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A new, recently extinct subspecies of the Kuroiwa's Leopard Gecko, *Goniurosaurus kuroiwae* (Squamata: Eublepharidae), from Yoronjima Island of the Ryukyu Archipelago, Japan

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Abstract. A new subspecies of the eublepharid gecko, *Goniurosaurus kuroiwae*, is described on the basis of fragmentary bones recovered from a midden on Yoronjima Island, Ryukyu Archipelago, Japan. It differs from the other conspecific subspecies in having a unique combination of osteological character states: in particular, the maxilla contains a posteriorly extended maxillary shelf and a scarcely inclined lateral wall above the posterior tooth row, and the frontal contains a widened anterior section and a laterally overhanging anterior part of lateral prefrontal facet, both of which differentiate this new subspecies from the morphologically most similar *G. k. kuroiwae*. The new subspecies, endemic to Yoronjima Island, may have gone extinct, together with several other amphibians and reptiles on the island — most likely due to human-related deforestation and increased predation pressure from introduced weasels.

Keywords. Biodiversity, extinction, human impacts, lizard, subfossil.

INTRODUCTION

Kuroiwa's Leopard Gecko, *Goniurosaurus kuroiwae* (Namiye, 1912), sensu Grismer et al. (1994), is a eublepharid gecko endemic to the central part of the Ryukyu Archipelago, Japan, in the subtropical northwestern Pacific. It is isolated from the rest of its congeners occurring in southeastern continental China, northern Vietnam, and adjacent coastal islands (Grismer et al., 2002; Ziegler et al., 2008; Orlov et al., 2008; Wang et al., 2010, 2013), and the species represents the easternmost Old World member of the family (Grismer, 1988; Grismer et al., 1994). Because this species (or species complex, see below) consists of a number of allopatric and apparently diagnosably divergent insular populations, its classification has been the subject of much controversy. In the latest revision (Grismer et al., 1994), its populations were combined into a single species comprising five extant subspecies: *G. k. kuroiwae* (Namiye, 1912); *G. k. orientalis* (Maki, 1930); *G. k. splendens* (Nakamura and Uéno, 1959); *G. k. toyamai* Grismer et al., 1994; and *G. k. yamashinae* (Okada, 1936). Later, Grismer et al. (1999, 2002), adopting the evolutionary species concept, referred to each of these taxa as full species, and this taxonomic treatment has been widely accepted in the context of the recent trend of disuse of the subspecies rank by herpetologists. However, we believe that such changes in taxonomic rank are premature, because diagnostic characters originally proposed to define each of these taxa are few in number and, moreover, include those with highly variable character states. For example, yellow-brown to gold iris color was considered as one of the character states that

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discriminates *G. k. yamashinae* from the other subspecies whose irises are blood-red in color (Grismer et al., 1994), but *G. k. kuroiwae* populations from Okinawajima and adjacent islets also include individuals with more or less yellow irises (H.Ota, unpublished observations). We therefore prefer to take a conservative stance with respect to the taxonomic treatment of *G. kuroiwae* sensu lato by maintaining the framework of Grismer et al. (1994).

The species has been recorded from 10 islands of the Okinawa Island Group and one island of the Amami Island Group (Grismer et al., 1994; Kurita and Kawamura, 2011). Its patchy insular distribution has baffled biogeographers. This is best exemplified in the species' absence from islands between Tokunoshima Island in the Amami Island Group, where *G. k. splendens* occurs, and islands of the Okinawa Island Group, where the other four subspecies occur (Grismer et al., 1994). This distributional gap is now partially filled by our discovery of bone fragments from a presumed cultural deposit on Yoronjima Island, an islet representing the southwesternmost extremity of the Amami Group (Nakamura et al., 2013; Fig. 1).

The available skeletal elements of the Yoronjima *G. kuroiwae* are rather few in number and fragmentary, but they deserve careful morphological investigation as these are the only available evidence for the population on Yoronjima that has recently become extinct (see below). Our detailed morphological investigations using comparative specimens, including representatives of all known conspecific subspecies, revealed that the Yoronjima *G. kuroiwae* has a unique suite of character states that differentiates it from the others, warranting recognition as a new subspecies as described below. Given the presumed recency of the bones, the present finding most likely represents a human-induced extinction of an insular squamate taxon, which has never before been documented in Japan (including the Ryukyus).

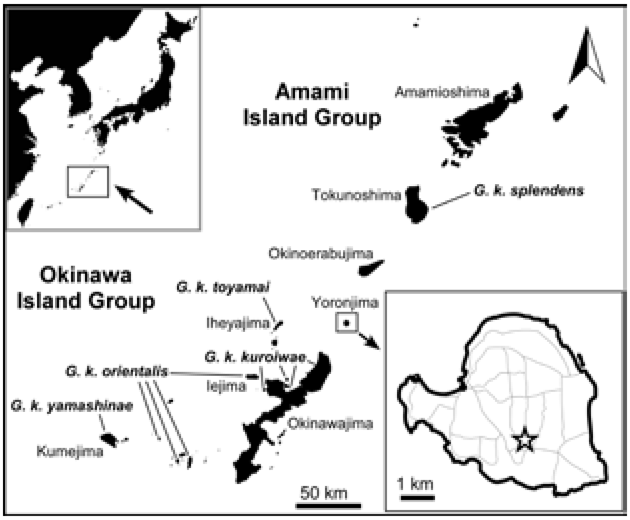

Fig. 1. Map of the Central Ryukyus showing the location of Yoronjima Island and the distribution of *Goniurosaurus kuroiwae* subspecies. Star indicates the study site.

MATERIAL AND METHODS

Yoronjima is a small (20.5 km^2), flat (97 m elevation) limestone island lying 40 km southwest of Okinoerabujima Island in the Amami Island Group, and 30 km northeast of Okinawajima Island of the Okinawa Island Group (Fig. 1). Brief descriptions of Yoronjima and the sampling site are presented in Nakamura et al. (2013). The skeletal remains of *Goniurosaurus kuroiwae* subspecies that are described here were retrieved from deposits under a limestone rock shelter located approximately 150 m east of the Takachiho Shrine, Asato (27°02'05"N, 128°26'02"E; Fig. 1). The site appeared to be a midden, as the deposits were mixed with soil, numerous marine fish bones, and modern artifacts (such as fragments of tableware and glass bottles). Among the artifacts, the fragmentary glass bottles were estimated to be from no earlier than the 19th century. Based on the species composition and preservation of terrestrial vertebrate elements (four species of frogs, ten species of squamate reptiles [including *G. kuroiwae*], a shrew, and some non-native rodents such as the Black Rat [*Rattus rattus*], all of which were mostly preserved in fine condition), we believe that this accumulation of skeletal remains is derived from animals that were attracted by invertebrates associated with garbage (Nakamura et al., 2013).

