Acta Herpetologica 8(1): 19-34, 2013

Recent cryptic extinction of squamate reptiles on Yoronjima Island of the Ryukyu Archipelago, Japan, inferred from garbage dump remains

Yasuyuki Nakamura[1,*], Akio Takahashi[2], Hidetoshi Ota[3]

[1] *Tropical Biosphere Research Center, University of the Ryukyus, Senbaru 1, Nishihara, Okinawa 903-0213, Japan. *Corresponding author.* E-mail: ynaka.riukiaria@gmail.com
[2] *Department of Zoology, Faulty of Science, Okayama University of Science, Ridai-cho 1-1, Kita-ku, Okayama, Okayama 700-0005, Japan*
[3] *Graduate School of Human Science and Environment, University of Hyogo, Yayoi-gaoka 6, Sanda, Hyogo 669-1546, Japan*

Submitted on 2012, 28th December; revised on: 2013, 24th February; accepted 2013, on 24th April.

Abstract. We report recent skeletal remains of squamate reptiles screened from an old garbage dump deposit found on Yoronjima Island, a small island of the Ryukyu Archipelago, in the subtropical northwestern Pacific. Identified remains include at least three species of terrestrial snakes, one sea snake, and seven species of lizards. Among these, the Ryukyu Short-legged Skink, *Ateuchosaurus pellopleurus*; Kuroiwa's Leopard Gecko, *Goniurosaurus kuroiwae*; and one unidentified *Gekko* species constitute entirely new findings. For a further two snake species and one lizard species, the evidence presented here is the first specimen-based documentation that these species existed on this island, where they are now evidently absent. The present absence of these species on Yoronjima is mainly attributable to predation by the Japanese Weasel, *Mustela itatsi*, introduced in the mid-1950s. Our results demonstrate a prominent case of recent, sizable deterioration of insular herpetofaunal diversity, which has never been documented with certainty in the Ryukyu Archipelago, and suggest that human influence should be taken into account in biodiversity research in this area.

Keywords. Extinction, Ryukyu Archipelago, Squamata, weasel, Yoronjima.

INTRODUCTION

Our knowledge of the natural diversity of many insular terrestrial vertebrate faunas in subtropical and tropical regions remains comparatively limited. Currently, these faunas are often depauperate in indigenous elements compared to their original states, due mainly to past activities of humans and their associated animals (e.g., Henderson, 1992; Case et al., 1998). Even where documentation of past faunal states is regarded as comprehensive, caution should be exercised not to underestimate an island's natural biodiversity, as this renders unreliable conclusions from biogeographical and ecological studies that consider only the historically known fauna (Steadman, 2006; Whittaker and Fernández-Palacios, 2007). In a number of islands in the lower latitudes, reptilian bone fragments associated with buried human contexts have offered unique opportunities to reveal the existence of several currently missing elements as well as to investigate the history of insular terrestrial reptile communities under anthropogenic influence (e.g., Pregill, 1998; Pregill and Worthy, 2003; Pregill and Steadman, 2004). However, there have not been many previous studies focusing on reptile remains (which tend to be small and easily overlooked), suggesting there remains a large gap in our understanding of the diversity of insular reptiles.

The Ryukyu Archipelago, forming the most southwesterly part of Japan, is a cluster of more than one hundred continental fragments in the subtropical northwestern Pacific. The islands have been explored zoologically since the mid-19th century (Stejneger, 1907), so the extant herpetofauna is considered to be well documented

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

www.fupress.com/ah

(Ota, 1998; Maenosono and Toda, 2007). Habitat degradation by humans has been the most serious threat to the biological diversity of indigenous amphibians and reptiles (Ota, 2000; Ministry of the Environment, 2010), which are predominant elements of the terrestrial vertebrate faunas. As is the case with many islands in other regions, there has recently been a growing concern for the negative effects of exotic mammalian predators such as domestic dogs, cats, mongooses, and weasels (e.g., Watari et al., 2008; Yamada et al., 2009; Ministry of the Environment, 2010).

Until recently, the herpetofaunas of this archipelago have nevertheless been regarded as healthy because neither extinction nor serious, irreparable population extirpation (such as on a whole-island level) of Japanese indigenous amphibians and reptiles has been known (Environment Agency, 2000; Ministry of the Environment, 2010); this concerns the period at least since the mid-19th century, which marked the start of the westernization and modernization of Japan. This view is however no longer warranted, stemming merely from a past scarcity of knowledge. Indeed, Hikida et al. (1992) and Ota (2003b) have suggested that documented and possibly unique *Plestiodon* skink populations may have disappeared from Tairajima and Akusekijima Islands in the northern part of this archipelago, due to predation by the introduced Japanese Weasel, *Mustela itatsi*. As shown below, it seems appropriate that such instances not be regarded as isolated cases.

On Yoronjima Island, a small island in the Central Ryukyus, we confirmed the recent disappearance of a rhacophorid tree frog (*Rhacophorus viridis*) population by examining some very recent skeletal remains collected from an old garbage dump (Nakamura et al., 2009). This is the first confirmed case of an island-level extirpation in modern terrestrial herptiles in Japan. Vertebrate remains collected at the same time include several species of snakes and lizards, some of which seem to have no previous record or only old unverified records for this island. In this study, we report the results of a detailed identification of these recent reptilian remains and demonstrate the first specimen-based evidence for recent and sizable losses of components of the squamate faunas in this archipelago.

MATERIAL AND METHODS

Brief description of Yoronjima and its terrestrial vertebrate fauna

Yoronjima is a relatively small (area 20.5 km^2) and flat (elevation 97 m) island, lying 30 km northeast of Okinawajima Island and 40 km southwest of Okinoerabujima Island in the Central Ryukyus (Fig. 1). It consists mainly of terraced limestone beds deposited in the middle Pleistocene (Odawara and Iryu, 1999). Yoronjima has a relatively long history of human settlement. Archaeological records indicate that this island was first colonized more than two thousand years ago (the late Jomon Period; Takamiya and Chinen, 1984). At a minimum, this island is likely to have been occupied continuously since the early 15th century, at which time a medieval fort was constructed (Motoyama, 1988).

The known terrestrial non-volant vertebrate fauna on Yoronjima is poor in species when compared to other islands in the Central Ryukyus. All the recorded species are common on islands of the Central Ryukyus, and no endemic taxa have been found. The current terrestrial herpetofauna on Yoronjima consists of three species of frogs (Hallowell's Tree Frog, *Hyla hallowellii*; Ryukyu Kajika Frog, *Buergeria japonica*; Okinawa Narrow-mouth Toad, *Microhyla okinavensis*), four species of lizards (Hokou Gecko, *Gekko hokouensis*; House Gecko, *Hemidactylus frenatus*; Ryukyu Five-lined Skink, *Plestiodon marginatus*; Okinawa Green Grass Lizard, *Takydromus smaragdinus*), and two species of snakes (Okinawa Green Snake, *Cyclophiops semicarinatus*, and Brahminy Blind Snake, *Ramphotyphlops braminus*) (Ota, 1986; Maenosono and Toda, 2007). Of these, *Hemidactylus frenatus* has presumably been unintentionally introduced to Yoronjima by humans (Lever, 2003; Ota et al., 2004), which may also be the case for *Ramphotyphlops braminus* (e.g., Ota et al., 2004). The occurrence of four other reptile species (Okinawa Keelback Snake, *Amphiesma pryeri*; Ryukyu Odd-tooth Snake, *Dinodon semicarinatum*; Okinawan Tree Lizard, *Japalura polygonata polygonata*; Common Four-clawed Gecko, *Gehyra mutilata*) has also been reported (Koba, 1956; Nakamura and Uéno, 1959; Takara, 1962; Morita, 1988; Samejima, 1991), but it has been pointed out that these insufficient and mostly verbal records need further confirmation (Ota, 2003a; Maenosono and Toda, 2007). Terrestrial mammals are poorly represented and consist of the Ryukyu Flying Fox, *Ptero-*

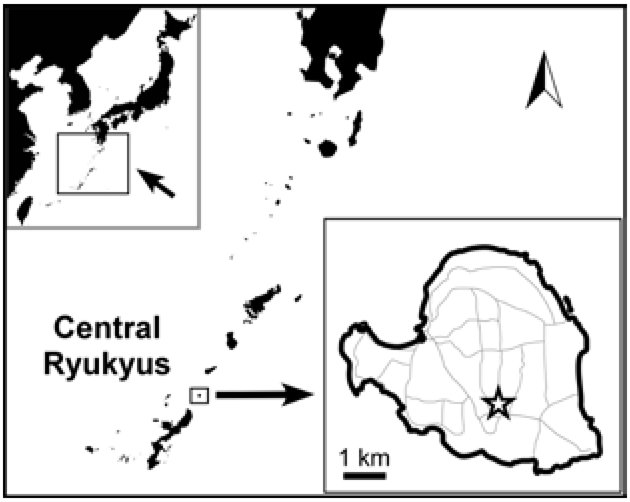

Fig. 1. Map of the northern and central parts of the Ryukyu Archipelago, showing the location of Yoronjima Island. Star indicates the study site.

pus dasymallus; Watase's Shrew, *Crocidura watasei*; Musk Shrew, *Suncus murinus*; Norway Rat, *Rattus norvegicus*; Black Rat, *R. rattus*; and House Mouse, *Mus musculus* (see Morita, 1988; Funakoshi et al., 2006; Motokawa, 2007). In addition, the Oriental Free-tailed Bat, *Tadarida insignis*, was recorded (Morita 1988). All rodents and the musk shrew are believed to have been introduced (e.g., Motokawa, 2007), as has the Japanese Weasel, *Mustela itatsi* (see Morita, 1988).

Study site

Skeletal remains of terrestrial vertebrates examined here were collected from an old garbage dump, which was found by A. Takahashi in 2007, deposited under the sheltered overhang of a limestone rock wall located in Asato (27°02'05"N, 128°26'02"E; Fig. 1). Precise deposition dates are unknown but probably no earlier than the late 19th century, as they were found in mixture with fragments of various modern artifacts such as tableware and glass bottles. Apart from the remains of livestock and marine fishes, there were remains of small terrestrial vertebrates. These were collected by careful fine-scale (1 mm) sieving of sandy soil deposits. Four frog species identified from the remains have already been reported (Nakamura et al., 2009). Mammalian remains identified included *Crocidura watasei*, *Rattus norvegicus*, *R. rattus*, and *Mus musculus*. All these species live on Yoronjima today (see above).

