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Taxonomic revision and re-description of *Ateuchosaurus pellopleurus* (Hallowell, 1861) (Reptilia, Squamata, Scincidae) with resurrection of *A. okinavensis* (Thompson, 1912)

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Abstract

The scincid lizard *Ateuchosaurus pellopleurus* (Hallowell, 1861) has been recognized as a single species widely distributed in the Osumi, Tokara, Amami, and Okinawa Groups of the Ryukyu Archipelago, southern Japan. However, a recent molecular phylogenetic study suggested that this skink should be divided into two species: one distributed in the Osumi to Amami Groups, and another distributed in the Okinawa Group. For *A. pellopleurus*, two extant syntypes collected from an island of the Amami Group were confirmed. Therefore, we identified the species in the Osumi to Amami Groups as *A. pellopleurus* sensu stricto by designating one of the syntypes as the lectotype for this species. For the species in the Okinawa Group, we resurrected *A. okinavensis* (Thompson, 1912), of which the type locality is on Okinawajima Island in the Okinawa Group. *Ateuchosaurus pellopleurus* and *A. okinavensis* can be differentiated by the following characteristics: usually separated frontonasal and frontal, 8–14 subdigital scales on the fourth toe (mode = 11), and usually two or three pairs of dorsal median scale rows with black stripes in *A. pellopleurus*; usually fused frontonasal and frontal, 10–16 subdigital scales on the fourth toe (mode = 13), and usually no stripe on the dorsal scales or a pair of dorsal median scale rows with black stripes in *A. okinavensis*.

Key Words

lectotypification, morphological diagnosis, Ryukyu Archipelago, scalation

Introduction

Ateuchosaurus pellopleurus (Hallowell, 1861) is a scincid lizard occurring in the northern and central parts of the Ryukyu Archipelago, southern Japan (sites 1–22 in Fig. 1). This species and its congener, *A. chinensis* Gray, 1845, constitute the genus *Ateuchosaurus* Gray, 1845. The phylogenetic distinctness and morphological diagnoses of this genus have been well described (Mittleman 1952; Makino et al. 2020). Additionally, the phylogenetic distinctness and morphological diagnosis between *A. pellopleurus* and *A. chinensis* have been provided in detail (Nguyen et al. 2008; Makino et al. 2020; Okamoto and Kurita 2021).

A recent molecular phylogenetic study elucidated the existence of two genetically divergent lineages within *A. pellopleurus*: the northern lineage distributed in the Osumi, Tokara, and Amami Groups (sites 1–13 in Fig. 1), and the southern lineage distributed in the Okinawa Group (sites 14–22) (Makino et al. 2020). Then, Makino et al. (2020) concluded that these lineages deserved full species recognition. *Ateuchosaurus pellopleurus* was originally described based on the specimens from Ousima (= Amamioshima Island, site 11) and “Loo-Choo” (= the Ryukyu Kingdom, often interpreted as Okinawajima Island, site 15; e.g., Stejneger 1907; Okada 1939) (Hallowell 1861). Therefore, the syntypes of *A. pellopleurus* sensu lato may encompass both lineages, and thus lectotype designation is needed to clarify which lineage should finally bear the species name *A. pellopleurus*.

Stejneger (1927) stated that the syntypes of *A. pellopleurus* were missing in 1907 after transferring them from Philadelphia to USNM (now the NMNH) (see Appendix 1), but two syntypes were finally found and re-deposited as USNM 42110 and USNM 42114. We were able to identify the two syntypes USNM 42110 and USNM 42114 in the NMNH collection database (Smithsonian Institution 2021), both of which were from Amamioshima Island (site 11) according to the metadata. Here, we designate USNM 42110 as the lectotype for *A. pellopleurus*, concluding that the northern lineage is *A. pellopleurus* sensu stricto (hereafter referred to as *A. pellopleurus*). For the southern lineage, we resurrect *Ateuchosaurus okinavensis* (Thompson, 1912), of which the type locality was Okinawajima Island (site 15 in Fig. 1; Thompson 1912).

Even though the distinct genetic divergence of these species was confirmed by the molecular study (Makino et al. 2020), and their nomenclatural statuses were resolved above, their morphological diagnoses have not been well established. Although several scalation differences were pointed out in the original descriptions of *A. okinavensis* and *A. pellopleurus* (referred to as *Lygosaurus pellopleurus browni* Van Denburgh, 1912a) (Thompson 1912; Van Denburgh 1912a, b), Okada (1939) negated substantial differences between the Okinawajima and Amamioshima populations and synonymized them with *A. pellopleurus*. Thereafter, Ota et al. (1999) investigated the morphological variation of *A. pellopleurus* sensu lato based on morphometric and scalation characters, and found a geographic divergence between the populations of northern (sites 1, 5–7, and 9–12) and southern (sites 15, 16, 19, and 22) areas. Although Ota et al. (1999) finally failed to identify a clear-cut boundary of the divergence supported by any single character, the geographic divergence in frequencies of single and separated frontal scales seemed to be concordant with the genetic divergence, except for two island samples including the geographically intermediate sample of Okinoerabujima Island (site 13).

In this study, we conducted a morphological investigation of *A. pellopleurus* and *A. okinavensis* to identify their diagnostic characters. Finally, we re-describe these *Ateuchosaurus* species.

