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

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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 occurences 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.

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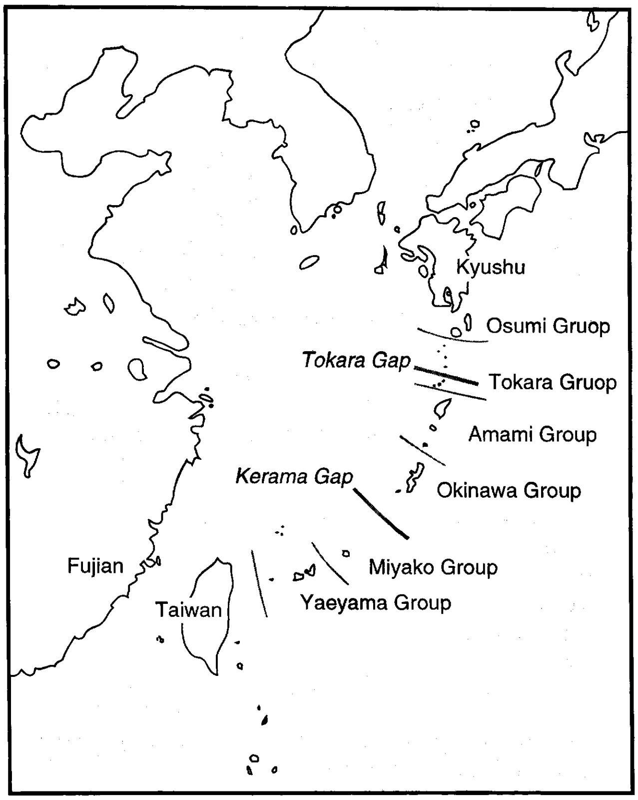

Fig. 1. Map of East Asia showing the location of the Ryukyu Archipelago.