Identification

Collected reptile skeletal elements were identified with the help of comparisons to skeletal specimens of extant squamata species occurring in the Central Ryukyus and adjacent regions (Appendix). Owing to the virtual absence of useful information on the systematic identification of most fragmentary squamate reptile bone elements, our comparisons were based on overall similarity. However, for major taxonomic assignment of lizard bones we mostly followed available apomorphy-based systematic hypotheses. Our identifications at species level were primarily based on the current distributions of certain taxa. In particular, we regarded a present occurrence on Yoronjima or nearby islands as important information for species-level identification, unless contradictory evidence was present. This approach appears justified because of the very recent status of the bone remains examined here. We present brief descriptions of identified remains (for snakes in particular) to provide basic information for the systematic identification of their isolated skeletal elements.

All observations were made under stereoscopic microscopes (Nikon SMZ-10 or SMZ-1000). Measurements were taken with an embedded micrometer. Osteological terminology follows LaDuke (1991) and Holman (2000) for snakes and Rieppel (1984) and Estes et al. (1988) for lizards. Division of the regions of snake vertebral columns followed Hoffstetter and Gasc (1969), and for subregions of the trunk vertebrae, LaDuke (1991). The described skeletal remains were deposited in the collection of the Museum of the University of the Ryukyus (Fujukan), Nishihara, Okinawa, Japan.

RESULTS

Systematic accounts

Suborder Serpentes

Family Colubridae

Subfamily Colubrinae

Cyclophiops semicarinatus (Hallowell, 1861) (Fig. 2A)
Referred specimens—24 middle and posterior trunk vertebrae (RUMF-GF-4060).
MNI = at least two individuals, on the basis of size.

The referred vertebrae are as long as wide and nearly square across the zygapophyseal articular facets. The neural spine is square anteriorly and angularly undercut posteriorly. It is of moderate height at the anterior edge, roughly twice as long as high, and below the height of the neural canal. Viewed anteriorly, the zygosphene is dorsally convex; viewed from above, its anterior edge is weakly convex. The lateral inclinations of the zygosphenal articular facets are moderate, ~40° from the sagittal plane. The neural arch is slightly depressed. The posterior neural arch swells dorsally, so that the height of the posterior part of the neural spine is less than half the height of the anterior part. Posteriorly, the neural arch laminae bear barely developed epizygapophyseal spines, which extend posterolaterally beyond the margins of the postzygapophyseal articular facets. The shapes of the prezygapophyseal articular facets are ovoid, while those of the postzygapophyseal articular facets are rounded. The prezygapophyseal accessory processes are blunt and directed laterally in dorsal view. Viewed from above, the anterior edges are usually bowed posteriorly. The cotyle and the condyle are rounded, except for those of small-sized vertebrae where they are usually depressed. They are equal in size to the neural canal, but large-sized vertebrae tend to have relatively large cotyles and condyles. In lateral view, the condyle is moderately oblique; viewed ventrally, the transverse width of the condyle almost equals the width of the precondylar part of the centrum. The subcentral ridges are weakly defined, and are straight or somewhat bowed dorsally in lateral view. The hemal keel is deep and narrow, and laterally deeply excavated by the deep subcentral grooves.

The presence of the distinct neural spines, well-developed prezygapophyseal accessory processes, well separated diapophyses and parapophyses, and the lack of the hypapophysis indicate that the referred vertebrae are middle or posterior trunk vertebrae of colubrine snakes (Rage, 1984; but see also Malnate, 1972; Ikeda, 2007). They would thus expect to be derived from either *Cyclophiops semicarinatus* or *Dinodon semicarinatum*, representatives of colubrine snakes in the Central Ryukyus. The trunk vertebrae

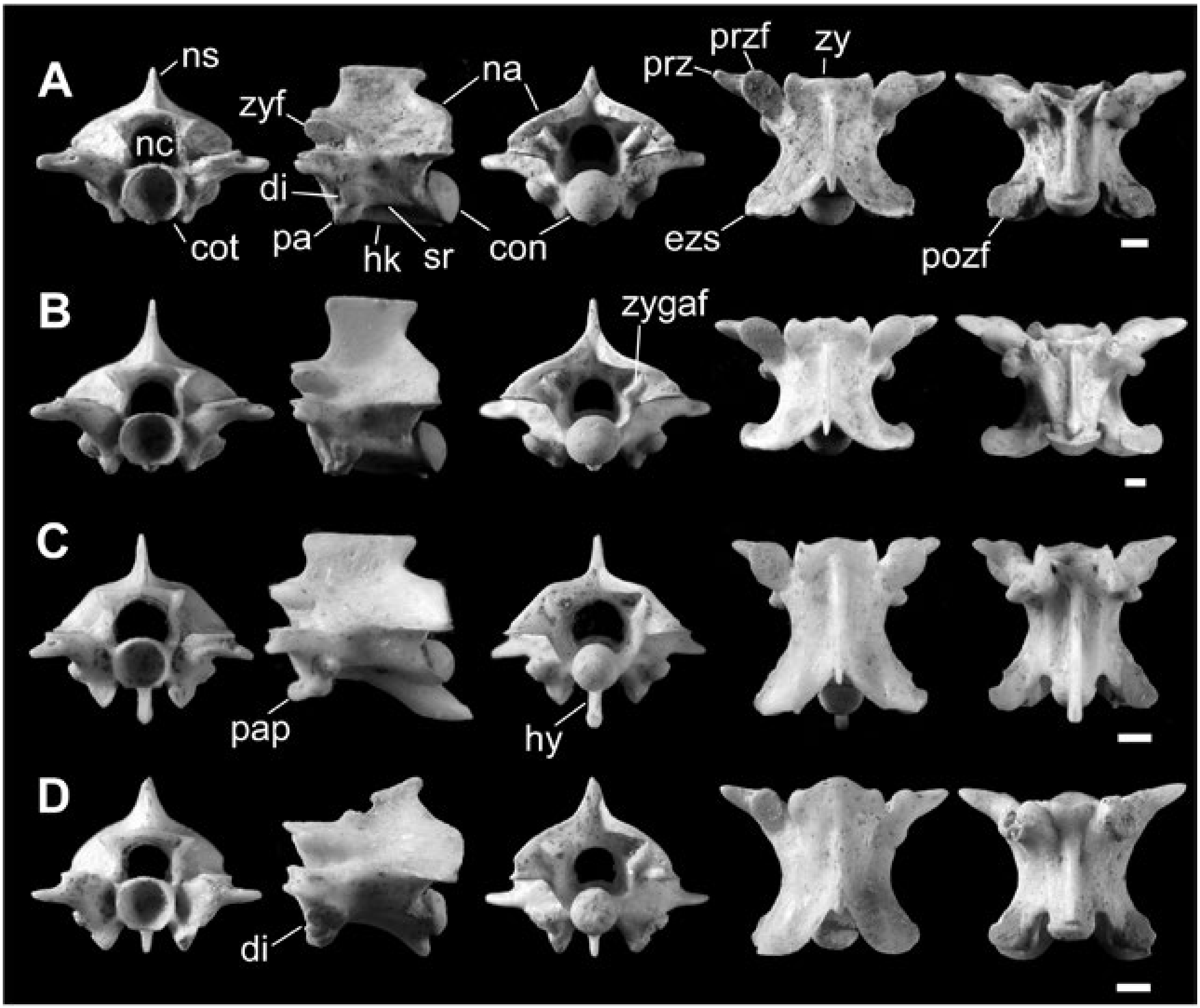

Fig. 2. Trunk vertebrae of snakes. (A) referred vertebra of *Cyclophiops semicarinatus* (one of 24 registered as RUMF-GF-4060), (B) referred vertebra of *Dinodon semicarinatum* (one of 21 registered as RUMF-GF-4061), (C) referred vertebra of *Amphiesma pryeri* (one of 39 registered as RUMF-GF-4062), and (D) referred vertebra of Hydrophiinae sp. (unidentified sea snake) (RUMF-GF-4063). Left to right: anterior, lateral (left), posterior, dorsal, and ventral views. Abbreviations are: con, condyle; cot, cotyle; di, diapophysis; ezs, epizygapophyseal spine; hk, hemal keel; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; pa, parapophysis; pap, parapophyseal process; prz, prezygapophyseal accessory process; przf, prezygapophyseal articular facet; pozf, postzygapophyseal articular facet; sr, subcentral ridge; zy, zygosphene; zyf, zygosphenal articular facet; zygaf, zygantral articular facet. Scale bars equal 1 mm.

have been identified as those of *C. semicarinatus*, on the basis of their relatively low neural spines lower than the height of the neural canals, square anterior margins of the neural spines, rounded cotyles and condyles (except for small-sized vertebrae), posteriorly bowed anterior edges of the prezygapophyseal accessory processes, the presence of epizygapophyseal spines that extend beyond the margins of the postzygapophyseal articular facets, rounded postzygapophyseal articular facets, and very weak precondylar constrictions of the centra.

Dinodon semicarinatum (Cope, 1860) (Fig. 2B)

Referred specimens—21 middle and posterior trunk vertebrae (RUMF-GF-4061).

MNI = at least two individuals (one juvenile and one adult), on the basis of size.

Referred vertebrae are short and broad, with relatively large cotyles and condyles. The neural spine is thin, short, and high, and about as high as long. Its height is greater than that of the neural canal in anterior view. It overhangs anteriorly and posteriorly, and the anterodorsal corner is rounded. The dorsal roof of the zygosphene is convex; its anterior margin is convex anteriorly. The lateral inclinations of the zygosphenal articular facets are moderate, ~40° from the sagittal plane. Viewed posteriorly, the neural arch is more or less depressed. Viewed laterally, its posterodorsal part swells, so that the depth of the posterior neural spine is half the depth of the anterior edge. The neural arch laminae above the zygantra extend posteriorly beyond the posterior ends of the facets of the zygantra (hereafter referred to as zygantral articular facets). The epizygapophyseal spines are usually absent, or rudimentary if present. The blunt and gently tapered prezygapophyseal accessory processes are directed laterally in dorsal view, with rounded or weakly pointed tips. The shapes of the prezygapophyseal articular facets are ovoid; those of the postzygapophyseal articular facets are rectangular, more extensive mediolaterally than anteroposteriorly. The cotyle and the condyle are oval in outline, broader transversely than sagittally, with moderate inclinations. Viewed ventrally, the centrum tapers posteriorly to the condyle, and the condyle is much wider than the precondylar part of the centrum. The subcentral ridges are weakly to moderately defined and bowed dorsally in lateral view. The hemal keel is narrow but widens at the posterior part. It is shallow in middle trunk vertebrae (Fig. 2B) and deep in posterior trunk vertebrae. The state of the subcentral grooves ranges from shallow in middle trunk vertebrae (Fig. 2B) to deep in posterior trunk vertebrae.