The site yielded at least 19 bone fragments of *G. kuroiwae*, of which some were reported preliminarily in our preceding paper, along with associated remains of several other squamates (Nakamura et al., 2013). The Yoronjima *G. kuroiwae* material was compared with partially skeletonized specimens of known *G. kuroiwae* subspecies (see Appendix). One of the difficulties in this study arose from the scarcity of available *G. kuroiwae* specimens for osteological comparisons. Most of the subspecies are poorly represented by museum specimens because their populations are currently endangered due to loss of habitat, predation by exotic mammals, and frequent illegal collections for pet trade; thus, they are under the strict protection of the prefectural laws of Okinawa and Kagoshima (Tanaka, 2005a, b, c, d; Ota, 2010). Unfortunately, we were unable to examine the maxilla of *G. k. toyamai*, and the axis and the frontal of *G. k. toyamai* and *G. k. yamashinae*. Likewise, disarticulated skeletal elements, such as frontals, available for comparison were very limited (see Table 2). Moreover, with regard to some specimens of *G. k. kuroiwae* (derived from roadkill), some of the elements were not observable due to fracture.

Body size (snout–vent length, SVL) of the Yoronjima material was estimated based on measurements taken from certain elements of extant *G. kuroiwae* skeletons with size data. The relevant regressions (where x = bone measurement and y = SVL) were: length of the dentary tooth row (right), $y = -9.8 + 9.04x$, $r^2 = 0.79$, $P < 0.0001$, n = 16; interorbital width of the frontal, y = -20.8 + 45.5x, $r^2 = 0.73$, $P < 0.01$, n = 8; length of the humerus, y = -29.5 + 8.54x, $r^2 = 0.96$, $P < 0.0001$, n = 8 (five right and three left bones from eight individuals); and the length of the femur, y = -33.4 + 7.39x, $r^2 = 0.9$, $P < 0.01$, n = 8 (the same side as the humerus).

Morphological comparisons were performed using a binocular microscope (Nikon SMZ-10), and drawings were made using a camera lucida. Measurements were taken with ImageJ (US National Institutes of Health, Bethesda, MD; http://imagej.nih.gov/ij/) or an ocular micrometer. Numerical calculations were performed using the program R (R Development Core Team, 2011). Osteological terminology followed that of Camp (1923), Estes et al. (1988), and Conrad (2004). All of the examined subfossil material was deposited in the Fujukan, Museum of the University of the Ryukyus, Nishihara, Okinawa, Japan (RUMF).

RESULTS

Systematics

Goniurosaurus kuroiwae yunnu Nakamura, Takahashi and Ota, subsp. nov. (Figs. 2-4; Tables 1, 2)

Type material

Holotype: RUMF-GF-4076, a well-preserved left maxilla, collected by Akio Takahashi, Kentaro Hagari, and Motohiro Okade on 19 November 2011. Paratypes: One right maxilla (RUMF-GF-4075), three right and three left dentaries (RUMF-GF-4077 to 4082), six frontals

Table 1. Summary of selected morphometric and meristic data for the subspecies of *Goniurosaurus kuroiwae.* Numerals in parentheses indicate sample sizes, and those in brackets indicate medians (for ratios) or means ± 1 standard error (for others). NC = not compared. R = right, L = left. All measurements are in mm.

Subspecies	*yunnu*	*kuroiwae*	*orientalis*	*splendens*	*toyamai*	*yamashinae*
n		5	4	6	2	1
Maxilla (left)						
Tooth count	52 (1)	41-50 (4) [45.5 ± 1.85]	42-51 [47 ± 1.96]	44-50 [46.2 ± 0.83]	NC	43
Frontal						
Width at the point of the base of the anterolateral processes (Wbap)	3.22 (1)	2.74-3.27 (4) [3.12 ± 0.13]	2.8 (1)	2.98-3.25 (4) [3.09 ± 0.06]	NC	NC
Interorbital width (Wi)	1.92, 1.94, 2.08, 2.13 (4) [2.02 ± 0.05]	2.04-2.47 (4) [2.3 ± 0.09]	2.08 (1)	2.0-2.16 (4) [2.09 ± 0.04]	NC	NC
Wbap/Wi (%)	168 (1)	132-142 (4) [134.5]	135 (1)	144-152 (4) [148]	NC	NC
Dentary (right, unless noted)						
Surface length of anterodorsal margin of lateral coronoid facet (Lalcf)	1.09, 0.96, 0.83 (2R, 1L) [0.96 ± 0.08]	0.65-0.96 (4R, 1L) [0.85 ± 0.06]	0.63-1.41 [1.06 ± 0.16]	0.68-0.9 [0.74 ± 0.03]	0.79, 0.9	0.79
Length of ventral margin of lateral coronoid facet (Lvlcf)	2.18, 1.97, 1.95 (2R, 1L) [2.03 ± 0.07]	1.41-2.6 (4R, 1L) [1.99 ± 0.2]	1.06-1.76 [1.33 ± 0.15]	0.91-1.53 [1.23 ± 0.09]	1.3, 1.74	1.09
Lvlcf/Lalcf (%)	200, 205, 235 (2R, 1L) [205]	198-280 (4R, 1L) [227]	114-168 [119.5]	125-187 [173]	165, 193	138
Tooth count	50, 53, 51, 52 (2R, 2L) [51.5 ± 0.65]	41-53 [47.6 ± 2.23]	47-51 [49.5 ± 0.96]	46-52 [49.8 ± 0.98]	52, 50*	48
Tooth row length	9.8, 10.4, 10, 9.9 (2R, 2L) [10.1 ± 0.12]	8.5-11.4 [10.4 ± 0.51]	9.1-10.2 [9.7 ± 0.27]	8.9-9.8 [9.4 ± 0.15]	11, 10.7*	10.3

* Denotes unreliable character observation due to breakage or abnormality.

Table 2. Comparisons of morphological characteristics of the subspecies of *Goniurosaurus kuroiwae*. Numerals in parentheses indicate sample sizes. NC = not compared.

