Toward a synthesis of paleontological and neontological information on the terrestrial vertebrates of the Ryukyu Archipelago. I. Systematic and biogeographic review

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Abstract

Paleontological and neontological information relevant to the evolutionary and biogeographical history was reviewed for non-volant terrestrial vertebrate taxa of the Ryukyu Archipelago. This is the first step toward an attempt to integrate paleontological and neontological information on these organisms to address problems on the paleogeography of the Ryukyus. Results demonstrated a substantial advantage of such an integrative approach to the inference of past morphological and geographical changes in a few taxa. On the other hand, the present review elucidated a few essential problems in each of the paleontological and neontological fields that require intensive efforts.

1. Introduction

The Ryukyu Archipelago (sensu Kizaki, 1985: Fig. 1) is an island chain extending between Kyushu of Japan and Taiwan. Most recent geologists and geographers consider that the area corresponding to the current archipelago initially emerged as the eastern margin of Eurasian Continent in no later than the middle Tertiary, and then has been subjected to radical, complicated tectonic movement partially involving volcanism. It is also postulated that such movements, together with occasional eustatic sea level fluctuations, have involved dramatic changes of land configuration in this area (e.g., Kizaki and Oshiro, 1977, 1980; Kimura, 2002).

From the biological viewpoint, the Ryukyu Archipelago is noted for the high ratio of endemic taxa in its biota (Hotta, 2003; Motokawa, 2000; Ota, 2000a,b; Nishida et al., 2003). This is particularly true with non-volant terrestrial vertebrates that, as a whole, are not capable of long distance dispersals across the sea primarily by way of swimming and rafting (Motokawa, 2000; Ota, 2000a). It has also been pointed out that the non-volant terrestrial vertebrate fauna of the Ryukyus exhibits prominent discontinuity in taxonomic composition at the Tokara Gap
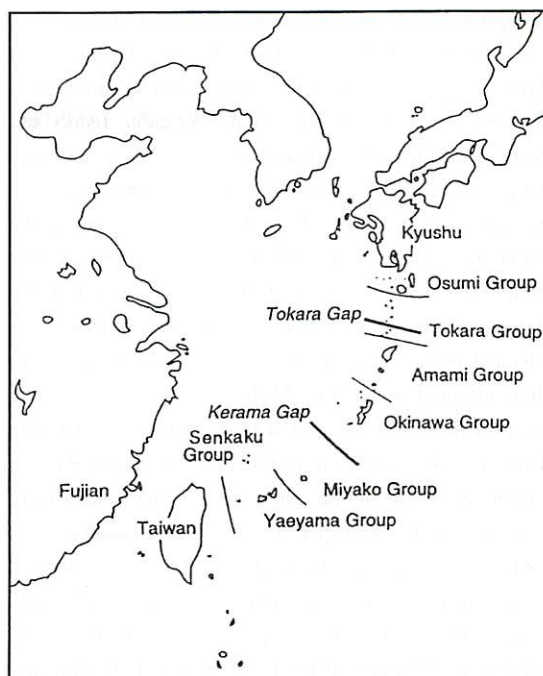

Fig.1. Map of East Asia showing the location of each island group of the Ryukyu Archipelago referred to in the text.

(or Tokara Tectonic Strait, located between Kodakarajima and Akusekijima of the Tokara Group: Fig. 1), and that taxa occurring on the southwestern side of this strait exhibit close affinity with those from the Oriental Faunal Realm (i.e. Taiwan, southeastern continental China, and Southeast Asia) rather than with taxa from the Palaearctic Faunal Realm (i.e., the main islands of Japan, Korea, and eastern continent: e.g., Okada and Koba, 1931; Kuroda, 1931; Tokuda, 1941a). Furthermore, it has been argued that some vertebrate taxa of the archipelago, mostly from the central Ryukyus (an area located between the Tokara Gap and the Kerama Gap: Fig. 1), are in the relict state because of the absence of their close relatives in the adjacent regions (e.g., Tokuda, 1941b, 1969; Ota, 1998).

Temporal changes in configuration of a particular land area, involving its isolation from the continent through partial subsidence, division into a number of smaller islands, and subsequent landbridge connection, should play a crucial role in the formation of its fauna, because these geographical events may lead each taxon thereon to allopatric differentiation, range extension, and extinction. It is, therefore, not surprising that a number of geologists, attempting to infer the chronological changes of land configuration in some parts or whole of the Ryukyus, have paid a serious attention to geographical arrangement and chronological changes of terrestrial fauna in this region. Hanzawa (1935), for example, postulated submergence and recent up-lifting of the Miyako Group chiefly on the basis of the absence of the venomous *Trimeresurus* snakes in this island group (note: *Trimeresurus* is present in the neighboring Yaeyama and Okinawa Groups). Kizaki and Oshiro (1977, 1980), on the other hand, assumed an Early Pleistocene, peninsular-shaped landbridge (EPLB) that extended from southeastern continent to the Tokara Gap. They, although suspecting Middle Tertiary origins for a few taxa that were considered to be in highly relict state (Tokuda, 1941b, 1969), argued that most terrestrial Ryukyu vertebrates on the southwestern side of the Tokara Gap, were originated from dispersals by using this landbridge.

More recently, chiefly on the basis of chronological changes in fossil foraminifera from the Okinawa Trough, Ujiié and his colleagues (e.g., Ujiié, 1990; Ujiié and Nakamura, 1996) argued for the formation of an additional landbridge during the Late Pleistocene Glacial Maxima (LPGM: ca. 0.018 million year ago [Mya]) that extended from southeastern continent, passed trough the northern vicinity of the Yaeyama and Miyako Groups, and reached to the Okinawa and Amami Groups. Primarily on the basis

of fault arrangements, sediment properties, and geomorphology of the Tokara and Kerama Gap bottoms, Kimura (1996 a, b) went even further to hypothesize an involvement of the whole Ryukyus into the formation of a more extensive landbridge that ranged from the southeastern continent and Taiwan to Kyushu during LPGM. All these authors emphasized the advantage of the hypotheses in explaining the apparently recent migration of the Minatogawa man and the wild boar into the Ryukyus (e.g., Hasegawa, 1980: also see below).

However, based on data available at that date, Hikida and Ota (1997) and Ota (1998) claimed for a serious discrepancy between landbridge formation during the LPGM as postulated by those authors and the phylogeographical pattern illustrated by most extant reptiles and amphibians of the Ryukyus. They also doubted the validity of the EPLB because of a predominance of relict taxa particularly in the central Ryukyus. They, however, did not provide any concrete values for estimated divergence time of taxa in question. Thus, large part of their argument seriously needs verification based on additional data that accompany reliable chronological information.