Most of the middle and posterior trunk vertebrae of *Dinodon semicarinatum* are separated from those of *Cyclophiops semicarinatus* by their short and wide general shapes, high neural spines that are usually higher than the neural canals, anteriorly overhanging anterior edges of the neural spines, dorsoventrally depressed cotyles and condyles (except for small-sized vertebrae), anteriorly bowed anterior edges of the prezygapophyseal accessory processes, much wider transverse width of the condyles than the precondylar parts of the centra, laterally elongated postzygapophyseal articular facets, posteriorly elongated neural arch laminae that hide the zygantral articular facets from above, and the lack of the epizygapophyseal spine.

Subfamily Natricinae

Amphiesma pryeri (Boulenger, 1887) (Fig. 2C)
Referred specimens—39 precaudal trunk vertebrae (RUMF-GF-4062).
MNI = 1.

Referred precaudal vertebrae have generally slender and elongate overall shapes. The neural spine is thin, and is much thinner laterally than the hypapophysis. It is moderately high and long. The length is more than twice the height at the anterior edge, and the height is about equal to that of the neural canal. The neural spine overhangs anteriorly and posteriorly. The zygosphene is very slightly dorsally convex; its anterior margin is convex. The lateral inclinations of the zygosphenal articular facets are slight, ~25° from the sagittal plane. Viewed posteriorly, the neural arch laminae are bent at the midpoints. The dorsal elevation of the posterior neural arch is slight; it is confined to almost the same level as the zygosphene. The epizygapophyseal spines are barely developed, with tips extending posteriorly to the margins of the postzygapophysial articular facets. The distinct parapophyseal processes protrude anteriorly. The shapes of the prezygapophyseal articular facets are sub-round or ovoid, while those of the postzygapophysial articular facets are rounded. The cotyle and the condyle are rounded and smaller than the neural canal. The condyle is slightly wider than the precondylar part of the centrum in ventral view, and the dorsoventral inclination is moderate. The prezygapophyseal accessory processes are thin or blunt and directed anterolaterally. The hypapophysis is broad, deep, pointed posteriorly, and squared anteroventrally. Its distal part extends posteriorly beyond the condyle tip. Viewed laterally, the subcentral ridges are well defined and slightly bowed dorsally, and viewed ventrally, the shallow subcentral grooves run throughout the ventral side of the centrum.

Precaudal vertebrae of *Amphiesma pryeri* differ from the middle and posterior trunk vertebrae of *Cyclophiops semicarinatus* and *Dinodon semicarinatum* in being narrow and elongate and having well developed hypapophyses, distinct and anteriorly projected parapophyseal processes, anterolaterally directed prezygapophyseal accessory processes (e.g., Ikeda, 2007), less inclined laterally facing zygosphenal articular facets, a posterior neural arch that extends dorsally very slightly, posterior neural arch laminae bent at the midpoints, and small condyles and cotyles smaller than the neural canals. It differs further from middle and posterior trunk vertebrae of *C. semicarinatus* in having overhanging anterior edges of the neural spines and anteriorly bowed anterior edges of the prezygapophyseal accessory processes; and from *D. semicarinatum* in having rounded condyles and cotyles, rounded postzygapophysial articular facets, and weaker precondylar constrictions. Although anterior trunk vertebrae of these colubrine snakes also possess hypapophyses, these vertebrae are easily identified on the basis of their dorsoventrally elongate and anteroposteriorly short general shapes (LaDuke, 1991).

These precaudal vertebrae highly resemble those of *Amphiesma pryeri*, while there are some other non-colubrine cenophidian snakes in the Central Ryukyus that display hypapophyses throughout their precaudal vertebrae (e.g., Ikeda, 2007; see Suppl. Fig. S1-3). Precaudal vertebrae of the Amami odd-scaled snake, *Achalinus werneri*, may be distinguished from those of *Am. pryeri* by e.g., less elongated centra, less developed hypapophyses, thick neural spines that are flattened on the dorsal edges, and flat neural arch laminae. Likewise, those of elapid snakes (the coral snakes *Sinomicrurus japonicus japonicus* and *S. j. boettgeri*, and the sea kraits *Laticauda colubrina*, *L. laticaudata*, and *L. semifasciata*) differ in being heavily-built and having short centra, lower and thicker neural spines (of the same thickness as the hypapophyses), depressed posterior neural arches (which are even laterally expanded in *Laticauda*), and mostly spine-like hypapophyses (see also Ikeda, 2007). Precaudal vertebrae of the black-headed sea snake, *Hydrophis melanocephalus*, and the turtle-headed sea snake, *Emydocephalus ijimae*, resemble those of *Am. pryeri* in being elongate, lightly-built, and having thin neural spines, but they are readily distinguished by high neural spines that are confined to the posterior of the zygosphenes and by less developed hypapophyses. Viperid vertebrae can easily be excluded, as they are generally anteroposteriorly short and have both short accessory processes and thick hypapophyses that are dorsoventrally long and anteroposteriorly short (Szyndlar, 1991; Ikeda, 2007). Unfortunately, no information is available on vertebral characteristics of the Kikuzato's stream snake, *Opisthotropis kikuzatoi*, an extremely rare snake endemic to Kumejima Island in the Central Ryukyus. This species is substantially smaller-bodied than *Am. pryeri* and is strictly confined to a small number of mountain stream systems of an island far from Yoronjima (Okinawa Prefectural Board of Education, 1993). Therefore, here, we tentatively reject the possibility that *O. kikuzatoi* is represented.

Family Elapidae

Hydrophiinae sp. (unidentified sea snake) (Fig. 2D)
Referred specimen—one trunk vertebra (RUMF-GF-4063).
MNI = 1.

One trunk vertebra is referred to a sea snake. This specimen displays a characteristic elongated neural arch that extends posteriorly beyond the condyle tip. Viewed posteriorly, the neural arch is broad and vaulted, with the posterior margin around the midline rising dorsally to near the posterodorsal corner of the neural spine. The neural spine lost the anterodorsal corner, but the anterior edge is clearly inclined posteriorly and the base is located considerably behind the zygosphene. The dorsal edge slopes up posteriorly, and the posterior corner overhangs. The height of the neural spine is less than its length. The dorsal roof of the zygosphene is weakly convex dorsally, and the rounded anterior margin strongly protrudes when viewed from above. Lateral inclinations of the small zygosphenal articular facets are moderate (38°). The prezygapophyseal accessory processes are thin, long, pointed, and directed anterolaterally. They are positioned distinctly ventrally of the prezygapophyseal articular facets, which are rounded and small. The parapophyseal processes barely protrude anteriorly. The diapophyses are anterolaterally directed, reaching the level of the cotyle rim, and are almost invisible from above. Weakly developed epizygapophyseal spines are present. Viewed laterally, the condyle is truncated with a slight inclination, and viewed ventrally, it is slightly wider than the precondylar part of the centrum. The hypapophysis is shallow, and its tip directs ventrally and extends posteriorly only to the level of the condyle base. In lateral view, the weakly defined subcentral ridge is bowed dorsally. The subcentral grooves are weak and confined to the regions along with the anterior part of the hypapophysis.

The referred material clearly differs from vertebrae of the three species discussed above. Among cenophidian snakes occurring in and around the Central Ryukyus, some character states possessed by this vertebra are confined to sea snakes, without being universal. These are the neural spine, which rises out considerably behind the zygosphene; the neural arch, which extends posteriorly beyond the condyle; and anterolaterally directed diapophyses, which are almost invisible from above (Suppl. Fig. S2, 3). However, this vertebra specimen differs from examined sea snakes (three *Laticauda* species, *Emydocephalus ijimae*, and *Hydrophis melanocephalus*) in the sloping dorsal edge of the neural spine, the posterior neural arch that flares out dorsally at the midline, and the pronouncedly anteriorly protruding zygosphene. Although we were unable to examine respective skeletal specimens, we consider this unique vertebra to be derived from one of three other hydrophiine sea snake species known from the waters surrounding the Central Ryukyus: *Hydrophis cyanocinctus*, *H. ornatus maresinensis*, and *Pelamis platura* (see Toriba, 1996).

Suborder Lacertilia
Family Agamidae

Japalura polygonata polygonata (Hallowell, 1861) (Fig. 3A, B)
Referred specimens—six right and four left maxillae (RUMF-GF-4064), three right and three left dentaries (RUMF-GF-4065), a proximal part of the right humerus, and a proximal part of the left femur.
MNI = 6.

