5.4, median=4.8, and 2.6–3.3, median=3.1, respectively: $U_{6,3}=0$, $p=.02$).

There was no significant difference between six sympatric and three allopatric (population median ACV=4.5–5.0, median of population medians=4.5) populations of the Japanese stream toad ($U_{6,3}=5$, $p=.38$).

Table 60. Difference in the T-EL ACV between the Japanese stream toad (t) and the Japanese common toad (j) from the zone of sympatry. For populations with sample size over 20, only 20 samples were used for Mann-Whitney's U test (signified by an asterisk).

Age/sex group	Form	Population	N	ACV range	ACV median	U	p
Young	t	104	4	4.2– 5.1	4.6	0	<.05
	j	57	5	1.6– 3.0	2.6		
	t	105	6	4.4– 5.3	4.8	0*	<.05
	j	58	23	2.5– 4.1	3.3		
	t	106	5	4.5– 5.7	5.4	0	<.05
	j	59	10	2.3– 3.8	3.1		
♂Adults	t	101	3	4.6– 5.2	4.9	0	<.05
	j	51	12	1.9– 3.1	2.5		
	t	103	9	4.1– 5.3	4.4	0*	<.05
	j	55	25	1.8– 3.8	2.7		
	t	105	6	4.7– 5.1	4.9	0	<.05
	j	58	6	3.2– 3.7	3.5		
	t	106	4	4.1– 5.0	4.7	0*	<.05
	j	59	59	1.4– 3.7	2.7		

In the Japanese common toad, the range of medians in the seven adjacent allopatric populations (3.4–4.3) did not ovelap that for three sympatric populations, and the medians differed significantly between these two groups ($U_{3,7}=0$, $p=.02$; median of population medians for allopatric populations=4.1). The adjacent allopatric populations of the Japanese common toad had T-EL ACVs closer to the Japanese stream toad than the sympatric populations.

Among 39 populations of the common toad, 23 (59.0%) had medians of ACV different from stream toad populations: all of the sympatric and three of seven (42.9%) adjacent allopatric populations significantly differed from all the Japanese stream toad populations in medians. These included four type A and two type B populations (Table 66). Out of 29 more distant allopatric populations, 17 (58.6%) differed. These common toad populations had smaller medians than the stream toad, and all but two were type A. A single population of the Miyako toad did not differ from at least one population of the stream toad in median of ACV.

adult males.—In all the corresponding sympatric populations, the range of ACV did not overlap, and all the four combinations resulted in significant differences (Table 60). The Japanese stream toad had medians of ACV 1.41–1.95 times larger than those of the common toad. Thus, four populations of the stream toad and five of the common toad from the sympatric zone differed significantly in the median of population medians (4.4–4.9, median of population medians=4.8 and 2.2–3.5, median=2.7, respectively; $U_{4,5}=0$, $p=.02$).

There was no significant difference in population medians between four sympatric and four allopatric (population medians=4.4–4.9, median of population medians=4.6) populations of the Japanese stream toad ($U_{4,4}=5$, $p=.49$).

In the Japanese common toad, the range of medians in the 11 allopatric populations from the surrounding localities (2.3–3.9) overlapped that for five sympatric populations, but the median of population medians in the allopatric populations (3.0) was closer to that for the Japanese stream toad than in the sympatric populations. All the five sympatric and 11 adjacent allopatric populations of the common toad differed from all populations of the stream toad.

When the 42 allopatric populations of the Japanese common toad from more distant localities were compared, 38 (90.5%) differed significantly from all populations of the stream toad. Populations of the common toad which did not differ from stream toad populations were all type B. In Honshu, only one population from the western extremity (Pop. 80) had a median that did not differ from those for three of eight populations of the Japanese stream toad. Three populations from Shikoku (Pops. 84, 85, 87) had ACVs overlapping those for the populations of the stream toad.

Thus, as many as 54 (93.1%) of total 58 populations of the common toad had ACV medians different from all the stream toad populations, and the populations of the common toad having T-EL ACV's similar to those of the stream toad were all from the localities markedly distant from the range of the stream toad.

All the three populations of the Miyako toad had significantly smaller medians than any of the Japanese stream toad populations.

adult females.—Each of the two corresponding sympatric populations of the Japanese stream and common toad differed significantly in ACV (Pop. 103 vs. 55: $U_{4,5}=0$, $p=.02$; Pop. 105 vs. 58: $U_{4,12}=0$, $p<.05$), and all of the five common toad populations from the sympatric zone had significantly smaller population medians (3.0–3.4, median of population medians=3.1) than each of the five stream toad populations (range of population medians, 4.8–5.1).

The ranges of ACV overlapped between the sympatric and allopatric populations of the Japanese stream toad. In the Japanese common toad, the range of medians (2.8–4.5, median of population medians=3.2) was larger in the neighbouring allpatric populations (including type A and type B) than in the sympatric populations (all type A), but the difference in population medians was insignificant ($U_{8,5}=17$, $p>.05$).

Only one of eight adjacent allopatric populations of the common toad (Pop. 62 =type B) did not differ from some of the five ppulations of the stream toad, and all the seven remaining populations (87.5%) were significantly smaller than all populations of the Japanese stream toad in ACVs.

Among the remaining 37 more distantly distributed allopatric populations of the common toad, 11 did not differ from at least one of five stream toad populations in medians. Of these, four were from Honshu (Pops. 12, 78, 79, 80), four from Shikoku (Pops. 84, 85, 86, 87), and three from Kyushu (Pops. 88, 89, 91), and all were type B. The remaining 26 populations (70.3%) had significantly smaller medians than all the stream toad populations. Therefore, in total, as many as 38 out of 50 (76.0%) populations of the Japanese common toad had smaller ACV medians than any of the stream toad populations.

Four populations of the Miyako toad had significantly smaller medians than all of the Japanese stream toad populations.

4) TD: When the medians for the stream toad and for the common toad were compared in the corresponding populations from the zone of sympatry, all the six combinations resulted in significant differences ($p<.05$, Table 61). In all the corresponding populations, the Japanese stream toad had a smaller tympanum than the Japanese common toad, and the magnitude of difference was 1.66–2.02 times. Only between Pop. 103 and Pop. 55, did the ranges of ACV slightly overlap.

Table 61. Difference in the TD ACV between corresponding Japanese stream toad (t) and the Japanese common toad (j) populations from the zone of sympatry. For populations with sample size over 20, only 20 samples were used for Mann-Whitney's U test (signified by an asterisk).

Form	Population	N	ACV		U	p
			range	median		
t	101	8	3.3– 4.2	4.1	0	<.05
j	51	17	4.9– 8.3	6.8		
t	103	17	2.1– 5.1	3.3	1*	<.05
j	55	33	4.9– 7.9	6.7		
t	104	6	3.3– 4.2	3.8	0	<.05
j	57	7	5.4– 7.2	6.3		
t	105	16	2.4– 4.4	3.6	0*	<.05
j	58	41	5.2– 8.4	6.6		
t	106	9	3.1– 4.6	3.5	0*	<.05
j	59	81	5.1– 8.4	6.7		
t	112	9	2.6– 3.6	3.1	0	<.05
j	72	4	4.7– 6.5	5.6		

Thus, six corresponding sympatric populations of the stream toad and the common toad had a significantly different median of population ACV medians (3.1–4.1, median $=3.6$, and 5.6–6.8, median$=6.6$, respectively; $U_{6,6}=0$, $p=.001$).

There was a significant difference between six sympatric and four allopatric (population medians$=3.1$–3.4, median of population medians$=3.1$) populations of the Japanese stream toad ($U_{6,4}=2$, $p=.038$), and the allopatric populations had smaller ACV.

In the Japanese common toad, the range of population medians was larger (4.7–7.6, median$=6.2$) in 15 neighbouring allopatric populations than in nine populations from the sympatric zone (5.6–6.8, median$=6.8$), but the medians of population medians did not differ significantly ($U_{9,15}=34$, $p>.05$). All the nine sympatric and 14 of 15 adjacent allopatric (93.3%) populations of the common toad had significantly larger medians than any of the Japanese stream toad populations. Only one type B population from an adjacent locality (Pop. 64, Settsu) had an insignificantly different median from two populations of the stream toad (Pop. 101: $U_{4,8}=6$, $p=.11$; Pop. 104: $U_{4,6}=3$, $p=.07$).

When 59 allopatric populations of the common toad from more distant localities were compared with the stream toad in medians of TD ACV, only one type B population from Kyushu (Pop. 90) was insignificantly different from three of ten populations of the Japanese stream toad, probably due to small sample size (Pop. 90 vs. Pop. 101: $U_{8,\,3}=6$, $p=.27$; Pop. 104: $U_{6,\,3}=2$, $p=.10$; Pop. 106: $U_{9,\,3}=3$, $p>.05$). Therefore, 58 out of 59 populations (98.3%) of the Japanese common toad from distant localities had larger medians than any of the stream toad populations. Thus, as many as 81 out of a total of 83 populations (97.6%) of the common toad differed from all populations of the stream toad.

All of the four populations of the Miyako toad differed from populations of the Japanese stream toad in medians, and had larger values than the latter.

From these results it was obvious that only a few populations of the Japanese common toad had medians of ACV similar to those of the Japanese stream toad, and that, even in such cases, more distantly distributed populations of the common toad tended to have more similarities with the stream toad.

5) HW: young.—Each of the corresponding three populations of the Japanese stream and common toad (Pop. 104 vs. 57; Pop. 105 vs. 58; Pop. 106 vs. 59) did not differ significantly in ACV median ($p>.05$).

Medians of population medians of the six sympatric and three allopatric populations did not differ in the stream toad (38.3–40.5, median=38.9, and 37.1–40.7, median=38.7, respectively; $U_{6,\,3}=8$, $p=.90$). Also, in the common toad, three populations from the sympatric zone and seven from the adjacent allopatric zone had insignificantly different medians (36.5–40.8, median=38.6 and 35.8–40.2, median=39.4, respectively; $U_{3,\,7}=10$, $p=1.0$).

No populations of the Japanese common toad, including those from more distant localities, differed from any of the Japanese stream toad populations in medians. A single population of the Miyako toad (Pop. 97) had a median insignificantly different from five out of nine stream toad populations.

adult males.—Only one (Pop. 106 vs. Pop. 59) of the four corresponding populations of the stream and common toads differed significantly in medians ($U_{4,\,20}=11$, $p<.05$), and in this combination, the common toad had a smaller median.

Medians for the four sympatric and four allopatric populations of the Japanese stream toad did not differ (37.2–38.1, median=37.6 and 35.3–39.0, median=37.5, respectively; $U_{4,\,4}=10$, $p>.1$). Similarly, in the common toad, five populations from the sympatric zone and 11 from the adjacent allopatric region did not differ in the median of population medians (35.6–38.0, median=36.5 and 34.9–40.2, median=36.8, respectively; $U_{5,\,11}=22$, $p>.05$).

Among 42 more distantly distributed allopatric populations of the common toad, only two (4.8%; Pops. 1 and 24) differed from all populations of the Japanese stream toad in medians. The locations of these two type A populations (Hakodate and Togane) were far from the range of the stream toad. Thus, only 3.5% of a total of 58 populations of the common toad differed completely from the stream toad. Of the three populations of the Miyako toad, two (Pops. 97 and 99) differed from seven of eight populations of the Japanese stream toad, but none differed completely from the latter.

adult females.—Each of the two corresponding sympatric populations of the stream and common toad did not differ significantly in medians.

In the Japanese stream toad, two sympatric populations had slightly larger medians than three allopatric populations, but no difference was observed between Pop. 103 (sympatric) and Pop. 110 (allopatric). Five sympatric and seven adjacent allopatric populations of the common toad had similar medians (38.4–40 8, median=39.6, and 37.7–41.4, median=39.0, respectively; $U_{5,7}=14$, $p=.63$).