Ota (2002) discussed the advantages and disadvantages of neontological approaches to the Ryukyu paleogeography and emphasized the importance of gathering and evaluating all relevant data available irrespective of scientific disciplines. Indeed, the effort has been made to some extent in order to integrate data from neontological and geological studies (e.g., Kizaki and Oshiro, 1977, 1980; Ota, 1998). However, very little has been attempted to formulate or test paleogeographical hypotheses of the Ryukyus by integrating pertinent data from paleontological and other approaches.

As the first step toward such an integration, I here review paleontological and neontological information on the evolutionary and biogeographical history of each of non-volant terrestrial vertebrate taxa in the Ryukyus.

2. Review of available information on each fossil taxon with pertinent neontological data

1) Amphibia
① *Rana holsti* (Anura)

Fossils of this frog species were reported from the Late Pleistocene fissure filling deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Also, Hasegawa and Nohara (1978) tentatively identified a few skeletal

remains from the Late Pleistocene or Holocene fissure deposit at Ishisukuyama, Ishigakijima, as this species.

Current range of this large forest-dwelling species is confined to the northern part of Okinawajima and Tokashikijima of the Okinawa Group (Maeda and Matsui, 1999). The fossil record from the southern part of Okinawajima indicates much broader distribution of this species on this island in the past. It explains the process of its migration into Tokashikijima, which is located southwest to Okinawajima.

Identification of the southern Ryukyu materials needs careful verification. Phylogenetically, *Rana holsti* seems to be closest to *R. subaspera* from the Amami Group, and they constitute a clade much distinct from the other *Rana* species (Matsui and Utsunomiya, 1983).

② *Rana ishikawae* (Anura)

Fossils of this frog species are relatively abundant in the Late Pleistocene fissure filling deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Otsuka (2002) also referred to fossils from the lowest Pleistocene stratum at Imadomari-Akagimata site, the northern part of Okinawajima, as being similar to *Rana ishikawae*.

Current distribution of this large stream-dwelling frog is confined to the northern part of Okinawajima and several mountains of Amamioshima, the central Ryukyus (Maeda and Matsui, 1999). Thus, the Late Pleistocene fossil record from the southern part of Okinawajima indicates a much broader distribution of this frog and its rapid reduction on this island during or after LPGM.

A relatively well-preserved fossil specimen, identified to *Rana ishikawae* on the basis of skeletal shape and proportions, was discovered from the Early Pleistocene deposit (1.3 ± 0.2 Mya) on Tanegashima of the Osumi Group, northern Ryukyus (Otsuka and Kuwayama, 2000). Otsuka and Kuwayama (2000) and Otsuka (2002) assumed that this specimen was derived from a landbridge dispersal of *R. ishikawae* from the central to the northern Ryukyus across current Tokara Tectonic Strait area before the initiation of the strait in the Late Pliocene or Early Pleistocene.

There are a few prominent morphological and chromosomal differences between the two extant populations of *R. ishikawae*, suggesting that each of them should be recognized as a distinct taxon (Maeda and Matsui, 1999).

③ *Rana limnocharis* (Anura)

Fossils of this frog species were found from the Late Pleistocene fissure filling deposits at Minatogawa, southern

part of Okinawajima (Hasegawa, 1980), and from the Holocene deposit at Ishisukuyama, Ishigakijima (Hasegawa and Nohara, 1978). This frog is currently broadly distributed from tropical to temperate East Asia, including the southern half of the main islands of Japan, the central and southern Ryukyus, Taiwan, and most area of Southeast Asia (Maeda and Matsui, 1999). On most islands of the central and southern Ryukyus, this is the commonest frog in open lowland habitats (Ota, unpublished data).

Recent biochemical genetic analyses of geographic variation revealed that *Rana limnochris* in the current sense actually refers to a composite of several morphologically poorly diverged but genetically distinct species (Toda et al., 1998a). With respect to the East Asian assemblage, populations from southern Ryukyus are distinct from the others (i.e., those from the main islands of Japan, central Ryukyus, Taiwan, and eastern continental China), whereas variation in the latter is quite meager (Toda et al., 1997). Such a pattern of variation is interpreted as reflecting relatively long isolation and speciation of the southern Ryukyu populations, and much more recent dispersals of, or very frequent gene flows among, the remaining populations (Toda et al., 1997, 1998b; Toda, 1999).

Based on these results, as well as its slightly larger body and relatively longer hind limbs, Maeda and Matsui (1999) referred to the southern Ryukyu population as a distinct undescribed species, *Rana* sp. (but also see Sumida et al. [2002] for a different view). It is almost certain that the remains from Ishisukuyama reported by Hasegawa and Nohara (1978) actually belong to this species rather than *R. limnocharis*.

Absence of distinct genetic differentiation between the central Ryukyu *Rana limnocharis* and conspecific Taiwanese/continental populations may suggest a recent artificial origin of the former (Toda et al., 1997). However, the discovery of the Late Pleistocene fossils of this species from Okinawajima (Hasegawa, 1980) negates this possibility.

④ *Rana namiyei* (Anura)

Fossils of this frog species were reported from the Late Pleistocene fissure filling deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Also, Hasegawa and Nohara (1978) identified a few remains from the fissure deposit at Ishisukuyama, Ishigakijima, as this species. The current distribution of this large stream-dwelling frog is confined to the northern part of Okinawajima (Maeda and Matsui, 1999). The fossil record from the southern part of Okinawajima indicates a much

broader distribution of this species on this island in the past.

Recent chromosomal and morphological studies suggested a close phylogenetic affinity of *Rana namiyei* with the Taiwanese population of *R. kuhlii* (Kuramoto, 1984; Emerson and Berrigan, 1993). It is therefore particularly desired to reexamine the identity of the fossils from Ishisukuyama by comparing them with the latter.

⑤ *Rana narina* sensu lato (Anura)

Based on morphological and allozyme analyses, Matsui (1994) recognized four species within *Rana narina*. Whereas restricting an application of the original name to the Okinawajima population, he described the Amami Group populations, and the large and small forms of the Yaeyama Group as *R. amamiensis*, and *R. supranarina* and *R. utsunomiyaorum*, respectively. To explain the phylogeographical pattern in this species complex, Matsui (1994) hypothesized two times of its migrations from Taiwan to the southern Ryukyus, the first one giving rise to *R. utsunomiyaorum*, and the second one to *R. supranarina*. The process for emergences of the two central Ryukyu species remains uncertain.