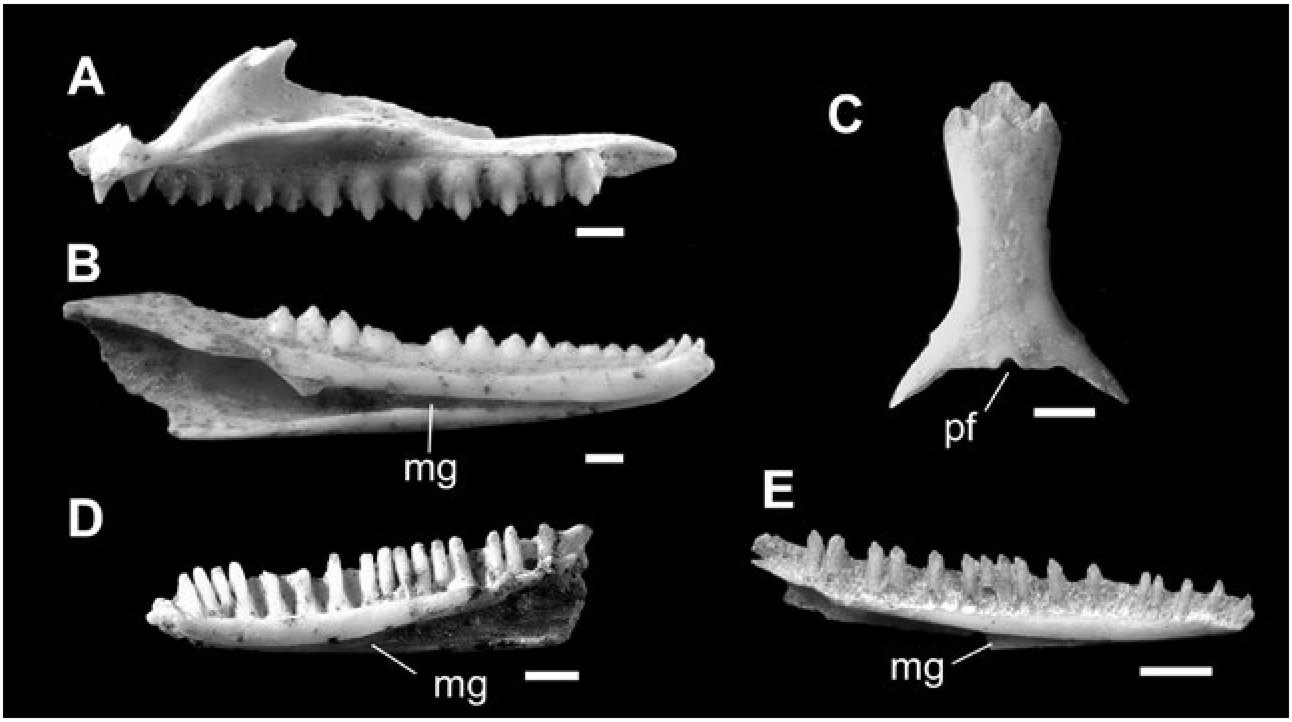

Fig. 3. Lizard remains referred to *Japalura polygonata polygonata* (A, B), *Ateuchosaurus pellopleurus* (C), *Plestiodon marginatus* (D), and *Takydromus smaragdinus* (E). (A) right maxilla (one of 10 registered as RUMF-GF-4064) in medial view, (B) left dentary (one of 6 registered as RUMF-GF-4065) in medial view, (C) frontal (RUMF-GF-4066) in dorsal view, (D) right dentary (RUMF-GF-4067) in medial view, and (E) left dentary (RUMF-GF-4068) in medial view. Abbreviations are: mg, Meckelian groove; pf, parietal foramen. Scale bars equal 1 mm.

The referred dentaries are labiolingually flattened, with anterior tips that are curved dorsally (Fig. 3B). The Meckelian groove is open along the entire length. Four specimens preserve complete tooth rows, which are composed of three canine-like anterior teeth and 12 (right: n = 1) or 13 (left: n = 3) tricuspid posterior teeth. The anterior teeth are conical and curved, and attach to the inner aspect of the labial wall (i.e., pleurodont), while the posterior teeth are firmly united with the dorsal portion of the labial wall (acrodont). Posterior teeth are compressed laterally, with a pair of small additional cusps on each anterior and posterior side. Dentition of the maxillae is identical to that of the dentaries (Fig. 3A), consisting of two or three canine-like pleurodont anterior teeth and 12 (right: n = 2), 13 (right: n = 2), or 14 (left: n = 1) acrodont posterior teeth.

Dentition of the referred maxillae and dentaries exhibits a combination of character states exclusive to agamid lizards: canine-like pleurodont anterior teeth and deltoid, tricuspid, and labiolingually flattened acrodont posterior teeth, as well as a lack of indentation for the coronoid in the posterolateral dentaries (Estes et al., 1988; see also Smith et al., 2011). These specimens were positively identified as *Japalura polygonata polygonata*, the only representative of agamid lizards in the Central Ryukyus. Additionally, fragments of a humerus and a femur were also identified. All of these referred bones are essentially identical to the same elements in living *J. p. polygonata*.

Family Scincidae

Ateuchosaurus pellopleurus (Hallowell, 1861) (Fig. 3C)
Referred specimen—one frontal (RUMF-GF-4066).
MNI = 1.

The referred material is an intact frontal. It is undivided and fused completely, thin and slightly convex dorsally, and the lateral descending processes are shallow downturned lobes that have no ventral contact. Posteriorly, it bears a prominent notch for the parietal foramen at the midline and a pair of posterolateral projections at the lateral sides. Such a single, unpaired frontal bone with shallow lateral descending processes is unique among Japanese lizards to so-called lygosomine skinks. Among them, or even among scincid species, the only known species to possess a single frontal with a parietal foramen are members of the genus *Ateuchosaurus* (see Greer, 1970). This material was definitely identified as *A. pellopleurus*, as *Ateuchosaurus* is exclusively represented by this species in the Ryukyu Archipelago.

Plestiodon marginatus Hallowell, 1861 (Fig. 3D)
Referred specimens—one right dentary (RUMF-GF-4067), two right and one left posterior mandibles, five right and one left humeri, one right femur, and one right and one left pelvic girdle.
MNI = 5.

The referred dentary fragment is deep and truncated. The Meckelian groove is fully open to the symphysis. Dentition is pleurodont; there are 17 teeth and seven vacant tooth positions. Teeth are blunt and tapering cylinders whose crowns are slightly thinner than the rest of the teeth. Each of the intact teeth has a concave and striated lingual surface at the crown and a pair of cusps that are labiolingually doubled and lingually inclined.

This dentary specimen is referred to scincids on the basis of the cylindrical teeth and striated and lingually concave tooth crowns (e.g., Estes, 1983). Of the three currently recognized scincid species in the Central Ryukyus, *Ateuchosaurus pellopleurus* and the Barbour's Blue-tailed Skink, *Plestiodon barbouri*, may be excluded because the dentary is of too great a size and depth (see Suppl. Fig. S4). Although the use of the body size for identification of lizard remains requires special caution (e.g., Pregill, 1986), the material could be referable to *P. marginatus*, and the present occurrence of the species on Yoronjima (see above) supports this conclusion. Certain elements of scincid remains were also referred to this species on the basis of size and general morphological similarities. Although two subspecies of *P. marginatus* have been recognized, we here have omitted subspecific status as the distinction of these subspecies has been cast into doubt by recent research (e.g., Honda et al., 2008).

Family Lacertidae

Takydromus smaragdinus (Boulenger, 1887) (Fig. 3E)
Referred specimens—one left dentary (RUMF-GF-4068), and one right and one left pelvic girdle.
MNI = 1.

The referred left dentary is small, thin, and shallow. The Meckelian groove is open and ventrally located in the anterior part. There are 16 slender and cylindrical pleurodont teeth and 10 or 11 vacant alveoli. Dentition is heterodont; some posterior intact teeth show tricuspid tooth crowns while anterior teeth are clearly unicuspid. These character states (especially of the teeth) are typical in *Takydromus* lizards (Arnold, 1997; Arnold et al., 2007). This specimen was assigned to *T. smaragdinus*, as this is the only representative of the genus in the Central Ryukyus. One right and one left pelvic girdle were also referred to this species on the basis of distinct tubercles on proximal dorsal edges of the ilia.

Family Gekkonidae

Gekko hokouensis Pope, 1928 (Fig. 4A-D)
Referred specimens—three right and three left maxillae (RUMF-GF-4069), two right and three left dentaries (RUMF-GF-4070), five frontals (RUMF-GF-4071).
MNI = 5

Dentary

The completely fused Meckelian grooves and pleurodont tooth rows of these shallow dentaries display the unique character states of geckos (Kluge, 1967; Estes et al., 1988), and the peg-like simple and slender teeth indicate a gekkonid origin (Fig. 4B). Among seven described and one undescribed species of gekkonid occurring in the Central Ryukyus (Toda, 2008; Toda et al., 2008), the moderately sized material from the garbage pile does not seem to be referable to any of the three relatively large-sized species (the Takara Gecko, *Gekko shibatai*, the Amami Gecko, *G. vertebralis*, and the undescribed species of the Okinawa Island Group) nor to the small-sized species, the Mourning Gecko, *Lepidodactylus lugubris* (see Ota, 1996; Toda, 2008; Toda et al., 2008).

Among the remaining four equivalent-sized gekkonid species (*Gehyra mutilata*; *Gekko hokouensis*; the Bowring's Gecko, *Hemidactylus bowringii*; and *H. frenatus*), *Gehyra mutilata* apparently differs from the referred specimens in having thin teeth and elongated tooth crowns (Suppl. Fig. S5A). For the rest of the species, however, we were unable to find any useful morphological difference between these and the referred gekkonid dentaries. We have tentatively referred these dentary fragments as *Gekko hokouensis* because other certain elements of gekkonid remains from this site were also assigned to *Gekko* species, whereas none have been clearly identified as *Hemidactylus*.

Maxilla

An intact specimen of the referred maxillae displays a pronounced process at the anterior part of the medial shelf, the anteromesial process (Fig. 4A), which is one of the synapomorphies of geckos (Rieppel, 1984;