Among 37 allopatric populations of the common toad distant from the sympatric zone, five (13.5%; Pops. 1, 23, 24, 38, 43; all type A) had significantly smaller medians than any of the five stream toad populations. Populations other than these five had medians not different from at least one population of stream toad. Thus, of the total number of 49 common toad populations, only 10.2% differed completely from all the stream toad populations.

Of the three Miyako toad populations, two (Pops. 97 and 98) had smaller medians than all of the stream toad populations, and one (Pop. 100) had an insignificantly different median from only one of five stream toad populations (Pop. 109; $U_{3,20}=17$, $p>.05$).

6) PL: The comparison of ACVs in the corresponding six sympatric populations of the Japanese stream and common toad all resulted in significant differences (Table 62), and populations of the common toad had medians 1.17–1.35 times larger than those of the corresponding populations of the stream toad.

Sympatric and allopatric populations of the stream toad did not differ in medians (16.4–17.8, median=17.0, and 16.1–18.3, median=17.4, respectively; $U_{6,4}=11.5$, $p>1$). Only one of the nine sympatric and 15 adjacent allopatric populations of the

Table 62. Difference in the PL ACV between corresponding Japanese stream toad (t) and the Japanese common toad (j) populations from the zone of sympatry. For populations with sample size 20 or larger, only 20 samples were used for Mann-Whitney's U test (signified by an asterisk).

Form	Population	N	ACV range	ACV median	U	p
t	101	9	14.1–19.5	17.8	6	<.05
j	51	17	18.1–24.8	21.3		
t	103	18	14.5–23.0	17.8	33*	<.05
j	55	33	17.7–25.0	21.5		
t	104	6	15.1–18.4	16.2	1	<.01
j	57	7	18 3–24.4	21.8		
t	105	16	14.2–20.8	16.1	16.5*	<.05
j	58	40	17.6–23.9	21.0		
t	106	10	16.4–18.7	17.0	5*	<.05
j	59	40	17.5–24.2	21.6		
t	112	9	13.1–20.2	18.3	3	<.05
j	72	4	19.5–22.5	21.3		

common toad had medians not different from those of the stream toad populations. The single exception was Pop. 68 (Ise), which did not differ from one of 10 stream toad populations (Pop. 112).

Among more distantly distributed 59 allopatric populations of the common toad, only seven did not differ from some populations of the Japanese stream toad in medians (Pops. 3, 13, 14, 40, 82, 83, 87). These populations were from far east of the sympatric zone in Honshu (type A) or from Shikoku (type B). Thus, as many as 75 out of a total of 83 populations (90.4%) of the Japanese common toad had medians different from those of all populations of the Japanese stream toad.

All the four populations of the Miyako toad had medians insignificantly different from those of the stream toad.

7) PW: young.—All the corresponding populations of the Japanese stream and common toad (Pop. 104 vs. 57; Pop. 105 vs. 58; Pop. 106 vs. 59) differed singnificantly in medians ($p>.05$).

In the Japanese stream toad, population medians for the six sympatric and three allopatric populations did not differ (6.3–6.9, median=6.7, and 6.1–6.7, median=6.3, respectively; $U_{6,3}=2$, $p=.10$), whereas in the common toad, three sympatric and seven adjacent allopatric populations differed significantly in medians (6.5–6.7, median =6.6, and 6.9–8.3, median=7.0, respectively; $U_{3,7}=0$, $p=.02$).

Among 39 populations of the Japanese common toad, only one (2.6%; Pop. 73= type B) had a significantly larger median than those of the nine populations of the stream toad. All the remaining populations of the common toad did not differ from at least one population of the stream toad. A single population of the Miyako toad did not differ from any of the stream toad populations.

adult males.—Only one (Pop. 106 vs. 59) of the four corresponding populations of the stream and common toads differed significantly in medians ($U_{4,20}=8$, $p<.05$). In this combination, the common toad had a larger median than the stream toad.

Medians for four sympatric and four allopatric populations of the Japanese stream toad did not differ (6.1–6.9, median=6.5, and 6.2–7.5, median=6.7, respectively; $U_{4,4}=5$, $p=.49$), and similarly in the common toad, five sympatric and 11 adjacent allopatric populations did not differ in medians (6.5–7.7, median=7.4, and 6.6–7.6, median=7.3, respectively; $U_{5,11}=24$, $p>.05$).

Among the populations of the Japanese common toad, only one (1.7%: Pop. 19 =type A) had a significantly larger median than those of eight populations of the stream toad, and all the remaining populations of the common toad did not differ from at least one population of the stream toad. None of three populations of the Miyako toad differed from any of the Japanese stream toad populations.

adult females.—The two available corresponding populations of the stream and common toad from sympatric zone had almost similar medians (6.0 and 6.3, respectively). Likewise, no difference was observed between sympatric and adjacent allopatric populations of the Japanese common toad in medians (6.9–8.6, median of population medians=7.5, and 6.9–7.6, median=7.3, respectively; $U_{5,7}=11$, $p=.34$), and medians were significantly larger than those for the Japanese stream toad (sympatric and allopatric populations combined: $U_{5,5}=0$, $p=.008$, and $U_{5,7}=0$, $p=.002$, respectively).

Among 50 populations of the Japanese common toad, 31 (62.0%) differed completely from all the stream toad populations: three out of five type B populations (60.0%) from the sympatric zone and four (two type A and two type B) out of eight populations (50.0%) from the adjacent allopatric region significantly differed from all populations of the Japanese stream toad. Of the remaining 37 more distant populations, 24 (64.9%) differed from all of the stream toad populations. These populations included 16 of type A, one intermediate, and seven of type B, and invariably had larger ACVs than in the stream toad. By contrast, each of the four populations of the Miyako toad differed from at most two of the five stream toad populations.

8) LAL: The comparison of the medians between stream and common toad from the zone of sympatry resulted in significant differences in all the six corresponding combinations ($p<.05$, Table 63), notwithstanding the slight overlap of ACV range in three populations. Six populations of the stream toad and nine of the common toad from the zone of sympatry differed significantly in medians (53.5–56.1, median=54.8, and 47.5–51.5, median=49.5, respectively; $U_{6,9}=0$, $p<.05$). In the sympatric zone, the Japanese stream toad had medians in LAL ACV 1.05–1.06 times larger than in the common toad, and only between distantly located populations did medians not differ (Pop. 101 vs. Pop. 58: $U_{9,20}=56$, $p>.05$; Pop. 101 vs. Pop. 71: $U_{5,9}=8$, $p>.05$).

In the Japanese stream toad, no significant difference was found between six populations from the sympatric zone and four from the allopatric zone (allopatric=54.2–55.2, median=54.9; $U_{6,4}=12$, $p>1$).

The range of medians was larger (46.1–51.3) in the 15 neighbouring allopatric

Table 63. Difference in the LAL ACV between corresponding Japanese stream toad (t) and the Japanese common toad (j) populations from the zone of sympatry. For populations with sample size 20 or larger, only 20 samples were used for Mann-Whitney's U test (signified by an asterisk).

Form	Population	N	ACV		U	p
			range	median		
t	101	9	50.2–56.9	53.5	10	<.05
j	51	17	44.4–53.9	48.0		
t	103	18	50.1–58.1	54.6	37*	<.05
j	55	34	46.0–56.3	50.4		
t	104	5	52.6–60.1	56.1	0	<.05
j	57	7	45.2–50.8	48.8		
t	105	16	50.3–56.6	54.3	49*	<.05
j	58	41	46.7–55.8	51.5		
t	106	10	52.2–57.0	54.9	0*	<.05
j	59	50	43.1–51.3	47.5		
t	112	9	52.8–57.3	55.6	0	<.05
j	72	4	48.7–50.1	49.5		

populations of the common toad than in nine sympatric populations, but the median of population medians of the former (49.5) did not differ from that of the latter ($U_{15,9}=57$, $p>.05$).

Six out of nine populations (66.7%) of the common toad from the sympatric zone differed from all populations of the Japanese stream toad. Among 15 allopatric populations ranging adjacent to the sympatric zone, only five (three type A and two type B) slightly overlapped some geographically more distant populations of the stream toad (Pop. 101 vs. Pops. 47, 53, 64, 69, 70; Pop. 105 vs. Pop. 69; Pop. 113 vs. Pop. 70), and the remaining 10 populations (66.7%: five type A and five type B) differed from all of the stream toad populations.

Of the remaining 59 populations of the common toad from more distant localities, 21 (36.8%, 10 type A and 11 type B) did not differ significantly in medians from at least one population of the stream toad. Among them, populations of the common toad which did not differ from as many as 6–10 stream toad populations were Pops. 13, 40, 46, 82, 83, 84, 85, 89, 90. All of these populations are distributed distantly from the zone of sympatry, and the number of type B populations was larger than that of type A.

Thus, among the total of 83 populations, 54 (65.1%) had significantly smaller ACV medians than all populations of the stream toad.

All of four populations of the Miyako toad had significantly smaller ACVs than any population of the Japanese stream toad.

9) TL: young.—Two of three populations of the Japanese stream toad (Pops. 105, 106) had medians 1.08–1.09 times significantly larger than the corresponding sympatric populations of the Japanese common toad ($U_{6,20}=18$, $p<.05$, and $U_{6,6}=0$, $p=.002$, respectively), whereas in the remaining one population (Pop. 104), the median did not differ from the corresponding common toad population ($U_{4,5}=4$, $p=.19$).

Medians for six populations from sympatric and three from allopatric zone did not differ in the stream toad (36.0–38.4, median=37.6, and 36.8–38.8, median=38.1, respectively; $U_{6,3}=5$, $p=.38$), and similarly in the common toad, three populations from sympatric and seven from adjacent allopatric region did not differ in the median of population ACV medians (34.4–36.2, median=35.6, and 34.0–36.7, median=35.2, respectively; $U_{3,7}=10$, $p=1$).

All populations of the common toad including those from more distant localities did not differ from at least one of the stream toad populations in medians, notwithstanding occurrence of many different combinations. A single comparable Miyako toad population had a significantly smaller ACV median than those of all the stream toad populations.

adult males.—All of four populations of the stream toad had 1.08–1.12 times larger medians than the corresponding sympatric common toad populations (Table 64).

In the Japanese stream toad, medians of the four populations from the sympatric zone were larger than those of four allopatric populations (40.1–41.1, median=40.6, and 38.5–40.0, median=39.9, respectively; $U_{4,4}=0$, $p=.03$). By contrast, between five sympatric and 11 adjacent allopatric populations of the common toad, medians did not differ significantly (36.4–37.9, median=36.8, and 35.3–38.9, median=37.1,

Table 64. Difference in the adult male TL ACV between corresponding Japanese stream toad (t) and the Japanese common toad (j) populations from the zone of sympatry. For populations with sample size 20 or over, only 20 samples were used for Mann-Whitney's U test (signified by an asterisk).

Form	Population	N	ACV range	ACV median	U	p
t	101	3	39.1–41.3	40.3	1	<.05
j	51	12	32.7–39.5	36.3		
t	103	10	38.2–43.1	41.1	13.5*	<.05
j	55	25	34.2–41.1	37.5		
t	105	6	38.0–42.7	40.1	1	<.01
j	58	7	35.6–38.8	36.7		
t	106	4	39.6–41.6	41.0	0*	<.05
j	59	57	33.1–39.0	36.6		

respectively; $U_{5,11}=24.5$, $p>.05$). These latter two median values were significantly smaller than those of the stream toad.