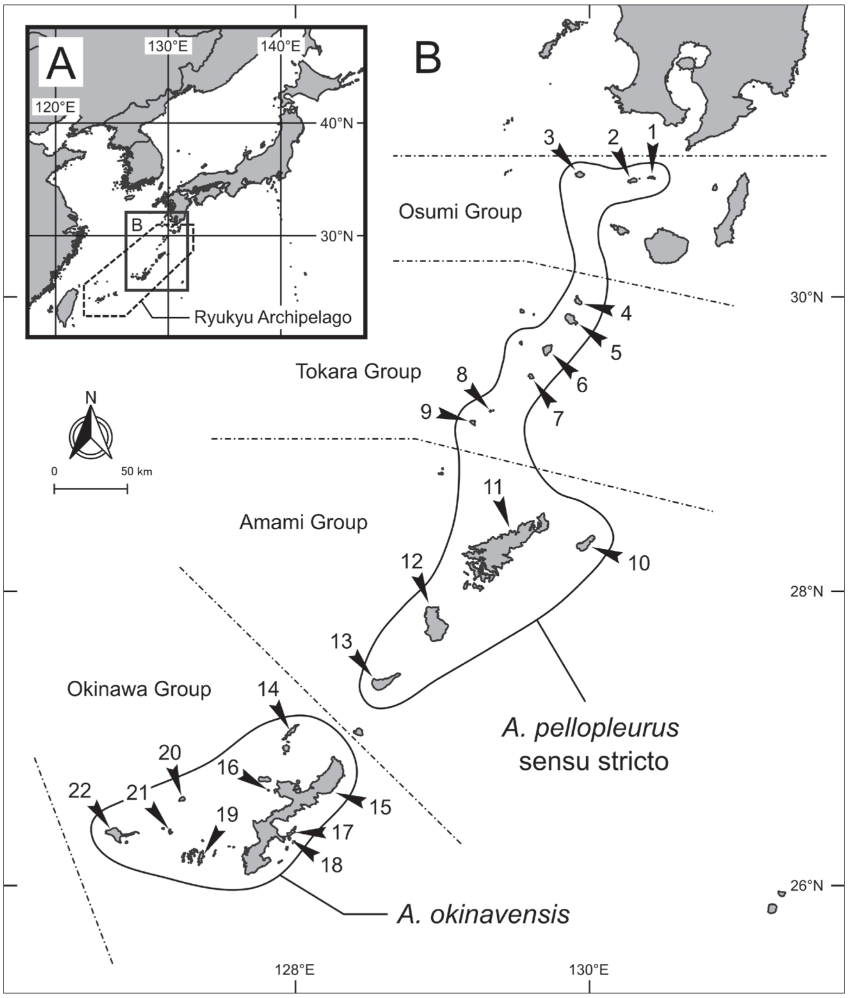

Figure 1. Map of the geographic range of *Ateuchosaurus pellopleurus* and *A. okinavensis* in the Ryukyu Archipelago, and the sampling sites of the specimens examined in this study. **A.** The geographic location of the Ryukyu Archipelago; **B.** Sampling sites in the northern and central parts of the Ryukyu Archipelago. Each solid line indicates the geographic range of the *Ateuchosaurus* species revealed by Makino et al. (2020). Site numbers correspond to the locality numbers in Tables 1–2 and Suppl. materials 1–3.

Materials and methods

Morphological comparison

In total, 305 specimens of *A. pellopleurus* from 13 islands (sites 1–13 in Fig. 1) and 126 specimens of *A. okinavensis* from nine islands (sites 14–22) were examined. We also examined two specimens of *A. chinensis* for comparison (see Suppl. material 1 for the materials examined). The sex and maturity of each specimen were determined based on gonadal examination (Okada et al. 1992).

Variation in external morphology within and between species was explored by observation using a stereoscopic binocular microscope. For bilateral characters, we used the character state of the right side. This morphological investigation was conducted for the following characters, which were previously pointed out as differences between the populations of Amamioshima and Okinawajima Islands (sites 11 and 15) (Thompson 1912; Van Denburgh 1912a, b) or known to be geographically variable (Ota et al. 1999): the condition of frontonasal and frontal (see below for the revised definition of these scales), the number of midbody scale rows (MSR, counted around midbody), the number of dorsal median scales (DMS, counted from the scale behind the parietal to the one above the vent), and the number of subdigital scales of the fourth toe (TIV, measured only for specimens with an undamaged fourth toe). We also counted the number of dorsal scale rows with black stripes (DSRBS), in which the four ordered states were recognized in most of the specimens: no stripe, one, two, and three rows from the dorsal median line to the right and left sides (Fig. 2). DSRBS was counted on the midbody because the number of striped scale rows was sometimes variable across the longitudinal axis. In addition, the following head scales were investigated qualitatively: separate/fusion of nasal and first supralabial (SuLa), and the condition of supranasal (see below for the definition of supranasal).

We also examined several morphometric and meristic characters for mature specimens from Amamioshima and Okinawajima Islands (sites 11 and 15). The morphometric characters included the following: snout-vent length (SVL, from snout tip to vent), head length (HL, from snout tip to posterior margin of interparietal), head width (HW, width at position of ear opening), head height (HH, height at position of ear opening), snout-eye length (SEyL, from snout tip to anterior corner of eye), eye length (EyL, between anterior and posterior corners of eye), eye-ear length (EyEaL, from posterior corner of eye to anterior border of ear opening), ear diameter

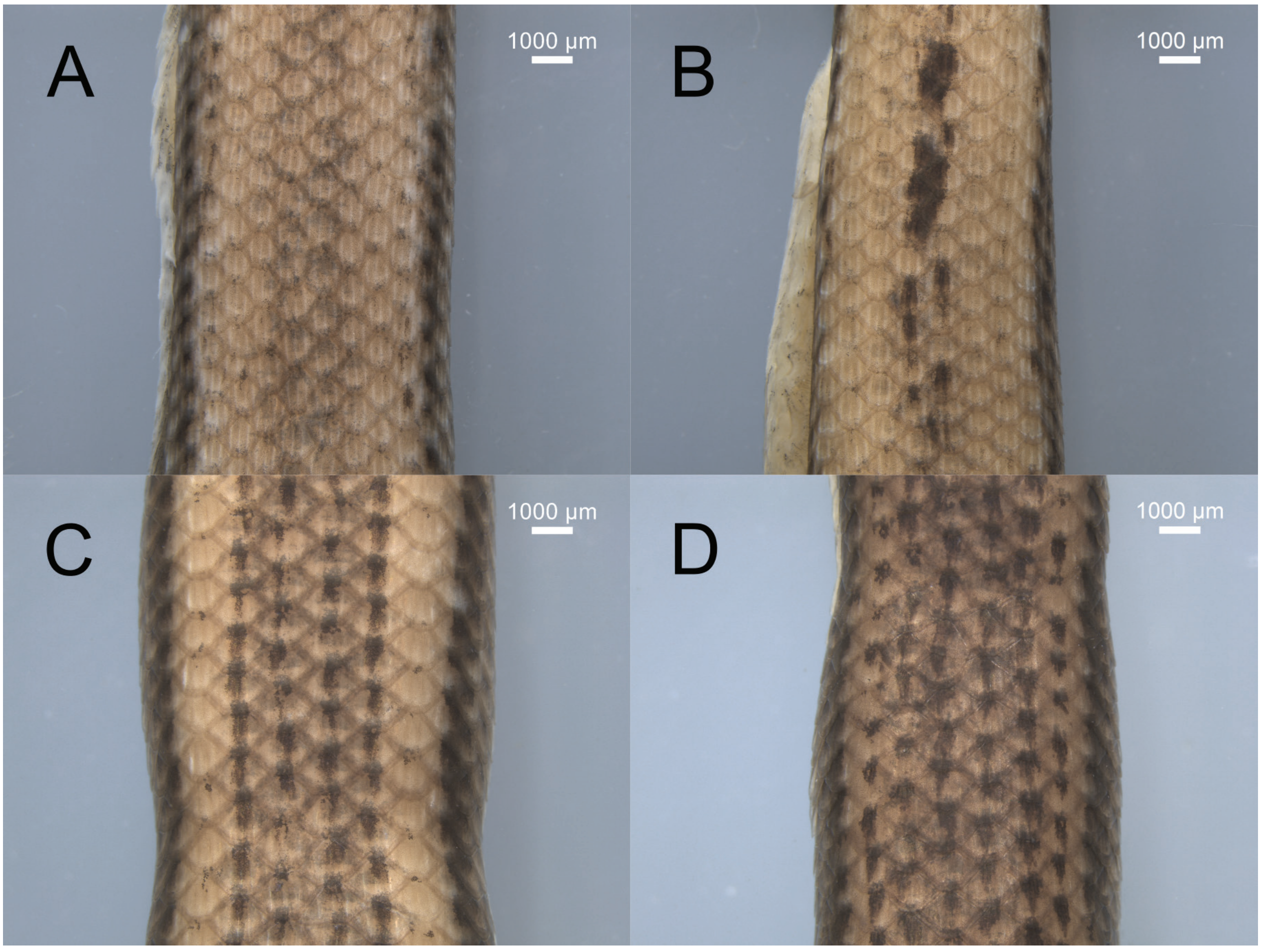

Figure 2. Observed major character states in dorsal scale rows with black stripes in *Ateuchosaurus pellopleurus* and *A. okinavensis*. **A.** No stripe (KUZ R77453); **B.** One pair of scale rows with black stripes (KUZ R70133); **C.** Two pairs of scale rows with black stripes (KUZ R77707); **D.** Three pairs of scale rows with black stripes (KUZ R77692).

