

## Geographic Patterns of Endemism and Speciation in Amphibians and Reptiles of the Ryukyu Archipelago, Japan, with Special Reference to their Paleogeographical Implications

Hidetoshi Ota<sup>1)</sup>

Tropical Biosphere Research Center, University of the Ryukyus, Nishihara, Okinawa 903–0213, Japan

**Abstract.** This paper analyzes the phylogeographical patterns of amphibian and reptile lineages distributed in the Ryukyu islands south of the Tokara Gap on the basis of relevant distributional data and phylogenetic hypotheses hitherto published. Results indicate the numerical dominance of highly relict lineages in the central Ryukyus, and the occurrences of a few more or less relict lineages in the Miyako Group as well. On the other hand, most species and subspecies endemic to the Yaeyama Group or to the Yaeyama and Miyako Groups are considered to be direct consequences of vicariance with adjacent regions. Three major hypotheses regarding the Cenozoic paleogeography of the central and the southern Ryukyus are examined in the light of the present results and a modified hypothesis is proposed accordingly.

**Key words:** amphibians, dispersal, paleogeography, phylogeny, reptiles, speciation.

### Introduction

The Ryukyu chain is a fairly long archipelago consisting of approximately 140 subtropical islands ranging between Kyushu and Taiwan (Fig. 1; Kizaki 1985). Cenozoic land configuration of the current Ryukyu region is considered to have varied extensively and temporarily, involving more than one period of landbridge connection of the islands in various combinations with adjacent land masses. Such paleogeographical dynamics of the Ryukyu Archipelago should have enhanced range extension through dispersal and vicariance through geographic isolations in each lineage of terrestrial organisms in this region.

Twenty-one native species and subspecies of amphibians and 52 native species and subspecies of terrestrial reptiles, both including a number of endemic taxa, are distributed in the southern and central parts of the Ryukyu Archipelago, i.e., islands located between the Tokara Gap (or Tokara Tectonic Strait) and Taiwan (Fig. 1; Ota 1997a). Because of their limited ability for over sea dispersal, these vertebrate groups are expected to be good model organisms for research on the historical biogeography of islands having a complicated geohistory.

In this paper, I first review the phylogeographical

patterns illustrated by the amphibians and reptiles of the Ryukyu Archipelago to infer the temporal and geographical patterns of their dispersal and divergence. I then examine consistencies between such patterns and the currently prevailing hypotheses on the paleogeography of this and adjacent regions to seek and, when necessary, devise the best fitting explanatory scenario as a subject for future criticism.

In these processes, I took four *a priori* assumptions: 1) Currently recognized genera, species and subspecies are monophyletic unless otherwise claimed; 2) in fairly small islands like those of the Ryukyus, within-island diversification of a given species or subspecies is negligibly small compared to its between-island diversification; 3) recognizable phylogenesis initiates only through between-island vicariance; 4) lineages showing apparent disjunct distributions with their sister lineages are relict at their taxonomic levels *sensu* Darlington (1957).

### Phylogeography of amphibian lineages in the Ryukyus

Distributional ranges of amphibian species of the Ryukyus are summarized in Table 1, together with those of their possible closest relatives.

1) E-mail: ota@sci.u-ryukyu.ac.jp

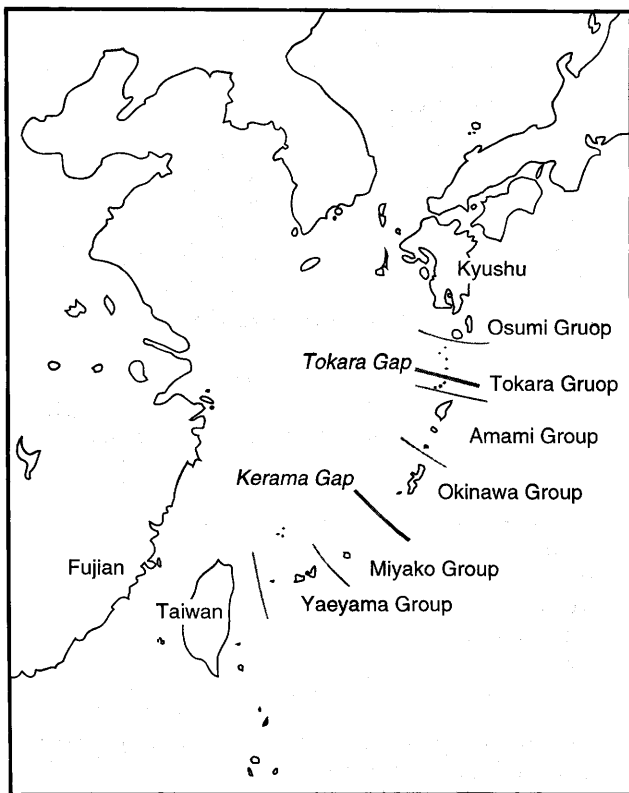


Fig. 1. Map of East Asia showing the location of the Ryukyu Archipelago.

### Newts

Based on morphological and allozyme data, Inger (1947) and Hayashi and Matsui (1988), respectively, demonstrated the occurrence of primary intraspecific variation in *Cynopus ensicauda* between populations of the Amami and the Okinawa Groups. Hayashi et al. (1992) also compared samples of *Tylototriton andersoni* from Amami-oshima, Tokunoshima and Okinawajima by allozyme electrophoresis, and reported that the former two, while closely resembling each other, are quite differentiated from the latter genetically.

### Toads

The Miyako population of *Bufo gargarizans* is endemic to this island group at the subspecific level. This subspecies, *B. g. miyakonis*, seems to be most closely related to conspecific eastern continental populations and rather distant from other congeneric taxa in Taiwan and the main-islands of Japan (Matsui 1984; Nishioka et al. 1990a). A few previous authors considered such a pattern of distribution as indicative of an artificial origin of the Miyakojima population (Inger 1947; Nakamura and Uéno 1963; Kuramoto 1979), but this view was rejected by the discov-

ery of late Pleistocene ( $>0.025$  Ma) fossils of this toad from Miyakojima (Okinawa Prefectural Board of Education 1985).