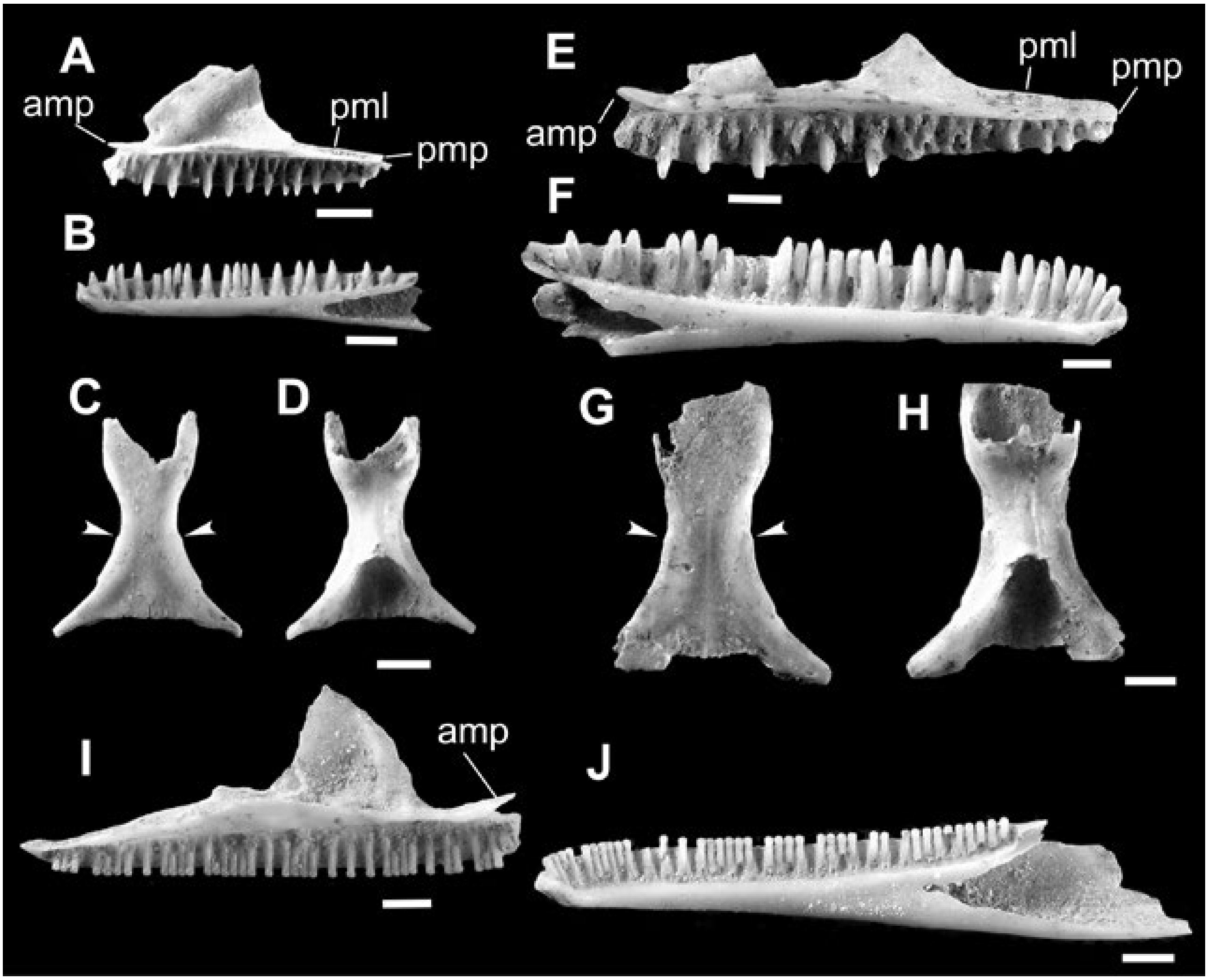

Fig. 4. Lizard remains referred to *Gekko hokouensis* (A-D), *Gekko* sp. (a large-sized *Gekko* species) (E-H), and *Goniurosaurus kuroiwae* (I, J). (A) right maxilla (one of 6 registered as RUMF-GF-4069) in medial view, (B) right dentary (one of 5 registered as RUMF-GF-4070) in medial view, (C, D) frontal (one of 5 registered as RUMF-GF-4071) in dorsal (C) and ventral (D) views, (E) right maxilla (one of 3 registered as RUMF-GF-4072) in medial view, (F) right dentary (one of 3 registered as RUMF-GF-4073) in medial view, (G, H) frontal (one of 3 registered as RUMF-GF-4074) in dorsal (G) and ventral (H) views, (I) left maxilla (RUMF-GF-4076) in medial view, and (J) right dentary (RUMF-GF-4077) in medial view. Abbreviations are: amp, anteromesial process; pml, posterior maxillary lamina; pmp, posterior maxillary process. Arrows in C and G indicate the posterior extents of the prefrontal sutures. Scale bars equal 1 mm.

Estes et al., 1988). The posterior maxillary process bears a short ascending wall (hereafter referred to as the posterior maxillary lamina) at the lateral side of the medial shelf. This character state was found in examined species of *Gekko*, which possess jugals that are laterally covered by the posterior maxillary laminae (Suppl. Fig. S6B-E), but is lacking in examined *Hemidactylus* species and in *Gehyra mutilata*, whose jugals wrap almost throughout these parts (Suppl. Fig. S6A, F, G). These maxillae can thus be identified as those of *Gekko hokouensis*, the only extant representative of *Gekko* species on Yoronjima.

Frontal

These referred frontals are lightly built and unpaired (Fig. 4C, D). They were assigned to geckos because they form depressed cylinders due to the lateral descending processes that meet and fuse ventrally (Kluge, 1967; Estes et al., 1988). Their anteroposteriorly truncated general shapes and rounded ventral sides indicate that these frontals are of gekkonid origin and do not belong to the eublepharid *Goniurosaurus*. The dorsal surfaces of the referred frontals are concave, the lateral edges of the orbital margins are acute, and the prefrontal sutures laterally extend posteriorly beyond the narrowest parts of the bones (Fig. 4C). Among the four equivalent-sized gekkonid species of the Central Ryukyus (see above), the frontal of *Gehyra mutilata* is distinguished from the referred frontals by the heavily-built body, the posterior dorsal surface without a concavity, and rolled orbital margins (Suppl. Fig. S7A). Likewise, frontals of *Hemidactylus* differ in that the prefrontal sutures do not extend posteriorly beyond the narrowest parts of the bones (Suppl. Fig. S7F, G). *Gekko hokouensis* is the only species that has comparable size and morphological details to those of the Yoronjima specimens.

Gekko sp. (A large-sized *Gekko* species) (Fig. 4E-H)
Referred specimens—three right maxillae (RUMF-GF-4072), two right and one left dentaries (RUMF-GF-4073), three frontals (RUMF-GF-4074), and three left pterygoids.
MNI = 3.

Certain elements of the referred material appear identical to bones of *Gekko hokouensis*, but the specimens are too large to belong to this species. Some of the material's character states, especially the presence of posterior maxillary laminae of the maxillae (Fig. 4E) and the prefrontal sutures of the frontals which extend to the narrowest parts of the bones (Fig. 4G), readily exclude all Japanese lizards examined other than species of the genus *Gekko* (see above). However, the widths at the narrowest parts of the two frontals (1.8 and 1.9 mm) and the length of the maxillary tooth row (8.7 mm) show that these elements were derived from animals with ~56, 59, and 65 mm snout-vent lengths (SVLs), respectively (estimates were obtained from measurements of 14 *Gecko* specimens from Yoronjima and Okinawajima Islands). By contrast, the SVL range of the extant Yoronjima population of *G. hokouensis*, the only known *Gekko* species from Yoronjima (see above), is merely up to 51.1 mm (male: 43-47.9 mm, n = 2; female: 48-51.1 mm, n = 4; see also Toda, 2008 for SVL of *G. hokouensis* from four islands in the Okinawa Island Group [~56.4 mm, n = 170]). Although lizard fossils have frequently exhibited aberrant body size when compared with those of modern counterparts (Arnold, 1976; Pregill, 1986), in this case certain elements referred to *G. hokouensis* at a size comparable to those of the extant conspecific population were recovered.

The referred elements compare favorably with large-bodied *Gekko* species, particularly those widely distributed in the Central Ryukyus: *G. vertebralis* of the Amami Island Group and the undescribed *Gekko* species known from the Okinawa Island Group (Toda, 2008; Toda et al., 2008). Skeletons of these species and *G. hokouensis* resemble each other, and since in sum these Yoronjima specimens do not preserve enough traits to permit specific identification, here we simply refer to them as a large-sized *Gekko*.

Family Eublepharidae

Goniurosaurus kuroiwae (Namiye, 1912) [sense Grismer et al., 1994] (Fig. 4I, J)
Referred specimens—one right and one left maxillae (RUMF-GF-4075 to 4076) and four right and three left dentaries (RUMF-GF-4077 to 4083).
MNI = 4.

The occlusal margins of tooth crowns in these maxillae and dentaries are expanded. The unique dental character is a derived feature diagnosing some mostly insular species of *Goniurosaurus* including *G. kuroiwae* (e.g., Grismer et al., 1999, 2002). No other *Goniurosaurus* occurs in and around the Ryukyu Archipelago (Grismer et al., 1994). We therefore refer these bones to *G. kuroiwae*. Five subspecies of *Goniurosaurus kuroiwae* are currently recognized (Grismer et al., 1994; but see Grismer et al., 1999), but none of these are known to originate from Yoronjima. A detailed morphological comparison of the Yoronjima material and known *G. kuroiwae* subspecies will be presented in a separate paper.

DISCUSSION

In total, three species of terrestrial snakes, one sea snake, and seven species of lizards were recovered from the old garbage dump deposits, in addition to four frog species previously reported by us (Nakamura et al., 2009). Among these, the discovery of skeletal elements of the Ryukyu Short-legged Skink, *Ateuchosaurus pellopleurus*; one large-sized *Gekko* species; and Kuroiwa's Leopard Gecko, *Goniurosaurus kuroiwae*, are of particular note, as none of these species have ever been recorded from Yoronjima. The results not only increase the total number of indigenous terrestrial squamate species on Yoronjima to 10, but also provide the first specimen-based documentation that some of these species once existed on this island. With regard to *Amphiesma pryeri*, *Dinodon semicarinatum*, and *Japalura polygonata polygonata*, their previous records from Yoronjima were not supported by extant voucher specimens or results of recent surveys. Hence, their occurrence on Yoronjima has been questioned (Ota, 2003a; Maenosono and Toda, 2007). The occurrence of *Takydromus smaragdinus* on Yoronjima was for the first time reported by Toda and Takahashi (2002), with some doubt regarding its native status. The present results confirm the native occurrence of these species on Yoronjima. By contrast, the occurrence of a sea snake bone from these inland deposits is seemingly unnatural; it is likely to have been deposited as a result of consumption by humans (as like *Laticauda* species are consumed locally) or by a bird. Although the site appeared to be an old garbage dump, the possibility that these animals had been brought from nearby islands by humans is very low, because this subfossil assemblage is comprised mainly of small non-attractive species, which possess no economic value. Additionally, the small and easily overlooked bones (size of the vertebrae are usually ~1 mm) of *Ramphotyphlops braminus* apart, it may also be significant that the absence of *Hemidactylus frenatus* in the subfossil assemblage. Conceivably the environment around the site was unsuitable for this synanthropic species, which prefers buildings and artificially lighting places, or the remains concerned predate the invasion of the gecko (before 1958: Nakamura and Uéno, 1959).

It is evident that the natural species diversity of the terrestrial squamate fauna on Yoronjima has been seriously underestimated. Three out of 10 indigenous species that historically existed on the island were missing from previous accounts, together with another three species whose occurrence in the fauna has been doubted (see above). There is a parallel case in Yoronjima amphibians: until we recovered the species' bones from garbage dump deposits, the native status of the Okinawa Green Tree Frog, *Rhacophorus viridis*, had been questioned because there was no plausible record from this island other than a few old museum specimens (Nakamura et al., 2009). It is notable that these newly documented species of herptiles have never been recorded in faunal surveys conducted in the past five decades (Maenosono and Toda, 2007; Nakamura et al., 2009), although based on literature records and museum specimens (see below), three of them (*Japalura polygonata polygonata*, *Dinodon semicarinatum*, and *Rhacophorus viridis*) are considered to have occurred there at least in the 1950s. Despite the infrequency of surveys, the faunal impoverishment shown by recent investigations is considered to be an accurate reflection of the current state of the herpetofauna due to Yoronjima's small scale, flat profile and resulting thoroughly surveyable nature. It seems safe to state that most of the remains examined here are no older than the late 19th century (although the possibility of intrusions of some heterochronic elements cannot be entirely ruled out; see below). Together, these conclusions suggest that the present results illustrate a prominent case of recent mass disappearance of indigenous herptile populations from an island, something that has never been documented in the Ryukyu Archipelago. The markedly recent character of the event suggests human involvement in the present case.