(EaD, diameter of ear opening measured horizontally), snout-axilla length (SAL, from snout tip to posterior junction of forelimb and body wall), axilla to groin length (AGL, from posterior junction of forelimb and body wall to anterior junction of hindlimb and body wall when limbs held at right angle to body), tail length (TaL, from vent to tail tip); forelimb length (FlL, from middle point between anterior and posterior junctions of forelimb and body wall on ventral side to tip of third finger including claw when forelimb held at right angle to body), third finger length (FIIIL, from corner between second and third fingers to tip of third finger including claw), hindlimb length (HlL, from posterior junction of hindlimb and body wall to tip of fourth toe including claw when hindlimb held at right angle to body), and fourth toe length (TIVL, from corner between third and fourth toes to tip of fourth toe including claw). These measurements were taken to the nearest 0.1 mm using a digital caliper. Meristic characters included the followings: supraoculars (SuO), supraciliaries (SuCi), supralabials (SuLa), infralabials (InLa), DMS, MSR, and subdigital scales on third finger (FIII) and fourth toe (TIV).

We noted that nasal and first SuLa are fused in most of the specimens of *A. pellopleurus*, *A. okinavensis* and *A. chinensis* (300/300, 106/109 and 2/2 specimens, respectively); this feature has not been observed in most other skinks (but see Greer 1973; Greer et al. 2006; Nguyen et al. 2010). The fused state of those scales seems to have been overlooked by most previous studies (Hallowell 1861; Stejneger 1907; Okada 1939; Nakamura and Uéno 1963; Nguyen et al. 2008; but see Greer 1970).

Although the terminology of head scalation basically followed those of Taylor (1936), we re-defined the names for several head scales based on a revised interpretation of their homology with the scales of other skinks. The scale formerly treated as "frontonasal" was a single scale with a concave posterior edge in most specimens (Figs 4, 6), but was laterally divided into two scales in some specimens. The posteromedially concave shape and potentially paired nature that was implied by the variation in scale division, in addition to the anterior contact with rostral and the lateral contact with nasal and loreal, suggest its homology to be supranasal, rather than frontonasal, which usually has a posteriorly convex shape. Therefore, we re-defined the "frontonasal" of *Ateuchosaurus* as supranasal (SuNa) here.

The scale formerly treated as "frontal" is a long single scale that is weakly constricted at the middle ("hourglass shape" in Greer and Shea 2000) (Fig. 6) or two scales divided at a constricted point (Fig. 4). The separable nature as well as the constricted shape suggests that "frontal" consists of two elements with different homology. Considering their positions and relationships with surrounding scales, we re-interpreted the anterior and posterior parts of the "frontal" as frontonasal (FrNa) and frontal respectively.

Under the revised definition of FrNa, the scale formerly treated as "prefrontal" is located on the anterolateral side of FrNa. It may not be homologous with the prefrontal of other skinks. Therefore, we re-defined "prefrontal" of *Ateuchosaurus* as supraloreal (SuLo).

In *Ateuchosaurus*, parietal has been considered to be absent or undeveloped (Smith 1935; Zhao and Adler 1993). However, our observation confirmed the large paired scale at the rear of frontoparietal and interparietal, which was recognizable as parietal (Figs 4, 6). Conversely, we found a scale enclosed with supraocular, frontoparietal, parietal, and upper pretemporal. Other scincid lizards may not possess a scale similar in position and size to this scale. Thus, we defined this specific scale as ectoparietal (EcP).

Sexual differences and ontogenetic changes in variable characters were investigated for the Amamioshima, Okinoerabujima, Okinawajima, and Tokashikijima samples (sites 11, 13, 15, and 19), and we could not detect a statistically significant sexual difference in most of the island samples, nor variation correlated with body size in all the island samples. Therefore, we pooled the data of all the specimens from the same island to compare island populations, except for the characters showing sexual variation. For MSR, we excluded the Amamioshima sample from the comparison among island populations because males of this island sample showed a significantly smaller number of scale rows than the females of this island (Suppl. material 2). To test sexual and ontogenetic variation, we used the chi-squared test for the FrNa and frontal condition data, and the Mann-Whitney *U* test for the MSR, DMS, TIV, and DSRBS data. These statistical tests were conducted using PAST software (Hammer et al. 2001).

Genetic distances

Genetic distance among *Ateuchosaurus* species was calculated by Kimura (1980)'s two-parameter (K2P) correction using MEGA7 (Kumar et al. 2016); sequence data of mitochondrial cytochrome *b* gene in Makino et al. (2020) were analyzed (INSD accession numbers: LC492502–LC492663).

Results

Morphological variation

Regarding the condition of FrNa and frontal, most samples of *A. pellopleurus* exhibited high frequencies of the separated type (ca. 70.0%–100.0%, Table 1), except for the Takeshima and Iojima samples (sites 1 and 2, 50.0% and 47.1%, respectively). In contrast, the island samples of *A. okinavensis* exclusively exhibited the fused type, except for the separated type in two out of eight

Table 1. Variation of the condition of frontonasal-frontal and the number of subdigital scales of the fourth toe (TIV) in *Ateuchosaurus pellopleurus* and *A. okinavensis*.