Fossils of *Rana narina* sensu lato were found in large quantity from the Late Pleistocene fissure deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Also, several recent remains of *R. narina* sensu lato were found from Ishisukuyama, Ishigakijima. Considering aforementioned taxonomic changes in the last decade, it is highly likely that the specimens from Minatogawa represent *R. narina* sensu stricto, and the specimens from Ishisukuyama either *R. supranarina* or *R. utsunomiyaorum*, or both.

On Okinawajima, current distribution of *Rana narina* is confined to the northern part (Maeda and Matsui, 1999). The fossil record from the southern part of Okinawajima thus indicates its much broader distribution on this island in the past.

⑥ *Rana nigromaculata* (Anura)

Hasegawa and Nohara (1978) tentatively identified a few frog remains from the Late Pleistocene or Holocene fissure filling deposit of Ishisukuyama, Ishigakijima, as *Rana nigromaculata*. They stated that, although this species does not occur in the Ryukyus at present, it may have been distributed in the whole archipelago as a result of migration from Honshu, the main-island of Japan.

Since then, however, no additional evidence has been obtained for the past occurrence of this species or its relatives (i.e., *Rana porosa*, *R. plancyi*, and *R. fukienensis*:

see Sumida et al. [2000] and publications cited therein) in the Ryukyu Archipelago (e.g., Oshiro, 2001, 2002; Otsuka, 2002). Because *R. fukienensis*, a close relative of *R. nigromaculata*, occurs in Taiwan and southeastern continental China (Zhao and Adler, 1993), it is probable that the fossils from Ishisukuyama are actually allied to this species rather than to *R. nigromaculata*. If this is the case, biogeographical significance of the Ishisukuyama specimens should be fundamentally different from that assumed by Hasegawa and Nohara (1978: see above). Detailed reinvestigation of the materials is thus much desired by comparing them not only with *R. nigromaculata*, but also with all of its relatives including *R. fukienensis*.

⑦ *Rana okinavana* (Anura)

Fossils of this frog species were reported from the Late Pleistocene fissure filling deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Also, Hasegawa and Nohara (1978) identified several skeletal remains from the Late Pleistocene or Holocene fissure deposit at Ishisukuyama, Ishigakijima, as this species.

The current range of this small forest-dwelling species is confined to Kumejima, the northern part of Okinawajima, Tokunoshima, and Amamioshima of the central Ryukyus (Maeda and Matsui, 1999). The fossil record from the southern part of Okinawajima indicates a much broader distribution of this species and its rapid reduction on this island during or after LPGM. This also explains the process of migration of *R. okinavana* into Kumejima, which is located southwest to Okinawajima. The southern Ryukyu materials need careful taxonomic reevaluation.

Phylogenetically, *Rana okinavana* is closely related to the clade consisting of *R. tsushimensis* from Tsushima, Japan, and *R. sauteri* from Taiwan (Tanaka-Ueno et al., 1998). Considering the geographical proximity of the Yaeyama Group with Taiwan and the close biogeographical relationships assumed for the two regions (e.g., Ota, 1998), comparisons of the Ishisukuyama materials with skeletal specimens of *R. sauteri* should be particularly crucial.

While demonstrating a remarkable genetic divergence between the Okinawajima and Amamioshima populations, Tanaka et al. (1996) also clarified a great deal of differentiation of *Rana okinavana* as a whole from the other brown frogs, including the closest *R. tsushimensis* and *R. sauteri* (Tanaka-Ueno et al., 1998). They inferred the date of migration of ancestral *R. okinavana* into the central Ryukyus as some time in the Pliocene.

⑧ *Rana rugosa* (Anura)

Fossils identified to this species occur in large quantity in the Late Pleistocene fissure filling deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Otsuka (2002) also referred to fossils from the lowest Pleistocene stratum at Imadomari-Akagimata site in the northern part of Okinawajima as being similar to *Rana rugosa*.

Rana rugosa is usually regarded as a typical Palearctic element, and is currently broadly distributed in the main islands of Japan (including several adjacent islets), Korean peninsula, and eastern continental China (Maeda and Matsui, 1999; Zhao and Adler, 1993). Once introduced, however, this frog may be successful under the tropical insular environment (see the case of feral populations in Hawaii: Hunsaker and Breese, 1967). Presence of this species in the Late (and probably Early: Otsuka, 2002) Pleistocene Okinawajima is thus puzzling in both its origin and its fate. Further comparative studies are desired to verify the taxonomic status of the specimens from Minatogawa and Imadomari-Akagimata.

⑨ *Rana tagoi* (Anura)

A few specimens identified to *Rana tagoi* were obtained from the Late Pleistocene fissure filling deposits at Minatogawa, southern part of Okinawajima, and Ishisukuyama, Ishigakijima (Hasegawa and Nohara, 1978; Hasegawa, 1980). The current distribution of *R. tagoi* is confined to the main islands of Japan and a few adjacent islands with Yakushima of the northern Ryukyus being the southernmost extremity (Maeda and Matsui, 1999). As in the case of *R. rugosa* (see above), occurrence of *R. tagoi* in the Late Pleistocene Okinawajima and Ishigakijima is quite puzzling and obviously requires an *ad hoc* explanatory hypothesis. However, because some other brown frogs that might be confused with *R. tagoi* occur in the Oriental portion of the East Asian islands (e.g., *R. sauteri* from Taiwan, *R. longicurus* from Taiwan and southeastern continental China, and *R. okinavana* from the central Ryukyus) (Zhao and Adler, 1993; Maeda and Matsui, 1999), careful verification for taxonomic allocations of the Minatogawa and Ishisukuyama materials is much desired by comparing them with those Oriental brown frogs in detail before determining further.

⑩ *Buergeria japonica* (Anura)

A fossil of this frog species was found from the Late Pleistocene or Holocene fissure filling deposit at Ishisukuyama, Ishigakijima. *Buergeria japonica* is currently broadly distributed in the subtropical East Asian islands, from southern Taiwan to Kuchinoshima of the

Tokara Group, except for the Miyako Group (Toyama and Ota, 1991). Nishioka et al. (1987) demonstrated a substantial genetic differentiation between the Okinawajima and Amamioshima populations, and very poor divergence between the latter and the population of Nakanoshima, an island located north of the Tokara Tectonic Strait. Thus, Hikida et al. (1992) suspected a recent oversea dispersal of this frog to north across the strait.