Due to the relatively impoverished state of the current Yoronjima vegetation (e.g., Ohno, 1991), it is likely that deforestation played a major role in the demise of these mostly woodland-dwelling species. Current vegetation cover (including forest, shrub, and grassland) is estimated at 4.94 km^2 (National Institute for Japanese Islands, 1994), less than a quarter of the total surface area, and much of the forest has been fragmented. However, the current species diversity of indigenous terrestrial squamates on Yoronjima (four species) is far lower than would be expected from the carrying capacity of the remnant forest. According to available data, at least 11 out of 21 major islands (> 1 km^2) in the Central Ryukyus hold comparable or smaller vegetated areas than Yoronjima (National Institute for Japanese Islands, 1994). All but one of these islands are known to possess richer indigenous terrestrial squamate faunas, based on records of existent specimens (Maenosono and Toda, 2007; Kojima et al., 2012). The exception, Kudakajima Island (area: 1.38 km^2, vegetated area: 0.65 km^2), has only four known species and mirrors the disproportionally poor nature of Yoronjima's current squamate fauna. Therefore, deforestation does not satisfactorily account for the disappearance of the discussed reptile and frog species from Yoronjima. Some other mechanism must have been at work.

A more plausible explanation for the disappearance of these herptiles assumes an exotic mammalian predator, the Japanese Weasel, *Mustela itatsi*, which was introduced in the mid-1950s (see below), as the causal agent. This agile and mostly nocturnal mustelid (Masuda and Watanabe, 2009) had been introduced to several islands of the Ryukyu Archipelago to control introduced rodents (e.g., Uchida, 1969; Shiraishi, 1982). In this archipelago where most islands lack native carnivorous mammals, these weasels have in multiple instances (at least 14 islands) been implicated in the declines of certain indigenous reptiles (e.g., Shibata, 1964; Toyama, 1983; Hikida et al., 1992; Ota and Masunaga, 2004; Toyama, 2005 and cited therein). A good deal of notoriety has attended the weasel because its introduction resulted in near extinction of an indigenous skink (*Plestiodon latiscutatus*, as *Eumeces okadae*) on Miyakejima Island in the Izu Islands of Japan (Hasegawa, 1999). Yoronjima is a small and isolated island, and as a consequence the population size of native herptiles would have been limited. There is little doubt that predation by weasels was sufficient to rid the island of these squamate reptiles and of the frog *Rhacophorus viridis*. Although *J. p. polygonata* and *R. viridis* are arboreal species, their frequent use of ground habitats may have left them vulnerable to the weasels' predation.

Chronological correlation also corroborates the idea that predation by weasels might have been responsible for the herptile extinctions on Yoronjima. The introduction of weasels to Yoronjima occurred in 1953, when 13 individuals were imported, and in 1955 or 1956, 60 more individuals (possibly more than 200: Iha, 1966) followed (Yotsumoto, 1959; Morita, 1988). The last records for *Japalura polygonata polygonata* and *Dinodon semicarinatum* are from 1955, those for *Rhacophorus viridis* from 1959 (Koba, 1956; Nakamura et al, 2009). In both cases, cessation of sightings seems to have followed closely on the introduction of the weasel. Causes and timing of the disappearance of the other species concerned (*Amphiesma pryeri*, *Ateuchosaurus pellopleurus*, a large-sized *Gekko* species, and *Goniurosaurus kuroiwae*) are unknown; it is however likely that they shared the same fate.

The extent to which recent or earlier human activities have affected the composition of local herpetofaunas in the Ryukyu Archipelago remains to be clarified by expanding records of Late Quaternary fossils and subfossils of terrestrial vertebrates. Documenting anthropogenic losses of terrestrial vertebrates would allow us to predict the relative ability of species or populations to persist under human impacts, as well as informing conservation management of currently endangered species/populations. The present study shows that some populations of indigenous squamates vanished from Yoronjima. Although their conspecifics (or members of the same subspecies) still exist on other islands, their disappearance from Yoronjima may be a matter of serious concern because there is no guarantee that the currently accepted taxa provide appropriate units for conservational considerations (Ota, 2000). Moreover, these populations have disappeared before their taxonomic status could have been verified by modern taxonomic techniques. Taxonomic investigation of amphibians and reptiles of the Ryukyu Archipelago is far from completion, as illustrated by a series of recent findings (e.g., Toda et al., 2008; Matsui, 2011). It is now evident that in terms of population genetics and morphology, there are several levels of intraspecific diversity in certain island populations of amphibians and reptiles in this archipelago (e.g., Shibaike et al., 2009). These circumstances raise the question about whether the losses on Yoronjima can be treated as just the demise of local populations.

A concluding question to be addressed here is how the rich accumulation of terrestrial vertebrate remains in the investigated garbage dump was developed. This site appears to have no structural peculiarity that would turn it into a natural trap for these animals, but it has to some extent acted as a sink for surface waste. Owl activity as the most frequently attributed factor for the accumulation of small terrestrial vertebrate remains is not in evidence here, as the components of this bone assemblage are a mixture of diurnal (*Japalura* and skinks) and nocturnal species (others) with a considerable range of body sizes, ranging from tiny *Ateuchosaurus* to *Rattus norvegicus*. The only known resident owl on Yoronjima is the Brown Hawk-owl, *Ninox scutulata* (Amami Ornithologists' Club, 2009); it is a relatively small-sized bird (~30 cm in total length) and therefore its exclusive involvement in the accumulation of these vertebrate remains seems to be improbable. With the exception of the sea snake, dietary use of these vertebrates by humans is also unlikely; many of the identified species of squamates and frogs seem to be too small to use as food resources for humans, and none of the material from the site showed any sign of cooking or having been worked. We suppose that some of the finds may be incidental remains from animals died in the vicinity, but mostly the animals found here may have foraged in the dump for arthropods and small vertebrates associated with garbage and leftovers from the inhabitants, and have died or been killed there. Co-occurrence of their remains suggests that rodents and shrews were likely to be involved, although none of the examined reptilian and amphibian remains showed clear evidence of marks attributable to these scavengers. If this conjecture holds true, remains of old garbage dumps, very common facilities anywhere in the world, would offer effective data sources to reveal recent changes in the biodiversity of terrestrial vertebrate faunas, particularly those of limestone islands in lower latitudes.

ACKNOWLEDGEMENTS

We thank Seiji Moriyama and the late Shinichiro Moriyama for permission to carry out sampling on his land; Jumpei Ichikawa, Shun`ichi Matsumura, and Yoshitaka Tahara for providing us with comparative material; Mamoru Toda (University of the Ryukyus) for permission of use of specimens in his care; and Kentaro Hagari and Motohiro Okade for help of part of fieldwork. We also thank Julien Claude (ISE-M, France) and Krister T. Smith (Senckenberg Research Institute and Natural History Museum, Germany) for valuable comments to the manuscript. This study was partially supported by a Grant-in-Aid to The 21st Century COE Program at the University of the Ryukyus from the Ministry of Education, Culture, Sports, Science and Technology, Japan (Monbu-Kagaku-Sho). Supplementary material associated with this article can be found at http://www.unipv.it/webshi/appendix Manuscript number 11924.

REFERENCES

Amami Ornithologists' Club (2009): Birds of Amami. Bun-ichi Sogo Shuppan, Tokyo. (in Japanese)

Arnold, E.N. (1976): Fossil reptiles from Aldabra Atoll, Indian Ocean. Bull. Br. Mus. (Nat. Hist.) Zool. **29**: 85-116.

Arnold, E.N. (1997): Interrelationships and evolution of the east Asian grass lizards, *Takydromus* (Squamata: Lacertidae). Zool. J. Lin. Soc. **119**: 267-296.

Arnold, E.N., Arribas, O., Carranza, S. (2007): Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa **1430**: 1-86.

Boulenger, G.A. (1887): On a collection of reptiles and batrachians made by Mr. H. Pryer in the Loo Choo Islands. Proc. Zool. Soc. Lond. **1887**: 146-150.

Case, T.J., Bolger, D.T., Richman, A.D. (1998): Reptilian extinctions over the last ten thousand years. In: Conservation Biology: for the Coming Decade, Second Edition, pp. 157-186. Fiedler, P.L., Kareiva, P.M., Eds, Chapman & Hall, New York.

Cope, E.D. (1860): Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia, with notes and descriptions of new species. Part 2. Proc. Acad. Nat. Sci. Philadelphia **12**: 241-266.

Environment Agency (2000): Threatened Wildlife of Japan. Red Data Book Second Edition, Volume 3, Reptilia and Amphibia. Japan Wildlife Research Center, Tokyo. (in Japanese)

Estes, R. (1983): Sauria Terrestria, Amphisbaenia. Encyclopedia of Paleoherpetology, Part 10A. Gustav Fischer Verlag, Stuttgart.

Estes, R., de Queiroz, K., Gauthier, J. (1988): Phylogenetic relationships within Squamata. In: Phylogenetic Relationships of the Lizard Families, Essays Commemorating Charles L. Camp, pp. 119-281. Estes, R., Pregill, G., Eds, Stanford University Press, Stanford.

Funakoshi, K., Osawa, Y., Osawa, K. (2006): Distribution of the Ryukyu flying-fox (*Pteropus dasymallus inopinatus*) on islands adjacent to Okinawa Island, with special reference to their ecology on Yoron Island. Mammalian Science **46**: 29-34. (in Japanese with English abstract)

Greer, A.E. (1970): A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool. **139**: 151-183.

Grismer, L.L., Ota, H., Tanaka, S. (1994): Phylogeny, classification, and biogeography of *Goniurosaurus kuroiwae* (Squamata: Eublepharidae) from the Ryukyu Archipelago, Japan, with description of a new subspecies. Zool. Sci. **11**: 319-335.

Grismer, L.L., Viets, B.E., Boyle, L.J. (1999): Two new continental species of *Goniurosaurus* (Squamata: Eublepharidae) with a phylogeny and evolutionary classification of the genus. J. Herpetol. **33**: 382-393.

Grismer, L.L., Shi, H., Orlov, N.L., Ananjeva, N.B. (2002): A new species of *Goniurosaurus* (Squamata: Eublepharidae) from Hainan Island, China. J. Herpetol. **36**: 217-224.