Locality	Frontonasal and frontal				TIV										
	Separated	Fused	*N*	Frequency of the separated type (%)	8	9	10	11	12	13	14	15	16	*N*	Frequency of the individual of 8–12 TIV (%)
Ateuchosaurus pellopleurus															
1. Takeshima Island	6	6	12	50.0		1	7	2	1					11	100.0
2. Iojima Island	8	9	17	47.1	1	3	6	6	1					17	100.0
3. Kuroshima Island	18		18	100.0			10	8						18	100.0
4. Kuchinoshima Island	3		3	100.0			2							2	100.0
5. Nakanoshima Island	7	2	9	77.8			3	5						8	100.0
6. Suwanosejima Island	7	3	10	70.0			3	4						7	100.0
7. Akusekijima Island	3	1	4	75.0			1	3						4	100.0
8. Kodakarajima Island	9	4	13	69.2			3	5	3					11	100.0
9. Takarajima Island	41	6	47	87.2			7	27	10					44	100.0
10. Kikaijima Island	7	1	8	87.5				4	3	1				8	87.5
11. Amamioshima Island	64	20	84	76.2			2	27	27	13	4			73	76.7
12. Tokunoshima Island	22	4	26	84.6				1	12	6	2			21	61.9
13. Okinoerabujima Island	42	10	52	80.8		1		19	17	5	1			43	86.0
Total	237	66	303	78.2	1	5	44	111	74	25	7			267	88.0
Ateuchosaurus okinavensis															
14. Iheyajima Island		15	15	0.0					3	6	2	1		12	25.0
15. Okinawajima Island		39	39	0.0				1	4	13	12	2	1	33	15.2
16. Minnajima Island		14	14	0.0										n/a	n/a
17. Miyagijima Island		2	2	0.0					1		1			2	50.0
18. Hamahigajima Island		3	3	0.0					1	1	1			3	33.3
19. Tokashikijima Island		30	30	0.0					2	8	17	3		30	6.7
20. Agunijima Island	2	6	8	25.0			1		5	2				8	75.0
21. Tonakijima Island		1	1	0.0						1				1	0.0
22. Kumejima Island		13	13	0.0					5	6	3			14	35.7
Total	2	123	125	1.6			1	1	21	37	36	6	1	103	22.3

specimens (25.0%) from Agunijima Island (site 20). The interspecific difference in frequency of the separated types was statistically significant (chi-squared test, $p < 0.05$), and the boundary samples (sites 12–14) did not show intermediate frequencies.

The examined specimens showed variation in TIV from eight to 16 subdigital scales (Table 1). The *A. pellopleurus* samples possessed 8–14 subdigital scales (mode = 11), and these samples also seemed to show clinal variation from fewer to more scales from the northern to southern islands. Conversely, the *A. okinavensis* samples showed 10–16 subdigital scales (mode =13), and a larger number of subdigitals in TIV than the *A. pellopleurus* samples (Mann-Whitney *U* test, $p < 0.05$).

For MSR, only the Amamioshima sample (site 11) showed a significant sex-related difference (Mann-Whitney *U* test, $p < 0.05$). This sample, especially the males, also showed a considerably higher frequency of 24 scale rows than the other samples (Suppl. material 2). Males and females of *A. pellopleurus*, except for the Amamioshima specimens, showed 24–30 (mode = 26) and 26–30 scale rows (mode = 26), respectively, whereas males and females of *A. okinavensis* showed the same number of 25–28 scale rows (mode = 28). A significant interspecific difference in MSR was not detected (Mann-Whitney *U* test, excluding the Amamioshima sample, $p \geq 0.05$).

For DMS, significant sexual differences were detected among the Amamioshima, Okinoerabujima, and Tokashikijima samples (sites 11, 13, and 19; Mann-Whitney *U* test, $p < 0.05$). Therefore, the data for males and females were compared separately. Males and females of *A. pellopleurus* showed 53–70 (mode = 62) and 56–69 scales (mode = 63), respectively, and males and females of *A. okinavensis* showed 54–64 (mode = 59) and 55–67 scales (mode = 58), respectively (Suppl. material 3). *Ateuchosaurus pellopleurus* tended to have larger numbers of DMS than *A. okinavensis* in both sexes (Mann-Whitney *U* test, $p < 0.05$).

The DSRBSs of most specimens could be categorized as one of the four character states described above (Fig. 2), except for a few specimens with sparse stripes (41/304 for *A. pellopleurus*, 8/113 for *A. okinavensis*), which were excluded from statistical tests and inter-population comparison. Most of the island samples in *A. pellopleurus* showed high frequencies of individuals with two or three DSRBSs (78.3%–100.0%, Table 2), except for Suwanosejima Island (50%, $N = 4$, site 6). In contrast, most of the island populations of *A. okinavensis* showed low frequencies of two or three DSRBSs (0%–40.0%). *Ateuchosaurus pellopleurus* more frequently possessed two or three DSRBSs than *A. okinavensis* (Mann-Whitney *U* test, $p < 0.05$).

Table 2. Variation of the number of dorsal scale rows with black stripes (DSRBS) in *Ateuchosaurus pellopleurus* and *A. okinavensis*. Columns 0–3 correspond to the four major character states of DSRBS, none to three pairs of scale rows with black stripes, respectively.

Locality	0	1	2	3	*N*	Frequency of the individual of 2–3 scale rows with black stripe (%)
Ateuchosaurus pellopleurus						
1. Takeshima Island			6	4	10	100.0
2. Iojima Island	1		9	1	11	90.9
3. Kuroshima Island			11	6	17	100.0
4. Kuchinoshima Island				2	2	100.0
5. Nakanoshima Island	1		6		7	85.7
6. Suwanosejima Island	2		1	1	4	50.0
7. Akusekijima Island			1	1	2	100.0
8. Kodakarajima Island			3	4	7	100.0
9. Takarajima Island	1		25	18	44	97.7
10. Kikaijima Island		1	2	5	8	87.5
11. Amamioshima Island	4	2	55	15	76	92.1
12. Tokunoshima Island	5		12	6	23	78.3
13. Okinoerabujima Island	10	1	24	17	52	78.8
Total	24	4	155	80	263	89.4
Ateuchosaurus okinavensis						
14. Iheyajima Island	9	2	1	3	15	26.7
15. Okinawajima Island	19	11	1	5	36	16.7
16. Minnajima Island		2		1	3	33.3
17. Miyagijima Island		2			2	0.0
18. Hamahigajima Island	1	1		1	3	33.3
19. Tokashikijima Island	19	2		6	27	22.2
20. Agunijima Island		3		2	5	40.0
21. Tonakijima Island		1			1	0.0
22. Kumejima Island	9	1		3	13	23.1
Total	57	25	2	21	105	21.9

Discussion

The results indicate that *A. pellopleurus* can be differentiated from *A. okinavensis* by usually having separated FrNa-frontal, two or three DSRBSs, and a tendency to have larger numbers of DMSs (mode = 62 and 63 in males and females, respectively) (Tables 1, 2, Suppl. material 3), whereas *A. okinavensis* usually has fused FrNa-frontal, either no or one DSRBS, and a tendency to have a smaller number of DMSs (mode = 59 and 58 in males and females, respectively), although there were some geographic variations in both species. While Ota et al. (1999) found the difference in frequencies of fused and separated states of FrNa-frontal between the populations of the Amami (= *A. pellopleurus*) and Okinawa Groups (= *A. okinavensis*), they concluded it was a geographically gradual variation because their Okinoerabujima sample (site 13) showed intermediate frequencies. However, the results of the present study, which are based on a larger number of samples ($N = 52$) than Ota et al. (1999)'s study ($N = 10$), showed that the Okinoerabujima population usually possesses the separated type (80.8%, Table 1); therefore, this character shows distinct geographic differentiation concordant with their genetic divergence (Makino et al. 2020). In addition, the results of the present study revealed morphological differences between these species in some other characters, as mentioned above. Thus, *A. pellopleurus* and *A. okinavensis* can be regarded as species that are genetically and morphologically well differentiated.