⑪ *Rhacophorus viridis* (Anura)

Fossils of this frog species were reported from the Late Pleistocene fissure filling deposit at Minatogawa, southern part of Okinawajima (Hasegawa, 1980). Current distribution of this species includes almost whole of Okinawajima, Kumejima and Iheyajima of the Okinawa Group (nominotypical subspecies), and Tokunoshima, Ukejima, Yorojima, Kakeromajima and Amamioshima of the Amami Group (*Rhacophorus viridis amamiensis*: Toyama and Ota, 1991). It is assumed on the basis of morphological and acoustic similarity that this species is most closely related to *R. schlegeli* of the main islands of Japan (Maeda and Matsui, 1999).

⑫ *Microhyla ornata* (Anura)

Fossils of this frog species have been found from the Late Pleistocene or Holocene deposits in fissures at Minatogawa of the southern part of Okinawa (Hasegawa, 1980), and Pinza-Abu Cave on Miyakojima (Nokariya and Hasegawa, 1985). Otsuka (2002) also referred to fossils from the lowest Pleistocene stratum at Imadomari-Akagimata site, the northern part of Okinawajima, as being similar to *Microhyla ornata*.

This species is currently broadly distributed in the subtropical East Asian islands, from southern Taiwan to Amamioshima of the Amami Group (Toyama and Ota, 1991). Kuramoto (1976, 1987) reported substantial differentiation in acoustic characters among the central Ryukyu, southern Ryukyu, and Taiwanese populations of this frog.

⑬ *Bufo gargarizans miyakonis* (Anura)

Fossils of this toad species have been found from the Late Pleistocene deposit of Pinza-Abu Cave on Miyakojima, Miyako Group (Nokariya and Hasegawa, 1985). Until then, the current toad population on Miyakojima was regarded as a consequence of recent artificial introduction from the eastern part of the Eurasian Continent (e.g., Inger, 1947), but its native status is now unquestionable.

There are neither other native populations nor any fossil

record of the genus *Bufo* in the southern or central Ryukyus. Results of morphological and allozyme analyses indicated that *Bufo gargarizans miyakonis* is phylogenetically closest to the continental populations, *B. g. gargarizans*, rather than the Taiwanese *Bufo, B. bankorensis* (Matsui, 1984; Nishioka et al., 1990).

⑭ *Cynops ensicauda* (Urodela)

Fossils of this newt species have been found in large quantity from the Late Pleistocene and Holocene fissure deposits at Minatogawa, southern part of Okinawajima. Currently, *Cynops ensicauda* occurs on Okinawajima and some other islands of the Okinawa Group, and Amamioshima and a few other islands of the Amami Group (Toyama and Ota, 1991).

Based on allozyme data, Hayashi and Matsui (1988) estimated a fairly large genetic divergence between *Cynops ensicauda* and its putative sister species, *C. pyrrhogaster*, from the main islands of Japan. They also demonstrated a prominent genetic difference between the Okinawa Group and Amami Group populations. Interestingly, application of the electrophoretic clock calibrated from data for the North American salamanders (Maxon and Maxon, 1979) yielded estimates of isolation periods between *C. ensicauda* and *C. pyrrhogaster*, and between the Okinawa and Amami Group *C. ensicauda* that, respectively, corresponded grossly to the geologically estimated dates of the formation of the Tokara Tectonic Strait (Late Miocene: 8 Mya), and of final isolation of the Okinawa and Amami Groups (Early–Middle Pleistocene: 1.5–1 Mya) (Kizaki and Oshiro, 1977, 1980).

2) Reptilia

① *Geoemyda japonica* (Testudines)

The central Ryukyu populations of the turtle genus *Geoemyda* had long been regarded as a subspecies of *G. spengleri* from southern China and northern Indochina until Yasukawa et al. (1992) gave a full species status to it on the basis of a number of external and skeletal characters. Fossils of *G. japonica* have been reported from the Late Pleistocene fissure filling deposits on Okinawajima (Futenma-gu in the central part of the island: Oshiro, 1994) and cave deposits on Iejima (Hasegawa, 1980) and Kumejima (Takahashi et al., 2003) as well as archaeological sites on Okinawajima (Seifa in the southern part of the island: Kaneko, 1999). Recently, fossils of this turtle were reported from a stratum dated as Early Pleistocene (1.5±0.3 Mya) at an Imadomari-Akagimata site in the northern part of Okinawajima (Takahashi et al.,

2003).

Current distribution of *G. japonica* is confined to the northern forested area of Okinawajima, and Tokashikijima and Kumejima (Yasukawa et al., 1992), suggesting a recent disappearance of its populations from the southern and central parts of Okinawajima and Iejima. Much isolated occurrence of its sister taxon (*G. spengleri*: Yasukawa et al., 1992) is interpreted as reflecting the highly relict status of *G. japonica* (see Yasukawa and Ota, 1999).

② *Cuora* sp. (Testudines)

Fossils of the box turtle genus *Cuora* (sensu lato, including *Cistoclemmys*: Honda et al., 2002a) have been found from the Late Pleistocene fissure filling deposits in the northern (Bise) and southern parts of Okinawajima (Kurukubaru: Otsuka, 2002) as well as on Kumejima (Takahashi et al., 2003). Otsuka (2002) noted that the reconstructed specimen from the northern part measured 25 cm in carapace length, a value much larger than the corresponding value in *Cuora flavomarginata evelynae* from southern Ryukyus (<19 cm: Ota, 1995), the only extant representative of the genus from the Ryukyus.

The range of the genus is currently confined to the southern Ryukyus, Taiwan, southeastern continent, and Southeast Asia (Iverson, 1992). Phylogenetic analyses of mitochondrial (mt) DNA sequence data strongly suggest a poor divergence between the Taiwanese (*C. f. flavomarginata*) and the southern Ryukyu populations of this species (*C. f. evelynae*) while showing relatively large divergence between *C. flavomarginata* and other congeneric species (Honda et al., 2002a). Furthermore, the analyses indicated nonmonophyly of the genus *Cistoclemmys* (as consisting of *Cuora flavomarginata* and *C. galbinifrons*), although its monophyly had been well supported by cladistic analysis of morphological data (Yasukawa et al., 2001).

Judging from the fossil record, however, it is almost certain that *Cuora* also occurred in more northeastern area including the central part of Honshu, Japan, until at least as late as Middle Pleistocene (Yasukawa and Hirayama, 2001).

③ *Mauremys mutica* (Testudines)

Some turtle fossils from the southern part of Okinawajima (Minatogawa: Hasegawa, 1980), and Miyakojima (Pinza-Abu: Manabe and Hasegawa, 1985) and Ishigakijima (Ishisukuyama: Hasegawa and Nohara, 1978), all from Late Pleistocene or Holocene fissure or cave deposits, were tentatively assigned to *Mauremys mutica* (Oshiro, 2001). However, because of rather

fragmented states of all these fossils, their identifications are not sufficiently convincing (Takahashi et al., 2003).