Subspecies	*yunnu*	*kuroiwae*	*orientalis*	*splendens*	*toyamai*	*yamashinae*
n		5	4	6	2	1
Maxilla						
Maxillary shelf width at level of posterior-most tooth: one tooth's width more (+) or less (-) than a half of one tooth's width	+ (1)	-	+	-	NC	-
Lateral wall above posterior tooth row: nearly upright (+) or inclined considerably (-)	+ (1)	-	+	-	NC	+
Frontal						
Anterior part of lateral prefrontal facet: overhangs laterally (+) or not (-)	+ (2)	- (4)	- (1)	NC	NC	NC
Dentary						
Lateral coronoid facet: ventral margin straight (+) or bowed ventrally (-)	+ (3)	+	-	-	-	-
Posterolateral margin below lateral coronoid facet	convex (1)	convex (4)/ straight (1)	convex (3)/ straight (1)	recessed	straight (1)/ recessed (1)	convex
Posterior mandible						
Retroarticular process: longitudinal ridge present (+) or absent (-)	+ (2)	+	+ (3)/- (1)*	-	+	+
Prearticular-surangular suture below posterior mylohyoid foramen: position to the midpoint between the foramen and ventral edge	dorsal (1)/ same (1)	dorsal (4), (1)**	same (1)/ ventral (3)	ventral (3), (1)**	ventral	same**
Axis						
Hypapophysis: ventral keel thick (+) or not (-)	+ (1)	+ (4)	+ (1)	- (3)	NC	NC

* Denotes unreliable character observation due to breakage or abnormality. ** Denotes inferred state owing to the overlying angular.

(RUMF-GF-4083 to 4088), two right posterior mandibles (RUMF-GF-4089 and 4090), one axis (RUMF-GF-4091), one right humerus (RUMF-GF-4092), and one right femur (RUMF-GF-4093). Of these, two right (RUMF-GF-4077 and 4078) and one left (RUMF-GF-4080) dentaries have the same data as the holotype; others were collected by Akio Takahashi and Yasuyuki Nakamura on 24-25 November 2007.

Etymology

The subspecific name is derived from "yunnu," an old vernacular name for Yoronjima Island.

Diagnosis

The bone fragments recovered are referred to the genus *Goniurosaurus* based on their association with maxillary and dentary teeth having the derived condition of an expanded and ridged occlusal margin that is unique to *Goniurosaurus* among gekkotans (Grismer, 1988), and to *G. kuroiwae* based on its exclusive occurrence in the Ryukyus (see also accounts of certain skeletal elements presented below). *Goniurosaurus kuroiwae yunnu* is a relatively small-sized (estimated adult SVL 66.6-84.2 mm) subspecies. It differs from all known conspecific subspecies in having the following combination of morphological characteristics: posteriorly extended maxillary shelf one tooth's width wide at level of posterior-most tooth; scarcely inclined lateral wall of posterior maxilla above posterior part of tooth row; ratio of width at the point of base of anterolateral processes of frontal to interorbital width high (1.68); laterally overhanging anterior parts of lateral prefrontal facets of frontal; ventral margin of lateral coronoid facet of dentary straight or slightly curved dorsally — more than twice as long as surface length of anterodorsal margin of facet; convex posterolateral margin of dentary ventral to lateral coronoid facet, forming a broad and posteriorly-oriented process; prearticular-surangular suture below posterior mylohyoid foramen situated at, or dorsal to, midpoint between foramen and ventral edge of prearticular; longitudinal ridge on dorsal surface of retroarticular process; thick keel on axial hypapophysis.

Description of holotype

Nearly complete left maxilla lacking part of posterior margin of facial process and a number of teeth (Figs. 2A-D). Teeth pleurodont, peg-like, undifferentiated, set closely (ctenodont), forming continuous straight edge ventrally, 52 tooth loci and 36 functional teeth (including posteriormost one) (Fig. 2B); tooth crowns exposed