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 discovery 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
Salamandridae			
Cynops ensicauda	AM, OK	*C. pyrrhogaster* (MJ)	Hayashi and Matsui (1988)
Tylototriton andersoni	AM, OK	*T.* spp. (SW)	Assumption 1) of this review
Bufonidae			
Bufo gargarizans	MY, SW, WE	*B. bankorensis* (TW)	Nishioka et al. (1990a)
Hylidae			
Hyla hallowellii	AM, OK	*H. chinensis* (TW, SW)	Riehl et al. (1995)
Microhylidae			
Microhyla ornata	AM-YY, TW SW,WE	unknown	
Ranidae			
R. amamiensis	AM	*R. narina* (OK)	Matsui (1994)
R. holsti	OK	*R. subaspera* (AM)	Matsui and Utsunomiya (1983)
R. ishikawae	AM, OK	unknown	
R. limnocharis	AM-YY, TW MJ, SW, WE	unknown	
R. namiyei	OK	*R. kuhlii* (TW, SW)	Emerson and Berrigan (1993)
R. narina	AM	*R. amamiensis* (OK)	Matsui (1994)
R. okinavana	AM, OK	(*R. tsushimaensis* (NE), *R. sauteri* (TW)) clade	Tanaka-Ueno et al. (1998)
R. psaltes	YY, TW	*R. adenopleura* (TW, SW)	Kuramoto (1985)
R. subaspera	AM	*R. holsti* (OK)	Matsui and Utsunomiya (1983)
R. supranarina	YY	*R. swinhoana* (TW), (*R. swinhoana* (TW), *R. utsunomiyaorum* (YY)) clade, or (*R. amamiensis* (AM), *R. narina* (OK)) clade	Matsui (1994)
R. utsunomiyaorum	YY	*R. swinhoana* (TW), or (*R. amamiensis* (AM), *R. narina* (OK)) (*R. supranarina* (YY), *R. swinhoana* (TW)) clade	Matsui (1994)
Rhacophoridae			
Buergeria japonica	NT-OK, YY TW	unknown	
Chirixalus eiffingeri	YY, TW	*C. idiootocus* (TW)	Kuramoto and Wang (1987)
Rhacophorus viridis	AM, OK	(*Rh. schlegelii* (MJ), *Rh. arboreus* (MJ)) clade	Nishioka et al. (1987a) Wilkinson et al. (1996)
Rh. owstoni	YY	*Rh. moltrechti* (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
Bataguridae			
Cistoclemmys flavomarginata	YY, TW, SW	*C. galbinifrons* (SW)	Assumption 1) of this review
Geoemyda japonica	OK	*G. spengleri* (SW)	Yasukawa et al. (1992)
Mauremys mutica	YY, TW, SW	*M. annamensis* (SW)	Iverson and McCord (1994)
Gekkonidae			
Gekko hokouensis	OS-YY, SK TW, MJ, SW	unknown	
Hemidactylus bowringii	AM-TW, SW	unknown	
Eublepharidae			
Goniurosaurus kuroiwae	AM, OK	*G. lichtenfelderi* (SW)	Grismer (1988)
Agamidae			
Japalura polygonata	AM-TW	unknown	
Scincidae			
Ateuchosaurus pellopleurus	OS-OK	*A. chinensis* (SW,WE)	Assumption 1) of this review
Emoia atrocostata	MY, TW, SW	unknown	
Eumeces barbouri	AM, OK	(*E. marginatus* (NT-OK), *E. stimpsonii* (YY)) *E. elegans* (SK, TW, SW, WE) clade	Hikida (1993), Kato et al. (1994)
E. kishinouyei	MY, YY	*E. chinensis* (TW, SW, WE)	Hikida (1993)
E. marginatus	NT-OK	*E. stimpsonii* (YY)	Hikida (1993)
E. stimpsonii	YY	*E. marginatus* (NT-OK)	Hikida (1993)
Scincella boettgeri	MY, YY	*S. modesta* s. lat. (TW, SW, WE)	Ouboter (1986)
Lacertidae			
Takydromus dorsalis	YY	*T. sylvaticus* (SW)	Arnold (1997)
T. smaragdinus	ST-OK	*T. sauteri* (TW)	Arnold (1997)
T. toyamai	MY	(*T. sauteri* (TW), *T. smaragdinus* (ST-OK)) clade	Arnold (1997)
Typhlopidae			
Ramphotyphlops braminus	NT-TW, SK, SW	unknown	
Colubridae			
Achalinus formosanus	YY, TW	unknown	
A. werneri	AM, OK	unknown	
Amphiesma concelarum	MY	(*Am. ishigakiense* (YY), *Am. pryeri* (AM, OK)) clade	Ota and Iwanaga (unpublished)
Am. ishigakiense	YY	*Am. pryeri* (AM, OK)	Ota and Iwanaga (unpublished)
Am. pryeri	AM, OK	*Am. ishigakiense* (YY)	Ota and Iwanaga (unpublished)
Calamaria pavimentata	YY, TW, SW	unknown	
C. pfefferi	MY	*C. pavimentata* (YY, TW, SW)	Inger and Marx (1965)
Cyclophiops herminae	MY, YY	*Cy. semicarinatus* (ST-OK)	Ota (unpublished)
Cy. semicarinatus	ST-OK	*Cy. herminae* (MY, YY)	Ota (unpublished)
Dinodon rufozonatus	MY-TW, SK SW, WE, NE,	unknown	
D. semicarinatus	AM, OK	unknown	
Elaphe carinata	YY, SK, TW SW	*E. quatrivirgata* (MJ)	Schulz (1996)
E. taeniura	MY-TW, SW	*E. moellendorffi* (SW)	Schulz (1996)