Hallowell, E. (1861 ["1860"]): Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U.S.N. P. Acad. Nat. Sci. Phila. **12**: 480-510.

Hasegawa, M. (1999): Impacts of the introduced weasel on the insular food webs. In: Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation, pp. 129-154. Ota, H., Ed, Elsevier Science B.V., Amsterdam.

Henderson, R.W. (1992): Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies. Caribb. J. Sci. **28**: 1-10.

Hikida, T., Ota, H., Toyama, M. (1992): Herpetofauna of an encounter zone of Oriental and Palearctic elements: Amphibians and reptiles of the Tokara Group and adjacent islands in the Northern Ryukyus, Japan. Biol. Mag. Okinawa **30**: 29-43.

Hoffstetter, R., Gasc, J.-P. (1969): Vertebrae and ribs of modern reptiles. In: Biology of the Reptilia, pp. 201-310. Gans, C., Bellairs, A.d'A., Parsons, T.S., Eds, Academic Press, London.

Holman, J.A. (2000): Fossil Snakes of North America. Origin, Evolution, Distribution, Paleoecology. Indiana University Press, Bloomington.

Honda, M., Okamoto, T., Hikida, T., Ota, H. (2008): Molecular phylogeography of the endemic five-lined skink (*Plestiodon marginatus*) (Reptilia: Scincidae) of the Ryukyu Archipelago, Japan, with special reference to the relationship of a northern Tokara population. Pac. Sci. **62**: 351-362.

Iha, K. (1966): Introduction records of the Japanese Weasel as a natural enemy of the rodents. Journal of Okinawa Agriculture **5**: 45-53. (in Japanese)

Ikeda, T. (2007): A comparative morphological study of the vertebrae of snakes occurring in Japan and adjacent regions. Curr. Herpetol. **26**: 13-34.

Kluge, A.G. (1967): Higher taxonomic categories of gekkonid lizards and their evolution. Bull. Am. Mus. Nat. Hist. **135**: 1-59, pls. 1-5.

Koba, K. (1956): Herpetofauna of the Amami Group of the Loo Choo Islands, I. Memoirs of the Faculty of Education, Kumamoto University **4**: 148-164, 2pls. (in Japanese with English abstract)

Kojima, K., Honda, M., Takiguchi, I., Ota, H. (2012): Genetic diversification in *Dinodon semicarinatum* (Squamata, Colubridae) from the Central Ryukyus, Japan, inferred from mitochondrial DNA. Bulletin of the Herpetological Society of Japan **2012**: 62-63. (in Japanese)

LaDuke, T.C. (1991): The fossil snakes of Pit 91, Rancho La Brea, California. Contrib. Sci. Natur. Hist. Mus. Los Angeles County **424**: 1-28.

Lever, C. (2003): Naturalized Reptiles and Amphibians of the World. Oxford University Press, Oxford.

Maenosono, T., Toda, M. (2007): Distributions of amphibians and terrestrial reptiles in the Ryukyu Archipelago: A review of published records. Akamata **18**: 28-46. (in Japanese)

Malnate, E.V. (1972): Observations on the vertebral hypapophyses and associated musculature in some snakes, with special reference to the Colubridae. Zool. Med. Leiden **47**: 225-239.

Masuda, R., Watanabe, S. (2009): *Mustela itatsi*. In: The Wild Mammals of Japan, pp. 240-241. Ohdachi, S.D., Ishibashi, Y., Iwasa, M.A., Saitoh, T., Eds, Shoukadoh, Kyoto.

Matsui, M. (2011): On the brown frogs from the Ryukyu Archipelago, Japan, with descriptions of two new species (Amphibia, Anura). Curr. Herpetol. **30**: 111-128.

Ministry of the Environment (2010): Japan Biodiversity Outlook. Report of Comprehensive Assessment of Biodiversity in Japan. Ministry of the Environment, Tokyo.

Morita, T. (1988): Terrestrial animals. In: History of Yoron Town (Yoron Cho-shi), pp. 36-49. History of Yoron Town Editing Committee, Ed, Yoron Town Board of Education, Yoron. (in Japanese)

Motokawa, M. (2007): Distribution and new localities of small mammals in the central part of the Ryukyu Archipelago, Japan. Bull. Biogeogr. Soc. Japan **62**: 3-9. (in Japanese with English abstract)

Motoyama, F. (1988): Social system and its environment. In: History of Yoron Town (Yoron Cho-shi), pp. 78-112. History of Yoron Town Editing Committee, Ed, Yoron Town Board of Education, Yoron. (in Japanese)

Nakamura, K., Uéno, S.-I. (1959): The geckos found in the limestone caves of the Ryu-Kyu Islands. Mem. Coll. Sci. Univ. Kyoto Ser. B **26**: 45-52, pl. 1.

Nakamura, Y., Takahashi, A., Ota, H. (2009): Evidence for the recent disappearance of the Okinawan tree frog *Rhacophorus viridis* on Yoronjima Island of the Ryukyu Archipelago, Japan. Curr. Herpetol. **28**: 29-33.

Namiye, M. (1912): On the gekkonid lizards of Okinawa. Zool. Mag. (Tokyo) **286**: 442-445, pl. 6. (in Japanese)

National Institute for Japanese Islands (1994): Annual Report of Statistics on Japanese Islands 1994. National Institute for Japanese Islands, Tokyo. (in Japanese)

Odawara, K., Iryu, Y. (1999): Pleistocene coral reef deposits (the Ryukyu Group) on Yoron-jima, Kagoshima Prefecture, Japan. Journal of the Geological Society of Japan **105**: 273-288. (in Japanese with English abstract)

Ohno, T. (1991): Flora of Yoronjima. Minaminihon-bunka **24**: 113-139. (in Japanese)

Okinawa Prefectural Board of Education (1993): Kikuzato's Stream Snake (*Opisthotropis kikuzatoi*): Its Status and Conservation. Survey Reports on Natural Monuments of Okinawa Prefecture, 33. Okinawa Prefectural Board of Education, Naha. (in Japanese)

Ota, H. (1986): A review of reptiles and amphibians of the Amami Group, Ryukyu Archipelago. Mem. Fac. Sci., Kyoto Univ., Ser biol. **11**: 57-71.

Ota, H. (1996): Gekkonidae. In: The Encyclopedia of Animals in Japan, pp. 69-71. Sengoku, S., Hikida, T., Matsui, M., Nakaya, K., Eds, Heibonsha, Tokyo. (in Japanese)

Ota, H. (1998): Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res. Popul. Ecol. **40**: 189-204.

Ota, H. (2000): Current status of the threatened amphibians and reptiles of Japan. Popul. Ecol. **42**: 5-9.

Ota, H. (2003a): *Japalura polygonata polygonata*. In: Threatened Wild Animals and Plants in Kagoshima Prefecture, Animal Edition, p. 90. Kagoshima Prefectural Government, Ed, Society for Environmental Technology of Kagoshima, Kagoshima. (in Japanese)

Ota, H. (2003b): *Eumeces latiscutatus* populations on Akusekijima and Tairajima Islands, Tokara Island Group. In: Threatened Wild Animals and Plants in Kagoshima Prefecture, Animal Edition, p. 101. Kagoshima Prefectural Government, Ed, Society for Environmental Technology of Kagoshima, Kagoshima. (in Japanese)

Ota, H., Masunaga, G. (2004): Herpetofauna of the Kerama Islands, Ryukyu Archipelago, Japan. Midoriishi **15**: 29-35. (in Japanese)

Ota, H., Toda, Mi., Masunaga, G., Kikukawa, A., Toda, Ma. (2004): Feral populations of amphibians and reptiles in the Ryukyu Archipelago, Japan. Global Environ. Res. **8**: 133-143.

Pope, C.H. (1928): Four new snakes and a lizard from South China. Am. Mus. Novit. **325**: 1-4.

Pregill, G. (1986): Body size of insular lizards: A pattern of Holocene dwarfism. Evolution **40**: 997-1008.

Pregill, G. (1998): Squamate reptiles from prehistoric sites in the Mariana Islands. Copeia **1998**: 64-75.

Pregill, G.K., Steadman, D.W. (2004): South Pacific iguanas: human impacts and a new species. J. Herpetol. **38**: 15-21.

Pregill, G.K., Worthy, T.H. (2003): A new iguanid lizard (Squamata, Iguanidae) from the Late Quaternary of Fiji, Southwest Pacific. Herpetologica **59**: 57-67.

Rage, J.-C. (1984): Serpentes. Encyclopedia of Paleoherpetology, Part 11. Gustav Fischer Verlag, Stuttgart.

Rieppel, O. (1984): The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). Zool. J. Lin. Soc. **82**: 291-318.

Samejima, M. (1991): Animals of Yoronjima Island. Minaminihon-bunka **24**: 71-84. (in Japanese)

Shibaike, Y., Takahashi, Y., Arikura, I., Iiizumi, R., Kitakawa, S., Sakai M., Imaoka, C., Shiro, H., Tanaka, H., Akakubo, N., Nakano, M., Watanabe, M., Ohne, K., Kubota, S., Kohno, S., Ota, H. (2009): Chromosome evolution in the lizard genus *Gekko* (Gekkonidae, Squamata, Reptilia) in the East Asian islands. Cytogenet. Genome Res. **127**: 182-190.

Shibata, Y. (1964): Amphibians and reptiles from Okierabujima, Amami Group. Research Report of Kansai Nature and Culture Research Group **1**: 13-16. (in Japanese)

Shiraishi, S. (1982): The weasel as a rat-control agent. Collecting and Breeding **44**: 414-419. (in Japanese)

Smith, K.T., Schaal, S.F.K., Sun, W., Li, C.-T. (2011): Acrodont iguanians (Squamata) from the middle Eocene of the Huadian Basin of Jilin Province, China, with a critique of the taxon "*Tinosaurus*". Vert. Pal. Asiat. **49**: 69-84.

Steadman, D.W. (2006): Extinction and Biogeography of Tropical Pacific Birds. University of Chicago Press, Chicago.

Stejneger, L. (1907): Herpetology of Japan and adjacent territory. Bull. U. S. Natl. Mus. **58**: 1-577.

Szyndlar, Z. (1991): A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estud. Geól. **47**: 237-266.