### Frogs

Currently prevailing taxonomy indicates that *Microhyla ornata* is widely distributed almost throughout the Ryukyu Archipelago, and in other subtropical and tropical East Asian areas (Frost 1985). However, Kuramoto (1987) recognized a significant acoustic differentiation between samples from Taiwan and the Ryukyus. This suggests that populations of these regions have actually diverged from each other to some extent.

*Rana limnocharis* is widely distributed in the central and southern parts of the archipelago, as well as in the southern main-islands of Japan, Taiwan, continental China, and Southeast and South Asia (Frost 1985). Recent biochemical analyses revealed that the southern Ryukyu populations are genetically distinct from the other East Asian populations, whereas populations of the central Ryukyus are poorly diverged from those of the main-islands of Japan, eastern continent, and Taiwan (Nishioka and Sumida 1990; Toda et al. 1997a). It is likely that southern Ryukyu populations actually constitute a distinct, long-isolated cryptic species (Toda et al. 1997a). By contrast, most other populations of the East Asian islands seem to represent relatively recent over sea dispersals from the eastern continent (Toda et al. 1997a, 1998).

The other non-endemic *Rana* of the Ryukyus, *Rana psaltes*, occurs in Ishigakijima and Iriomotejima Islands of the Yaeyama Group and Taiwan (Kuramoto 1985; Chou 1994). *Rana psaltes* closely resembles *Rana adenopleura* from Taiwan and eastern continental China (Kuramoto 1985) and it is probable that these species diverged from each other through isolations in the southern Ryukyus and Taiwan, respectively. Current Taiwanese populations of *R. psaltes* may have been derived from dispersals from the southern Ryukyus subsequent to such allopatric speciation.

Tanaka et al. (1996) reported a relatively large difference in mitochondrial DNA sequence between the Amami-oshima and Okinawajima samples of *R. okinavana*, which probably reflects a substantial divergence of the two island populations. Likewise, populations of *R. ishikawae* on these islands seem to be much diverged morphologically and chromosomally (Seto et al. 1984; Maeda and Matsui 1993).

No information is available regarding the phylogenetic relationship of *R. ishikawae* or a clade consisting of *R. holsti* and *R. subaspera* with other congeneric species. Nevertheless, it is almost certain that each of these represents a highly relict state (Maeda and Matsui 1993; Matsui and Utsunomiya 1983).

**Table 1.** Geographic ranges of native amphibian species distributed in the Ryukyu Archipelago and their possible closest relatives. Distributional data were taken from Ota (1997a), Maeda and Matsui (1993), and Zhao and Adler (1993), unless otherwise stated in the text.

Species	Range	Possible closest relatives (ranges in parentheses)	Source of information for phylogenetic hypothesis
<b>Salamandridae</b>			
<i>Cynops ensicauda</i>	AM, OK	<i>C. pyrrhogaster</i> (MJ)	Hayashi and Matsui (1988)
<i>Tylototriton andersoni</i>	AM, OK	<i>T. spp.</i> (SW)	Assumption 1) of this review
<b>Bufo</b>			
<i>Bufo gargarizans</i>	MY, SW, WE	<i>B. bankorensis</i> (TW)	Nishioka et al. (1990a)
<b>Hylidae</b>			
<i>Hyla hallowellii</i>	AM, OK	<i>H. chinensis</i> (TW, SW)	Riehl et al. (1995)
<b>Microhylidae</b>			
<i>Microhyla ornata</i>	AM-YY, TW SW, WE	unknown	
<b>Ranidae</b>			
<i>R. amamiensis</i>	AM	<i>R. narina</i> (OK)	Matsui (1994)
<i>R. holsti</i>	OK	<i>R. subaspera</i> (AM)	Matsui and Utsunomiya (1983)
<i>R. ishikawae</i>	AM, OK	unknown	
<i>R. limnocharis</i>	AM-YY, TW MJ, SW, WE	unknown	
<i>R. namiyei</i>	OK	<i>R. kuhlii</i> (TW, SW)	Emerson and Berrigan (1993)
<i>R. narina</i>	AM	<i>R. amamiensis</i> (OK)	Matsui (1994)
<i>R. okinavana</i>	AM, OK	( <i>R. tsushimaensis</i> (NE), <i>R. sauteri</i> (TW)) clade	Tanaka-Ueno et al. (1998)
<i>R. psaltes</i>	YY, TW	<i>R. adenopleura</i> (TW, SW)	Kuramoto (1985)
<i>R. subaspera</i>	AM	<i>R. holsti</i> (OK)	Matsui and Utsunomiya (1983)
<i>R. supranarina</i>	YY	<i>R. swinhoana</i> (TW), ( <i>R. swinhoana</i> (TW), <i>R. utsunomiyaorum</i> (YY)) clade, or ( <i>R. amamiensis</i> (AM), <i>R. narina</i> (OK)) clade	Matsui (1994)
<i>R. utsunomiyaorum</i>	YY	<i>R. swinhoana</i> (TW), or ( <i>R. amamiensis</i> (AM), <i>R. narina</i> (OK)) ( <i>R. supranarina</i> (YY), <i>R. swinhoana</i> (TW)) clade	Matsui (1994)
<b>Rhacophoridae</b>			
<i>Buergeria japonica</i>	NT-OK, YY TW	unknown	
<i>Chirixalus eiffingeri</i>	YY, TW	<i>C. idiootocus</i> (TW)	Kuramoto and Wang (1987)
<i>Rhacophorus viridis</i>	AM, OK	( <i>Rh. schlegelii</i> (MJ), <i>Rh. arboreus</i> (MJ)) clade	Nishioka et al. (1987a) Wilkinson et al. (1996)
<i>Rh. owstoni</i>	YY	<i>Rh. moltrechti</i> (TW)	Kuramoto and Utsunomiya (1981)

OS, Osumi Group; NT and ST, Tokara islands north and south of the Tokara Strait, respectively; AM, Amami Group; OK, Okinawa Group; MY, Miyako Group; YY, Yaeyama Group; SK, Senkaku Group; TW, Taiwan; MJ, the main-islands of Japan; NE, northern extralimital; SW, southwestern extralimital; WE, western extralimital.