Table 2. continued

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

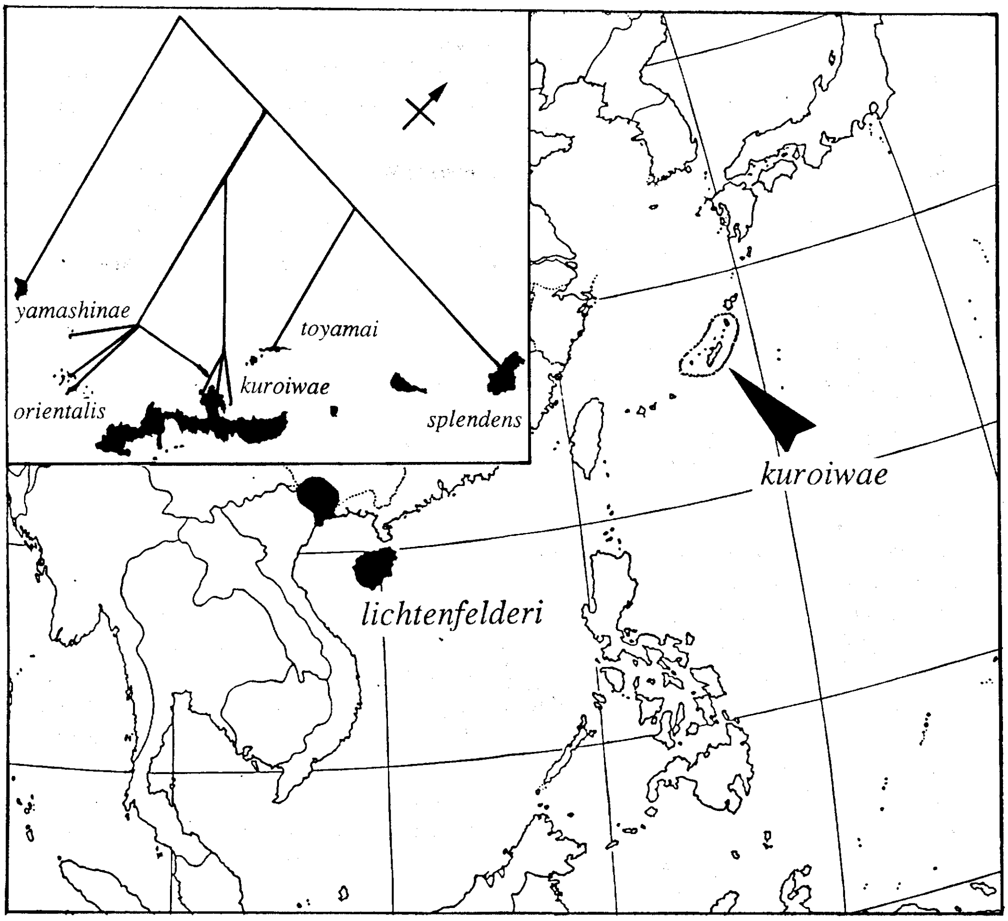

Fig. 2. Map of East Asia showing distributions of *Goniurosaurus kuroiwae*, a typical relict species of the central Ryukyus, and its closest relative, *G. lichtenfelderi*, from southern China and northern Vietnam. Cladogram drawn in the inset depicts the phylogenetic relationships of the five subspecies of *G. kuroiwae* 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 *Opheodrys* 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 cladgram suggesting a sister-group relationship between *A. pryeri* and *A. ishigakiense* (Ota and Iwanaga unpublished). Such incosistency 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 macclellandi 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, respectively (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 retatives 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 macclellandi 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 concelarum*);

(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 werneri*). 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 Ryukyu endemics, all belonging to groups 3 and 4, have closest relatives just northeast and southwest of their ranges, and thus seemingly represent vicariances 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 Ryukyu subspecies (*H. j. boettgeri* and *H. j. japonica*) is located between Tokunoshima and Yorojima Islands (Koba et al. 1977), and the *Trimeresurus flavoviridis–tokarensis* clade, in which the species border is located between Amamioshima and Takarajima Islands (Koba and Kikukawa 1969). These may reflect additional vicariances 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 concelarum*) seem to be more or less relict (see above).

More than 80% of the endemic southern Ryukyu 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 Ryukyu 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 Ryukyu 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-