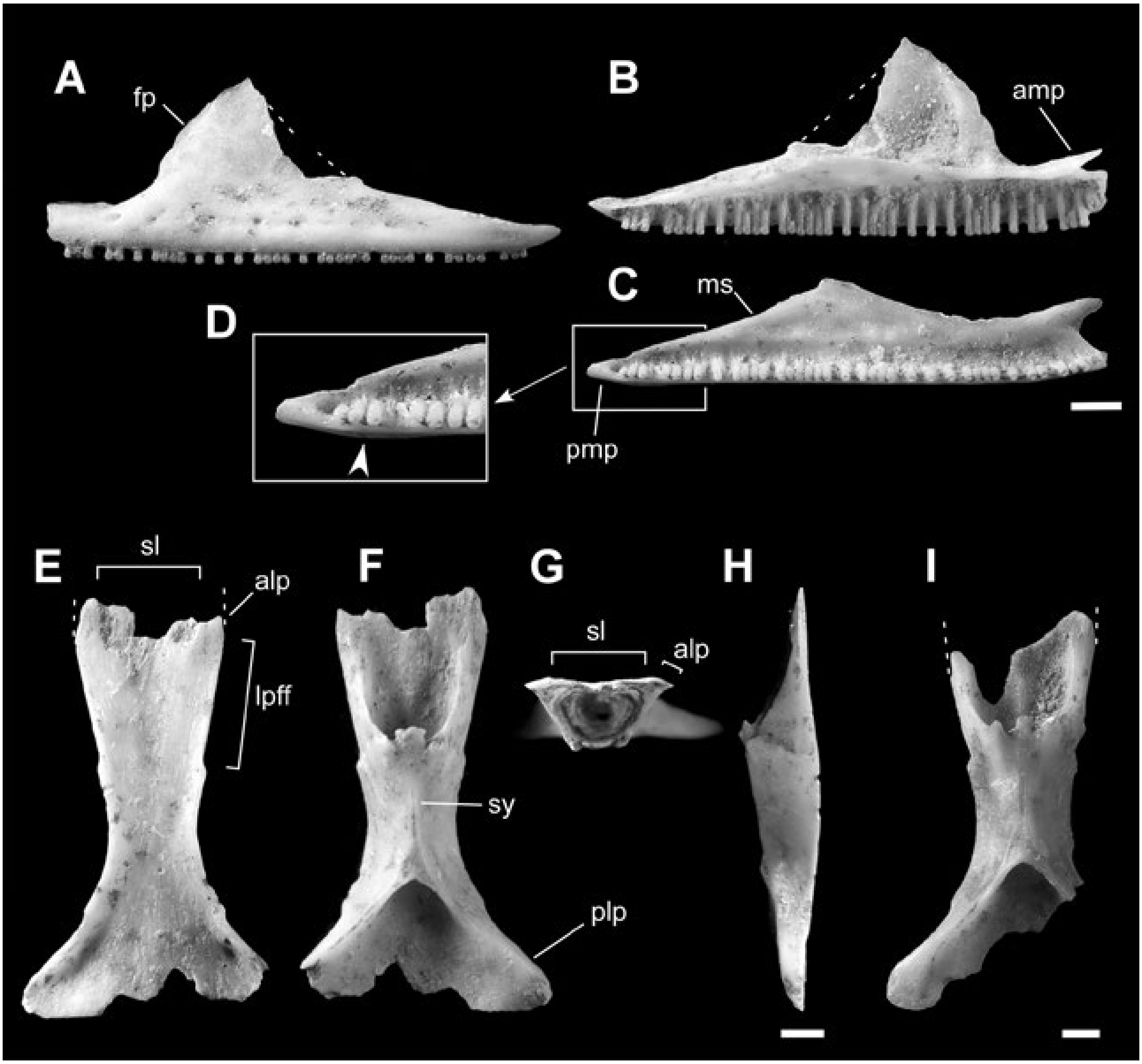

Fig. 2. Maxilla and frontals of *Goniurosaurus kuroiwae yunnu* new subspecies. A-D, the holotype left maxilla (RUMF-GF-4076) in lateral (A), medial (B), and ventral (C) views, and close-up of the posterior part in ventral view (D); E-H, frontal (RUMF-GF-4083) in dorsal (E), ventral (F), anterior (G), and left lateral (H) views; I, frontal (RUMF-GF-4084) in ventral view. Abbreviations: alp, anterolateral process; amp, anteromesial process; fp, facial process; lpff, lateral prefrontal facet; ms, maxillary shelf; plp, posterolateral process; pmp, posterior maxillary process; sl, subsurface lamina; sy, symphysis. The arrow in D indicates the lateral wall above the posterior tooth row, which is scarcely visible from the ventral side. Broken lines represent inferred original outlines. Scale bars equal 1 mm.

below labial wall (Fig. 2A), each expanded, more elongated mediolaterally than anteroposteriorly, and consisting of labiolingual series of (usually) four cusps, yielding flat occlusal surface in mediolateral views (Figs. 2A, B); facial process steep and three times the anterior height of bone, triangular in shape, with thin and acute dorsal tip (Figs. 2A, B); seven supralabial foramina, forming row at lateral surface, and additional row of two associated foramina dorsally (Fig. 2A); anteromesial process prominent, medial edge thick and ridged ventrally (Figs. 2B, C); maxillary shelf broadest at level of 30th tooth, extending posteriorly beyond tooth row by more than one tooth's width medially to posteriormost tooth (Figs. 2C, D); bases of some posteriormost teeth unexposed medially due to ventrally turned maxillary shelf (Fig. 2B); a toothless deep depression, the length of two teeth, follows posteriorly to tooth row (Fig. 2D); lateral wall above posterior part of tooth row scarcely inclined laterally, lateral surface hardly visible from ventral side (Fig. 2D); posterior maxillary process disproportionally truncated, with length from posteriormost tooth to tip of process smaller than length of four posteriormost teeth, although we cannot confirm the process is intact (Fig. 2D); tip of process curves dorsomedially (Figs. 2A-C). Measurements (mm): maximum length, 10.1; maximum width, 1.92; maximum height (without teeth), 3.49; tooth row length, 9.33; anteromesial process length, 1.1; maximum length of maxillary shelf from tooth row, 1.54; length from widest point of bone to posterior tip, 4.95.

Descriptions of paratypes

The paratypical maxilla (right: RUMF-GF-4075) is much more worn, so that it furnishes no morphological characteristics. Like the holotype, it is identified as this species on the basis of the expanded occlusal margins of the tooth crowns (a synapomorphy of *G. kuroiwae* and some other *Goniurosaurus* species: Grismer et al., 1999, 2002; Wang et al., 2010) usually with four cusps (a unique character state seen in *G. kuroiwae*: Sumida and Murphy, 1987; Grismer, 1988; Nikitina and Ananjeva, 2009).

Of the six paratypical frontals recovered, none is complete. These unpaired frontals possess ventrally fused lateral descending processes (subolfactory processes), which is a shared derived character state of the extant gekkotans (Kluge, 1967; Estes et al., 1988; see also Daza et al., 2013). The frontals also possess the posterolateral processes, which are anteroposteriorly elongated, unlike those of other Japanese gekkotans examined (all gekkonids) whose posterolateral processes are thin anteroposteriorly. The most complete of the referred frontals (RUMF-GF-4083: Figs. 2E-H) retains the anterior section of the bone, which is anteriorly elongated and widened, while the anterior third of both anterolateral processes and the intervening subsurface lamina for the nasals are lost. The length from the subsurface lamina to the parietal facet is 8.0 mm, and the width at the point of the base of the anterolateral processes (3.22 mm) is 1.68 times wider than the narrowest width of the interorbit (1.92 mm) (Figs. 2E, F; Table 1). The smooth dorsal surface is concave, most prominently posterior to the postorbitofrontal facets. The anterolateral processes are tilted laterally (Fig. 2G). In lateral view, the bone is deepest at the anterior end of the ventral contact of the lateral descending processes (Fig. 2H). Anteriorly, the paired lateral descending processes terminate at a much more posterior level of the nasal overlap, yielding a flat ventral surface of the more anterior part (Fig. 2F). Posterior to the ventral contact, the processes become a pair of swellings that extend posteriorly to the posterolateral edges. The ventral surface of the posterolateral margin is thin and flat. In this specimen and the second best preserved specimen of the referred frontals (RUMF-GF-4084: Fig. 2I), the lateral prefrontal facets are straight and overhang laterally throughout their length (Figs. 2E-G, I). Although the second best specimen lacks the anterior fourth or fifth of the lateral prefrontal facets (Fig. 2I), the width at the anteriormost intact part (3.15 mm) is much greater, 1.48 times, than that at the orbital constriction (2.13 mm), this suggests that the high ratio between the width at the point of the base of the anterolateral processes and interorbital width in the most complete specimen (see above) is not a malformation.