Matsui (1994) demonstrated the presence of five species in *R. narina* at that date (i.e. *R. narina* s. str., *R. amamiensis*, *R. supranarina*, *R. swinhoana* and *R. utsunomiyaorum*). Considering relationships from allozyme data illustrated by dendrograms (Matsui 1994),

the two southern Ryukyu species (*supranarina* and *utsunomiyaorum*) are likely to be the consequence of allopatric speciation and subsequent dispersal between the Yaeyama Group and Taiwan. The two central Ryukyu species (*narina* and *amamiensis*) seem to reflect a vicari-

**Table 2.** Geographic ranges of native reptile species distributed in the Ryukyu Archipelago and their possible closest relatives. Distributional data were taken from Ota (1997a), Sengoku (1979), and Zhao and Adler (1993), unless otherwise stated in the text. See Table 1 for abbreviations.

Species	Range	Possible closest relatives (ranges in parentheses)	Source of information for phylogenetic hypothesis
<b>Bataguridae</b>			
<i>Cistoclemmys flavomarginata</i>	YY, TW, SW	<i>C. galbinifrons</i> (SW)	Assumption 1) of this review
<i>Geoemyda japonica</i>	OK	<i>G. spengleri</i> (SW)	Yasukawa et al. (1992)
<i>Mauremys mutica</i>	YY, TW, SW	<i>M. annamensis</i> (SW)	Iverson and McCord (1994)
<b>Gekkonidae</b>			
<i>Gekko hokouensis</i>	OS-YY, SK TW, MJ, SW	unknown	
<i>Hemidactylus bowringii</i>	AM-TW, SW	unknown	
<b>Eublepharidae</b>			
<i>Goniurosaurus kuroiwae</i>	AM, OK	<i>G. lichtenfelderi</i> (SW)	Grismer (1988)
<b>Agamidae</b>			
<i>Japalura polygonata</i>	AM-TW	unknown	
<b>Scincidae</b>			
<i>Ateuchosaurus pellopleurus</i>	OS-OK	<i>A. chinensis</i> (SW, WE)	Assumption 1) of this review
<i>Emoia atrocostata</i>	MY, TW, SW	unknown	
<i>Eumeces barbouri</i>	AM, OK	( <i>E. marginatus</i> (NT-OK), <i>E. stimpsonii</i> (YY)) <i>E. elegans</i> (SK, TW, SW, WE) clade	Hikida (1993), Kato et al. (1994)
<i>E. kishinouyei</i>	MY, YY	<i>E. chinensis</i> (TW, SW, WE)	Hikida (1993)
<i>E. marginatus</i>	NT-OK	<i>E. stimpsonii</i> (YY)	Hikida (1993)
<i>E. stimpsonii</i>	YY	<i>E. marginatus</i> (NT-OK)	Hikida (1993)
<i>Scincella boettgeri</i>	MY, YY	<i>S. modesta</i> s. lat. (TW, SW, WE)	Ouboter (1986)
<b>Lacertidae</b>			
<i>Takydromus dorsalis</i>	YY	<i>T. sylvaticus</i> (SW)	Arnold (1997)
<i>T. smaragdinus</i>	ST-OK	<i>T. sauteri</i> (TW)	Arnold (1997)
<i>T. toyamai</i>	MY	( <i>T. sauteri</i> (TW), <i>T. smaragdinus</i> (ST-OK)) clade	Arnold (1997)
<b>Typhlopidae</b>			
<i>Ramphotyphlops braminus</i>	NT-TW, SK, SW	unknown	
<b>Colubridae</b>			
<i>Achalinus formosanus</i>	YY, TW	unknown	
<i>A. wernerii</i>	AM, OK	unknown	
<i>Amphiesma conelarum</i>	MY	( <i>Am. ishigakiense</i> (YY), <i>Am. pryeri</i> (AM, OK)) clade	Ota and Iwanaga (unpublished)
<i>Am. ishigakiense</i>	YY	<i>Am. pryeri</i> (AM, OK)	Ota and Iwanaga (unpublished)
<i>Am. pryeri</i>	AM, OK	<i>Am. ishigakiense</i> (YY)	Ota and Iwanaga (unpublished)
<i>Calamaria pavimentata</i>	YY, TW, SW	unknown	
<i>C. pfefferi</i>	MY	<i>C. pavimentata</i> (YY, TW, SW)	Inger and Marx (1965)
<i>Cyclophiops herminae</i>	MY, YY	<i>Cy. semicarinatus</i> (ST-OK)	Ota (unpublished)
<i>Cy. semicarinatus</i>	ST-OK	<i>Cy. herminae</i> (MY, YY)	Ota (unpublished)
<i>Dinodon rufozonatus</i>	MY-TW, SK SW, WE, NE,	unknown	
<i>D. semicarinatus</i>	AM, OK	unknown	
<i>Elaphe carinata</i>	YY, SK, TW SW	<i>E. quatrivirgata</i> (MJ)	Schulz (1996)
<i>E. taeniura</i>	MY-TW, SW	<i>E. moellendorffi</i> (SW)	Schulz (1996)

Table 2. continued

<i>Lycodon ruhstrati</i>	MY-TW, SW	unknown	
<i>Opisthotropis kikuzatoi</i>	OK	<i>O. spp.</i> (SW)	Assumption 1) of this review
<i>Pareas iwasakii</i>	YY	<i>P. formosensis</i> (TW)	Ota et al. (1997)
Elapidae			
<i>Hemibungarus japonicus</i>	AM, OK	<i>H. sauteri</i> (TW)	Ota et al. (in preparation)
<i>H. macclellandi</i>	YY, TW, SW	unknown	
Viperidae			
<i>Trimeresurus elegans</i>	YY	<i>T. mucrosquamatus</i> (TW, SW)	Brattstrom (1964), Koba (1973)
<i>T. flavoviridis</i>	AM, OK	<i>T. tokarensis</i> (ST)	Koba and Kikukawa (1969)
<i>T. tokarensis</i>	ST	<i>T. flavoviridis</i> (AM, OK)	Koba and Kikukawa (1969)
<i>Ovophis okinavensis</i>	AM, OK	<i>O. spp.</i> (TW, SW)	Assumption 1) of this review

ance between Okinawajima Island and the two northern Amami islands (Matsui 1994).