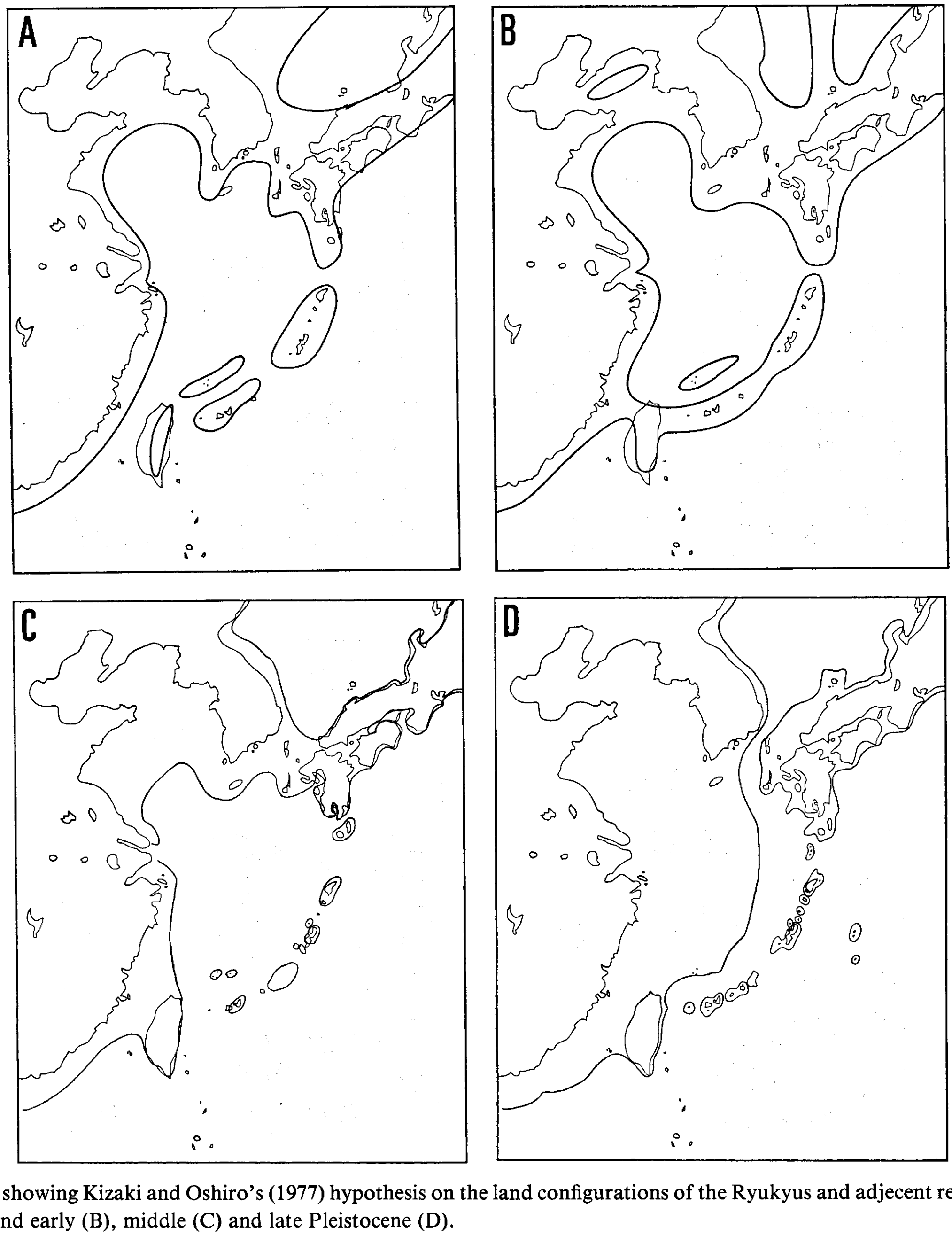

Fig. 3. Maps showing Kizaki and Oshiro's (1977) hypothesis on the land configurations of the Ryukyus and adjecent regions during the Pliocene (A), and early (B), middle (C) and late Pleistocene (D).

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 lead to temporary fluctuations of exposed land areas in this region almost throughout the Cenozoic era (e.g. Kizaki and Oshiro 1977, 1980; Ujiié 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 landmasses including two large islands in the Ryukyu region