Natural populations of this species are currently known from the southern Ryukyus, Taiwan, southeastern continental China, and northern Vietnam (Iverson, 1992). Of these, the southern Ryukyu populations are regarded as a distinct subspecies, *Mauremys mutica kami* (Yasukawa et al., 1996; Yasukawa and Ota, 1999). The result of recent molecular phylogenetic analyses of this and other congeneric species suggests that *M. mutica* represents a primitive stock of the genus (Honda et al., 2002b).

④ *Manouria oyamai* (Testudines)

Fossils of this extinct land turtle have been found from Late Pleistocene fissure and cave deposits in the southern (Kamikurukubaru), central (Hinigusuku and Futenma-gu) and northern parts of Okinawajima (Awa and Bise) as well as on Miyakojima (Amaga-do), Iejima (Gohezu) and Tokunoshima (Isen: Oshiro, 1994; Otsuka, 2002; Takahashi et al., 2003). The two extant species of the genus, *Manouria emys* and *M. impressa*, are distributed in the southern part of continental China, Indochina, Malay Peninsula, Sumatra, and Borneo (Iverson, 1992).

⑤ Trionychidae sp. (Testudines)

Oshiro and Hasegawa (1998) reported a piece of pleural plate of *Trionyx* sensu lato (see Meylan [1987] for strict definition of the genus) found from Late Tertiary stratum on Ogamijima, Miyako Group. Although one trionychid species, *Pelodiscus sinensis*, currently occurs on several islands of the Ryukyus, all these populations are of artificial origin (Sato and Ota, 1999). Therefore, their close affinity with the fossil species is unlikely.

⑥ *Dinodon semicarinatum* (Squamata)

Fossils identified as *Dinodon semicarinatum* were reported from Early Pleistocene strata at Imadomari-Akagimata site in the northern part of Okinawajima (Otsuka, 2002). Currently, this species occurs on almost all islands of the central Ryukyu (Toyama and Ota, 1991), and a recent genetic study suggested a much closer affinity of the Amamioshima and the Tokunoshima populations compared to the Okinawajima population (Kumazawa et al., 1998). The relationship of *D. semicarinatum* with other congeneric species is yet to be investigated.

Manabe and Hasegawa (1985) listed *Dinodon* sp. among fossil reptiles discovered from the Late Pleistocene deposit of Pinza-Abu Cave on Miyakojima. However, its specific identification and phylogenetic position still remain to be studied.

⑦ *Trimeresurus* spp. (Squamata)

Fossils of this venomous snake group have been found from Late Pleistocene fissure and cave deposits in the southern part of Okinawajima (Minatogawa) as well as Iejima and Miyakojima (Oshiro, 2001). Recently, fossils of *Trimeresurus* sp. were reported also from a stratum dated as Early Pleistocene (1.5 ± 0.3 Mya) at Imadomari-Akagimata site in the northern part of Okinawajima (Otsuka, 2002).

At present, representatives of the genus *Trimeresurus* occur in the Okinawa and Amami Groups (*T. flavoviridis* and *T. okinavensis*), southern islands of the Tokara Group (*T. tokarensis*), and the Yaeyama Group (*T. elegans*: Toyama and Ota, 1991). It should be noted that, although a representative of the genus obviously occurred on Miyakojima as late as LPGM (Manabe and Hasegawa, 1985), none of its descendants survive on this or adjacent islands of the Miyako Group. It is also noteworthy that Manabe and Hasegawa (1985) tentatively identified fossils from Pinza-Abu as *Trimeresurus flavoviridis* from the central Ryukyu, not *T. elegans* from the Yaeyama Group. Although they did not clarify the reason of such an identification, it is probable that they considered the size of those fossils, because *T. flavoviridis* is distinctly larger than the other extant congeners of the Ryukyus and the Pinza-Abu fossils also appear large in size (Manabe and Hasegawa, 1985).

Recent biochemical and molecular studies on the East Asian *Trimeresurus*, demonstrated the presence of substantial divergence between the central Ryukyu (*T. flavoviridis* -*T. tokarensis*) clade and the southern Ryukyu-Taiwan (*T. elegans* - *T. mucrosuqmatus*) clade while confirming a close affinity of *T. flavoviridis* and *T. tokarensis* and completely distant phylogenetic allocation of *T. okinavensis* (Toda et al., 1999; Tu et al., 2000). Phylogenetic analyses of mtDNA sequence data by Tu et al. (2000) also yielded results that suggest a sister group relationship of the central Ryukyu clade with a continental species, *T. jerdonii*, rather than with the southern Ryukyu-Taiwan clade. Tu et al. (2000), therefore, hypothesized independent ancestral migrations into the Ryukyus by the two clades, i.e., first by the central Ryukyu clade, and then by the southern Ryukyu-Taiwan clade after formation of the Kerama Gap.

Results of both Toda et al.'s (1999) and Tu et al.'s (2000) investigations, as well as those of many other neontological studies dealing with historical aspects of the formation of current diversity in the Ryukyu *Trimeresurus* (e.g., Takara, 1962), altogether emphasize role of the Kerama Gap as a

long-standing isolation barrier. The taxonomic allocation of the Pinza-Abu fossils is, therefore, quite crucial in that it may belong to *T. flavoviridis*, a species whose distribution is otherwise confined to the northeastern side of the Kerama Gap. Because body size of insular snake populations occasionally increases dramatically in a short period (a phenomenon often referred to as the "insular gigantism": see Boback [2003] for review), further detailed investigations of the Pinza-Abu specimens are desired to confirm their taxonomic relationships.

⑧ *Scincella boettgeri* (Squamata)

Fossils of *Scincella boettgeri* were reported from the fissure filling deposit at Ishisukuyama of Ishigakijima, the Yaeyama Group. Currently, *S. boettgeri* occurs on almost all islands of the southern Ryukyus (Toyama and Ota, 1991). Based on the morphological comparisons, Chen et al. (2001) considered this species to be closely related to *S. formosanus* from Taiwan.

⑨ *Japalura* spp. (Squamata)

Fossils of *Japalura polygonata* have been found from Late Pleistocene or Holocene fissure filling deposits and cave deposits on Okinawajima and Iejima of the Okinawa Group, Miyakojima of the Miyako Group, and Ishigakijima of the Yaeyama Group (Oshiro, 2001, 2002). Manabe and Hasegawa (1985) identified a large number of fossils from Pinza-Abu Cave deposits as *J. p. polygomata*, a subspecies confined to the central Ryukyus at present, rather than *J. p. ishigakiensis* which currently occurs on Miyakojima and other southern Ryukyu islands (Ota, 1991). In the Pinza-Abu fossil assemblage, Manabe and Hasegawa (1985) also recognized another species (*J.* sp.) that differed from *J. p. polygomata* in shape and arrangement of teeth.