Six dentaries (three right and three left, Fig. 3) are referred to *G. kuroiwae* on the basis of tooth morphology (Fig. 3F), which is identical to that of the maxillae (see above). The total tooth count is 50 and 53 in two right dentaries and 51 and 52 in two left dentaries (Table 1). The tooth crowns are exposed above the labial wall. The Meckelian groove is fused completely. The subdental shelf is well developed. The mental foramina are arranged in a longitudinal row at the middle of the lateral surface; there are a total of seven (n = 2) or eight (n = 3) foramina. These foramina are anteroposteriorly elongated and housed within depressions. The posterolateral margin is posterodorsally excavated for the lateral process of the coronoid (henceforth referred to as "the lateral coronoid facet"; Fig. 3B). The ventral margin of the lateral coronoid facet is straight (Figs. 3D, E) or weakly curved dorsally (Figs. 3B, C), and it is approximately twice as long as the surface length of the anterodorsal margin (Tables 1, 2). The best preserved right dentary (RUMF-GF-4077: Figs. 3A-C) retains an almost intact posterolateral mar-

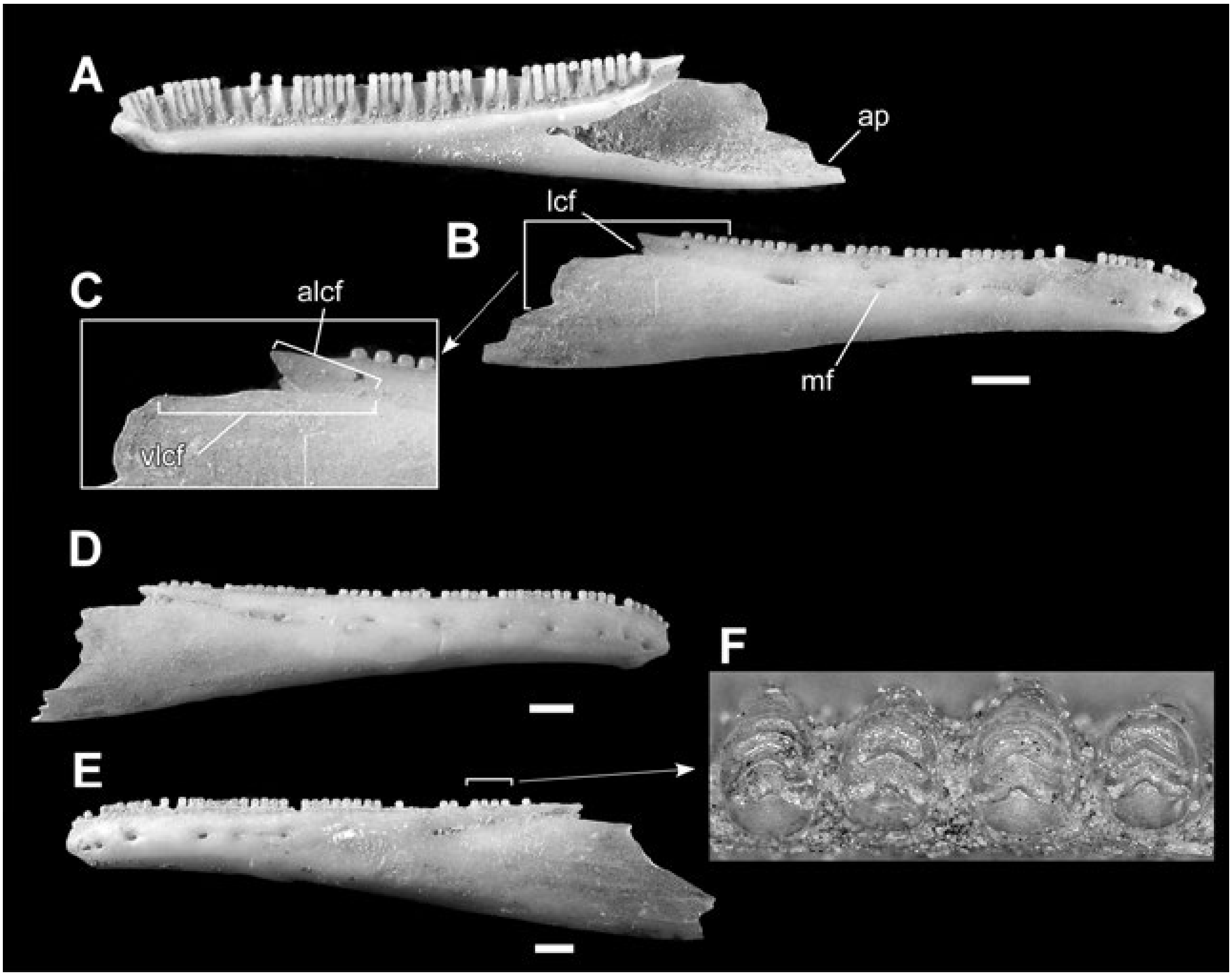

Fig. 3. Dentaries of *Goniurosaurus kuroiwae yunnu* new subspecies. A-C, right dentary (RUMF-GF-4077) in medial (A) and lateral (B) views, and close-up of the posterodorsal part in lateral view (C); D, right dentary (RUMF-GF-4078) in lateral view; E and F, left dentary (RUMF-GF-4080) in lateral view (E) and close-up of the posterior teeth in occlusal view (F). Abbreviations: alcf, anterodorsal margin of the lateral coronoid facet; ap, angular process; lcf, lateral coronoid facet; mf, mental foramen; vlcf, ventral margin of the lateral coronoid facet. Scale bars equal 1 mm.

gin, except for the tip of the angular process. Ventral to the lateral coronoid facet, the margin is strongly convex, forming a posteriorly-oriented broad process. Ventral to the process, it is weakly notched. Despite the posterolateral parts being broken, at least two other dentaries (RUMF-GF-4078, 4080: Figs. 3D, E) confirm that the posterolateral dentary margins are not excavated anteriorly beyond the levels of the posterior ends of the lateral coronoid facets.

Two specimens of right postdentary bones of mandibles are preserved (RUMF-GF-4089, 4090; Figs. 4A-C), both of which lacks the dentary, coronoid, angular, and splenial (plus posterior half of the retroarticular process in RUMF-GF-4090). They are referred to gekkotans on the basis of having an anteriorly constricted and spoon shaped retroarticular process with a medial offset and a lateral notch of the base (Estes et al., 1988; Daza et al., 2013; Fig. 4A) and to *G. kuroiwae* on the basis of having an angulated dorsal edge of the surangular (which is round in other examined Japanese gekkotans) (Fig. 4A). In both specimen, a short, anteroposteriorly oriented ridge is present immediately lateral to the foramen chorda tympani of the dorsal surface of the retroarticular process (Fig. 4A). Both the posterior surangular foramen and the posterior mylohyoid foramen are distinct at the posterior part, with the latter foramen being located at almost the midpoint of the mandible's height (Figs. 4B, C). In RUMF-GF-4090, the surangular-prearticular suture