Nishioka et al. (1987a) recognized little genetic variation between samples of *Buergeria japonica* from Nakano-shima Island of the northern Tokara Group and Amami-oshima Island [Nei's (1972)  $D=0.003-0.038$ ].  $D$  values for these two and the Okinawajima samples were much greater (0.175–0.270; Nishioka et al. 1987a).

The phylogeographical pattern exhibited by *Chirixalus eiffingeri* and *C. idiootocus* (see Kuramoto and Wang 1987) seems to be comparable with that of the *Rana psaltes-adenopleura* group (see above). It is probable that *C. idiootocus* and *C. eiffingeri* also first differentiated allopatrically in Taiwan and the southern Ryukyus, respectively, and that the latter secondarily dispersed into Taiwan.

*Rhacophorus viridis* of the central Ryukyus is divided into two subspecies, *Rh. v. viridis* endemic to the Okinawa Group and *Rh. v. amamiensis* endemic to the northern Amami islands. These are diverged from each other morphologically and genetically to some extent (Inger 1947; Nishioka et al. 1987a; Wilkinson et al. 1996).

### Phylogeography of reptile lineages in the Ryukyus

Distributional ranges of reptile species of the Ryukyus are summarized in Table 2, together with those of their possible closest relatives.

#### Turtles

Of the three batagurid species in the Ryukyus, *Cistoclemmys flavomarginata* and *Mauremys mutica*, both having endemic subspecies confined to the Yaeyama Group (*C. f. evelynae* and *M. m. kami*, respectively), exhibit similar phylogeographic patterns in having populations of different subspecies in Taiwan (McCord and Iverson 1991; Yasukawa et al. 1996). This seems to reflect a relatively

recent vicariance between these two regions (Yasukawa et al. 1996).

#### Lizards

Of the six gekkonid species currently known from the central and the southern Ryukyus, only two, *Hemidactylus bowringii* and *Gekko hokouensis*, seem to be native to this archipelago (Moritz et al 1993; Hikida and Ota 1997). Slight but significant morphological variation was recognized between populations of *G. hokouensis* from Okinawajima Island, northern Taiwan, and Lanyu Island (Ota et al. 1988). By use of allozyme electrophoresis, Toda et al. (1997b) recognized three genetically characterized groups of populations in the central Ryukyu-Kyushu region. Of these, one showing especially low genetic variability ranges across the Tokara Tectonic Strait, and thus suggests recent dispersal of *G. hokouensis* across the strait (Toda et al. 1997b).

*Goniurosaurus kuroiwae*, while being highly relict at the species level, shows a number of subspeciations, presumably as a result of a series of between-island vicariances (Grismer et al. 1994; Fig. 2). For *Japalura polygonata*, three subspecies are recognized on the basis of a few morphological characters — *J. p. polygonata* from the Amami and the Okinawa Groups, *J. p. ishigakiensis* from the Miyako and the Yaeyama Groups, and *J. p. xanthostoma* from northern Taiwan (Ota 1991a). Phylogenetic relationships among these subspecies remain uncertain.

*Emoia atrocostata*, while being confined to the Miyako Group within the Ryukyus, is widely distributed in Taiwan, the Philippines and the Indo-Australian Archipelago. Such distributional pattern is considered to reflect frequent over sea dispersals of this coast-dwelling lizard (Brown 1991).

Three scincid species belonging to the *Eumeces laticutatus* species group (*E. barbouri*, *E. marginatus* and *E. stimpsonii*; Hikida 1993) seem to have a rather complicated history of diversification in East Asian islands. According to Hikida (1993), species belonging to this group