Among 58 populations of the common toad, three out of five sympatric (60.0%) and six (five type A and one type B) out of 11 adjacent allopatric (54.5%) populations differed significantly from all populations of the stream toad. Out of 42 more distantly distributed populations, 21 (50.0%) differed significantly. Thus, a total of 51.7% of common toad populations had different medians from all populations of the stream toad. In these populations, medians were invariably smaller than those of the stream toad. Likewise, all the three populations of the Miyako toad differed from all populations of the Japanese stream toad, and had smaller ACVs than the latter form.

adult females.—Two stream toad populations had medians 1.09–1.13 times significantly larger than that of the corresponding sympatric populations of the common toad (Pop. 103 vs. Pop. 55: $U_{4,7}=1$, $p=.01$; Pop. 105 vs. Pop. 58: $U_{4,12}=0$, $p<.05$).

In the Japanese stream toad, two populations from the sympatric zone exhibited slightly larger medians than those for the three allopatric populations (39.6–40.0, and 36.8–38.5, median=37.9, respectively), and as stated previously, some combinations among these populations resulted in significant differences. In the common toad, five sympatric and seven adjacent allopatric populations did not differ in the median of population ACV medians (34.6–36.4, median=35.0, and 34.4–36.2, median=35.5, respectively; $U_{5,7}=13.5$, $p=.58$). Medians of the common toad populations were significantly smaller than those of the allopatric stream toad populations.

Among 50 populations of the common toad, 23 (46.0%) differed completely from all the stream toad populations. Two out of five sympatric (40.0%) and two out of eight adjacent allopatric (25.0%: one type A and one type B) populations differed significantly from all populations of the stream toad. Out of 37 more distant allopatric populations, 19 (51.4%) differed. Thus, 46.0% of the common toad populations differed from the stream toad and invariably had smaller medians. Similarly, all the four populations of the Miyako toad had significantly smaller ACVs than those of all the stream toad populations.

10) FL: young.—All of the three stream toad populations had medians 1.07–1.22 times significantly larger than those of the corresponding sympatric common toad populations (Table 65).

Table 65. Difference in the FL ACV between corresponding Japanese stream toad (t) and the Japanese common toad (j) populations from the zone of sympatry. For populations with sample size 20 or larger, only 20 samples were used for Mann-Whitney's U test (signified by an asterisk).

Age/sex group	Form	Population	N	ACV		U	p
				range	median		
Young	t	104	4	46.2–52.6	48.9	0	<.05
	j	57	5	37.0–42.6	40.1		
	t	105	6	45.4–48.4	45.8	1*	<.05
	j	58	23	38.1–45.5	42.9		
	t	106	6	45.8–49.4	47.6	0	<.01
	j	59	10	38.0–44.7	41.8		
♂ Adults	t	101	3	52.3–55.2	53.9	0	<.05
	j	51	12	40.1–48.0	44.0		
	t	103	10	46.3–57.4	52.7	6*	<.05
	j	55	25	37.5–48.6	44.3		
	t	105	6	49.0–55.8	52.7	0	<.01
	j	58	7	41.2–46.0	43.8		
	t	106	4	51.7–55.0	52.4	0	<.05
	j	59	58	37.7–48.2	43.3		

Medians of the six sympatric and three allopatric populations of the stream toad did not differ (45.8–48.9, median=46.3, and 47.7–49.2, median=47.7, respectively; $U_{6,3}=2$, $p=.10$). Similarly, in the three sympatric and seven adjacent allopatric populations of the common toad, medians did not differ significantly (40.1–42.9, median=41.8, and 38.4–42.1, median=42.1, respectively; $U_{3,7}=3$, $p=.12$). Medians of the Japanese common toad were significantly smaller than those of the Japanese stream toad.

Among 39 populations of the common toad, all the three sympatric (100%, type A) and six out of seven (85.7%, all type B) adjacent allopatric populations differed significantly from all populations of the stream toad. Out of 29 more distantly ranging populations, nine (31.0%) differed significantly. Thus, 46.2% of the common toad populations differed from all the stream toad populations in medians. A single Miyako toad population significantly differed from every population of the stream toad. In the populations mentioned above, medians were invariably smaller than in the stream toad.

adult males.—All of the four populations of the stream toad had medians 1.19–1.22 times significantly larger than those of the corresponding sympatric populations of the common toad (Table 65).

Medians for the four sympatric and four allopatric populations of the stream toad did not differ (49.8–53.5, median=52.7, and 52.4–53.9, median=52.7, respectively; $U_{4,4}=6$, $p=.68$). Similarly, in the five sympatric and 11 adjacent allopatric common toad populations, the median of the population medians did not differ (43.3–45.2, median=44.2, and 39.8–47.4, median=43.9, respectively; $U_{5,11}=27$, $p>.05$). Medians of the common toad were significantly smaller than those of the stream toad.

Among 58 common toad populations, as many as 50 (86.2%) differed completely from the populations of the stream toad. All the sympatric (100%) and 10 out of 11 adjacent allopatric (90.9%: five type A and five type B) populations differed significantly from all populations of the stream toad. Out of 42 more distantly located populations, 35 (83.3%; 26 type A, one intermediate, and eight type B) differed from all of the stream toad populations. All of the three Miyako toad populations also differed significantly from every population of the Japanese stream toad. All these different combinations included a larger ACV in the stream toad.

adult females.—Two stream toad populations (Pops. 103, 105) had 1.08–1.11 times significantly larger medians than in the corresponding sympatric common toad populations ($U_{4,7}=0$, $p=.006$ and $U_{4,12}=3$, $p<.05$).

Medians of the three allopatric populations (45.0–46.3, median=45.8) were only slightly larger than those of the two sympatric populations (44.6–44.7) in the stream toad. In the same manner, between the five sympatric and seven adjacent allopatric common toad populations, medians were similar (38.1–41.6, median=39.8 and 37.8–43.2, median=39.1, respectively; $U_{5,7}=16$, $p=.87$). The values for the stream toad were significantly larger than those for the common toad.

Among 50 populations of the Japanese common toad, 39 (78.0%) differed from all populations of the stream toad. All the five sympatric (100%) and six out of eight (75.0%: five type A and one type B) adjacent allopatric populations differed from all populations of the stream toad. Out of 37 more distantly distributed populations, 28 (75.7%: 17 type A, one intermediate, and 10 type B) differed significantly from all of the stream toad populations. All of the four populations of the Miyako toad significantly differed from all populations of the stream toad. In all these different combinations, the Japanese stream toad had invariably larger medians.

DISCUSSION

Hybrids between two different species sometimes resemble either of the parental species in some characters (Cory and Manion, 1955; Feder, 1979; Kobel et al., 1981), but the reciprocal hybrids artificially produced between the Japanese stream toad and the Japanese common toad are morphologically intermediate between the parental species, and have intermediate morphometric values in such characters as TD, PL and FL, which are important for distinguishing the two forms (Matsui, unpubl.; Kawamura et al., 1980: 34), though the brain morphology and the clutch size are apparently affected by maternal source (Masai et al., 1982; Kawamura et al., 1980). Consequently, if natural hybridizations actually occurred in nature, and hybrids were frequently produced in the zone of sympatry, the hybrids would mingle with parental forms and would show continuous morphological variation within the sympatric zone. Individuals showing intermediate morphology, however, have never been actually obtained in the zone of sympatry, and all of the collected specimens can be assigned to either of the two forms (e.g., by the relationship between T-EL and TD: Figs. 56–57).

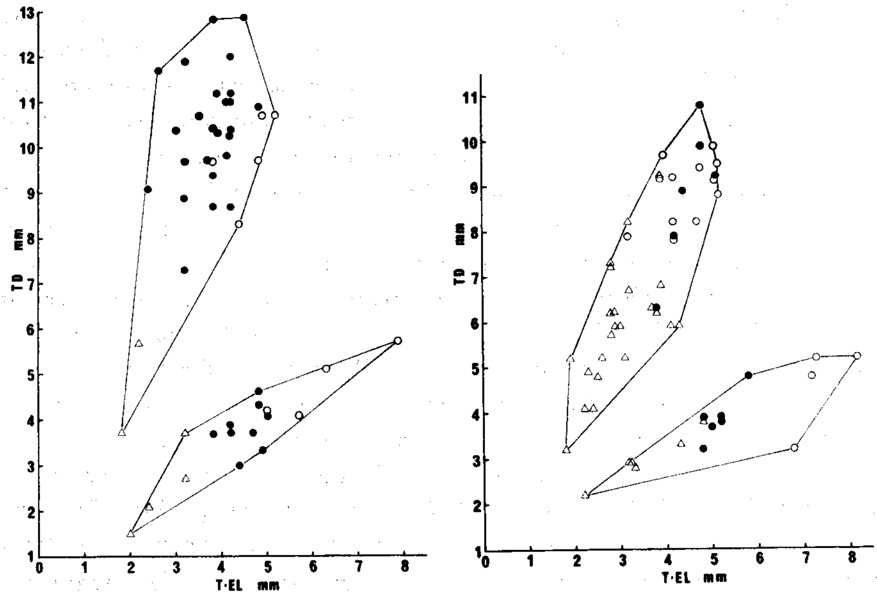

Fig. 56. Relationship between T-EL and TD in the sympatric Japanese stream toad (bottom) and the Japanese common toad (top) from Nogo Hakusan (left) and Kyoto Ashu (right).

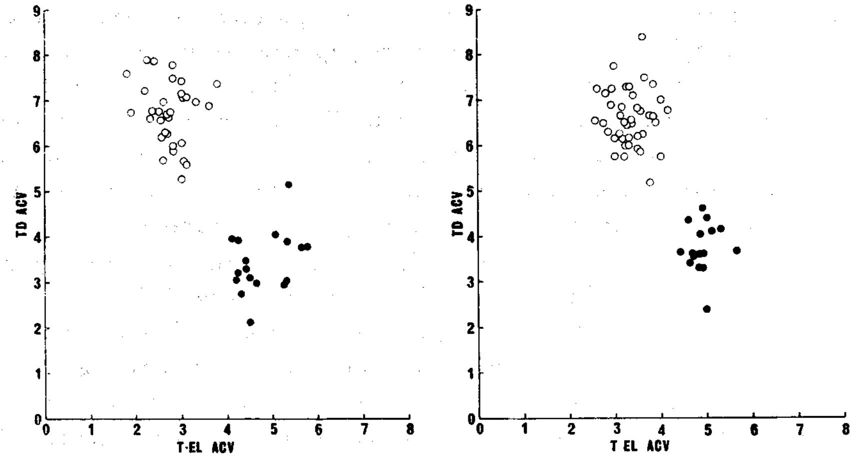

Fig. 57. Relationship between T-EL ACV and TD ACV in the sympatric Japanese stream toad (bottom) and the Japanese common toad (top) from Nogo Hakusan (left) and Kyoto Ashu (right).

Where individuals exhibiting distinct adult morphology of the Japanese stream toad occur, there are also found stream dwelling tadpoles with unique morphology. It is of course, very difficult to eliminate the possibility of natural hybridization or introgression, but the hitherto available data indicate very infrequent occurrence of such cases, and suggest the presence of complete pre-mating isolating mechanisms between the Japanese stream toad and the Japanese common toad.

Intrapopulation variation pattern: Most pronounced age variation in the Japanese stream toad was the relative elongation of TL and FL in males, and females also showed a tendency toward TL elongation. The results in males agreed well with those obtained from males of the Japanese common toad, but the trend found in the female stream toad somewhat differed from that observed in the female Japanese common toad. In the latter form, young and adult females were almost identical in TL. Thus, not only the male, but also the female of the stream toad had a long tibia, resulting in less evident sexual dimorphism in this character than in the common toad.

Among sexual dimorphisms found in the Japanese stream toad, the most remarkable ones were in HW and FL. This result is similar to that found in both type A and type B populations of the Japanese common toad. By contrast, the frequency of sexual dimorphism in T-EL and TL was lower than in the two types of the common toad, and the frequency of difference in HL was also slightly lower in the stream toad.