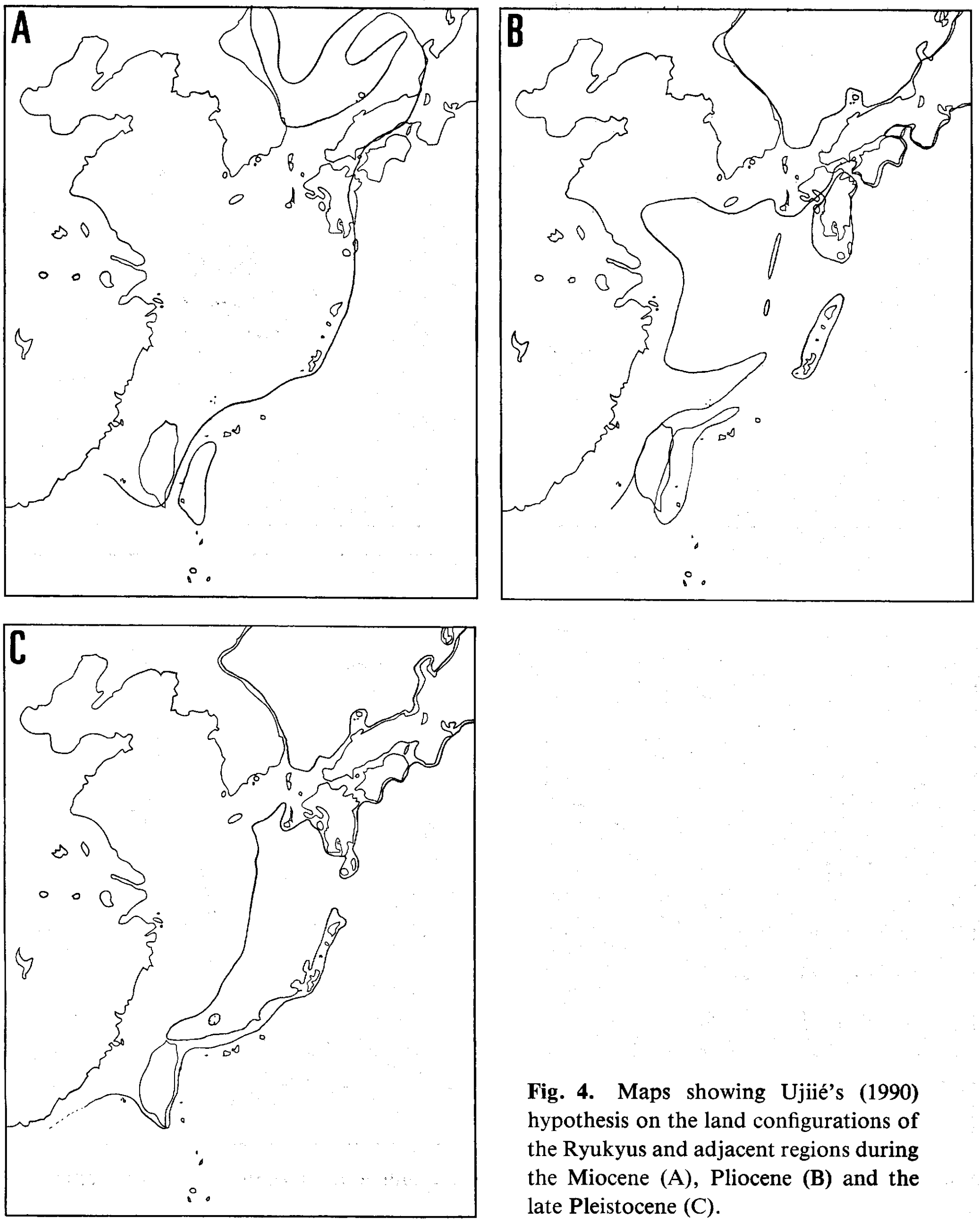

Fig. 4. Maps showing Ujiié's (1990) hypothesis on the land configurations of the Ryukyus and adjacent regions during the Miocene (A), Pliocene (B) and the late Pleistocene (C).

during the Pliocene — one extending from the current western Yaeyama to the northern Miyako islands, and the other from current Kumejima to Amamioshima Islands (Fig. 3A); ii) in the early Pleistocene (ca 1.5 Ma) a large magnitude of uplifting of the Ryukyu Cordillera base regenerated the landbridge from eastern China, which, however, did not reach the main-islands of Japan because of the truncation by the Tokara Gap (Fig. 3B); iii) large portions of this landbridge, including those corresponding to the current Miyakojima and adjacent islands, submerged again in the middle Pleistocene (ca 1 Ma), leaving relatively few islands above sea level (Fig. 3C); iv) in the late Pleistocene (0.02−0.015 Ma), land areas expanded to form several super-islands as a result of the sea level drop involved by continental glaciation (Fig. 3D). This hypothesis has been advocated by a number of subsequent authors, but sometimes with slight modifications mostly due to the changes in estimated value of the sea level drop during the Würm glaciation (200 m in Kizaki and Oshiro 1977 v.s., e.g., 140 m in Kizaki and Oshiro 1980, and 120 m in Ota et al. 1993].

The second hypothesis (hypothesis II), developed by H. Ujiié and his colleagues (Ujiié 1990; Ujiié et al. 1991; Ujiié and Nakamura 1996) chiefly on the basis of sedimental and microfossil data, postulates that: i) In the Miocene the southern Ryukyu islands were isolated from the continent, whereas the remaining Ryukyus, as well as the western main-islands of Japan, composed the western margin of the continent (Fig. 4A); ii) the central Ryukyus were first isolated from the continent as one large island occupying almost the whole area of the current Okinawa and Amami Groups in the Pliocene (Fig. 4B); iii) during the late Pleistocene glaciation (0.02 Ma) a large peninsular-shaped landbridge developed from southeastern China to Amamioshima Island, without passing through the southern Ryukyu islands (Fig. 4C). It is noteworthy that Ujiié and Nakamura (1996) further assumed the formation of an additional landbridge from Taiwan to the Miyako Group ca 3,800 yr ago.