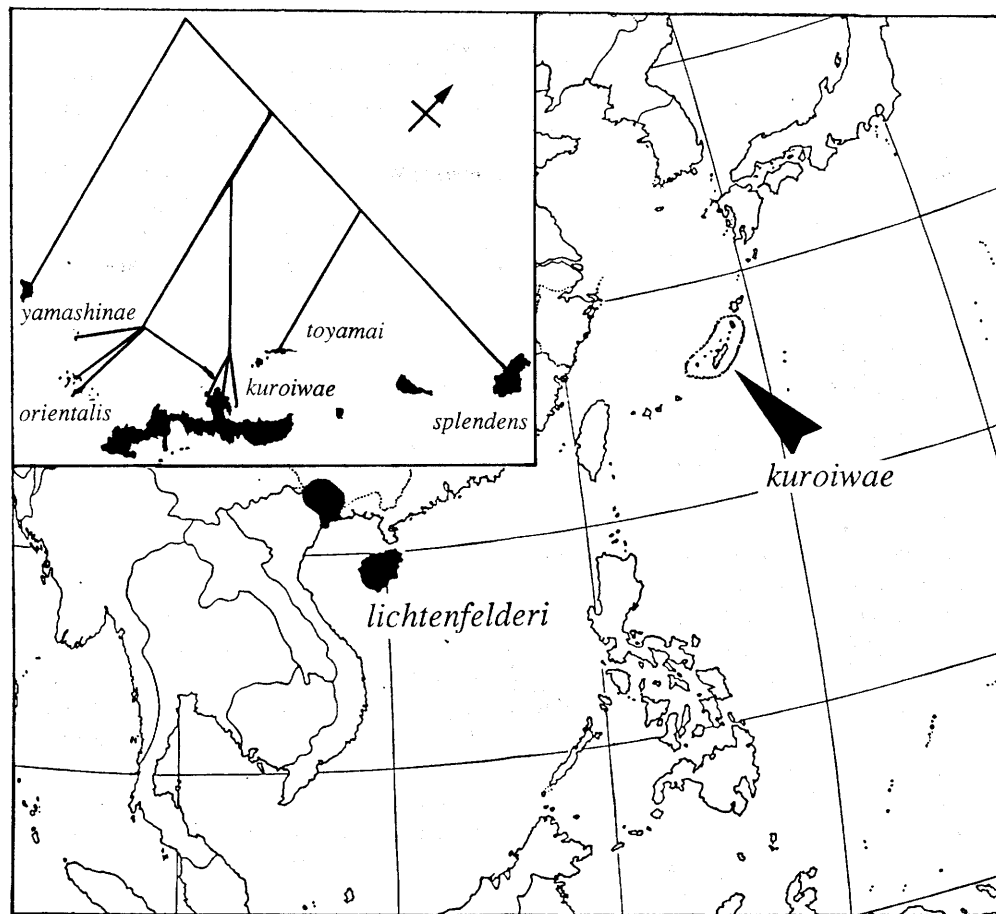


Fig. 2. Map of East Asia showing distributions of *Goniurosaurus kuroiwaie*, a typical relict species of the central Ryukyus, and its closest relative, *G. lichtenfelderi*, from southern China and northern Vietnam. Cladogram drawn in the inset depicts the phylogenetic relationships of the five subspecies of *G. kuroiwaie* inferred on the basis of morphological characters (Grismer et al. 1994).

in the central and the southern Ryukyus and Taiwan are monophyletic, of which *E. barbouri* seems to have first diverged from the others, followed by *E. elegans* from the Senkaku Group and Taiwan, and *E. stimpsonii* and *E. marginatus* in order. Such a relationship, also supported by biochemical data (Kato et al. 1994), seems to suggest that the ancestral stocks of the current *E. latiscutatus* species group dispersed into the central Ryukyus at least two times, of which the primary and the subsequent dispersals should have resulted in derivations of *E. barbouri* and *E. marginatus*, respectively (Hikida and Ota 1997). Within *E. marginatus*, further differentiations seem to have taken place between populations of the Okinawa plus southern Amami islands and the northern Amami plus southern Tokara islands (Kato et al. 1994).

Considerable morphological variation is recognized between populations of *Ateuchosaurus pellopleurus* from the Okinawa Group and the northern Amami islands, but with an intermediate population in Okierabujima Island of

the southern Amami Group. There is no distinct variation between populations south and north of the Tokara Tectonic Strait. This suggests recent over sea dispersals of this species across the strait (Ota et al. 1998).

### Snakes

Seven colubrid taxa, all endemic to the southern Ryukyus at the specific or subspecific level (*Achalinus formosanus chigirai*, *Calamaria pavimentata miyarai*, *Dinodon rufozonatus walli*, *Elaphe carinata yonaguniensis*, *E. taeniura schmackeri*, *Lycodon ruhstrati multifasciatus*, and *Pareas iwasakii*), have close relatives in Taiwan (Ota 1982, 1988, 1991b; Ota and Toyama 1989; Ota et al. 1997; Schulz 1996), and thus may possibly have emerged through vicariance between these regions. *Calamaria pfefferi* from Miyakojima and Irabujima Islands of the Miyako Group is supposedly closely related to *C. pavimentata miyarai* from western Yaeyama and *C. p. formosana* from Taiwan

(Inger and Marx 1965). However, the absence of congeneric species in the intermediate region (i.e. Iriomotejima and Ishigakijima Islands of the Yaeyama Group and Taramajima Island of the Miyako Group), as well as its distinctly small body size (Ota 1982; Ota and Hokama 1996), suggests a relict state of *C. pfefferi*.

Based on cranial morphology, Cundall (1981) examined the relationship among the green snakes (genus *Ophedryx* sensu lato) including the three East Asian species, *Cyclophiops major* from eastern continental China and Taiwan, *C. herminae* from the southern Ryukyus, and *C. semicarinatus* from the central Ryukyus. Results of the distance analyses applied in that study suggested the intermediacy of *C. herminae* between *C. major* and *C. semicarinatus*, and Cundall (1981) thus deferred a conclusion regarding their phylogenetic relationships. Results of my parsimony analysis using his data matrix [Table 1 in Cundall (1981)] suggests a sister-group relationship of *C. herminae* with *C. semicarinatus*, although this hypothesis needs verification on the basis of additional data. On the other hand, extensive variation is known among island populations of *C. semicarinatus*, and populations of the Okinawa Group seem to be much diverged from northern Amami and southern Tokara populations (Ota et al. 1995).

Malnate (1962) argued that *A. pryeri* (sensu lato: see Ota and Iwanaga (1997) for current taxonomic arrangements) is most closely related to *A. craspedogaster* from eastern continental China and then to the *A. vibakari-popei-sauteri* clade. A preliminary phylogenetic analysis using the latter two as the first and second outgroups in order yielded a cladogram suggesting a sister-group relationship between *A. pryeri* and *A. ishigakiense* (Ota and Iwanaga unpublished). Such inconsistency between the phylogenetic and geographical patterns among the three Ryukyu species seems to preclude any simple, indigenous, vicariance-dependent scenario.

Results of karyotypic comparisons of *Dinodon semicarinatus* from the central Ryukyus, and *D. rufosonatus* from the southern Ryukyus, Taiwan and eastern continental China seem to negate their close affinity (Toriba 1990; Ota unpublished observations), and it is likely that the former actually represent a relict state rather than a recent vicariance with the latter (Hikida and Ota 1997).

*Hemibungarus maccllellandi iwasakii*, a subspecies endemic to the Yaeyama Group, has another conspecific subspecies (*H. m. formosensis*) on the main island of Taiwan (Ota 1991b). It is thus probable that these, like several colubrid pairs mentioned above, represent a recent vicariance between the southern Ryukyus and Taiwan.