These trends in age and sexual variation coincide well with those reported for the species of *Bufo* (Boring, 1939; De Lange, 1973; Fang and Chang, 1931; Hemmer et al., 1978; Opatrný, 1974; Underhill, 1961b), and are considered to be general in this genus.

Interpopulation variation pattern: Since the main habitats of the Japanese stream toad are limited to areas around mountain streams, the degree of isolation among populations is thought to be stronger in the Japanese stream toad than in the Japanese common toad, which utilizes wider and more various habitats. The pattern of morphological variation of the Japanese stream toad seems to indicate that the influence of such isolated distribution does not increase interpopulation variation. Geographic variation in the morphometric characters of the Japanese stream toad was generally less prominent than in the Japanese common toad. This may partly be due to the narrower distribution range of the stream toad. The presence of more pronounced variation among Japanese common toad populations in and near the zone of sympatry with the Japanese stream toad, however, indicate that the Japanese stream toad, as a whole, is surprisingly uniform in the morphometry of each character.

SVL variation: The SVL of females of the Japanese stream toad was significantly larger than that of males, and average relative female and male SVL was 1.28. This value is large compared with that of the Japanese common toad, and corresponds to the value of type B populations of the latter form from the southern region. In the populations of the Japanese common toad distributed in and near the zone of sympatry with the stream toad, the sexual difference in SVL was much smaller. Relative female and male mean SVLs in the Japanese stream toad populations completely deviate from the clines exhibited by the common toad populations, and the sexual difference in SVL in the stream toad is thought to be caused by factors different from those affecting the

Japanese common toad populations. For the type B populations of the Japanese common toad, the sexual difference in SVL could be attributed to the variation in the breeding season and subsequent individual growth and development, but such considerations hardly apply to the Japanese stream toad.

The SVL of females in stream-breeding *Rana* and *Amolops* (often referred to as *Staurois*) is reported to be much larger than that of conspecific males (Pope, 1931: 55; Liu, 1950: 66). The female of a rhacophorid, *Buergeria buergeri*, which is another unique stream breeder from Japan and frequently cohabits with the Japanese stream toad, has also markedly larger SVL than the male. Since many species of Rhacophoridae often exhibit great sexual dimorphism in SVL, the larger female SVL in *B. buergeri* may partly reflect its phylogeny. In the case of the Japanese stream toad, however, the essentialy unique mode of life lies in its stream breeding, which differs from most of the toad species of *Bufo*, and the sexual dimorphism in SVL can be more directly attributable to the habit of stream breeding. According to Pope and Liu (op. cit.), the small body size of the male is regarded as advantageous to the mated pair to reduce resistance in the swift water, and to the female to have a light load while trying to swim about in a current. This assumption is considered to well explain the SVL sexual dimorphism in the Japanese stream toad.

When all the populations are combined, males of the Japanese common toad exhibited a cline on which the maximum SVL is attained at about 34° 35' N, which passes near the centre of the distribution range of the Japanese stream toad. The factors affecting the SVL cline of the Japanese common toad populations have been discussed elsewhere. In the zone of sympatry with the stream toad, males of each common toad population had SVL 1.2–1.6 times larger than the corresponding stream toad males, and this fact indicates that some ecological factors in relation to the sympatric distribution affect the SVL of the two forms.

In contrast to males, the SVL of the Japanese stream toad females was similar to that of the female Japanese common toad. The Japanese stream toad has a slenderer body shape than the common toad, and even a gravid female has a rather slim body and has a smaller number of eggs than a common toad with the same body size (Matsui, unpubl.). The relatively smaller number of eggs laid by a female stream toad seems to suggest that a certain size of SVL is required for the female stream toad to lay larger number of eggs than is critical for guaranteeing the conservation of the species (generally the number of eggs laid is proportionate to the size of the female within a toad population: Kadel, 1977). The larger SVL in the female also seems to guarantee a larger SVL difference between the sexes and hence easier breeding in a stream as discussed above.

Comparisons with the common toad and the Miyako toad in ACV: The difference in the morphometric characters between the Japanese stream toad and the Japanese common toad was more distinct in the zone of sympatry than in the allopatric regions, as represented by T-EL, TD and FL (Table 66; Fig. 58).

More than 75% of the Japanese common toad populations differed from all populations of the Japanese stream toad in T-EL (in both sexes of adults), TD, PL, and FL

Table 66. Percentage of the Japanese common toad populations showing significant differences in the SVL and in median of ACV from all populations of the Japanese stream toad.

Character	Age/sex group	Sympatric zone				Adjacent allopatric zone			
		type A		type B		type A		type B	
		N of pops.	% of differing pops.	N of pops.	% of differing pops.	N of pops.	% of differing pops.	N of pops.	% of differing pops.
SVL	♂ Adults	5	60.0	0	–	5	80.0	6	0
	♀ Adults	5	0	0	–	5	20.0	3	0
HL	Young	3	0	0	–	1	0	6	0
	♂ Adults	5	0	0	–	5	0	6	0
	♀ Adults	5	0	0	–	5	0	3	33.3
SL	Combined	8	0	1	0	8	0	7	0
T-EL	Young	3	100	0	–	1	100	6	33.3
	♂ Adults	5	100	0	–	5	100	6	100
	♀ Adults	5	100	0	–	5	100	3	66.7
TD	Combined	8	100	1	100	8	100	7	85.7
HW	Young	3	0	0	–	1	0	6	0
	♂ Adults	5	0	0	–	5	0	6	0
	♀ Adults	5	0	0	–	4	0	3	0
PL	Combined	8	87.5	1	100	8	100	7	100
PW	Young	3	0	0	–	1	0	6	16.7
	♂ Adults	5	0	0	–	5	0	6	0
	♀ Adults	5	60.0	0	–	5	40.0	3	66.7
LAL	Combined	8	62.5	1	100	8	62.5	7	71.4
TL	Young	3	0	0	–	1	0	6	0
	♂ Adults	5	60.0	0	–	5	100	6	16.7
	♀ Adults	5	40.0	0	–	5	20.0	3	33.3
FL	Young	3	100	0	–	1	0	6	100
	♂ Adults	5	100	0	–	5	100	6	83.3
	♀ Adults	5	100	0	–	5	100	3	33.3

(in both sexes of adults), and especially, more than 90% of the common toad differed in male T-EL, TD, and PL (three age/sex groups combined for the latter two characters). All of these characters have been regarded as diagnostic for differentiating the Japanese stream toad from the Japanese common toad (Matsui, 1976a).

All of the Japanese stream toad populations were differentiated from 97.6% of the Japanese common toad populations, and only two (Pop. 64=Settsu and Pop. 90=Iki) among 83 populations of the common toad used for comparison did not differ from only some of the stream toad populations in TD. The overlap of TD ACV in the two exceptional populations and the stream toad populations, however, was slight and the former population had TD ACVs similar to those of only two of ten stream toad populations, and the latter only three of ten. The number of samples included in these

(Table 66. Cont'd.)

Character	Age/sex group	Distant allopatric zone						Total	
		type A		Intermediate type		type B			
		N of pops.	% of differing pops.	N of pops.	% of differing pops.	N of pops.	% of differing pops.	N of pops.	% of differing pops.
SVL	♂ Adults	30	20.0	1	0	11	0	58	22.4
	♀ Adults	23	4.3	1	0	13	15.4	50	8.0
HL	Young	16	0	1	0	12	0	39	0
	♂ Adults	30	6.7	1	0	11	0	58	3.4
	♀ Adults	23	26.1	1	0	13	0	50	14.0
SL	Combined	38	0	1	0	20	0	83	0
T-EL	Young	16	93.8	1	100	12	8.3	39	59.0
	♂ Adults	30	100	1	100	11	63.6	58	93.1
	♀ Adults	23	100	1	100	13	15.4	50	76.0
TD	Combined	38	100	1	100	20	95.0	83	97.6
HW	Young	16	0	1	0	12	0	39	0
	♂ Adults	30	6.7	1	0	11	0	58	3.4
	♀ Adults	23	21.7	1	0	13	0	49	10.2
PL	Combined	38	89.5	1	100	20	85.0	83	90.4
PW	Young	16	0	1	0	12	0	39	2.6
	♂ Adults	30	3.3	1	0	11	0	58	1.7
	♀ Adults	23	69.6	1	100	13	53.8	50	62.0
LAL	Combined	38	73.7	1	100	20	45.0	83	65.1
TL	Young	16	0	1	0	12	0	39	0
	♂ Adults	30	50.0	1	100	11	45.5	58	51.7
	♀ Adults	23	60.9	1	100	13	30.8	50	46.0
FL	Young	16	31.3	1	0	12	33.3	39	46.1
	♂ Adults	30	86.7	1	100	11	72.7	58	86.2
	♀ Adults	23	73.9	1	100	13	76.9	50	78.0

populations was quite small (N=4 for Pop. 64 and N=3 for Pop. 90), and this small sample size assuredly has affected the results. Therefore, with ample samples, the Japanese stream and common toad can be actually differentiated from each other by the TD ACV alone.

PL ACV similarly differentiated all the stream toad populations from 90.4% of the common toad populations. Eight out of 83 populations of the common toad had PL ACVs insignificantly different from some of the stream toad populations, and among them, seven are distributed in northeastern Honshu or in Shikoku. The remaining one (Pop. 68=Ise) is sympatric with the stream toad population, and was not different from only one of ten stream toad populations. In this case also, the small number of the sample seems to have affected the results (N=4 for Pop. 68). The two populations not different in TD as mentioned above differed from the stream toad populations in

PL ACVs. Thus, by combining only two characters (TD and PL), the Japanese stream toad and the Japanese common toad can be completely differentiated.

Populations of the Japanese common toad showing similarities to the Japanese stream toad in some characters all belonged to type B, and those distributed in Shikoku (Pops. 82, 83, 84, 87) exhibited the most remarkable resemblance. These populations did not differ from some of the stream toad populations in more than two of the three

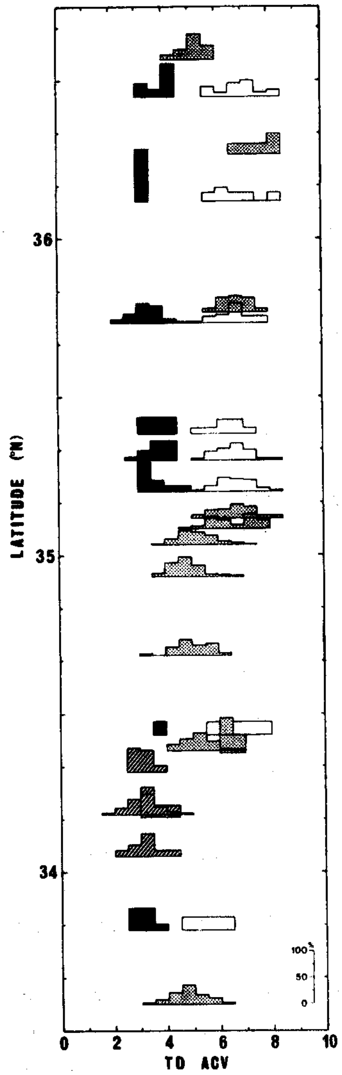

Fig. 58. Variation in TD ACV as represented by percentage histograms for the populations of the stream toad and the common toad from the sympatric and adjacent allopatric zone. Closed polygons = sympatric stream toad population; hatched polygons = allopatric stream toad population; dotted polygons = allopatric common toad population; open polygons = sympatric common toad population. Base line for each polygon corresponds to the latitude for the location of that population.

characters which are regarded as important in differentiating the two forms (T-EL, PL, and LAL). These results also indicate that the common toad differs from the stream toad more greatly in the zone of sympatry than in the allopatric regions.