Taxonomy

Ateuchosaurus pellopleurus **(Hallowell, 1861)**

Figs 3, 4

Japanese name: Heriguro-Hime-Tokage

Lygosaurus pellopleurus Hallowell, 1861: 496–497 (part); Stejneger 1907: 222–224 (part); 1927: 2; Sclater 1950: 114.

Lygosoma pellopleurum: Boulenger 1887: 319; Okada 1891: 70 (part).

Lygosoma (*Homolepida*) *pellopleurus*: Boettger 1895: 107.

Lygosaurus pellopleurus browni Van Denburgh, 1912a: 7; Van Denburgh 1912b: 240–241.

Ateuchosaurus pellopleurus: Smith 1937: 231; Tanaka 1979: 37 (part); Hikida 1996: 81 (part); Ota et al. 1999: 106 (part); Goris and Maeda 2004: 155–156 (part); Austin and Arnold 2006: fig. 2, table 1; Pyron et al. 2013: fig. 7; Hedges 2014: 322; Zheng and Wiens 2016: figs 1–2; Okamoto 2017: table 5.2; Makino et al. 2020: 6 ("northern lineage"); Okamoto and Kurita 2021: 142–143 (part).

Lygosoma pellopleurus: Okada 1939: 206–209 (part).

Lygosoma (*Ateuchosaurus*) *pellopleurum*: Nakamura and Uéno 1963: 123–125 (part).

Lectotype designation. One of the existing syntypes, USNM 42110, was designated as the lectotype for *A. pellopleurus*.

Lectotype. USNM 42110 collected from Amamioshima Island, Amami Group, Ryukyu Archipelago, Japan, in the United States North Pacific Surveying and Exploring Expedition in 1853–1856.

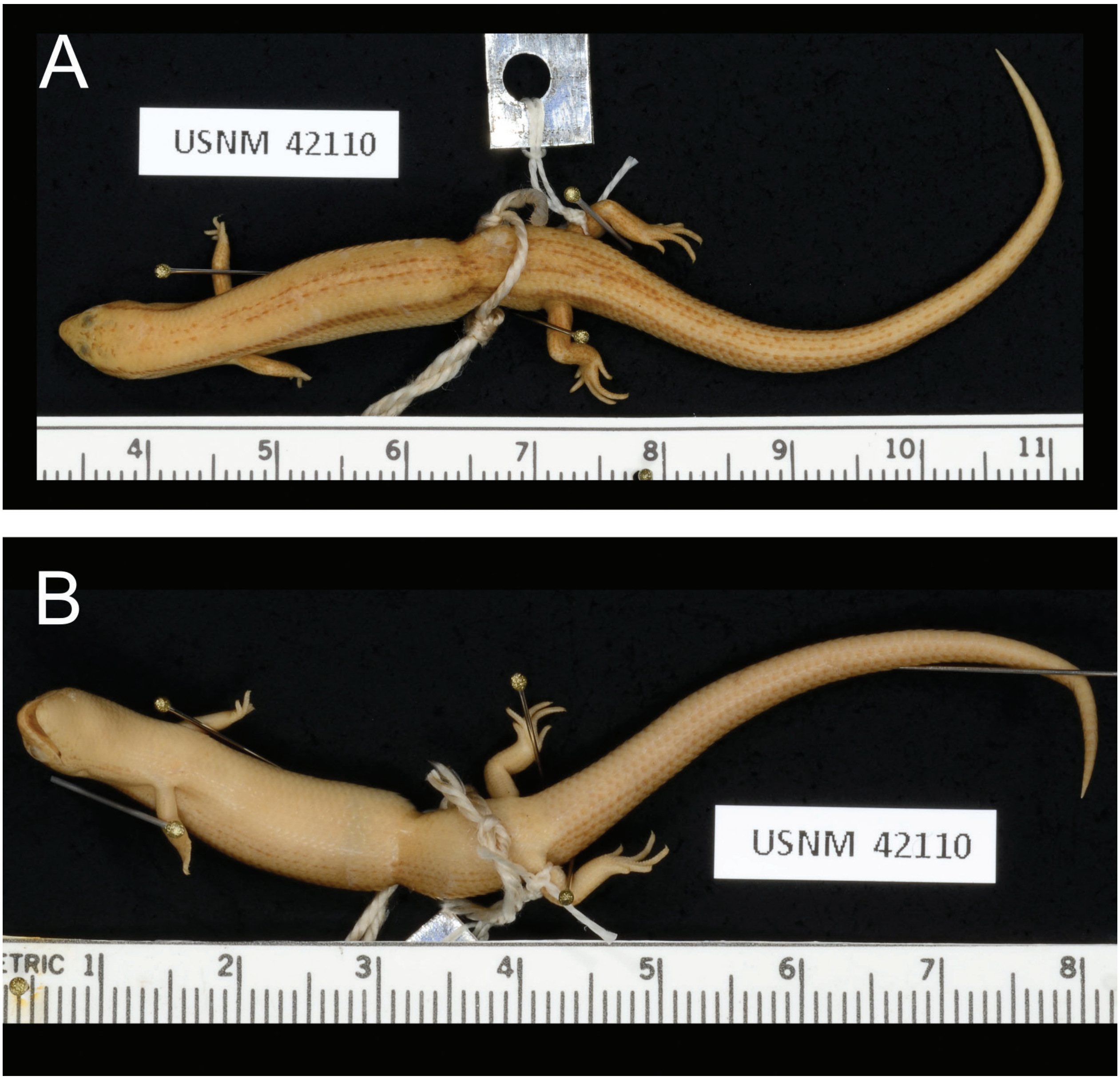

Figure 3. Dorsal (**A**) and ventral (**B**) views of the lectotype of *Ateuchosaurus pellopleurus* (USNM 42110). These photographs were cited from the collection database of the Division of Amphibians and Reptiles in the National Museum of Natural History at the Smithsonian Institution (EZID of the dorsal view: http://n2t.net/ark:/65665/m3c86ab460-1e75-4bb1-a19b-89e8439f129c, EZID of the ventral view: http://n2t.net/ark:/65665/m390991fa3-b108-4c49-bdb2-a4e443ac1cfe).

Paralectotype. USNM 42114. The locality of this specimen is the same as USNM 42110. Missing syntype(s) collected from Loo-Choo is also automatically fixed as the paralectotype(s) of *A. pellopleurus*. However, the specimen(s) may belong to *A. okinavensis*.