Kimura (1996a, b) published a third hypothesis (hypothesis III) by analyzing and synthesizing recently added stratigraphic, tectonostructural and geomorphic data for the Ryukyu Cordillera and adjacent regions. This hypothesis postulates that: i) In the late Pliocene, the Ryukyu region, as well as the main-islands of Japan, constituted an eastern margin of the Asian Continent, with a series of several small lakes arranged more inland along the shore-line (Fig. 5A); ii) with a formation and expansion of the East China Sea in the early Pleistocene (ca 1.7–1 Ma), most parts of the Ryukyus formed a large peninsula extending from the southeastern continent to the Tokara Gap; iii) large portions of the peninsula including the whole Miyako Group, as well as of eastern margin of the continent, submerged, retaining only a few islands (i.e. Iriomotejima, Ishigakijima, Okinawajima, Tokunoshima and Amamioshima) above the sea level in the middle Pleistocene (1−0.4 Ma); iv) a large landbridge was reformed from the southeastern continent to the main-islands of Japan, with exposures of both the Kerama and Tokara Gaps above the sea level during the middle to the

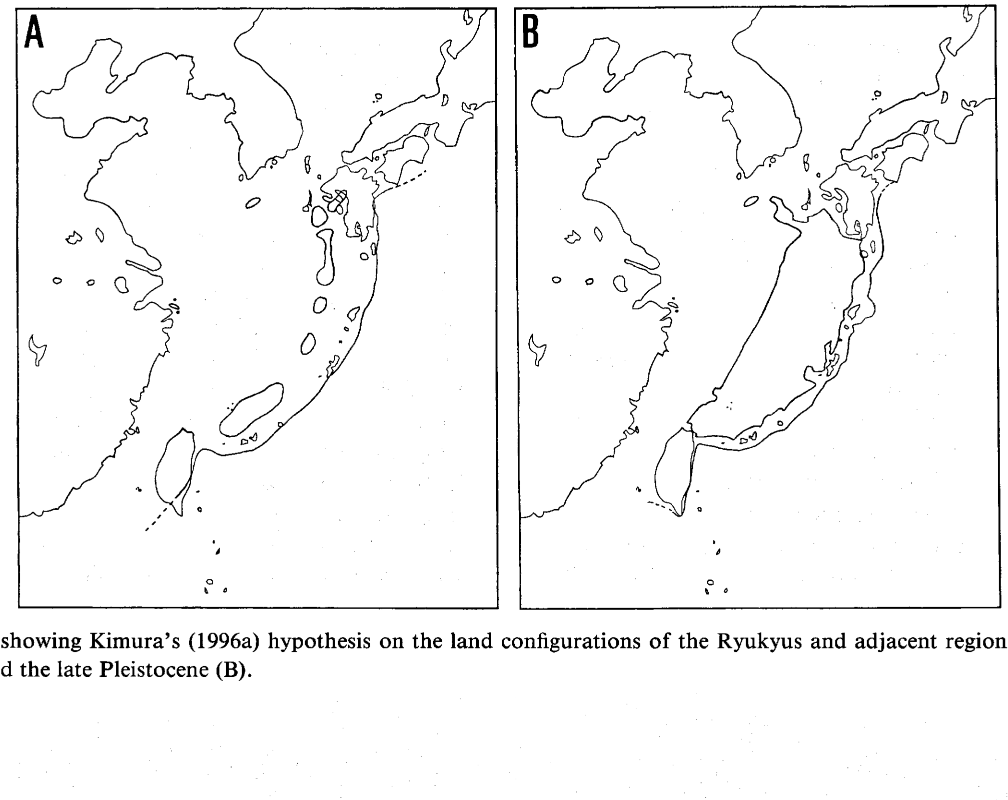

Fig. 5. Maps showing Kimura's (1996a) hypothesis on the land configurations of the Ryukyus and adjacent regions during the late Pliocene (A) and the late Pleistocene (B).

late Pleistocene (0.2−0.02 Ma: Fig. 5B).

Postulated land configulations for Pliocene and early to middle Pleistocene are largely similar between hypotheses I and II, and between hypotheses I and III, respectively. On the other hand, the Pliocene land configuration in hypothesis III differs much from those of the other hypotheses. It should be emphasized that hypothesis I assumes the consistent existence of the Tokara and the Kerama Gaps since their initial formations. By contrast, hypotheses II and III assume formations of extensive landbridges with almost complete closures of the Kerama Gap and both the Kerama and the Tokara Gaps during the late Pleistocene, respectively. It is also worth to note that hypotheses I and III assume the complete submergence of the Miyako Group during the middle Pleistocene (hypothesis II provides no account on this issue).