Two subspecies of *Hemibungarus japonicus*, *H. japonicus japonicus* and *H. j. boettgeri*, are endemic to the Okinawa Group and Tokunoshima Island, and Amamioshima Island and a few adjacent islets, respective-

ly (Koba et al. 1977; Toyama and Ota 1991). Recent morphological analysis (Ota, Ito and Lin in prep.) revealed that these subspecies are monophyletic against the other subspecies, *H. j. sauteri*, which shows a disjunct distribution in Taiwan with an absence of conspecific populations in the southern Ryukyus (Ota 1991b; Toriba in Golay et al. 1993). Such phylogenetic and distributional patterns seem to suggest that the two central Ryukyu subspecies, which most likely diverged from each other recently, collectively constitute a relict unit that are actually distant from the Taiwanese populations at the specific level (Ota et al. in preparation).

### General phylogeographical patterns recognized and putative geographic patterns of relict endemism and speciation

Based on the phylogeographical patterns surmised above, amphibian and reptile lineages in the central and southern Ryukyus could be classified into 14 groups:

- (1) those endemic to the central Ryukyus, with closest relatives occurring only on the continent or on the continent and Taiwan (*Tylototriton andersoni*, *Hyla hallowellii*, *Rana namiyei*, *Geoemyda japonica*, *Goniurosaurus kuroiwae*, *Takydromus smaragdinus*, *Ateuchosaurus pellopleurus*, *Opisthotropis kikuzatoi*, the *Hemibungarus japonicus japonicus-boettgeri* clade, and *Ovophis okinavensis*);
- (2) those endemic to the central Ryukyus, with closest relatives occurring only in Taiwan and the more northern region (*Rana okinavana*);
- (3) those endemic to the central Ryukyus, with closest relatives occurring only on the main islands of Japan and adjacent islets (*Cynops ensicauda*, *Rhacophorus viridis*);
- (4) those endemic to the central Ryukyus, with closest relatives occurring in the Miyako Group, Yaeyama Group, or both (the *Rana narina-amamiensis* clade, *Japalura polygonata polygonata*, *Eumeces marginatus*, *Cyclophiops semicarinatus*, *Amphiesma pryeri*, and the *Trimeresurus flavoviridis-tokarensis* clade);
- (5) those endemic to the Miyako Group, with possible closest relatives occurring on the continent (*Bufo gargarizans miyakonis*);
- (6) those endemic to the Miyako Group, with closest relatives occurring only in Taiwan and adjacent islands (*Calamaria pfefferi*);
- (7) those endemic to the Yaeyama Group or the Miyako and the Yaeyama Groups, with closest relatives occurring only in Taiwan or Taiwan and the continent (*R. supranarina*, *R. utsunomiyaorum*, *Rhacophorus owstoni*, *Cistoclemmys flavomarginata evelynae*, *Mauremys mutica kami*, *Japalura polygonata ishigakiensis*,

*Eumeces kishinouyei*, *Scincella boettgeri*, *Calamaria pavimentata miyarai*, *Pareas iwasakii*, *Elaphe carinata yonaguniensis*, *E. taeniura schmackeri*, *Dinodon rufozonatus walli*, *Lycodon ruhstrati multifasciatus*, *Achalinus formosanus chigirai*, *Hemibungarus maccellandi iwasakii*, *Trimeresurus elegans*).

(8) those endemic to the Yaeyama Group, or the Miyako and the Yaeyama Groups, with closest relatives occurring only in the central Ryukyus (*Eumeces stimpsonii*, *Cyclophiops herminae*, and *Amphiesma ishigakiense*);

(9) those endemic to the Yaeyama Group, with possible closest relatives occurring only on the continent (*Takydromus dorsalis*);

(10) those endemic to the Yaeyama Group and Taiwan, with possible closest relatives occurring only in Taiwan (*Rana psaltes*, *Chirixalus eiffingeri*);

(11) those widely distributed from Taiwan to the central Ryukyus (*Microhyla ornata*, *Rana limnocharis*, *Burigeria japonica*, *Gekko hokouensis*, *Hemidactylus bowringii*, *Ramphotyphlops braminus*);

(12) those endemic to the central Ryukyus, with closest relatives much diverged and widely distributed in the Ryukyus and adjacent regions (*E. barbouri*);

(13) those endemic to the Miyako Group, with the closest relatives occurring in both more northeastern and southwestern regions (*Takydromus toyamai*, *Amphiesma conelarum*);

(14) those exclusively shared between the Miyako Group, Taiwan and more southern islands (*Emoia atrocostata atrocostata*).

Besides these, there are several amphibian and reptile lineages, all from the central Ryukyus, for which no phylogenetic information/hypotheses are currently available at all (*Rana ishikawae*, the *R. holsti-subaspera* clade, *Dinodon semicarinatus*, and *Achalinus wernerii*). All these seem to be highly relict.

From these phylogeographical patterns, it is obvious that the central Ryukyus and the southern Ryukyus constitute two separate areas of endemisms. Most species and lineages endemic to the central Ryukyus (groups 1 and 2) have distinct geographical gaps or apparent secondary sympatry with their possible closest relatives, and thus are considered to be more or less relict. The remaining central Ryukyus endemics, all belonging to groups 3 and 4, have closest relatives just northeast and southwest of their ranges, and thus seemingly represent vicariations at the Tokara and Kerama Gaps, respectively. Gross coincidence between the time of divergence of *Cynops ensicauda* (group 3) from its sibling in the main-islands of Japan (*C. pyrrhogaster*) inferred from allozyme data, and the time of initial formation of the Tokara Gap (Hayashi and Matsui 1988) offer a robust support to the vicariance hypothesis for *ensicauda* and *pyrrhogaster* at this gap.

A number of endemic lineages of the central Ryukyus exhibit further variation, and the southwestern/northeastern divergence with major borders being located southwest of Tokunoshima Island is the most frequent geographic pattern of such variation (see above). This suggests a relatively recent occurrence of another vicariance between the Okinawa plus the southern Amami islands and the northern Amami plus the southern Tokara islands. A few exceptions include *Goniurosaurus kuroiwae* (in which the primary divergence is postulated between Kumejima and the remaining islands (Grismer et al. 1994), *Hemibungarus japonicus*, in which the border of the two Ryukyus subspecies (*H. j. boettgeri* and *H. j. japonica*) is located between Tokunoshima and Yorojima Islands (Koba et al. 1977), and the *Trimeresurus flavoviridistokarensis* clade, in which the species border is located between Amamioshima and Takarajima Islands (Koba and Kikukawa 1969). These may reflect additional vicariations and/or extensive dispersals. Further biochemical and molecular approaches are desired to examine the historical significances of such geographic-taxonomic patterns.