Since the number of populations treated was not adequate, and the range of distribution is restricted in the Japanese stream toad, it is difficult to analyze the geographic and climatic clines of SVL and ACV of each character. However, when the obtained data were compared with the clines found in the Japanese common toad (see the forgoing chapter), there are marked differences between the two forms in most of the characters, and the ACV for each character in the Japanese stream toad markedly deviated from the clines formed by type A or type B populations of the Japanese common toad. Therefore, the Japanese stream toad is regarded as markedly different from the Japanese common toad in the mode of adaptation to its habitat.

All of the Miyako toad populations completely differed from the Japanese stream toad in the ACVs of T-EL, TD, LAL, TL and FL. The relatively short parotoid of the stream toad, however, coincided with that of the Miyako toad. Among the distinguishing characters, relative lengths of limbs exhibited most marked differences: the Miyako toad tended to show relative shortening of the limbs, whereas the stream toad was characterized by the elongation of limbs. Thus, the Japanese stream toad is regarded as more remote from the Miyako toad than from the Japanese common toad.

The relatively small tympanum in the Japanese stream toad is regarded as correlated to its breeding habits. Although our knowledge of the breeding behavior of the Japanese stream toad is only fragmentary, observations made to date indicate that males of this species, unlike those of the Japanese common toad, neither call nor wait for the arrival of females near the water's edge, but wait for females on the deep bottom of the stream (Matsui, 1976f). It is, therefore, highly probable that the function of the mating call is further reduced in this form than in the Japanese common toad, and this might have led to the reduction of the tympanum. The allied stream-breeding *B. andrewsi* from Southwestern China also has a small tympanum, and the further specialized Korean *B. stejnegeri* has a tympanum completely concealed under the skin (Matsui, 1980b). A similar indistinct or cryptic tympanum is reported for most of the Middle American stream-breeding hylid species (Duellman, 1970: 24).

Along with the small tympanum, a short parotoid gland and long hindlimb also characterized the Japanese stream toad. The relatively long tibia in females of the stream toad contrasts to the short tibia of the common toad females as discussed above. These two organs exhibited some correlation in the Japanese common toad in relation to defence and escape against enemies, and the same interpretations can be applied to the Japanese stream toad. Escaping rapidly from the enemy by long hindlimbs possibly compensates for the probable small amount of poison secreted by the small parotoid glands. The presence of long hindlimbs in the Japanese stream toad is also regarded as an adaptation for swimming, since some semiaquatic *Bufo* species often possess long hindlimbs (e.g., *B. kisolensis*, *B. lemairi*, *B. rangeri*: Tandy and Keith, 1972). The Japanese stream toad also had longer lower arms than in most of the Japanese common toad populations, and this seems to be an adaptation for climbing and clinging to the surface of rocks near and in the mountain stream.

In conclusion, the Japanese stream toad completely differs from the sympatric common toad in more than two morphometric characters and no intermediate forms are found. The few common toad populations similar to the stream toad in some characters are all from regions completely isolated from the range of the Japanese stream toad. These facts demonstrate that the Japanese stream toad is a full species distinct from the Japanese common toad. Each of the morphometric features characterizing the Japanese stream toad is regarded as adaptive to the specialized mode of life— particularly the breeding habits— of this form.

VIII

Taxonomic Conclusions

As described above, Japanese toads can be divided into four forms (type A and type B of the Japanese common toad, the Miyako toad and the Japanese stream toad) by morphometric variation analysis. In this chapter, all the hitherto named forms are reexamined in the light of the morphometric characteristics and, by adding evidence from non-metric and non-morphological sources, conclusions on the classification of the Japanese toads will be drawn.

1. Reexamination of the Described Forms

The toad materials treated in the present study include either type series or samples from the type localities (topotypic specimens) of all forms hitherto described from Japan, including syntypes of *Bufo vulgaris japonicus*: *Bufo vulgaris japonicus* Schlegel (type locality =Japan; syntypes, RMNH 2109, 2115, 2116, 2117, 2119, 2119A); *B. formosus* Boulenger (type locality=Yokohama; Pop. 26, Yokohama=topotypic specimens), *B. smithi* Stejneger (type locality=Toza; Pop. 86, Kochi=including type series, USNM 31851, 31929, 31943, 31945–49, 31951); *B. v. hokkaidoensis* Okada (type locality=Hakodate; Pop. 1, Hakodate=topotypes); *B. v. yakushimensis* Okada (type locality=Yakushima; Pop. 96, Yakushima=topotypes); *B. v. montanus* Okada (type locality=Chokaizan; Pop. 10, Chokaizan=topotypes); *B. bufo miyakonis* Okada (type locality=Miyakojima; Pop. 97, Miyakojima=topotypes); *B. torrenticola* M. Matsui (type locality=Ohdaigahara; Pop. 109, Ohdaigahara=including type series, OMNH Am 2272–75, 4202–21, USNM 198427–28, AMNH 90768–69, SMF 68201–02). The validity of each form is reexamined on the basis of these samples.

a) Japanese Common Toad

Populations of the Japanese common toad were divided into northeastern type A and southwestern type B chiefly by the relative size of tympanum diameter.

1) Type A

formosus: Forms hitherto described from the distribution range of type A are *B. formosus*, *B. v. hokkaidoensis*, and *B. v. montanus* and all of these are characterized by a tympanum diameter twice as large as the tympanum-eye distance (Stejneger, 1907; Okada, 1930, 1931, 1937, 1966). Of these three forms, *formosus* is the oldest and was described from the specimens from Yokohama. My samples from this locality (Pop.

26) coincided well with the original description of *formosus*, and had large tympanums (ACV median=6.2), more than twice as long as the tympanum-eye distance (ACV median=2.8 for young, 2.6 for adult males, and 2.7 for adult females).

hokkaidoensis: This form has been regarded as being differentiated from *formosus* by the larger tympanum and longer hindlimb (Okada, 1928, 1930, 1931, 1966). My samples from the type locality (Pop. 1), however, had TD ACV ranging 5.1–7.1 (median=5.9), and these values completely overlapped those of Pop. 26 (topotypes of *formosus*, TD ACV=4.8–7.3, median=6.2). Further, most of the type A populations from the Tohoku District of Honshu had TD ACV medians larger than that of Pop. 1. As to TL and FL, which are regarded as representing the hindlimb length, there were almost no differences between young of Pop. 1 and Pop. 26, and the latter population had a larger value than the former in FL. Similar results were obtained for adult males. Only in adult females, Pop. 1 had slightly larger ACV medians in TL and FL than Pop. 26. Many type A populations from northeastern Honshu had larger ACV medians than Pop. 1 in these hindlimb characters. Population 1 and populations from the Tohoku District largely overlapped in the variation range of other characters and in some instances, Pop. 1 was nearer to more southern populations from the Chubu and Kanto districts From these results, it is morphometrically impossible to differentiate *hokkaidoensis* from the populations of northeastern Honshu.

montanus: *B. v. montanus* was reported to have a larger tympanum and a longer parotoid than in *formosus* (Okada, 1937: 190; 1966: 25). In the present study, I examined the samples from Chokaizan (Pop. 10=topotype). This population had a very large tympanum (TD ACV median=8.0), and differed from 85.4% of the other 82 populations of the Japanese common toad in this character. The ACV median for Pop. 10 was significantly larger than that for topotypes of *formosus* (Pop. 26, ACV=6.2). The large TD ACV, however, was found not only in Pop. 10, but also among populations from the localities distant from Pop. 10: Pop. 3 from the northernmost lowland of Tohoku District had a median of 8.3 and Pop. 43 from highland of Chubu District had a median of 7.7. In addition, the PL ACV of Pop. 10 (median=22.6) was not only about the same as that of Pop. 26 (median=22.1), but smaller than those of some populations of type A (Pop. 46: median=24.6 and Pop. 54: median=23.6). Thus, a longer parotoid in *montanus* was not validated. The most remarkable characteristic of Pop. 10 was a small body size and both sexes had smaller SVLs than in any other population. It is, of course, taxonomically difficult to differentiate Pop. 10 from other populations only by smaller body size, but the population is clearly more conspicuous in this regard than Pop. 1 (=*hokkaidoensis*).

Though not treated in this study, some comments on the body colour must be made: Okada (1966: 23–24) insisted that the reddish spots are a diagnostic character of *montanus*, but such spots are not confined to this form, and are found in almost every population of the Japanese common toad, though the degree of development varies considerably (Matsui, unpubl.). Thus, both morphometrically and non-metrically, it seems safe not to separate *montanus* from *formosus* as a distinct form, although the uniquely small body size of Pop. 10 suggests some ecological divergence of this population from others.

2) Type B

From the range of type B, *B. smithi* and *B. v. yakushimensis* have been described. Besides, *B. v. japonicus* is suggested to have originated from southwestern Japan, i.e., the range occupied by type B (Matsui, 1980c).

smithi: *Bufo smithi* was differentiated from *B. formosus* by the smaller tympanum, whose diameter is subequal to the tympanum-eye distance (Stejneger, 1907: 64). Samples for this form (Pop. 86) include the type series. In contrast to the original description, TD ACV for this population (median=5.3) was larger than T-EL ACV (median: young=4.1; adult males=3.8; adult females=4.1), but this TD median value was smaller than that of *formosus* (Pop. 26: median=6.2) whereas the T-EL values were larger than in the latter form (T-EL ACV median for Pop. 26: young=2.8, adult males=2.6, adult females=2.7). Thus, the two forms can be clearly separated by the relation of these two characters, as type A and type B have already been differentiated.

Some populations of type B from Honshu and Kyushu, however, had TD and T-EL ACVs similar to Pop. 86, and *smithi* from Shikoku cannot be differentiated from such populations. Therefore, Okada's treatment of placing the unique form from Shikoku into the synonymy of *japonicus* (Okada, 1930, 1931, but note that Okada's *japonicus* has been assigned to the common toad populations from southwestern Japan and not restricted to the type series of *japonicus*) is judged to be reasonable.

yakushimensis: This island form was described as distinguished from *japonicus* (=southwestern populations of the Japanese common toad as mentioned above) by the shorter hindlimb, smaller tympanum and different internostril—upper eyelid width relation (Okada, 1928: 269). The last character is not suitable for comparison as stated earlier (see chapter III). Samples from the type locality (Pop. 96) did not have markedly shorter hindlimbs than the populations from the adjacent Kyushu District. Some populations of type B from Honshu (e.g., Pop. 80) had even shorter hindlimbs than Pop. 96. TD ACV of Pop. 96 (median=5.0) was similar to, or in some case even larger than, those of some populations from Kyushu (e.g., Pops. 90 and 92). Therefore, *yakushimensis* cannot be morphometrically differentiated from some of the type B populations.

From these results, it seems morphometrically impossible to differentiate *hokkaidoensis* and *montanus* from other populations of type A, and they should be synonymized with *formosus*. Likewise, *smithi* and *yakushimensis* cannot be regarded as distinct from other populations of type B.

Bufo vulgaris japonicus: The name of *japonicus* is the oldest of the hitherto recognized Japanese forms. There are many problems, however, in this form, such as unknown exact locality and possibility of the presence of two forms in the type series as suggested by Stejneger (1907). I examined the type series and provided some answers to these questions (Matsui, 1980c). Although Stejneger (1907) considered some specimens with ill-developed webbing in the type series of *japonicus* as *formosus*, the variation in the degree of web development can be considered as ontogenetic and two forms cannot be recognized. The range of morphological variation is not extensive and all the specimens seem to have been collected from a narrow range in southwestern Japan.

The type series of *Bufo vulgaris japonicus* is composed of 15 individuals as shown in Table 67. When the allomorphic relation of each morphometric character against SVL was calculated and ACVs were derived (Tables 68 and 69), the relation of TD and T-EL in the type series clearly indicated that *japonicus* belonged to type B, confirming the reasonableness of Matsui's (1980c) suggestion.