In the Ryukyu Archipelago, two subspecies, *Japalura polygonata polygonata* from the central Ryukyus and *J. p. ishigakiensis* from the northern Ryukyus, are currently distributed, and the other subspecies, *J. p. xanthostoma*, occurs in northern Taiwan (Ota, 1991). Four additional species of the genus, morphologically closely resembling *J. polygonata*, occur in Taiwan, but the genus is completely absent in the eastern part of the continent (Ota et al., 1998). Therefore, detailed comparisons with these four Taiwanese species may be effective in determining the taxonomic status of *J.* sp. from Pinza-Abu.

⑩ *Takydromus smaragdinus* (Squamata)

Manabe and Hasegawa (1985) tentatively identified a dentary bone excavated from the Late Pleistocene Pinza-Abu (Miyakojima) deposit as *Takydromus smaragdinus*. They also noted the possibility of its allocation to *T. dorsalis*.

A population of the genus *Takydromus* in the Miyako Group had long been believed to be the southernmost representative of *T. smaragdinus* (a species otherwise confined to the central Ryukyu) until Takeda and Ota (1996) clarified its taxonomic status as an independent endemic species, *T. toyamai*. Moreover, while being phylogenetically distant from *T. smaragdinus* from the central Ryukyus or *T. dorsalis* from the Yaeyama Group, recent molecular studies revealed that *T. toyamai* is actually the closest taxon to the clade consisting of *T. stejnegeri* from Taiwan and *T. septentrionalis* from eastern continent (Lin et al., 2002; Ota et al., 2002). Lin et al. (2002) and Ota et al. (2002) also assumed a crucial role of the Kerama Gap in the formation of current phylogeographical arrangement of *Takydromus* lizards in the Ryukyus. Therefore, as in the case of *Trimeresurus* pit vipers mentioned above, it is essential to verify the identification of the Pinza-Abu fossil by Manabe and Hasegawa (1985) to discuss its biogeographical significance.

3) Aves

① *Gallirallus okinawae* (Gruiformes)

Fossils of this flightless rail, including those of young individuals, have been found from filling deposits of fissures in the central and southern parts of Okinawajima that had most likely been formed during the Late Pleistocene. Because the extant population of this species is confined to the northern part of the island, such an arrangement of the fossil sites obviously indicate occurrences of substantial reduction of its range after Late Pleistocene (Matsuoka, 2000). Matsuoka (op. cit.) assumed that *Gallirallus okinawae* was diverged from an ancestor common to *G. torquatus* (a volant species currently occurring in the Philippines, New Guinea, and their vicinity) just prior to Late Pleistocene.

② *Gallirallus* sp. (Gruiformes)

A few fossils of flightless rails found from Late Pleistocene deposits of Pinza-Abu Cave on Miyakojima were tentatively identified as *G. okinavana* (Ono and Hasegawa, 1985; Oshiro, 2001). However, Matsuoka (2000) recently reexamined the specimens and suggested that they represent an undescribed flightless species of the genus *Gallirallus*. No extant species of flightless rails are known from Miyakojima or other parts of the southern Ryukyus. The phylogenetic position of this fossil species remains to be determined.

③ *Grus* sp. (Gruiformes)

Besides the fossil remains of the flightless rail, those of a small-sized crane with poorly developed wings have also been found from Late Pleistocene deposits of Pinza-Abu Cave (Ono and Hasegawa, 1985). Matsuoka (2000) identified them as an undescribed flightless form of the genus *Grus*. There are no extant flightless cranes on Miyakojima or other parts of the Ryukyu Archipelago. Phylogenetic position of this fossil species is yet to be determined.

4) Mammalia
① *Pentalagus furnessi* (Lagomorpha)

Fossils of this distinct rabbit species, found only from filling deposits of the Ryukyu limestone fissures on Tokunoshima of the Amami Group, are likely to be dated back to no earlier than the Late Pleistocene (Tomida and Otsuka, 1993). Otsuka (2002) stated that fossils of its possible ancestral form, *Pliopentalagus* (see Tomida and Otsuka, 1993), occur in large number in the Late Pliocene stratum around the lower stream area of Yang-Tsu River, eastern continental China.

Yamada et al. (2002) conducted phylogenetic analyses using a partial mtDNA sequence and suspected that this taxon had diverged from lineages leading to other extant taxa in the Middle Miocene.

② *Rattus legata* (Rodentia)

This rat taxon was often treated as a species of the monotypic genus, *Diplothrix*. However, Suzuki et al. (2000) demonstrated its taxonomic placement within the genus *Rattus* based on sequence analyses of mtDNA and nuclear DNA (nDNA).

Fossils of this species have been found from filling deposits of the Ryukyu limestone fissures and cave deposits of no earlier than the Late Pleistocene on Tokunoshima and Kumejima as well as in the southern part of Okinawajima (Minatogawa, Gusigami-son: Takai and Hasegawa, 1971; Tomida and Otsuka, 1993; Oshiro and Nohara, 2000). Prehistoric (Holocene) remains of this rat were also reported from an archaeological site of Seifa in the southern part of Okinawajima (Kaneko, 1999). Besides these remains, a large number of fossils of this species was excavated from the Late Pleistocene cave deposits on Miyakojima, southern Ruykyus (Hasegawa, 1985). Otsuka (2002) reported a discovery of an extinct murine rodent of the genus *Leopoldamys* from Early Pleistocene stratum at the Imadomari-Akagimata site, northern part of Okinawajima. However, recent reinvestigation of the fossil specimen (first upper molar tooth) revealed its closer affinity with *Rattus legata* rather than *Leopoldamys* spp. (H. Otsuka, personal communication).

Current distribution of *Rattus legata* is confined to the northern forested area of Okinawajima, Tokunoshima, and Amamioshima (i.e., central Ryukyus), and this suggests a recent disappearance of its populations on Miyakojima and Kumejima as well as in the southern part of Okinawajima. Suzuki et al. (2000) estimated its divergence time from other *Rattus* species as 3–4 Mya, assuming the divergence of *Rattus* from its sister taxon, *Mus*, to be 12–14 Mya (Jacobs and Downs, 1994).