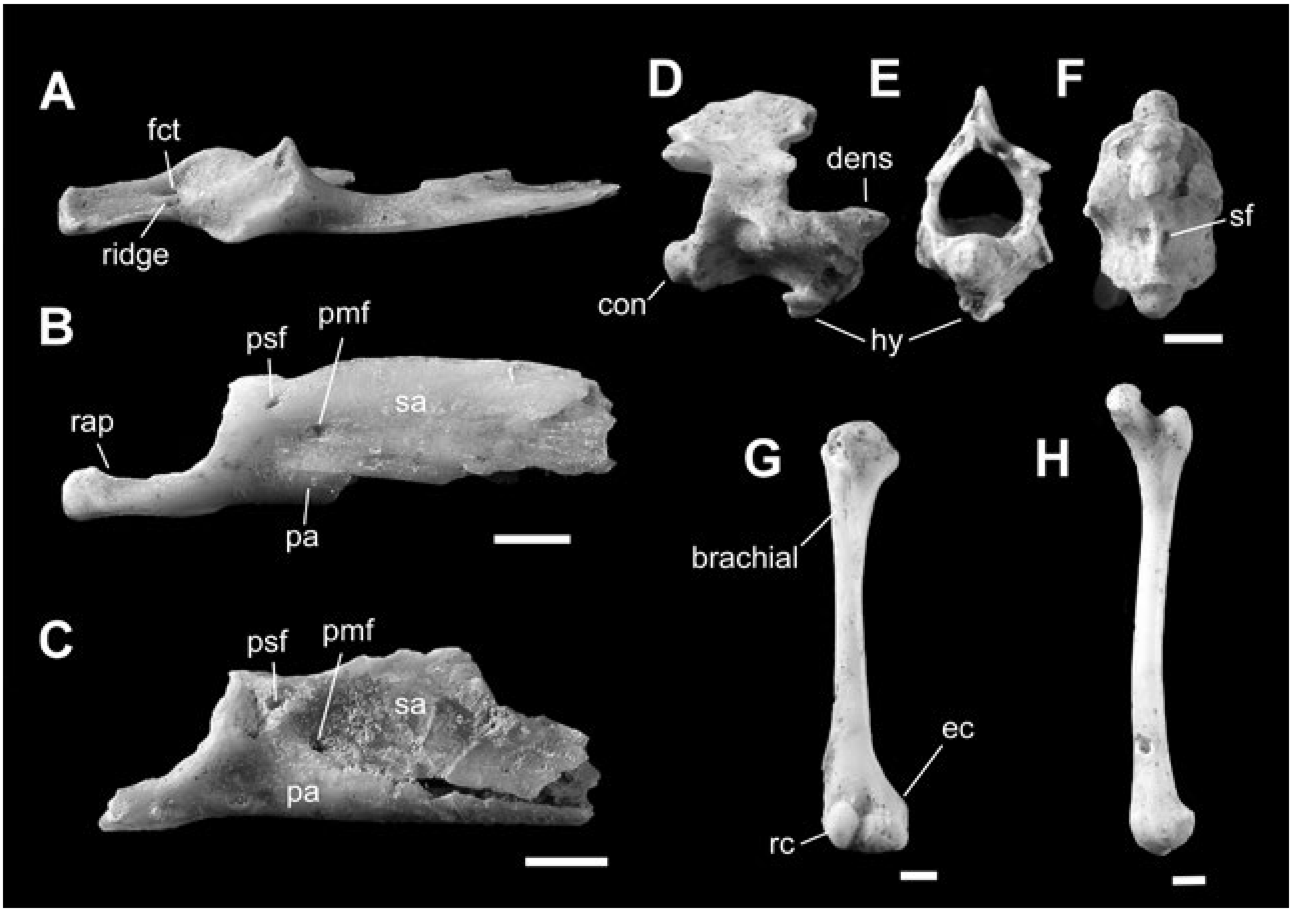

Fig. 4. Posterior mandibles, axis, humerus, and femur of *Goniurosaurus kuroiwae yunnu* new subspecies. A and B, right posterior mandible (RUMF-GF-4089) in dorsal (A) and lateral (B) views; C, right posterior mandible (RUMF-GF-4090) in lateral view; D-F, axis (RUMF-GF-4091) in right lateral (D), posterior (E), and ventral (F) views; G, right humerus (RUMF-GF-4092) in ventral view; H, right femur (RUMF-GF-4093) in medial view. Abbreviations: con, condyle; ec, entepicondyle; fct, foramen chorda tympani; hy, hypapophysis; pa, prearticular; pmf, posterior mylohyoid foramen; psf, posterior surangular foramen; rap, retroarticular process; rc, radial condyle; sa, surangular; sf, subcentral foramen. Scale bars equal 1 mm.

traverses across the lateral surface as nearly parallel with the ventral edge of the prearticular, although its posterior extent is unclear (Fig. 4C). At the position below the posterior mylohyoid foramen, the suture is situated at the midpoint (RUMF-GF-4089), or dorsally to the midpoint (RUMF-GF-4090), between the foramen and the ventral edge of the prearticular (Figs. 4B, C).

One nearly entire axis (RUMF-GF-4091: Figs. 4D-F) lacking the synapophysis and postzygapophysis on the left side is referred to the new subspecies. It is referred to gekkotans on the basis of having a squarish outline in the ventral view, distinct subcentral foramina, a round condyle, and posteriorly directed lateral projections at the lateral sides of the axial hypapophysis (Camp, 1923; Hoffstetter and Gasc, 1969); and to *G. kuroiwae* on the basis of having a procoelous condyle and a fused notochordal canal, both of which indicate a eublepharid origin (Camp, 1923; Hoffstetter and Gasc, 1969; Kluge, 1987; Grismer, 1988). It is 3.7 mm in length (without the dens, 3.2 mm), 2.3 mm in maximum width, and 3.7 mm in maximum height. The condyle is slightly inclined dorsoventrally. Its transverse width of 0.85 mm is much smaller than that of the posterior end of the centrum at 1.27 mm. The hypapophysis bears a thick and well-developed keel.