Table 67. Measurements (in mm) of syntypes of *Bufo vulgaris japonicus* Schlegel.

Sp. No.		Age/Sex	SVL	HL	SL	T-EL	TD	HW	PL	PW	LAL	TL	FL
RMNH	2109	young	20.0	7.2	3.1	—	0.9	6.7	4.2	1.8	8.8	6.3	6.4
do.	2109	do.	35.7	11.8	5.2	1.4	1.8	13.8	7.8	3.4	17.8	12.8	14.0
do.	2109	do.	36.8	12.7	5.2	1.3	1.8	13.8	7.8	3.8	19.2	13.3	14.2
do.	2109	do.	42.2	14.8	5.8	1.8	2.2	16.2	10.2	4.2	21.2	15.0	17.2
do.	2109	do.	44.2	15.3	6.8	1.9	2.8	18.0	9.8	3.8	21.6	14.9	15.2
do.	2109	do.	62.8	21.8	8.9	2.9	3.2	24.8	13.2	4.8	32.2	22.2	27.2
do.	2116	do.	76.5	26.8	9.9	4.2	4.2	31.2	16.2	6.4	36.2	26.5	31.0
do.	2116	do.	87.3	28.0	11.2	3.2	3.4	35.2	22.1	9.8	41.8	31.0	33.8
do.	2115	do.	89.6	30.8	12.8	3.9	5.2	38.8	21.0	8.2	45.2	31.2	35.2
do.	2115	♂ad.	108.8	35.8	13.9	3.2	5.1	40.0	21.8	9.8	53.2	39.8	51.2
do.	2119	do.	109.3	39.8	14.2	5.1	5.8	43.7	23.0	7.3	57.2	42.8	51.5
do.	2117	do.	112.7	34.2	14.1	4.1	4.8	38.2	27.8	8.2	55.3	42.9	50.0
do.	2117	♀ad.	115.0	38.0	15.8	4.2	6.5	46.2	27.8	9.2	59.8	42.1	49.2
do.	2115	do.	116.4	38.8	15.5	5.8	6.6	45.3	24.4	8.7	57.0	42.9	45.9
do.	2119A	do.	141.4	43.6	17.7	5.2	6.5	52.5	35.0	11.2	68.2	48.3	56.0

Although a holotype has been not designated, I here propose that the specimen RMNH 2119A be designated the lectotype of *Bufo vulgaris japonicus*, because it is a complete specimen (an adult female) and evidently figured in the original description (Schlegel, 1838: TAB. II. 5–6; Fig. 59). The other syntypes (RMNH 2109=6 young; 2115=1 young, 1 adult male and 1 adult female; 2116=2 young; 2117=1 adult male and 1 adult female; 2119=1 adult male) thus become paralectotypes of *Bufo vulgaris japonicus* Schlegel.

Description of lectotype.—Snout-vent length (SVL) 141.4 mm; tibia length 48.3 mm (34.2% of SVL); foot length 56.0 mm (39.6% of SVL); head length (HL) 43.6 mm (30.8% of SVL); head width 52.5 mm (37.1% of SVL); snout obtusely acuminate in dorsal view, blunt, slightly sloping in lateral profile; canthus rostralis moderately marked, and loreal region slightly concave; nostrils midway between tip of snout and anterior margin of upper eyelid, their distance from each other 9.7 mm, greater than their distance from eyes, 7.3 mm, but less than width of upper eyelid, 11.2 mm; eye diameter 1.7 times the distance from eye to nostril; interorbital space 9.2 mm, concave, narrower than width of upper eyelid, and 0.9 times the internarial distance; tympanum distinct, its diameter 6.5 mm, 1.25 times its distance from eye 5.2 mm; parotoid gland elongated and slightly elevated, diverged posteriorly, its length (PL), 35.0 mm (24.8% of SVL), about three times its width, 11.2 mm; forelimb stout, 84.2 mm (59.5% of SVL); fingers with remnant of webbing at their base, tips blunt, first and second fingers sub-

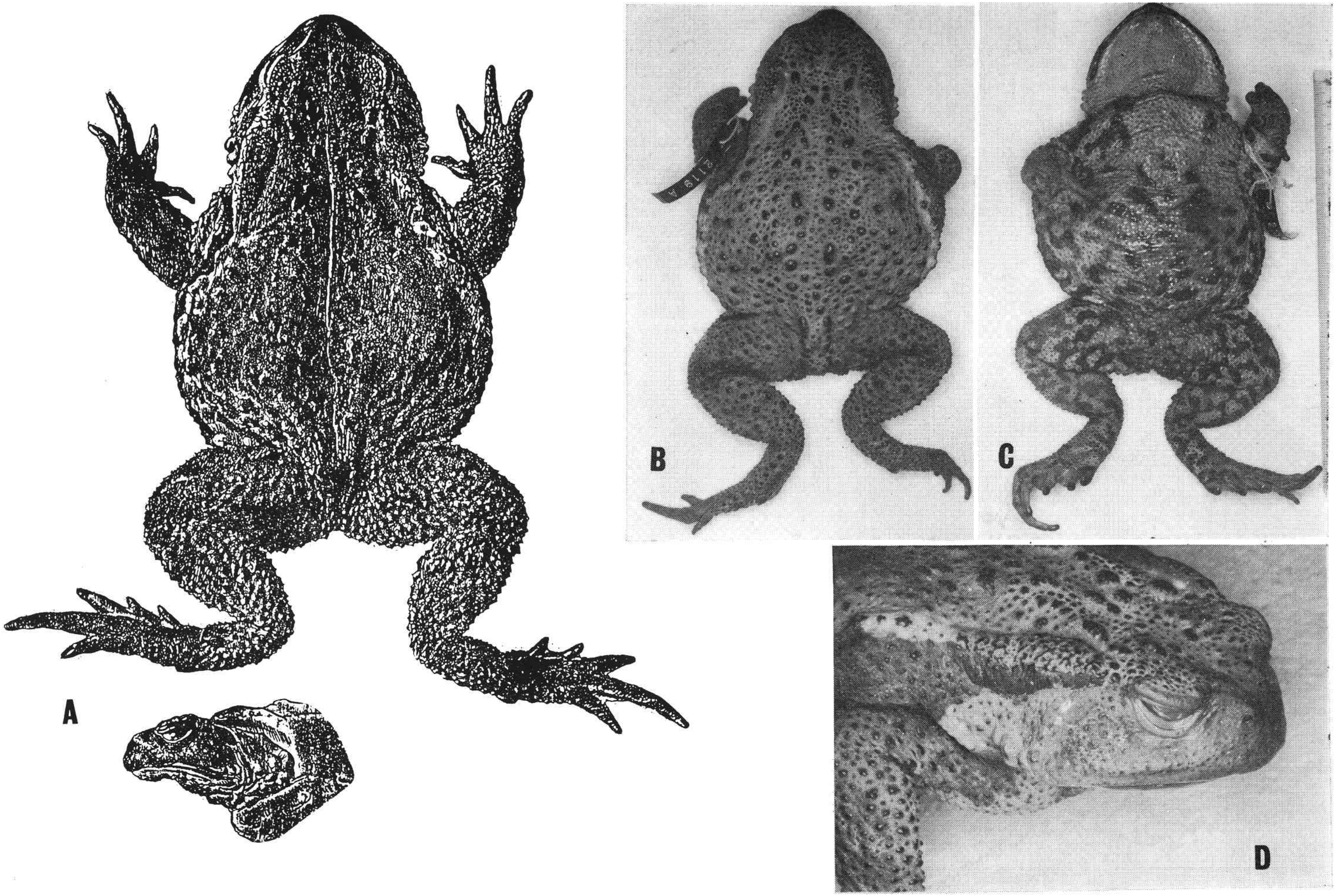

Fig. 59. The text figure shown by Schlegel, 1838 (TAB II, Fig. 6) (A) and the lectotype of *Bufo vulgaris japonicus* Schlegel, 1838 (=*Bufo japonicus japonicus*) (B: dorsal view;C: ventral view; D: dorsolateral view).

equal; two large palmar tubercles, inner one prominent, 5.3 mm, on base of inner margin of first finger, and outer one, 10.9 mm, on base of third and fourth fingers, large and elliptical, about 2.0 times the inner one in size; hindlimb short, 164.0 mm, 116.0% SVL, about twice the length of forelimb; heels slightly meeting when held at right angles to body; third and fifth toes with one phalanx free of broad web, though fringes extend to tips, fourth toe with three phalanges free; webs thick, not crenulate; inner metatarsal tubercle oval, with feeble cutting edge, its length 8.7 mm, shorter than first toe, which is 11.7 mm; outer metatarsal tubercle round, 6.2 mm, 0.7 times length of inner; no tarsal fold; distinct basal subarticular tubercles, some bifid; back covered by numerous keratinized tubercles of varying size; tubercles on hindlimb with spinose tips; a scattered row of medium-sized lateral tubercles running longitudinally from posterior edge of parotoid to groin; top of head only feebly granular without large warts; a group of conical tubercles behind rictus; venter coarsely granular; tibial gland not marked; no distinct tarsal gland.

Color (in alcohol).—Dorsum olive brown; tips of warts surmounted by black spots; vertebral stripe absent; evident black band on lower side of parotoid extending laterally along flanks, dorsally bordered by creamy band; underside of body and limbs dirty yellow, with many distinct dark blotches, except on throat, where only junctions of jaws are spotted with black.

Descriptive remarks.—The skin of an adult male (RMNH 2119) is badly damaged especially on the digits. A pair of specimens (RMNH 2117) are in amplexus and undoubtedly the female is gravid although I did not dissect it. Adult males are smaller in body size than adult females (Table 67). Adult males have dorsally a more acuminate snout than adult females. Laterally, the snout of adult males is more sloping than that of adult females. Most of the young and one adult female (RMNH 2115♀) have an evident canthus rostralis like the lectotype, but one young, all the adult males and one adult female (RMNH 2117♀) have a less marked canthus rostralis. Smaller young have a flat interorbital space, and in the larger ones, this space is slightly concave. All the adult specimens have a clearly concave interorbital space. Some of the young specimens have strongly elevated parotoid glands, but the others have rather flat parotoid glands as in the lectotype. All the adult males have flatter parotoids than the lectotype. All the adult males have dark nuptial asperities on the inner and upper sides of the first and second fingers and on the inner surface of the third finger. Adult males have relatively longer hindlimbs than adult females (Table 69). Toe webbing is less developed in young than in adults. Degree of web development is assessed by the method proposed by Dubois (1976: 43) and shown in Table 70. Nine specimens, including the lectotype, have webs not crenulated, and the remaining six have more or less crenulated webbing. The top of the head is covered by minute granules in the young. Adult specimens have a more or less smooth top, and granules, if present, are scattered or form weak wrinkles, and large warts are never present. Spines on warts are well developed in the lectotype and are found even on the warts on the flanks. Other specimens have less developed spines mostly only on the dorsal surface of the hindlimbs, and all the adult males have smooth warts, lacking these spines. In some of the paralecto-

Table 68. Allomorphic constants (α) and initial growth indices (B) for regression lines of each morphometric character—SVL in the syntypes of *Bufo vulgaris japonicus* Schlegel.

Character	N	α	log B	r
HL	15	0.951	−0.382	0.997
SL	15	0.902	−0.683	0.997
T-EL	14	0.972	−1.337	0.944
TD	15	0.997	−1.291	0.976
HW	15	1.031	−0.471	0.994
PL	15	1.039	−0.722	0.992
PW	15	0.878	−0.840	0.972
LAL	15	1.024	−0.351	0.997
TL	15	1.053	−0.546	0.998
FL	15	1.123	−0.621	0.993

Table 69. ACV (at SVL=100 mm) of syntypes of *Bufo vulgaris japonicus* Schlegel.