③ *Tokudaia osimensis* sensu lato (Rodentia)

Fossils, identified to this species complex (see below), have been found from the Late Pleistocene deposits on Tokunoshima and Iejima as well as Minatogawa in the southern part of Okinawajima (Takai and Hasegawa, 1971; Tomida and Otsuka, 1993; Oshiro and Nohara, 2000). Like *Rattus legata*, the current distribution of *Tokudaia osimensis* sensu lato is confined to the northern forested area of Okinawajima, Tokunoshima, and Amamioshima. This suggests a recent disappearance of its populations on Iejima and in the southern part of Okinawajima.

Recent morphological, chromosomal, and mtDNA studies revealed that *Tokudaia* populations from these three islands are much diverged, each deserving a full species status (i.e., Amamioshima population as *T. osimensis* sensu stricto, Okinawajima population as *T. muenninki*, and Tokunoshima population as an undescribed species of the genus: Tsuchiya et al., 1989; Suzuki et al., 1999; Kaneko, 2001). Because the above paleontological works did not consider such a taxonomic heterogeneity within *T. osimensis* sensu lato, re-identification of the fossil materials reported therein are strongly desired.

Suzuki et al. (1999) demonstrated that the mtDNA and nDNA divergences between the Amamioshima and Tokunoshima populations of *Tokudaia osimensis* sensu lato are comparable to those between related full species within the genus *Mus* or *Rattus*. Based on this result, they suspected that the two island populations have been reproductively isolated from each other for several million years.

④ *Microtus* spp. (Rodentia)

Many fossil teeth of microtine voles were found from the Late Peistocene deposits of Pinza-Abu Cave on Miyakojima, the Miyako Group, together with fossils of *Rattus legata* (see above). They were tentatively identified

to three *Microtus* species, *M. oeconomus*, *M. fortis*, and *M.* sp. (Kaneko, 1985).

Fossils of the subfamily Microtinae have not been found from other island groups of the Ryukyu Archipelago (Oshiro, 2001). Also, species of the genus *Microtus* do not occur anywhere in the Ryukyus at present, although the genus is broadly distributed in the Palearctic Eurasia including northeastern China, Korean peninsula, and the main-islands of Japan (Kaneko, 1985).

⑤ Felidae spp. (Carnivora)

Fossils representing two felid individuals were discovered from the Late Pleistocene deposits in Pinza-Abu Cave on Miyakojima, the Miyako Group (Hasegawa, 1985). Their taxonomic status remains controversial: Hasegawa (1985) assumed these fossils to represent species of the genus *Felis* (sensu lato), whereas some other authors (e.g., Otsuka, 2002) referred to them as the genus *Lynx*. Nevertheless, most authors consider their close affinity with felid taxa occurring in the Palearctic Eurasia rather than with the Oriental felids or *Prionailurus iriomotensis*, the only extant native felid species of the Ryukyus endemic to Iriomotejima of the Yaeyama Group (Otsuka, 2002). No other fossils of the family Felidae or other carnivoran mammals have been found anywhere in the central or southern Ryukyus (Oshiro, 2001).

Prionailurus iriomotensis was once believed, on the basis of some apparently primitive features, to represent an ancestral stock of the Felidae basal to all extant taxa, but recent molecular phylogenetic studies invariably indicated very close affinity of this species with *P. bengalensis* (Suzuki et al., 1994; Masuda and Yoshida, 1995; Johnson et al., 1999). Based on available genetic distance values, these authors estimated their divergence time to be 0.17–0.66 Mya, although the failure of examining the Taiwanese *P. bengalensis*, a population of the species geographically closest to *P. iriomotensis*, leaves the possiblity that the values still suffer overestimation.

⑥ *Mammuthus* sp. (Proboscidea)

Proboscid fossils were found from the Late Pleistocene deposit of Tanabaru cave in Miyakojima (Otsuka, 2001), and from near the lowest portion of Naha limestone stratum (corresponding to 1.0–1.2 Mya) at Kyan-Misaki, southern part of Okinawajima (Nohara and Hasegawa, 1973). This group of organisms, once diverged in the Palearctic Eurasia, is completely extinct at present. The taxonomic status of the fossils was a subject of active debate among mammalogists and paleontologists (e.g., see Otsuka [2001] for review). Recently, Otsuka (1978, 2001) suggested that

all these fossils are phylogenetically closely related to each other as well as to *Mammuthus shigensis* from Early Pleistocene in Kyushu and Honshu, Japan, and *M. armeniacuss taiwanicus* from Early Pleistocene Taiwan. I tentatively follow this account and consider the Miyakojima and Okinawajima fossils to be allied to each other, even though their specific allocation remains uncertain.

⑦ *Gomphotherium* sp. (Proboscidea)

Two fossil specimens of this proboscid taxon, initially referred to as *Trilophodon* (see Hasegawa et al., 1973), were found from Ogamijima of the Miyako Group. They are most likely to be dated back to the Late Meiocene or Early Pliocene (Hasegawa et al., 1973, 1978; Otsuka, 2002).

Fossils of this extinct mastodondid genus are relatively abundant in the middle and upper Tertiary strata of the Eurasian Continent and the main islands of Japan. The Ogamijima fossils thus suggest close geographical connections of the current Miyako area with the continent and the main islands of Japan at least by the Late Meiocene (Otsuka, 1983, 2002).

⑧ *Sus* spp. (Artiodactyla)

Fossils of this genus have been found from Late Pleistocene deposits of Pinza-Abu Cave, Miyakojima, and latest Pleistocene fissure deposits at several sites scattered in the southern and central parts of Okinawajima (Oshiro and Nohara, 1977; Hasegawa, 1980). It is interesting to note that, in the central Ryukyus and the Yaeyama Group, the wild boar fossil has never been found from strata lower than the uppermost Pleistocene series, although it often much outnumbers fossils of other vertebrates at latest Pleistocene sites as well as Holocene archaeological sites (e.g., Hasegawa, 1980; Nishinakagawa et al., 1994). The wild boars of the Late Pleistocene Miyakojima are much larger than those of the latest Pleistocene central Ryukyus, being similar to, or even larger than wild boars of the main islands of Japan and eastern continental China (Hayashi, 1985; Kawashima et al., 1985).

In the Ryukyu Archipelago, extant wild boar populations are confined to Iriomotejima and Ishigakijima of the Yaeyama Group, Okinawajima of the Okinawa Group, and Tokunoshima and Amamioshima of the Amami Group. Taxonomically, these Ryukyu populations are usually regarded as an endemic subspecies, *Sus sucrofa ruikiuanus*, chiefly on the basis of relatively small body size (Abe et al., 1994). Endo et al. (2002) compared mandible morphology among wild boar samples from

Iriomotejima (*S. s. riukiuanus*), Taiwan (*S. s. taivanus*), and the main islands of Japan (*S. s. leucomystax*), and confirmed a distinctly smaller size of the Iriomote sample. They also demonstrated a strong similarity in size between the latter two sample groups. They attributed such a pattern of variation to a dwarfism in the former, which had seemingly resulted from warm, insular environment of Iriomotejima.