Takamiya, H., Chinen, I. (1984): Survey on prehistoric and ancient archeological sites in the southeastern part of Yoronjima Island (preliminary report). Minaminihon-bunka **17**: 15-33. (in Japanese)

Takara, T. (1962): Studies on the terrestrial snakes in the Ryukyu Archipelago. Science Bulletin of the Division of Agriculture, Home Economics & Engineering, University of the Ryukyus **9**: 1-202, 22 pls. (in Japanese with English summary)

Toda, M. (2008): External characters useful to discriminate *Gekko hokouensis* and its cryptic undescribed species of the Okinawa Group, Japan: A preliminary report. Akamata **19**: 23-30. (in Japanese)

Toda, M., Sengoku, S., Hikida, T., Ota, H. (2008): Description of two new species of the genus *Gekko* (Squamata: Gekkonidae) from the Tokara and Amami Island Groups in the Ryukyu Archipelago, Japan. Copeia **2008**: 452-466.

Toda, M., Takahashi, H. (2002): A record of the green grass lizard, *Takydromus smaragdinus*, from Yoronjima Island of the Amami Group, Ryukyu Archipelago. Akamata **16**: 25-26. (in Japanese)

Toriba, M. (1996): Viperidae and Elapidae. In: The Encyclopedia of Animals in Japan, pp. 109-111. Sengoku, S., Hikida, T., Matsui, M., Nakaya, K., Eds, Heibonsha, Tokyo. (in Japanese)

Toyama, M. (1983): Preliminary reports on the herpetological fauna of the Okinawa Islands, Ryukyu Archipelago (II). In: General Survey Report of the Okinawa Prefectural Museum, III, Zamami Village, pp. 16-22. Okinawa Prefectural Museum, Ed, Okinawa Prefectural Museum, Naha. (in Japanese)

Toyama, M. (2005): *Eumeces kishinouyei*. In: Threatened Wildlife in Okinawa, Second Edition, Animals, Red Data Okinawa, pp. 121-122. Okinawa Prefectural Government, Ed, Okinawa Prefectural Government, Naha. (in Japanese)

Uchida, T. (1969): Rat-control procedures on the Pacific islands, with special reference to the efficiency of biological control agents. II. Efficiency of the Japanese weasel, *Mustela sibirica itatsi* Temminck & Schlegel, as a rat-control agent in the Ryukyus. J. Fac. Agric., Kyushu Univ. **15**: 355-385.

Yamada, F., Ogura, G., Abe, S. (2009): *Herpestes javanicus*. In: The Wild Mammals of Japan, pp. 264-266. Ohdachi, S.D., Ishibashi, Y., Iwasa, M.A., Saitoh, T., Eds, Shoukadoh, Kyoto.

Yotsumoto, T. (1959): Mink grazing to the island of Amami Oshima, Ryukyu. Japan Wildlife Bulletin **17**: 156-158. (in Japanese)

Watari, Y., Takatsuki, S., Miyashita, T. (2008): Effects of exotic mongoose (*Herpestes javanicus*) on the native fauna of Amami-Oshima Island, southern Japan, estimated by distribution patterns along the historical gradient of mongoose invasion. Biol. Invasions **10**: 7-17.

Whittaker, R.J., Fernández-Palacios, J.M. (2007): Island Biogeography: Ecology, Evolution and Conservation (Second Edition). Oxford University Press, Oxford.

APPENDIX

Skeletal specimens examined

Listed those of snakes and lizards occurring in the Central Ryukyus, extralimital taxa were omitted. Acronyms are KUZR = Kyoto University Museum Zoological Specimens and NPN = Y. Nakamura private collection.

Snakes—*Achalinus werneri*: Okinawajima (NPN 1091); *Amphiesma pryeri*: Amamioshima (NPN 774), Okinawajima (NPN 650, 651, 774, 775, 776, 1067, 1090); *Cyclophiops semicarinatus*: Okinawajima (NPN 511, 512, 648, 649, 858); *Dinodon semicarinatum*: Okinawajima (NPN 009, 513, 653, 777, 778, 779, 780, 859); *Emydoceph-

alus ijimae: Okinawajima (NPN 1085, 1087); *Hydrophis melanocephalus*: Iriomotejima (NPN 1080), Okinawajima (NPN 1086); *Laticauda colubrina*: Iriomotejima (NPN 857); *Laticauda laticaudata*: Iriomotejima (NPN 726); *Laticauda semifasciata*: Miyakojima (NPN 1074); *Protobothrops flavoviridis*: Okinawajima (NPN 1093); *Ovophis okinavensis*: Okinawajima (NPN 1094); *Ramphotyphlops braminus*: Okinawajima (NPN 1102); *Sinomicrurus japonicus japonicus*: Amamioshima (NPN 1088); *Sinomicrurus japonicus boettgeri*: Okinawajima (NPN 656). Lizards—*Ateuchosaurus pellopleurus*: Amamioshima (NPN 510), Okinawajima (NPN 1051, 1096); *Gehyra mutilata*: Ukejima (NPN 504); *Gekko hokouensis*: Okinawajima (KUZR 62307, 62308, 62317, 62319, 62424, NPN 1070, 1071), Ukejima (NPN 509), Yoronjima (KUZR 62240, 62264, 62265, NPN 644, 645); *Gekko shibatai*: Takarajima (KUZR 62272, 62274, 62275, 62279, 62345, 62364); *Gekko vertebralis*: Kotakarajima (KUZR 62266, 62267, 62268, 62269, 62280, 62388, 62389); *Gekko* sp.: Okinawajima (KUZR 62354, 62390, 62392, 62397, 62410, 62421, 62422, 62423, 62435, NPN 1095); *Goniurosaurus kuroiwae kuroiwae*: Okinawajima (KUZR 52392, 65827, 67952, 71631, 71909); *Goniurosaurus kuroiwae orientalis*: Tokashikijima (KUZR 71908); *Hemidactylus bowringii*: Ukejima (NPN 506); *Hemidactylu*s *frenatus*: Okinawajima (NPN 1068, 1069, 1097, 1098), Yoronjima (NPN 646, 647); *Japalura polygonata polygonata*: Amamioshima (NPN 767), Okinawajima (NPN 1042, 1051), Tokashikijima (NPN 632, 633, 634, 635, 636); *Lepidodactylus lugubris*: Okinawajima (NPN 1046, 1047); *Plestiodon barbouri*: Okinawajima (KUZR 62980, 62981); *Plestiodon marginatus*: Okinawajima (NPN 382, 654, 655); *Takydromus smaragdinus*: Okinawajima (NPN 285, 643, 1099, 1100).

SUPPLEMENTARY MATERIAL

Photographs of selected skeletal elements of snakes and lizards occurring in the Central Ryukyus

Fig. S1. Middle trunk vertebrae of typhlopid (A) and colubrid (B-E) snakes. (A) *Ramphotyphlops braminus* (NPN 1102), (B) *Achalinus werneri* (NPN 1091), (C) *Cyclophiops semicarinatus* (NPN 512), (D) *Dinodon semicarinatum* (NPN 513), and (E) *Amphiesma pryeri* (NPN 774). Left to right: anterior, lateral (left), posterior, dorsal, and ventral views. Scale bars equal 1 mm.

Fig. S2. Middle trunk vertebrae of viperid (A, B) and elapid (C, D) snakes. (A) *Ovophis okinavensis* (NPN 1094), (B) *Protobothrops flavoviridis* (NPN 1093), (C) *Emydocephalus ijimae* (NPN 1087), and (D) *Hydrophis melanocephalus* (NPN 1080). Left to right: anterior, lateral (left), posterior, dorsal, and ventral views. Scale bars equal 1 mm.

Fig. S3. Middle trunk vertebrae of elapid snakes (continued). (A) *Laticauda colubrina* (NPN 857), (B) *L. laticaudata* (NPN 726), (C) *L. semifasciata* (NPN 1074), and (D) *Sinomicrurus japonicus boettgeri* (NPN 656). Left to right: anterior, lateral (left), posterior, dorsal, and ventral views. Scale bars equal 1 mm.

Fig. S4. Maxilla and mandibles of agamid (A, B), scincid (C-E), and lacertid (F) lizards (in medial views). (A) right maxilla of *Japalura polygonata polygonata* (NPN 1051), (B) right mandible of *J. p. polygonata* (NPN 1051), (C) right mandible of *Ateuchosaurus pellopleurus* (NPN 1096), (D) right mandible of *Plestiodon barbouri* (KUZ R62980), (E) right mandible of *P. marginatus* (NPN 665), and (F) right mandible of *Takydromus smaragdinus* (NPN 643). Scale bars equal 1 mm.

Fig. S5. Mandibles of gekkotan lizards (in medial views). (A) right mandible of *Gehyra mutilata* (NPN 504), (B) right mandible of *Gekko hokouensis* (NPN 644), (C) right mandible of *G. shibatai* (KUZR 62274), (D) right mandible of *G. vertebralis* (KUZR 62267), (E) right mandible of *Gekko* sp. (KUZR 62392), (F) right mandible of *Hemidactylus bowringii* (NPN 506), (G) right mandible of *H. frenatus* (NPN 1098), (H) right mandible of *Lepidodactylus lugubris* (NPN 1046), and (I) left mandible of *Goniurosaurus kuroiwae kuroiwae* (KUZR 71631). Scale bars equal 1 mm.

Fig. S6. Maxillae of gekkotan lizards (in medial views). (A) left maxilla of *Gehyra mutilata* (NPN 504), (B) right maxilla of *Gekko hokouensis* (NPN 644), (C) right maxilla of *G. shibatai* (KUZR 62274), (D) right maxilla of *G. vertebralis* (KUZR 62267), (E) right maxilla of *Gekko* sp. (KUZR 62392), (F) right maxilla of *Hemidactylus bowringii* (NPN 506), (G) right maxilla of *H. frenatus* (NPN 1098), (H) right maxilla of *Lepidodactylus lugubris* (NPN 1046), and (I) right maxilla (dorsal part broken) of *Goniurosaurus kuroiwae kuroiwae* (KUZR 71631). Scale bar equals 1 mm.

Fig. S7. Frontals of gekkotan lizards (in dorsal [right] and ventral [left] views). (A) *Gehyra mutilata* (NPN 504), (B) *Gekko hokouensis* (NPN 644), (C) *G. shibatai* (KUZR 62274), (D) *G. vertebralis* (KUZR 62267), (E) *Gekko* sp. (KUZR 62392), (F) *Hemidactylus bowringii* (NPN 506), (G) *H. frenatus* (NPN 1098), (H) *Lepidodactylus lugubris* (NPN 1046), and (I) *Goniurosaurus kuroiwae orientalis* (KUZR 71908) with anterior part of the skull. Scale bars equal 1 mm.