Appendicular skeletons are represented by one almost complete right humerus (RUMF-GF-4092, 12.0 mm long; Fig. 4G) and one complete right femur (RUMF-GF-4093, 14.4 mm long; Fig. 4H). Association of the humerus is based on its size, straight overall shape, slender brachial, relatively undeveloped entepicondyle, and ovoid radial condyle that elongates in parallel with

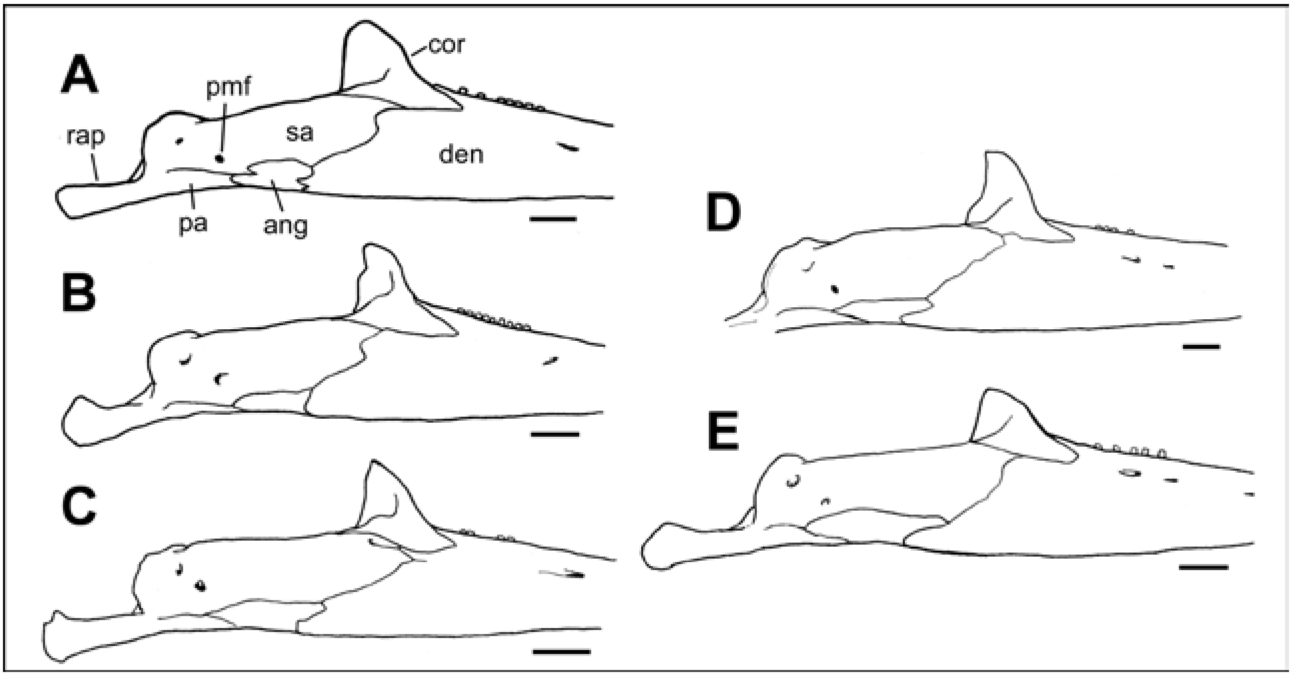

Fig. 5. Line drawings of mandibles (right, except *G. k. kuroiwae*) of extant *Goniurosaurus kuroiwae* subspecies in lateral views, showing variation in shapes of the posterolateral dentaries and the height of the prearticulars. A, *G. k. kuroiwae* (KUZ R67952) reversed left; B, *G. k. orientalis* (RUMF-ZH-570); C, *G. k. splendens* (KUZ R71533); D, *G. k. toyamai* (OMNH R3974) posterior retroarticular process is omitted; E, *G. k. yamashinae* (RUMF-ZH-206). Anterior dentaries and most teeth are omitted. In all specimens the posterior extent of the surangular-prearticular suture is unclear. Abbreviations: ang, angular; cor, coronoid; den, dentary; pa, prearticular; pmf, posterior mylohyoid foramen; rap, retroarticular process; sa, surangular. Scale bars equal 1 mm.

the bone's axis. The femur is referred on the basis of its size and straight and slender shape.

Body Size

SVL estimates of the Yoronjima material are 78.8-84.2 mm based on the length of three dentary tooth rows (9.8-10.4 mm, two right and one left: RUMF-GF-4077, 4078, and 4080), 66.6-76.1 mm based on the interorbital width of four frontals (1.92-2.13 mm, RUMF-GF-4083 to 4086), and 73.0 mm based on the length of the humerus (RUMF-GF-4092) and the femur (RUMF-GF-4093). The skeletal elements used for the estimation are considered to be derived from skeletally mature individuals judging from their fully ossified state and, in the dentaries, the large number of teeth.

Comparisons

The unique combination of osteological character states in those skeletal elements from the Yoronjima differentiates *Goniurosaurus kuroiwae yunnu* from all other currently recognized subspecies of *G. kuroiwae* (see Tables 1, 2). Most similar is the geographically closest *G. k. kuroiwae*. However, the Yoronjima material differs from *G. k. kuroiwae* (and some other known conspecific subspecies) in having: a posteriorly extended maxillary shelf that is one tooth's width wide at the level of the posteriormost tooth (the shelf is less posteriorly extended in *G. k. kuroiwae* [see also Fig. 6 in Grismer, 1988], *G. k. splendens*, and *G. k. yamashinae*; Table 2); a very weak lateral inclination of the lateral wall of the posterior part, above the posterior tooth row, of the maxilla (this part is considerably inclined in *G. k. kuroiwae* and *G. k. splendens*, as in their posterior maxillary processes, and the lateral surfaces are clearly visible from the ventral sides; Table 2); laterally overhanging anterior parts of lateral prefrontal facets of the frontal (vs. these parts vertical in *G. k. kuroiwae* and *G. k. orientalis*; Table 2); and an interorbital constriction and a widened anterior section of the frontal, resulting in a high ratio (1.68) of the width at the point of the base of the anterolateral processes to interorbital width (the ratio is lower in *G. k. kuroiwae*, *G. k. orientalis*, and *G. k. splendens*; Table 1). Additionally, the number of left maxillary teeth of *G. k. yunnu*, at 52, is greater than that observed in *G. k. kuroiwae* and other subspecies (Table 1). Indeed, a range of 46-50 left maxillary tooth counts from eight "*G. kuroiwae*" (presumably *G. k. kuroiwae*) has been reported by Nikitina and Ananjeva (2009). Moreover, the estimated adult SVL of *G. k. yunnu* at 66.6-84.2 mm, though apparently close to the adult SVL of most other subspecies (75-95 mm for *G. k. orientalis*, 65-81 mm for *G. k. splendens*, and 75-85 mm for *G. k. toyamai* and *G. k. yamashinae*: Ota, 2003; Tanaka, 2005a, b, c), is somewhat smaller, particularly at the upper limit, than that of *G. k. kuroiwae* (76-100 mm for the Okinawajima population: Tanaka and Nishihira, 1989; 80-92 mm for the Yagajijima population: Kurita and Kawamura, 2011). However, the body size of lizard populations can vary drastically in time and space (e.g., Pregill, 1986 and literature cited therein; Sumner et al., 1999), and, thus, caution should be used in using body size as a character.