Hongo et al. (2002), on the other hand, phylogenetically analyzed mtDNA data for wild boars and pigs from the Eurasian Continent and adjacent islands (including Taiwan, Ryukyu Archipelago, and the main islands of Japan). While confirming monophyly and poor genetic divergence among populations from Iriomotejima, Okinawajima and Amamioshima, their results suggested a close affinity of these three populations with the so-called large type of the Vietnamese pig. It also suggested close relationships of the Taiwanese wild boar with wild boars of the main islands of Japan and northeastern continent as well as with most East Asian domestic pigs including the so-called small type of the Vietnamese pig (Hongo et al., 2002). Wild boars of the Ryukyus and Taiwan, on the other hand, were rather distantly located from each other. Considering that the large type of the Vietnamese pig is even larger than the Taiwanese and Japanese (main island) wild boars despite its lower latitudinal (i.e., more tropical) location, it is likely that the insular dwarfism is the only factor responsible for the small body size of the Ryukyu wild boar. Relatively distant affinity between the Ryukyu and Taiwanese wild boars negates the possibility that the Ryukyu wild boar was originated from recent landbridge dispersal from southeastern continental China through Taiwan (contra Ujiié, 1990; Kimura, 1996a,b).

Large body size of fossil *Sus* sp. from Miyakojima may suggest its close affinity with northern continental populations of *S. sucrofa* (see Hayashi, 1985; Kawashima et al., 1985).

⑨ *Cervus astylodon* (Artiodactyla)

Fossils of this extinct deer have been found from Ishigakijima and Yonagunijima of the Yaeyama Group, Okinawajima, Kumejima and Iejima of the Okinawa Group, and Tokunoshima of the Amami Group (Oshiro, 2001, 2002; Otsuka and Takahashi, 2000; Otsuka, 2002). Whereas being most abundant in the Late Pleistocene cave and fissure deposits, fossils of this species have been obtained also from Early Pleistocene strata (1.3–1.7 Mya) at a few sites on Okinawajima (Otsuka, 2002). In contrast, no fossils have been found from more recent strata and

archaeological sites (Hasegawa, 1980; Nishinakagawa et al., 1994). It is, therefore, almost certain that this deer had first migrated into the Ryukyus by Early Pleistocene and became extinct around LPGM (Otsuka, 2002).

⑩ *Dicrocerus* sp. (Artiodactyla)

Fossils of this small-bodied extinct deer have been found from Okinawajima, Kumejima, and Iejima of the Okinawa Group, usually mixed with those of *Cervus astylodon* (Hasegawa, 1980; Oshiro, 2001). Like the latter species, *Dicrocerus* sp. is also quite common in the Late Pleistocene cave and fissure deposits, although fossils of the genus have also been found from Early Pleistocene strata (1.3–1.7 Mya) at a few sites on Okinawajima (Oshiro 2001; Otsuka, 2002). Taxonomic relationships of the Early Pleistocene and Late Pleistocene representatives of the genus are controversial: some researchers (e.g., Oshiro, 2001, 2002) consider them to illustrate a single ancestor-descendant lineage, whereas others (e.g., Otsuka, 2002) suspect the extinction of the former and migration of the latter in Middle Pleistocene.

⑪ *Capreolus miyakoensis* (Artiodactyla)

A large number of fossils, which represent a deer species but distinct from *Cervus astylodon* and *Dicrocerus* sp., have been found exclusively from the Late Peistocene deposits of Pinza-Abu and Tana-Baru Caves on Miyakojima, the Miyako Group. Several prominent characteristics, shared with extant *Capreolus capreolus* from Palearctic Eurasia, such as the presence of distinct but short blunt projections on the antler surfaces, indicate close affinity of this extinct species (*Ca. miyakoensis*) with *Ca. capreolus*. This further suggests that the Miyakojima population of *Capreolus* had initiated through migrations from the higher latitude (Zhen and Hasegawa, 1985), like those of *Microtus*, an unidentified felid, and *Sus* sp. (see above).

3. Directions of future studies

Present review highlighted a few cases, such as that on the evolution and biogeography of the genus *Sus* of the Ryukyus, in which a substantial advantage in integrating paleontological and neontological information is obvious. On the other hand, above reviews elucidated several important issues that need further investigations. For example, the currently accepted identifications of some Late Pleistocene or Holocene frog remains from Ishisukuyama (Ishigakijima) and Minatogawa (Okinawajima) indicate very recent occurrences of several, currently strictly Paleactic species in the southern and

central Ryukyus (Hasegawa and Nohara, 1978; Hasegawa, 1980). This contradicts with the currently prevailing view on the faunal pattern of amphibians in these regions that are characterized by the predominance, with very few exceptions, of the Oriental elements (Ota, 1998, 2000b). However, as was implicitly or explicitly written in the relevant paleontological works (Hasegawa and Nohara, 1978; Hasegawa, 1980), identifications of those crucial specimens are actually provisional yet. Therefore, future studies, particularly using skeletal specimens of Taiwanese and southeastern continental taxa as comparative mateirals (see above), are strongly desired to verify taxonomic allocations of those Ishisukuyama and Minatogawa specimens. Likewise, taxonomic status of some fossil reptiles from Pinza-Abu Cave, such as *Trimeresurus* and *Takydromus*, are essential in considering validity of the Kerama Gap as a long standing barrier against dispersals of terrestrial vertebrates between the central and the southern Ryukyus (Ota, 1998). This problem also requires further efforts for accurate identification of those fossils.

With respect to neontological studies, the greatest source of difficulties in their application to paleogeographical inference lies in the scarcity of taxa, for which reliable isolation date estimates are available. Molecular and biochemical data published to the present largely suggest long isolation of the central Ryukyus from the other land masses and much shorter isolation of the Yaeyama Group from Taiwan (see above). However, such data are yet limited to only a small number of taxa, and, moreover, very few of them accompany reliable calibrations on the basis of molecular and biochemical clock hypotheses. For evaluation of the currently prevailing paleogeographical hypotheses of the Ryukyus that invoke rather complicated process of landbridge formation and insularization (see Introduction; also see Kimura, 2002), accumulation of neontological data that can be used for calibration is strongly desired.

Acknowledgements

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