The Miyako Group, while sharing several lineages exclusively with the Yaeyama Group, accommodates a few others (groups 5, 6 and 13) endemic to itself. Of the latter, *Bufo gargarizans miyakonis* has conspecific populations only in continental China (Matsui 1984), and it is likely that the subspecies has emerged through a direct, relatively recent dispersal from the continent and subsequent short period of isolation. The remaining Miyako endemics (*Takydromus toyamai*, *Calamaria pfefferi*, and presumably *Amphiesma conelarum*) seem to be more or less relict (see above).

More than 80% of the endemic southern Ryukyus lineages occurring in the Yaeyama Group (group 7) seem to have closest relatives in Taiwan, and thus are most likely to have emerged through vicariance with the latter region. *Takydromus dorsalis* is unique in that it has a closest relative (*T. silvaticus*; Arnold 1997) only on the continent (e.g. Zhao and Adler 1993). This strongly suggests its relict nature which is quite exceptional among the amphibians and reptiles of the Yaeyama Group. The remaining southern Ryukyus endemics (group 8) have closest relatives exclusively in the central Ryukyus. This may be interpreted as reflecting the vicariance between the southern and the central Ryukyus (Hikida and Ota 1997).

Two amphibians of group 10 (*Rana psaltes* and *Chirixalus eiffingeri*), being shared between both the Yaeyama Group and Taiwan, may deserve special attention in that they also have their closest relatives in the latter sympatrically (Kuramoto 1985; Kuramoto and Wang 1987). Such a phylogeographical pattern seems to suggest the primary Taiwan-southern Ryukyus vicariance and subsequent dispersals from the latter to the former regions, although an



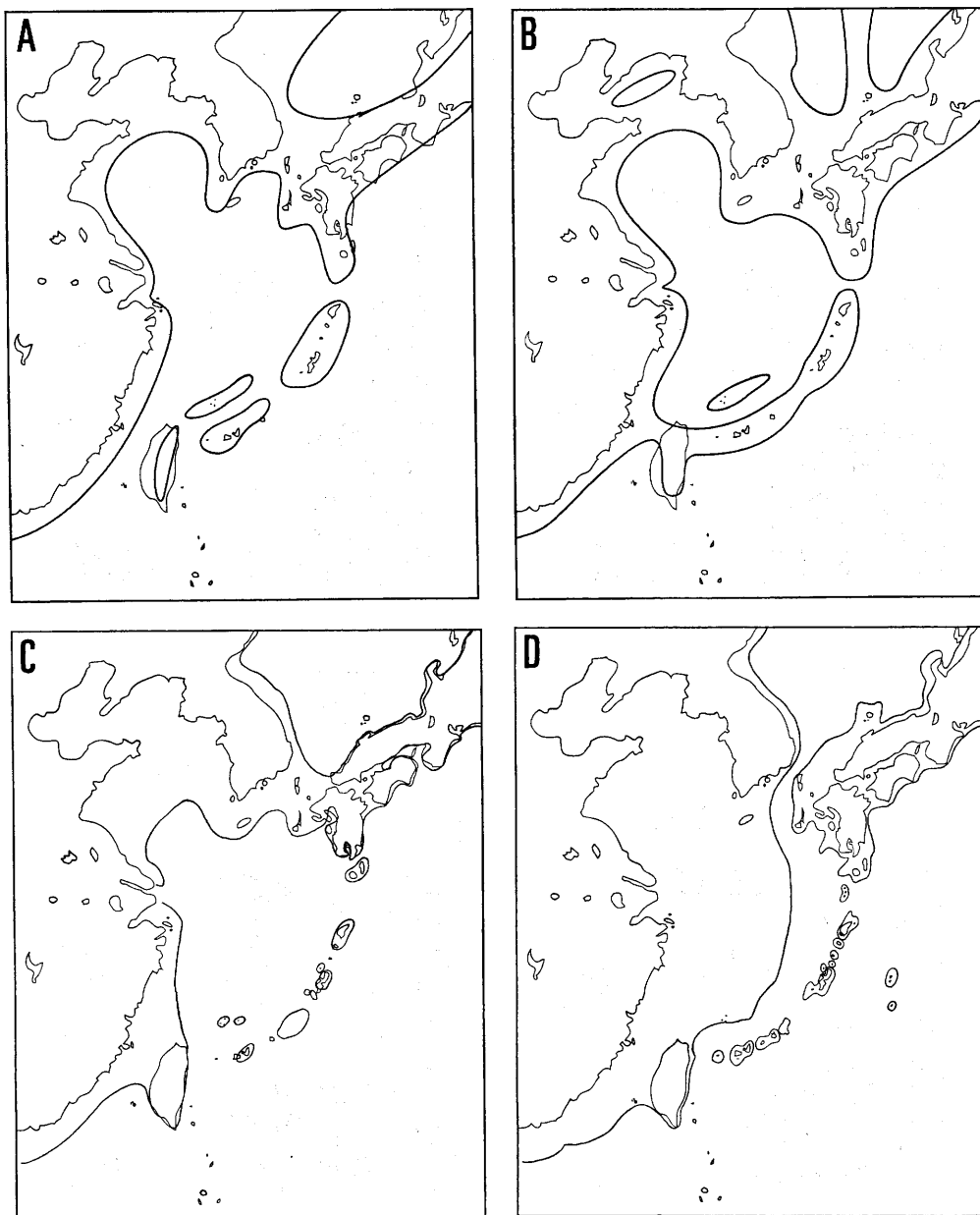
alternative explanation may be possible by assuming the primary *in situ* divergence within Taiwan (Ota 1997b) and subsequent dispersal of one of the resultant sister species into the Yaeyama Group.