Character	young			adult males			adult females			sex, age combined		
	N	range	median	N	range	median	N	range	median	N	range	median
HL	9	31.4–34.6	33.3	3	30.5–36.6	33.0	3	31.4–33.6	33.3		–	
SL		–			–			–		15	12.6–14.2	13.1
T-EL	8	3.4– 5.4	4.2	3	2.9– 4.7	3.7	3	3.7– 5.0	3.7		–	
TD		–			–			–		15	3.9– 6.3	5.1
HW	9	35.2–43.5	40.1	3	33.8–39.9	36.7	3	36.7–40.0	38.7		–	
PL		–			–			–		15	20.0–25.5	21.4
PW	9	7.2–11.0	8.4	3	6.8– 9.1	7.4	3	7.6– 8.3	8.1		–	
LAL		–			–			–		15	45.7–53.4	49.8
TL	9	34.3–38.1	35.8	3	36.4–39.0	37.8	3	33.5–36.6	36.6		–	
FL	9	38.0–45.9	41.9	3	43.7–46.6	46.6	3	38.0–42.1	38.7		–	

Table 70. Variation in extent of toe web in the syntypes of ***Bufo vulgaris japonicus*** Schlegel, as expressed by the formula proposed by Dubois (1976: 43). Figures indicate number of specimens.

Toe	Age/Sex	degree of webbing					
3rd outer		3/4	1–	1	1+	1 1/4	1 1/3
	young	1	6	2			
	♂ adults					3	
	♀ adults		1		1		1
	Total	1	7	2	1	3	1
4th inner		1/4	1/3	1/2	2/3		
	young	1	6	2			
	♂ adults			3			
	♀ adults		1	1	1		
	Total	1	7	6	1		
4th outer		1/4	1/3	1/2	2/3		
	young	5	4				
	♂ adults		2		1		
	♀ adults		1	2			
	Total	5	7	2	1		
5th inner		1	1+	1 1/4	1 1/3	1 2/3	
	young	3	5	1			
	♂ adults			1	1	1	
	♀ adults				3		
	Total	3	5	2	4	1	

types (RMNH 2109), the colour is badly faded. Nine specimens, including the lectotype, lack a vertebral line, and the remaining six possess it. The smaller specimens of RMNH 2116 and RMNH 2119 have an incomplete, but evident thin vertebral line. Except for specimens of RMNH 2109, which are discoloured, all the syntypes have a more or less evident dark stripe on each side of body. Adult specimens including the lectotype, have strongly defined stripes and one female (RMNH 2115) has reddish spots on these stripes. One young (RMNH 2116) has interrupted stripes and the other (RMNH 2115 young) has less defined weak stripes. Creamy light marking above the dark flank stripe is evident in one young of RMNH 2116, in RMNH 2115 male and in RMNH 2117 female, as in the lectotype. In another specimen of RMNH 2116 and in RMNH 2115 female and in RMNH 2117 male, the border between this light marking and the dorsal colour is not evident, and in RMNH 2119, the light marking is not seen. Ventral dark markings are found in all the paralectotypes, excepting discoloured RMNH 2109. One specimen of RMNH 2116, RMNH 2117 female and RMNH 2115 female have more developed dark markings than in the lectotype. By contrast, RMNH 2115 young and RMNH 2119 have fewer dark blotches than in the lectotype. Dark spots on the juncture of the jaws are present in all the paralectotypes, and some specimens have many dark markings over a wide range along the juncture of the upper and lower jaws.

3) Comparisons of *japonicus* with type B populations

Since *japonicus* is evidently closer to the type B than to type A, comparisons were made with other nominate forms of type B. Stejneger (1907) described *smithi* as a distinct species on the basis that it has a small tympanum, the diameter of which is subequal to its distance from the eye. Later, Okada (1930, 1931) synonymized *smithi* with *japonicus*, but the name *japonicus* was used by Okada, in opposition to northeastern *formosus*, for the populations from southwestern Japan except for *yakushimensis*. When the type series of *japonicus* was compared with Pop. 86 (including the type series of *smithi*), there were minor differences in some morphometric characters. The degree of toe webbing is the chief difference that Stejneger noted, but the type series of the two forms were not markedly different in this character (Matsui, 1980c).

Okada (1928) stated that *yakushimensis* has a smaller tympanum and shorter hindlimb than *japonicus*, but the type series of *japonicus* did not show such tendencies. The variation range of TD largely overlapped and the median was almost equal in the two forms. Of the hindlimb characters, the two forms largely overlapped in the variation range of TL, and in the adult female, *yakushimensis* had larger TL ACV than *japonicus*. The same tendency was found for FL. Thus, *yakushimensis* is not differentiated morphometrically from the type series of *japonicus*. The type series of *japonicus* is not conspicuous in every character when compared with populations of type B, other than *smithi* (Pop. 86) and *yakushimensis* (Pop. 96). Therefore, all the populations of type B should be called *japonicus*. Kawamura et al. (1980) retained the subspecific name *yakushimensis* on the basis of slight difference in the viability of the hybrids obtained by a cross with *japonicus*. The population from Yakushima has indeed some peculiarities in its ecology and physiology, for oviposition takes place before winter when the water temperature is rather high (Matsui, 1979a). The results of the hybridization by Kawamura et al. (1980), however, are not applicable for a taxonomic decision, because their data are meager regarding this form, and, generally, they provide no information how they correlate the various degree of genetic compatibility to the classification among the given animals.

4) Taxonomic relation of type A and type B populations

The Japanese common toad has long been treated as a subspecies of the European common toad, *Bufo bufo bufo* (Schlegel, 1838; Nakamura and Uéno, 1963; Okada, 1966), but as stated in the earlier pages of this paper, these two taxa show low genetic compatibility and are definitely different at specific rank. Since *japonicus* is the oldest name assigned to the Japanese common toad, it is appropriate taxonomically to call the Japanese common toad binominally *Bufo japonicus* Schlegel.

From the climatic clines shown in the morphometric characters, I concluded that type A and type B of the Japanese common toad should be divided into some taxonomic category below species. The two forms are almost identical in the fundamental patterns of mode of life and can hardly be regarded as different species.

It is difficult to decide whether or not the two types should be separated as different subspecies, since there are no abstract or generalized criteria invoked for the recognition of subspecies (Thorpe, 1981: 369).

The currently popular definition of subspecies was proposed by Mayr, Linsley and Usinger (1953) and was slightly modified by Mayr (1963: 348): a subspecies is an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species. As repeatedly pointed out by Mayr (1954, 1963), a subspecies is regarded as a purely subjective category. But even if most subspecies may be artificial or a category of convenience, some other subspecies, though smaller in number (Simpson, 1961), may represent a distinct evolutionary lineage (Wiley, 1981). Further, however subjective the category of subspecies may be, it is not sufficient to establish a subspecies simply because one population differs from others. What level of differentiation is sufficient or necessary for subspecific recognition should be tested repeatedly and seriously discussed (Thorpe, 1980).

Some morphometric characters exhibited clines in the Japanese common toad. The relation of subspecies to cline has been debated, and Moreau (1948) proposed as follows: the naming of subspecies which are segments of a cline can be justified only if discontinuities in the gradient can be defined and located. Bogert (1954) also stated that little is gained by the application of names to portions of a continuous cline and that subspecies should be recognized only when sharp discontinuities in the trends of one or more individual characters can be demonstrated. It is, of course, apparent as Sibley (1954) indicated, that in nature not all clines "step" conveniently at the same places.

In the Japanese common toad, two types are differentiated by the medians of TD ACV, although the variation range of this character is extensive even within a single population. The geographic cline of the median of TD ACV, however, suddenly changes around the Kinki District (Fig. 60). The distribution of several type B populations in the range of type A has been interpreted as artificial. The sudden "step" found in the geographic cline of TD ACV median seems to indicate the possibility of separating the two types as different subspecies. After dividing populations into two types (=aggregations of populations) around the region where such a "step" was found, the northeastern type A exhibited clear clines in a larger number of characters, whereas in the southwestern type B clearly clinal characters were few. Further, the male body size decreased in both directions around that "step". Thus, the "step" in the clines occurred in at least two characters at nearly the same place. The validity of Amadon's "75% rule" (Amadon, 1949; conventional level of subspecific difference by Mayr, 1963) was thrown in doubt by Gosline (1954) and its general applicability has not yet been well assessed. When type A and type B are regarded as an aggregation of populations, however, the rule apparently applies to the TD and T-EL ACV medians (Fig. 61).

From these considerations, it is not unreasonable to treat the two types as different subspecies, although the treatment may be somewhat artificial. Thus, type A and type B should be called as *Bufo japonicus formosus* and *B. j. japonicus*, respectively. As discussed previously, each subspecies is regarded as being in the evolutionary process of adapting to the environment of its own distributional range, and it seems more significant from the evolutional viewpoint to recognize two subspecies rather than to combine all the populations under a single subspecies. Such a division seems useful not only for taxonomists (Simpson, 1961) but also for the students of physiology and ecology. There are no evident physiographical barriers between the ranges of these two subspecies, but this fact alone does not negate the existence of two subspecies.

b) *Miyako Toad*

The morphometric characters of the Miyako toad exhibited little variation and only one form was recognized. The Miyako toad only slightly overlapped several populations of the Japanese common toad in its morphometric characters, and could be judged to be fairly divergent from the latter form. Further, the Miyako toad differed more from geographically adjacent *japonicus* than from distant *formosus*.

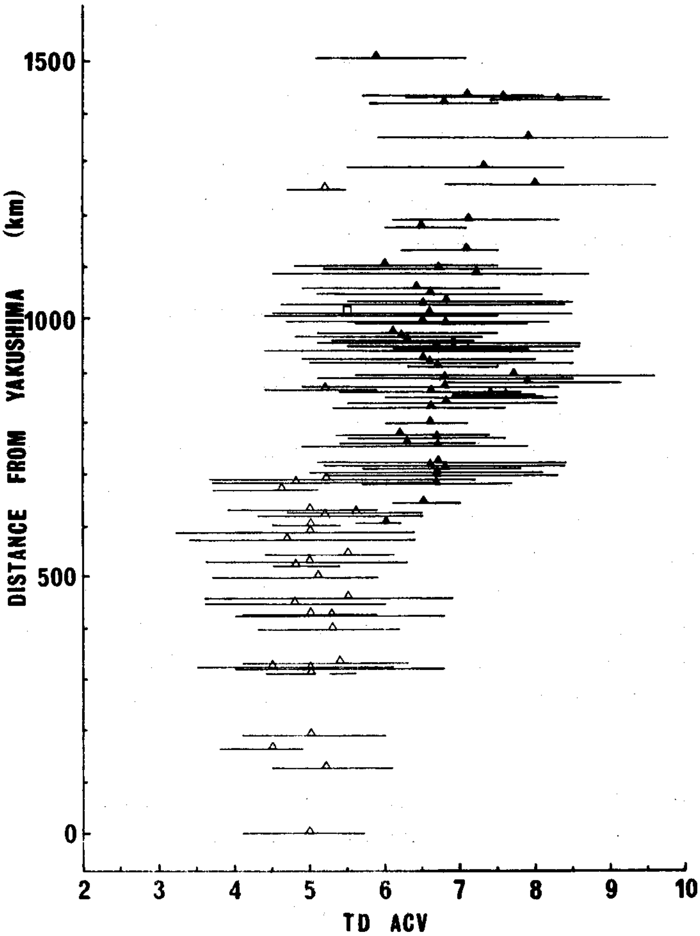

Fig. 60. Geographic cline of TD ACV expressed by the distance of each population from the southwesternmost population (Pop. 96=Yakushima). Closed triangles: type A; open triangles: type B; open square: intermediate type. Each symbol and horizontal line represents median and range, respectively.