Results of phylogeographical analyses of extant amphibians and reptiles of the Ryukyus confirm an extremely high frequency of relict taxa in the central part of this archipelago as was assumed by several previous authors (Hikida et al. 1989; Ota 1994; Matsui 1996; Kuramoto 1996). Also, results of the analyses indicate that most of such relict lineages have their closest relatives in more southwestern regions such as Taiwan and the southeastern continent. A few apparently relict species also occur in the Miyako Group. By contrast, except for the enigmatic *Takydromus dorsalis*, amphibians and reptiles endemic to the Yaeyama Group or the Yaeyama and the Miyako Groups were most likely derived from recent speciations through vicariance with adjacent regions. Likewise, speciation seems to have occurred in several endemic lineages of the central Ryukyus as a result of vicariance between the northern Amami-southern Tokara islands and the southern Amami-Okinawa islands.

It is obvious that such geographic patterns of relict endemisms and putative speciations do not support hypotheses II and III, and favor hypothesis I, because only the latter can explain numerical dominances of highly relict species in the central Ryukyus. With the recent closures of the Tokara Gap and the Kerama Gap, such faunal characteristics should have been much obscured or completely erased through landbridge dispersals. Distributions of a few species across the Tokara Gap (*Buergeria japonica, Gekko hokouensis, Ateuchosaurus pellopleurus* and *Eumeces marginatus*) appear supportive of the recent land connection of both sides of the gap. However, complete absence of possible cases of recent range extention from the north across this gap makes it more likely that those species actually crossed the gap by rafting under the predominant northeastwardly flowing sea current in this region (Hikida et al. 1992; Ota et al. 1994, 1998). The Pliocene land configurations in hypotheses III do not seem to be the case, either, considering the occurrences of a number of central Ryukyu endemics that most likely emerged through long insular isolations.

Numerical dominance of the species, subspecies and populations in the central and the southern Ryukyus that have hypothetical closest relatives in more southwestern regions appears to support the formation of an early Pleistocene landbridge from the southeastern continent to the Tokara Gap as in hypotheses I and II. However, this also makes it difficult to explain the much higher frequency of highly relict taxa in the central Ryukyus compared to the southern Ryukyus. As was recently assumed by Hikida and Ota (1997), it is likely that the land block of the central Ryukyus remained isolated even during the early Pleistocene when a landbridge connected the southern Ryukyus with Taiwan and southeastern continent. A few lineages showing closest phylogenetic affinities between the southern and the central Ryukyus [e.g. *E. stimpsonii* and *E. marginatus* (see Hikida 1993; Kato et al. 1994), and *Cyclophiops herminae* and *C. semicarinatus* (see above)] may represent over sea dispersals from the former to the latter areas after the submergence of the southern Ryukyu landbridges (Hikida and Ota 1997).

Occurrences of several endemic species and subspecies, including a few relatively relict ones, in the Miyako Group negate the recent submergence of this island group (contra hypotheses I and III), and suggest a relatively early isolation of the Miyako Group from the remaining early Pleistocene southern Ryukyu landbridge postulated above. Judging from their phylogeographical pattern, most amphibians and reptiles in the Yaeyama Group seem to have been isolated from their Taiwanese counterparts more recently, i.e. after the isolation of the Miyako Group. Those species and subspecies shared between the Yaeyama and Miyako Groups, all of which have closest relatives in adjacent regions and thus are not relict, could have dispersed from the Yaeyama Group to the Miyako Group by rafting, presumably when the distance between these regions decreased during the late Pleistocene glaciations (see above). Presence of a favorable current in this region (Nitani 1972) offers circumstantial support to this *ad hoc* assumption.

In conclusion, the phylogeographical patterns of amphibians and reptiles of the Ryukyus, inferred by best use of currently available information/data, obviously negate hypotheses II and III, and modifies hypothesis I as follows: i) Partial submergences of a large Miocene landbridge (extending from eastern China to the main-islands of Japan) formed several separate landmasses including two large islands (super-islands) in the Ryukyu region during the Pliocene — one extending from current western Yaeyama to the northern Miyako islands, and the other from current Kumejima to Amamioshima Islands; ii) in the early Pleistocene (ca 1.5 Ma) a large magnitude of uplifting of the Ryukyu Cordillera base regenerated the landbridge from eastern China, which, however, reached