Material examined. Japan • Kagoshima Prefecture, Mishima Village, Takeshima Island; KUZ R54830 to 54834, 70451, 70453 to 70456, 70458, 70461 • Kagoshima Prefecture, Mishima Village, Iojima Island; KUZ R70413 to 70417, 70420, 70422 to 70425, 70442 to 70443, 70445 to 70450 • Kagoshima Prefecture, Mishima Village, Kuroshima Island; KUZ R47185 to 47202 • Kagoshima Prefecture, Toshima Village, Kuchinoshima Island; KUZ R66811 to 66812, 68678 • Kagoshima Prefecture, Toshima Village, Nakanoshima Island; KUZ R66815, 66834 to 66835, OMNH R3024 to 3028, 6880 • Kagoshima Prefecture, Toshima Village, Suwanosejima Island; KUZ R69905 to 69910, OMNH R3022 to 3023, 6886, 6889 • Kagoshima Prefecture, Toshima Village, Akusekijima Island; KUZ R66781 to 66782, OMNH R3018 to 3019 • Kagoshima Prefecture, Toshima Village, Kodakarajima Island; KUZ R34983 to 34986, 70147 to 70151, 70153 to 70155, 70162 • Kagoshima Prefecture, Toshima Village, Takarajima Island; KUZ R13169 to 13207, OMNH R1 to 4, 2217, 3014 to 3016, 6890 • Kagoshima Prefecture, Kikai Town, Kikaijima Island; OMNH R3029 to 3036 • Kagoshima Prefecture, Amamioshima Island; KUZ R62708, 66187 to 66190, 69075, 69901 to 69904, 70700, 72543, 72545, 77679 to 77682, 77686, 77689 to 77690, 77692, 77694 to 77698, 77700, 77702 to 77708, OMNH R245 to 246, 248 to 249, 260, 621 to 623, 2777, 3077 to 3094, 3096 to 3100, 3102, 3105 to 3112, 6876, 6878 to 6879, 6881 to 6883, 6885, 6891 to 6892 • Kagoshima Prefecture, Tokunoshima Island; KUZ R70680, 77672, 77674, OMNH R3039 to 3042, 3044 to 3060, 6877, 6888 • Kagoshima Prefecture, Okinoerabujima Island; KUZ R34987 to 34996, 66740, 66780, 70675 to 70679, 70681 to 70682, 77637 to 77640, 77642 to 77644, 77647, 77649 to 77650, 77652 to 77661, 77664 to 77665, 77667 to 77671, OMNH R262 to 266, 3037.

Emended diagnosis. An *Ateuchosaurus* species characterized by the following characters: FrNa and frontal usually distinct; a pair of frontoparietals that do not contact each other; eight SuCis; anteroposteriorly reduced parietals separated from SuO and pretemporal by EcP; no distinct nuchals; usually six InLas; body size medium (SVL ca. 42–70 mm); widely separated forelimb and hindlimb when appressed; usually 26 or 28 MSRs (mode = 26, 24–30); 53–70 (mode = 62) and 56–69 DMSs (mode = 63) in male and female, respectively; 8–14 TIVs (mode = 11); 10 preanals not enlarged; usually 2–3 pairs of DSRBS.

Comparison. *Ateushosaurus pellopleurus*, together with *A. okinavensis* (see below), is distinguished from *A. chinensis* by having the following characters (Nguyen et al. 2008): usually six InLas (vs. seven InLas); smaller body size (SVL ca. 42–70 mm vs. 70.0–83.8 mm; see also Okamoto and Kurita 2021); usually 26 or 28 MSRs (vs. 30 scale rows); usually 10–14 TIVs (vs. usually 16–18 TIVs); 10 preanals (vs. usually six preanals); blackish line on dorsolateral surface from snout to midbody (vs. no such line). This species resembles *A. okinavensis* in MSR and body size but differs in usually having the separated state of FrNa and frontal (vs. the fused state), 53–70 and 56–69 DMSs in male and female (vs. 54–64 and 55–67 DMSs in male and female), 8–14 TIVs (vs. 10–16 TIVs), and usually 2–3 pairs of DSRBS (vs. usually 0–1 pair).

The mean K2P genetic distance ± standard deviation (range in parenthesis) based on cytochrome *b* sequences between *A. pellopleurus* and *A. chinensis* was 24.6% ± 0.3% (24.2%–25.5%); the distance between *A. pellopleurus* and *A. okinavensis* was 13.1% ± 0.9% (11.3%–16.0%).

Description. Mainly based on a topotype (KUZ R77703), an adult male collected from Amami City in Amamioshima Island (28°23'44.29"N, 129°28'04.32"E, 2 m above sea level) (followed by ranges of several morphometric and meristic characters in parenthesis; *N* = 23, topotypes, KUZ R66188, 72543, 77679–77682, 77686, 77689–77690, 77692, 77694–77698, 77700, 77702–77708); SVL 53.5 mm (53.5 ± 2.3, 49.0–57.0); HL 6.7 mm (6.5 ± 0.3, 6.0–7.0); HW 5.0 mm (5.4 ± 0.3, 4.8–6.0); HH 4.2 mm (4.2 ± 0.3, 3.7–5.0); SEyL 3.3 mm (3.2 ± 0.2, 2.8–3.6); EyL 2.1 mm (2.3 ± 0.1, 2.1–2.5); EyEaL 3.1 mm (3.2 ± 0.2, 2.9–3.5); EaD 1.1 mm (1.0 ± 0.1, 0.8–1.2); SAL 18.1 mm (17.2 ± 0.9, 15.5–18.6); AGL 31.4 mm (32.2 ± 1.7, 28.9–34.5); TaL 56.3 mm (original tail 32.6 mm; regenerated tail 23.7 mm; 66.1 ± 0.9, 65.5–66.8, *N* = 2 with undamaged original tail); FIL 9.0 mm (8.8 ± 0.6, 7.8–9.8); HIL 15.9 mm (14.8 ± 1.0, 12.5–16.5); FIIIL 1.8 mm (1.6 ± 0.2, 1.3–2.0); TIVL 4.3 mm (4.0 ± 0.3, 3.5–4.6).