Goniurosaurus kuroiwae yunnu also differs from extant conspecific subspecies other than *G. k. kuroiwae* in having: an elongated ventral margin of the lateral coronoid facet of the dentary that is twice as long as the surface length of the anterodorsal margin and that is straight or slightly curved dorsally (vs. a less-elongated and, as a whole, ventrally curved ventral margin in *G. k. orientalis*, *G. k. splendens*, *G. k. toyamai*, and *G. k. yamashinae*; Tables 1, 2); a strongly convex posterolateral margin of the dentary ventral to the lateral coronoid facet (vs. a straight or recessed margin in *G. k. splendens* and *G. k. toyamai*; Table 2); prearticular-surangular suture at the position below the posterior mylohyoid foramen situated at, or dorsal to, the midpoint between the foramen and the ventral edge of the prearticular (vs. a suture situated ventrally to the midpoint in *G. k. splendens* and *G. k. toyamai*; Table 2); a longitudinal ridge on the dorsal surface of the retroarticular process (vs. its absence in *G. k. splendens*; Table 2); and a thick keel of the axial hypapophysis (vs. an obscured or rudimentary keel in *G. k. splendens*; Table 2).

DISCUSSION

The Yoronjima *Goniurosaurus kuroiwae*, described here as a new subspecies, *G. k. yunnu*, can be regarded as an endemic form, morphologically distinguishable from all known conspecific subspecies. Further circumstantial support for this taxonomic conclusion is provided by the distributions of extant subspecies. Four currently recognized subspecies of the Okinawa Island Group are separated from each other by straits that are less than 300 m deep (see the bathymetry of Oshima et al., 1988). Separation from other landmasses by straits greater than 400 m deep suggests that Yoronjima has been isolated from other landmasses for a relatively long period, and it is therefore unlikely that the Yoronjima *G. kuroiwae* belongs to any known *G. kuroiwae* subspecies. In addition to its diagnosability, such putative geographical isolation warrants the recognition of *G. k. yunnu* as a distinct subspecies like all the others.

Our comparisons demonstrated the existence of a degree of morphological variation in certain skeletal elements of these *G. kuroiwae* subspecies, which in some cases could be comparable to that between full eublepharid species (Kluge, 1962; Grismer, 1988; and other papers) and there seems to be further inter-subspecies variation in some elements of their skulls (Y.N. unpublished data). Although our systematic interpretation of the osteological variation is inconclusive due to the lack of prepared skulls of some *G. kuroiwae* subspecies and the appropriate outgroup samples, the osteological information is seemingly promising and should be incorporated into future taxonomic studies of this group.

The discovery of *Goniurosaurus kuroiwae yunnu* should be marked as a highly likely instance of a taxon-level anthropogenic extinction in insular squamate reptiles. The excellent state of preservation of the material and its association with modern debris strongly suggest that this animal survived until recently, whereas the complete absence of sampling or observation records of live animals from the island, despite recent repeated herpetofaunal surveys (see literature cited in Maenosono and Toda, 2007), supports the idea of complete extinction of this gecko subspecies in recent times. There is little doubt that such recent extinction on an island at the post-modern human colonization stage was related to human activities (Case et al., 1998). Unlike the cases of large-sized lizards (Pregill and Worthy, 2003; Pregill and Steadman, 2004), the possibility of human exploitation can be discounted by the relatively small body size of the animal, although the remains were associated with artifacts.

The majority of historic extinctions of insular lizards are attributable to predation by introduced mammalian predators (Case et al., 1998). This may possibly be true with respect to *G. k. yunnu*, as well as at least three other species of Yoronjima's indigenous herptiles that disappeared after the 1960s, presumably as a result of predation by the exotic weasel, *Mustela itatsi*, which was introduced to the island in the middle of the 1950s (Nakamura et al., 2009, 2013). Nevertheless, the contribution of other factors to the extinction, such as deforestation, remains open to discussion.

On the other hand, there is a faint hope that this gecko still survives on Yoronjima, as it is usually difficult to confirm the extinction of relatively small, nocturnal, and secretive animals, even in such small, topographically-uncomplicated and hence thoroughly surveyable islands. It is, however, hardly conceivable that for several decades this obligate terrestrial, slow-moving gecko, which had long been isolated on the originally Carnivora-free island of Yoronjima, has been able to elude the established weasel, which is swift, predominantly nocturnal (Masuda and Watanabe, 2009), and notorious for predation on lizards when introduced to islands (e.g., Hasegawa, 1999; Sekiguchi et al., 2002).

Our findings illustrate the susceptibility of *G. kuroiwae* to population extinction, a notion which has been suggested previously (e.g., Tanaka, 1996, 2005d; Ota, 2010). Together with "rather incomplete" insular distribution of the species (Grismer et al., 1994), the present results may imply the existence of other recently eradicated (but nevertheless unnoticed) insular populations of this species. Documenting the missing pieces, particularly those wiped out by unnatural causes, demands priority, as it is a necessary complement to explain the diversity of the species and its relationship with the geohistory of the Ryukyus.

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APPENDIX

Specimens examined

Dissected specimens of *Goniurosaurus kuroiwae* examined. Acronyms are KUZ = Kyoto University Museum Zoological Specimens, OMNH = Osaka Museum of Natural History, and RUMF = Fujukan, University Museum of the University of the Ryukyus.

Goniurosaurus kuroiwae kuroiwae—Okinawajima (Kunigami Vil.): KUZ R52392 (male), R65827 (gender unknown), R67952 (female), R71631 (male), R71909 (male).

Goniurosaurus kuroiwae orientalis—Tokashikijima: KUZ R71908 (male), RUMF-ZH-569 (female), 570 (female), 572 (male).

Goniurosaurus kuroiwae splendens—Tokunoshima: KUZ R34580 (female), R71533 (female), R71895 (male), R71896 (female), R71897 (female), R71898 (female).

Goniurosaurus kuroiwae toyamai—Iheyajima: OMNH R3974 (male), R3975 (female).

Goniurosaurus kuroiwae yamashinae—Kumejima: RUMF-ZH-206 (male).