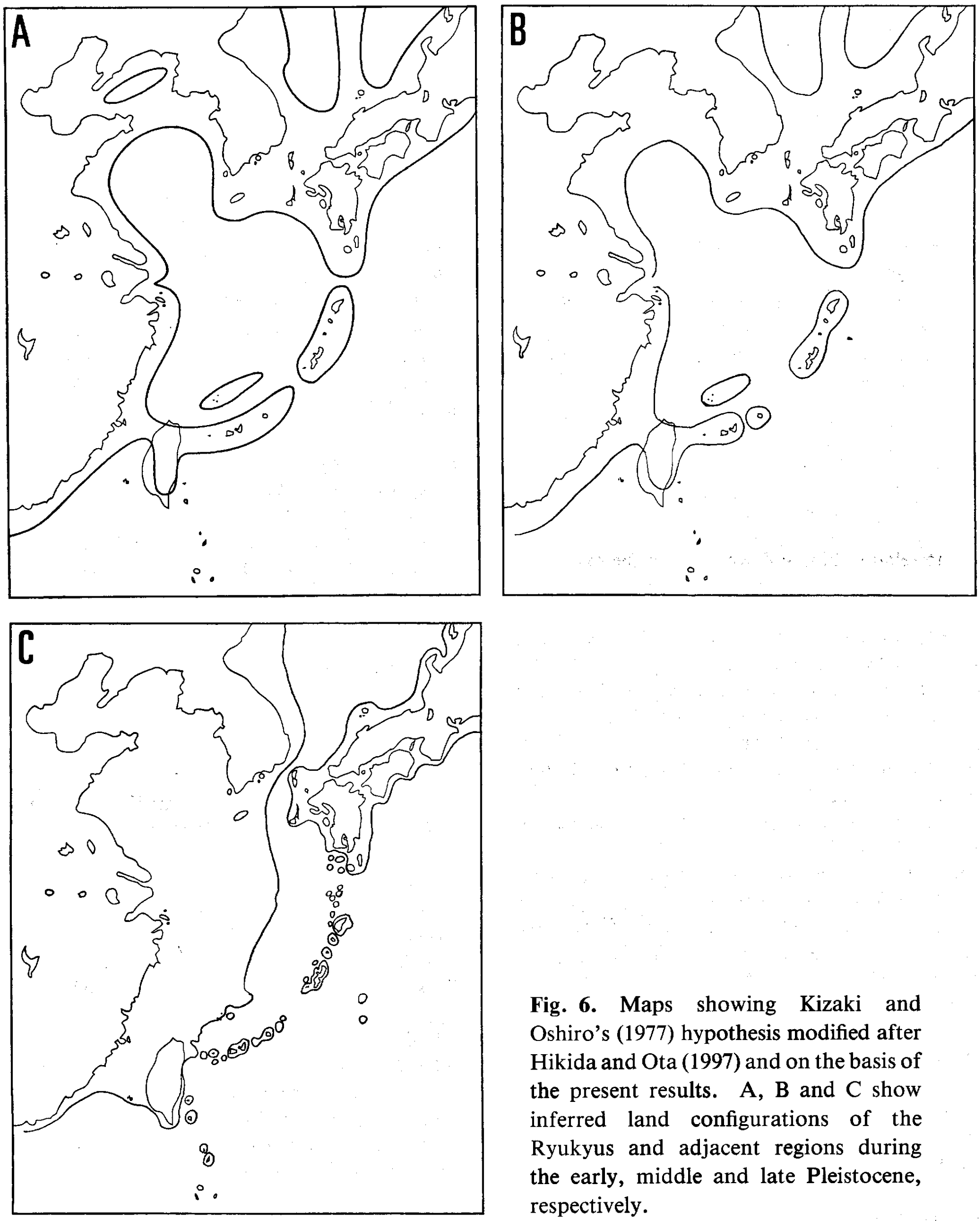

Fig. 6. Maps showing Kizaki and Oshiro's (1977) hypothesis modified after Hikida and Ota (1997) and on the basis of the present results. A, B and C show inferred land configurations of the Ryukyus and adjacent regions during the early, middle and late Pleistocene, respectively.

only to the southern Ryukyu super-island (Fig. 6A); iii) a portion of this landbridge corresponding to the current Miyako Group was isolated from the remainder first (Fig. 6B) and then was that corresponding to the current Yaeyama Group, presumably during the middle Pleistocene; iv) in the late Pleistocene (0.02−0.015 Ma), land areas expanded to form several super-islands as a result of a sea level drop by ca 120 m (Fairbanks 1989; Nakada et al. 1991; Fig. 6C).

This hypothesis should be tested on the basis of additional geological and biological data. Many of the phylogenetic hypotheses tentatively adopted in seeking a general phylogeographical pattern (e.g. those in Tables 1 and 2) actually depend on the general similarity criterion and thus definitely need verification, especially on grounds of parsimony. Validities of the four presumptions defined in the initial part of this review also need verification. Examinations of phylogeographical patterns in other groups of terrestrial animals diversified in the Ryukyus (e.g. land snails) are strongly desired as well.

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