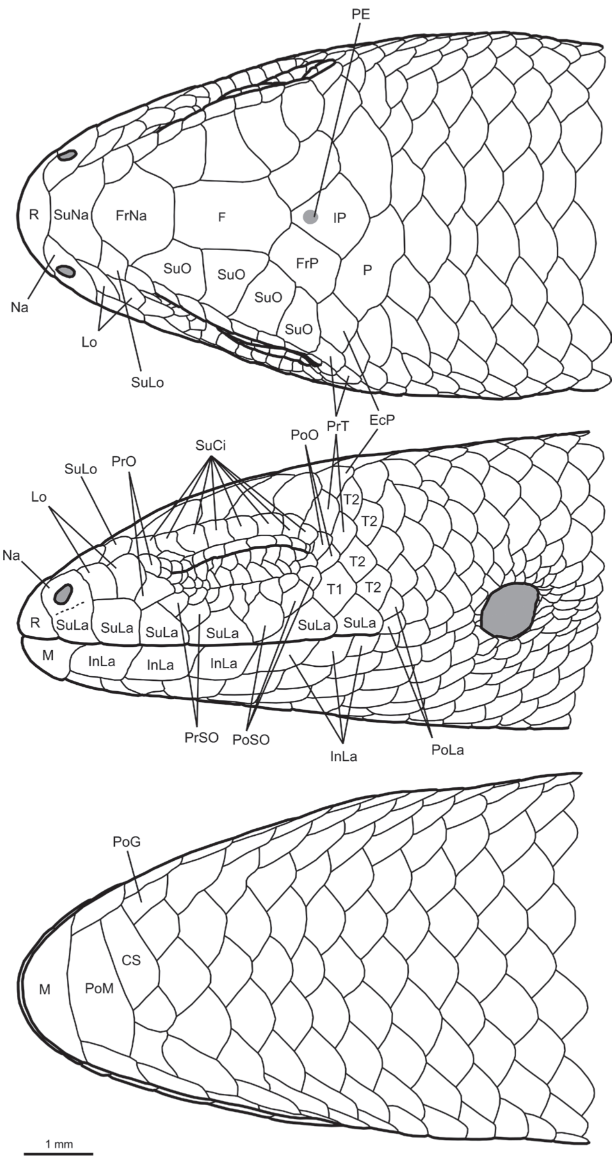

Figure 4. Dorsal, lateral, and ventral views of head scalation of *Ateuchosaurus pellopleurus* (KUZ R77703). CS, chinshield; EcP, ectoparietal; F, frontal; FrNa, frontonasal; FrP, frontoparietal; InLa, infralabial; IP, interparietal; Lo, loreal; M, mental; Na, nasal; P, parietal; PE, parietal eye; PoG, postgenial; PoLa, postlabial; PoM, postmental; PoO, postocular; PoSO, postsubocular; PrO, preocular; PrSO, presubocular; PrT, pretemporal; R, rostral; SuCi, supraciliary; SuLa, supralabial; SuLo, supraloreal; SuNa, supranasal; SuO, supraocular; T, temporal. The dashed line on the fused scale of Na and first SuLa in the lateral view indicates the line of a shallow groove on the scale.

Snout obtusely pointed; rostral visible from above, overlapping supranasal, nasal and first supralabial; nasal fused with first supralabial, with shallow groove on boundary between nasal and labial parts; nostril at center of nasal; supranasal unpaired with posterior edge concaved, overlapped by nasal; supraloreal overlapped by supranasal and anterior and posterior loreals, overlapping frontonasal and first supraciliary; frontonasal not fused with frontal, as large as supranasal, with flat posterior edge, overlapped by supranasal, overlapping first supraocular and frontal; no prefrontal; frontal large, shorter than distance from it to snout, longer than frontonasal, a part between first supraoculars narrower anteriorly, overlapping frontoparietals and interparietal; four supraoculars (no variation), anterior ones overlapping posterior ones, first one overlapped by first, second and third supraciliaries, first and second ones overlapping frontal, third and fourth ones overlapping frontoparietal; a pair of frontoparietals as long as width, separated from each other by interparietal, overlapping interparietal, parietal and ectoparietal; interparietal with short arrowhead-like tetragonal shape, similar length and width of frontoparietal, overlapping parietals; ectoparietal pentagonal and similar size to fourth supraocular, overlapped by fourth supraocular and upper pretemporal, overlapping parietal; parietals shorter and 1.5 times wider than interparietal, left one overlapped by right one; no distinct nuchal.

Two loreals with a half length and similar height of second supralabial, anterior one overlapped by nasaland second supralabial, overlapping supranasal and posterior one, posterior one overlapped by second supralabial, overlapping first supraciliary and upper and lower preoculars; eight supraciliaries (mode = 8, 7–8), anterior ones overlapping posterior ones, first one overlapped by upper preocular, third and fourth ones overlapping second supraocular, fourth to sixth ones overlapping third supraocular, sixth and seventh ones overlapping fourth supraocular, eighth one overlapping upper pretemporal and upper postocular; two preoculars, upper one similar size to first supraciliary, overlapped by lower one, lower one three times larger than upper one, overlapping third supralabial and anterior presubocular; two presuboculars overlapped by third supralabial, anterior one overlapping posterior one, posterior one overlapping fourth supralabial; three postsuboculars, lower ones overlapping upper ones, lowermost one largest, overlapped by fourth supralabial, lowermost and middle ones overlapping fifth supralabial, middle and uppermost ones overlapping primary temporal, uppermost one overlapping lower postocular; two postoculars, upper one overlapping lower one (usually three postoculars, anterior one overlapped by uppermost postsubocular, overlapping upper and lower ones); two pretemporals, upper one overlapped by fourth supraocular and upper postocular, overlapping lower one and uppermost secondary temporal, lower one smaller than upper one, overlapped by upper and lower postoculars, overlapping first to third secondary temporals; temporals with similar shape and size of body scales; single primary temporal overlapped by lower postocular and fifth supralabial, overlapping sixth supralabial; four secondary temporals, uppermost one overlapped by ectoparietal, second one overlapped by uppermost one, third one overlapped by primary temporal, overlapping second one, lowermost one overlapped by primary temporal, third one and sixth supralabial, overlapping upper postlabial; six supralabials (no variation), anterior ones overlapping posterior ones, fourth and fifth ones largely interrupted by lower-anterior postsubocular, fifth one longest, third to fifth ones under eye; two postlabials overlapped by sixth supralabial, upper one overlapping lower one.

Mental wider than and as high as rostral, overlapping postmental and first infralabial; single postmental, right part enlarged relative to left part, overlapped by first infralabial, overlapping chinshields; six infralabials on left side (five on right side) (mode = 6, 5–6), anterior ones overlapping posterior ones, first one overlapping chinshield and postgenial, sixth one smallest; a pair of chinshields, separated from each other, left one enlarged toward right side, right one distorted and smaller than left one, overlapping postgenial; a postgenial only in left side, smaller than chinshields, overlapped by second infralabial, no right postgenial.

Ear opening with oval shape, no ear lobule; forelimbs with five short but distinct fingers, third one longest; third finger with two rows of supradigitals at base and seven subdigital scales (mode = 7, 5–7); 25 scale rows around midbody (mode = 26, 24–26); 61 pairs of dorsal median scales from posterior side of parietal to position of posterior margin of preanal (mode = 57, 53–62); usually three keels on a dorsal scale; hindlimbs with five short but distinct toes, fourth one longest; fourth toe with two rows of supradigitals at base and 13 subdigital scales (mode = 11, 10–14); 10 preanals, central ones with shorter length and similar width of midbody scales, overlapped by outer ones, right-central one overlapped by left-central one, outer ones small; subcaudal not enlarged; 15 scale rows around tail at 10^{th} subcaudal position.