These geographically disjunct morphometric differences between the Miyako and the Japanese common toad strongly indicate the presence of physiological differences

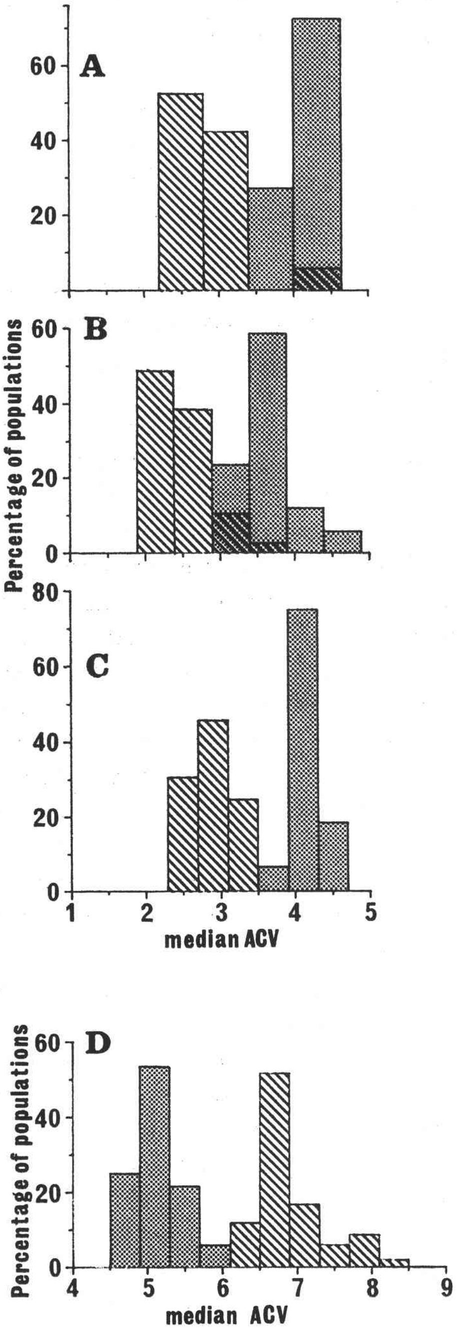

Fig. 61. Percentage of populations of each form (hatched: type A; dotted: type B) tabulated by population ACV median of T-EL (A: young; B: adult males; C: adult females) and of TD (D).

between the two forms. In addition, other features of the Miyako toad such as karyology, skull morphology, and coloration differ from those of the Japanese common toad, indicating that the two forms represent different evolutionary lineages.

The Miyako toad, like the Japanese common toad, clearly differs from the European common toad at specific rank as indicated by the results of artificial hybridization (Matsui, unpubl.; Kawamura et al., 1980). It is not easy to determine the taxonomic relation with the Japanese common toad since they are allopatrically distributed. The results of analyses of morphometry as well as of other non-metric characteristics discussed above, however, suggest that the Miyako toad is specifically distinct from the Japanese common toad.

I (Matsui, 1976b) reported that hybrids artificially produced between female *japonicus* and male *miyakonis* possessed gonads with an inner structure not much different from the gonad structure of the control *japonicus* × *japonicus*. I did not discuss taxonomic relationship of the two forms since the examined material was a small sample and reciprocal crosses were not tried at that time. Kawamura et al. (1980) made extensive hybridization experiments and concluded that the Miyako toad is a subspecies of the Japanese common toad, *Bufo japonicus*. Their taxonomic conclusion, however, seems not in accordance with the vast amount of data they exhibited. Half of the male hybrids between female *miyakonis* and male *japonicus* were triploid and sterile, and when back-crossed with female *japonicus* or *miyakonis*, the descendants usually did not metamorphose. These authors repeatedly stressed that the Japanese stream toad, *Bufo torrenticola*, is "scarcely" (*sic*) isolated reproductively from the Japanese common toad, *Bufo japonicus*, and relegated the former to a subspecies of *japonicus*. The Miyako toad, when crossed with the Japanese stream toad, exhibited even worse results than those obtained in the cross with the Japanese common toad. When female *miyakonis* and male *torrenticola* were crossed, the male hybrids were either triploid and sterile or diploid with abnormal testes. The female hybrids were triploid; some did not lay eggs and others laid eggs most of which did not hatch. It seems to me quite difficult from these results to conclude that the Miyako toad is conspecific with the forms of main islands, especially with the Japanese stream toad.

These examples indicate that the taxonomical interpretation of the results of artificial hybridization is rather complex. When inviable or sterile hybrids are obtained between two forms, it contributes much to the taxonomic decision (i.e., the indication of separate species), whereas if viable hybrids show various degrees of abnormality in the gonads, the interpretation is rather difficult. There is yet no general criterion for taxonomic judgement on the forms of animals showing various degrees of genetic compatibility. It is, however, natural to consider that hybrids showing low fertility under artificial conditions would be selected more severely under natural conditions and would hardly contribute much to the reproduction of the species.

Kawamura et al. (1980) indicated that artificial hybrids between female *miyakonis* and male *yakushimensis* are inferior to the control *miyakonis* × *miyakonis* in the rate of metamorphosis. My results with the same combination exhibited fewer normal sperms in the hybrids than in the controls (Matsui, unpubl.). This genetic incompatibility indicates the presence of a great gap between the Miyako toad and the southernmost population of the Japanese common toad (i.e., *yakushimensis*, synonymized with *japonicus* in the present study), as indicated by their morphological divergence.

Thus, from both morphological and genetic evidence, the Miayko toad should be given specific recognition different from the Japanese common and stream toads. Recently, Kawamura et al. (1982) made artificial hybridization experiments between forms of the Japanese toads and the Chinese common toad (*Bufo gragarizans*) from Peking, in which they found a high genetic compatibility of the Miyako toad and the Chinese toad from Peking. Since the Miyako toad is morphologically similar to the northeastern populations of the Chinese common toad, but at the same time somewhat differs from the southwestern populations (Matsui, 1974b, 1980a), it seems at present proper to consider *miyakonis* and *gargarizans* (type locality=Chu-zan=northeastern population) to be subspecifically related.

c) Japanese Stream Toad

The Japanese stream toad, *Bufo torrenticola*, is sympatrically distributed with the still-water type Japanese common toad in some parts of its range. Most of the Japanese stream toad populations are sympatric with common toads of the subspecies *formosus* and only in a few locations has sympatry with *japonicus* been ascertained. Namely, *formosus*, characterized by a large tympanum, is sympatric with the morphologically contrasting *torrenticola* which has an extremely small tympanum, whereas most populations of *japonicus*, intermediate between the above two forms in the diameter of the tympanum, are allopatric with *torrenticola*. As a result, the morphological difference is the greatest between the Japanese stream toad and the common toad in the zone of sympatry. The difference is not limited to the size of the tympanum, but other characters such as male body size and limb length also markedly differ between the two forms in the sympatric zone. Even if allopatrically distributed common toad populations are taken into consideration, *torrenticola* is still significantly differentiated morphologically from almost all populations of *japonicus* and *formosus*.

The clear morphological difference found in the sympatric zone indicates that each form maintains its own identity and that they rarely interbreed in natural conditions. Artificially produced hybrids between the two forms are fertile (Matsui, 1977b, 1979a), and Kawamura et al. (1980) considered *torrenticola* as a subspecies of *japonicus* on the basis of the results of artificial hybridization. The latter authors' idea of regarding two forms as conspecific when they produce fertile hybrids seems to be based on the Mayr's earlier definition that a species is groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups (Mayr, 1940). It must, however, be noted that the same author (Mayr, 1963: 15) admitted that he was accused by 'hasty' readers of having a species concept "based on cross-sterility." He distinguished the capacity to produce fertile hybrids (=fertility) and the exercise of this capacity in nature (=crossability), and at the same time clearly pointed out that the two subspecies are never sympatrically distributed.

There are many reports which indicate that fertile hybrids can artificially be produced between two apparently different natural species or even between two species of different genera, although not so commonly in animals as in plants. Hybrids between *Tharitimus maritimus* and *Ursus arctos*, between *Alopex lagopus* and *Vulpes vulpes*, between *Anas platyrhynchos* and *A. acuta*, between *Taricha torosa* and *T. rivularis*, and between *Notropis lutrensis* and *N. venustus*, are some examples of vertebrates (Twitty, 1961, 1964; Imaizumi, 1966; Yoshiyuki, 1981). The taxonomical value of the results of artificial hybridization has been summarized by Cain (1954), and as indicated by Simpson (1961), such results cannot be taxonomically decisive criteria. Davis and Heywood (1965) followed the idea of Simpson (op. cit.) and noted "Despite the undoubted importance of intersterility in the evolution of species, crossability criteria must be assessed, for purposes of a general classification, like any other taxonomic character and not be unduly weighted". More recently, Grant (1971) clearly postulated a similar idea: "Viewed from the standpoint of the evolutionary species concept, the important question is not whether two species hybridize, but whether two species do or do not lose their distinct ecological and evolutionary roles. If, despite some hybridization, they do not merge, then they remain separate species in the evolutionary perspective". A more generalized definition of species in relation to hybridization is well analyzed and summarized by Wiley (1978, 1981). Thus, successful crossing is subject to many interpretations, only one of which is the conclusion that the two forms belong to the same species (Wiley, 1981: 68).

On the basis of these generalized views, it seems reasonable to regard the Japanese stream toad as a distinct species. Kawamura et al. (1980), in the course of deciding the taxonomic position of the Japanese stream toad, considered the great variability of the Japanese common toad to be a result of natural hybridization, and believed that the Japanese stream toad and the Japanese common toad "inevitably" interbreed. Such an idea obviously neglects the actual distribution pattern of the two forms under natural conditions.

The Japanese stream toad is clearly separated from the European common toad (*Bufo bufo*) at specific rank. Likewise, it is specifically different from *Bufo gargarizans miyakonis* as discussed above. These decisions can be made on the basis of the results of artificial hybridization (Matsui, unpubl.; Kawamura et al., 1980). I consider that "sterile" or "extremely abnormal" artificial hybrids can be a good indication of the different taxonomic status of the parental species, but not *vice versa*. From these views, *Bufo torrenticola* is regarded as being recognizably distinct from both *Bufo japonicus* and *Bufo gargarizans miyakonis* at specific rank.

2. *Summary of the Taxonomic Conclusions*

Thus, the Japanese toads are separated into three species:

Bufo japonicus japonicus Schlegel, 1838
Bufo japonicus formosus Boulenger, 1883
Bufo gargarizans miyakonis Okada, 1931
Bufo torrenticola M. Matsui, 1976

These forms may be separated by the following key:

A. Stream breeding; tadpoles with large mouth, dental formula II/III; metamorphosed toads with small and indistinct tympanum

<4.1, and long foot >49.8 in adult males and >44.6 in adult females at SVL 100 mm; Western Chubu and Kinki, Honshu...... *B. torrenticola*

AA. Still-water breeding, tadpoles with small mouth, dental formula I: 1+1/III; metamorphosed toads with moderate to large tympanum >4.3, and short foot <50.1 in adult males and <44.6 in adult females at SVL 100 mm

B. Short parotoid <18.0 at SVL 100 mm; interorbital flat; seldom with dark stripe on flanks; web well developed; Ryukyu Archipelago .... *B. g. miyakonis*

BB. Long parotoid >19.1 at SVL 100 mm; interorbital concave; usually with dark stripe on flanks; web ill developed; from Yakushima Isl. northwards.

C. Medium tympanum 4.5< <5.6 at SVL 100 mm; southwestern Honshu, Shikoku, Kyushu .... *B. j. japonicus*

CC. Large tympanum >5.9 at SVL 100 mm; northeastern Honshu, Hokkaido .... *B. j. formosus*

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