Species of group 11 still need careful examination from a population systematic view point before any hypothetical scenarios are constructed to explain their current distribution. This is because most, if not all, of these seem to have been involved in substantial genetic divergence in the absence of discernible morphological differentiations (see

e.g. Kuramoto 1987; Nishioka et al. 1987a; Toda et al. 1997a, b).

**Paleogeographical implications**

Geologically the islands of the Ryukyus can be regarded as exposed portions of the Ryukyu Cordillera, which is located northwest of the Ryukyu Trench and southeast of the Ryukyu Trough. In response to the progress of subsi-

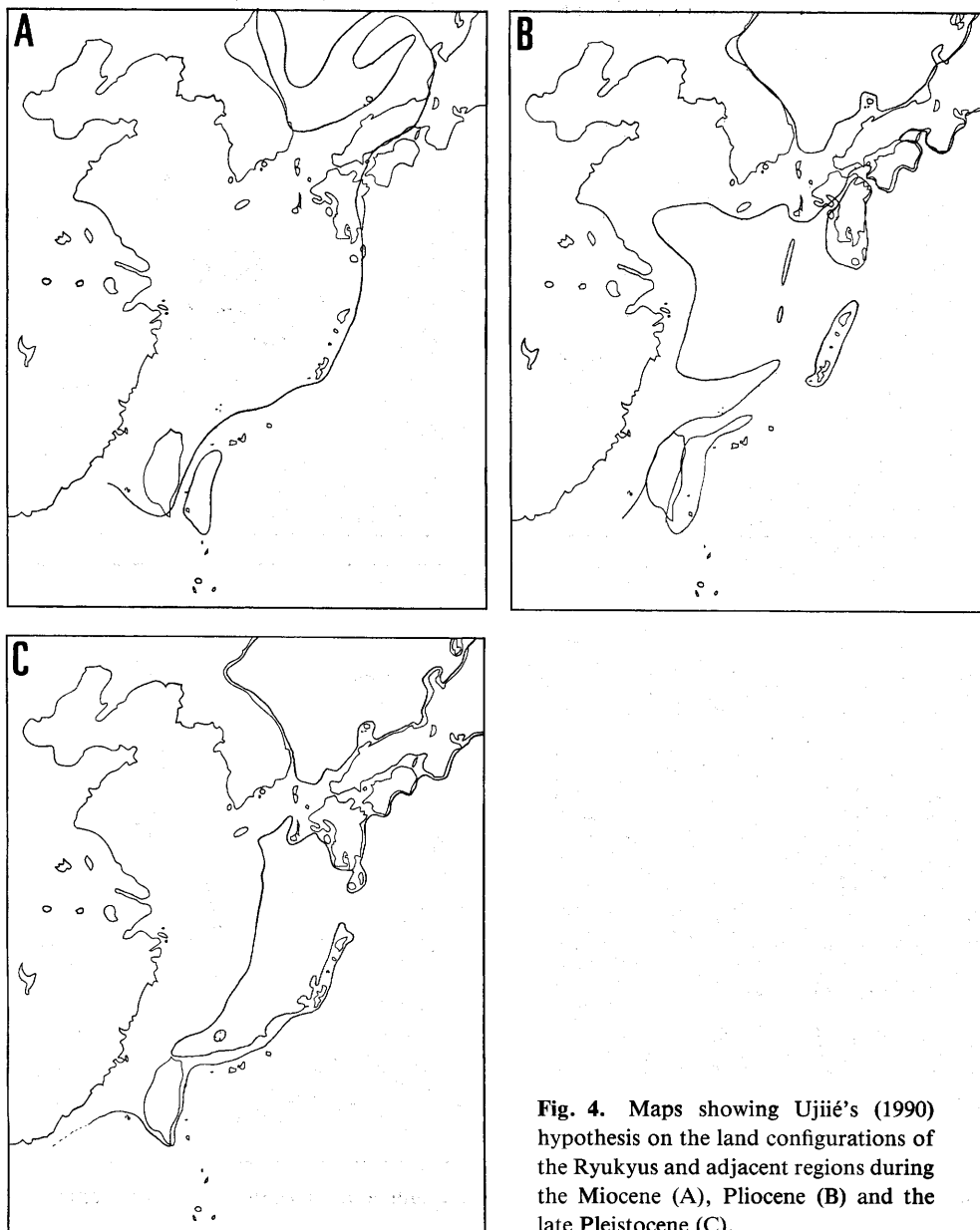


**Fig. 3.** Maps showing Kizaki and Oshiro's (1977) hypothesis on the land configurations of the Ryukyus and adjacent regions during the Pliocene (A), and early (B), middle (C) and late Pleistocene (D).

dence of the Philippine Plate into the Ryukyu Trench and subduction of the Ryukyu Trough, the Ryukyu Cordillera has been subjected to highly complicated vertical and horizontal movements, and these, along with glaciation-associated sea level changes, have led to temporary fluctuations of exposed land areas in this region almost throughout the Cenozoic era (e.g. Kizaki and Oshiro 1977, 1980; Ujiie 1990). For the formation of current phylogeographical patterns in terrestrial organisms of the Ryukyus, post-Tertiary dynamics of land configurations in this region should have made an especially great contribution by providing their ancestors with opportunities of

dispersal through landbridge connections and differentiations through insular-isolations.

Recently there are three major comprehensive hypotheses on the Cenozoic paleogeography of the Ryukyus which conflict with each other in the postulated changes of land configurations since the Miocene. The first hypothesis (hypothesis I: Kizaki and Oshiro 1977), chiefly on the basis of available sedimental and bathymetric data, postulates that: i) Partial submergences of a large Miocene landbridge (extending from eastern China to the main-islands of Japan) formed several separate land-masses including two large islands in the Ryukyu region



**Fig. 4.** Maps showing Ujiie's (1990) hypothesis on the land configurations of the Ryukyus and adjacent regions during the Miocene (A), Pliocene (B) and the late Pleistocene (C).