In alcohol, dorsal surface of head to tail light brown, first and second scale rows from dorsal median line with many blackish spots; no distinct blackish stripe on dorsal scale row (mode = 2, 0–3, *N* = 21); first scale row from dorsal median line on original tail with a pale blackish stripe; upper and lower eyelids whitish with blackish edge; blackish line on dorsolateral surface from snout to midbody interrupting dorsal and lateral sides, with narrower width of second supralabial on snout, interrupted by eye, with similar width of dorsolateral scale from eye to neck, 1.0–1.5 times as wide as dorsolateral scale at position above forelimb, gradually obscure from that position to midbody; upper margin of blackish line distinct from posterior corner of eye to midbody, located on middle position of scales on fourth scale row from dorsal median line; lateral surface of head to posterior position of forelimb whitish with small blackish spots; lateral surface of midbody to tail dark brown with small blackish spots; ventral surface of head to tail whitish, with a small number of blackish spots on head, small gray spots on midbody, rough blackish stripe on each trunk scale row around hindlimb including preanal scales, and a blackish spot on each subcaudal scale; forelimb and hindlimb light brown on dorsal surface and whitish on ventral surface with a blackish speckle on each scale row.

Variation. *Ateuchosaurus pellopleurus* usually has a single SuNa with a concave posterior edge (248/299 specimens), but sometimes has a SuNa with a straight posterior margin (28/299 specimens) or two laterally separated SuNas (23/299 specimens).

This species usually has distinct FrNa and frontal, but sometimes these are fused (Table 1). The Takeshima and Iojima populations (sites 1 and 2) also show comparable frequencies for the separated and fused types.

This species has 8–14 TIVs (mode = 11) (Table 1). This character shows clinal geographic variation from northern to southern populations: 8–12 (mode = 10, sites 1–7), 10–12 (mode = 11, sites 8 and 9), 10–14 (mode = 11, sites 10 and 11), and 9–14 TIVs (mode = 12, sites 12 and 13).

The Amamioshima population has smaller MSRs, especially in males (mode = 24, 24–28 in males; mode = 26, 24–26 in females), than the other populations, which usually have 26 or 28 MSRs (mode = 26, 24–30 in males; mode = 26, 26–30 in females) with few sexual differences (Suppl. material 2).

Males have smaller DMSs (mode = 62, 53–70) than females (mode = 63, 56–69) (Suppl. material 3). This species usually has 2–3 pairs of DSRBS, but sometimes has no stripe on the dorsum or one pair of DSRBS.

The populations of the Osumi and Tokara Groups (sites 1–9), Kikaijima and Amamioshima Islands (sites 10 and 11), and Tokunoshima and Okinoerabujima Islands (sites 12 and 13) have different mitochondrial DNA (mtDNA) sequences (Makino et al. 2020). The Osumi-Tokara populations have extremely low genetic diversity in the partial sequences of mtDNA and recombination activating gene 1 (*RAG1*) (Makino et al. 2020).

Distribution. Mishima (sites 1–3 in Fig. 1) of the Osumi Group, and the Tokara (sites 4–9 and surrounding islets) and Amami Groups (sites 10–13 and surrounding islets) of the Ryukyu Archipelago.

A skeletal remain, probably dating from the late 19th century, is known from Yoronjima Island (the island between sites 13 and 15) (Nakamura et al. 2013), although it remains unknown whether the specimen represents this species or *A. okinavensis*.

Natural history. This species occurs in leaf litter of grasslands and forest floors, including small vegetation around urban areas. Its reproductive season may range from May to August (Okada et al. 1992).

This skink is more active on sunny days (56/75 specimens) than on cloudy (11/75 specimens) or rainy days (8/75 specimens). This species is usually seen in the daytime (10:03–17:52, 79/84 specimens) in spring to autumn, but is sometimes seen in the evening to nighttime (18:11–21:48, 5/84 specimens) on Takeshima, Iojima, Kodakarajima, Amamioshima, Tokunoshima and Okinoerabujima Islands (sites 1, 2, 8, and 11–13 in Fig. 1). It is found in warm microhabitats with temperatures of more than 20.0 °C (25.2 ± 2.5 °C, 20.8–30.2 °C, 84 specimens) (T.M., personal observation).

Conservation. The island population of Iojima (site 2) is endangered by predation from the non-native Indian Peafowl *Pavo cristatus* Linnaeus, 1758, and the populations of Mishima (sites 1–3) are designated as Threatened Local Population (LP) in the Red Data Book of Japan (Ota 2014).

Ateuchosaurus okinavensis (Thompson, 1912)

Figs 5–7

Suggested Japanese name: Okinawa-Hime-Tokage

Lygosaurus pellopleurus Hallowell, 1861: 496–497 (part); Stejneger 1907: 222–224 (part); 1927: 2; Van Denburgh 1912a: 7 (part); 1912b: 240–241 (part); Sclater 1950: 114.

Lygosoma pellopleurum: Boulenger 1887: 319; Okada 1891: 70.

Lygosoma (*Homolepida*) *pellopleurus*: Boettger 1895: 107.

Lygosoma okinavensis Thompson, 1912: 4.

Ateuchosaurus pellopleurus: Smith 1937: 231; Tanaka 1979: 37 (part); Hikida, 1996: 81 (part); Ota et al. 1999: 106 (part); Goris and Maeda 2004: 155–156 (part); Austin and Arnold 2006: fig. 2, table 1; Pyron et al. 2013: fig. 7; Hedges 2014: 322; Zheng and Wiens 2016: figs 1–2; Okamoto 2017: table 5.2; Makino et al. 2020: 7 ("southern lineage"); Okamoto and Kurita 2021: 142–143 (part).

Lygosoma pellopleurus: Okada 1939: 206–209 (part).

Lygosoma (*Ateuchosaurus*) *pellopleurum*: Nakamura and Uéno 1963: 123–125 (part).

Holotype. CAS 21537 collected from Nago, Okinawajima Island, Okinawa Group, Ryukyu Archipelago, Japan.

Material examined. Japan • Okinawa Prefecture, Iheya Village, Iheyajima Island; KUZ R55183 to 55185, 77521 to 77529, 77531 to 77533 • Okinawa Prefecture, Okinawajima Island; KUZ R65611, 66980 to 66982, 68039 to 68040, 69900, 70122 to 70123, 70125, 70130 to 70131, 70673 to 70674, 77442, 77445 to 77446, 77450 to 77454, 77458 to 77462, 77464, 77466 to 77467, 77470 to 77471, 77587, OMNH R745, 1143, 3061 to 3064 • Okinawa Prefecture, Motobu Town, Minnajima Island; KUZ R77438 to 77440, 77574 to 77584 • Okinawa Prefecture, Uruma City, Miyagijima Island; KUZ R70132 to 70133 • Okinawa Prefecture, Uruma City, Hamahigajima Island; KUZ R70126 to 70128 • Okinawa Prefecture, Tokashiki Village, Tokashikijima Island; KUZ R47122 to 47141, 47143, 70501 to 70503, 70505 to 70507, OMNH R1102, 1107 to 1108 • Okinawa Prefecture, Aguni Village, Agunijima Island; KUZ R77623 to 77625, 77628 to 77632 • Okinawa Prefecture, Tonaki Village, Tonakijima Island; KUZ R66983 • Okinawa Prefecture, Kumejima Town, Kumejima Island; KUZ R70480, 70483 to 70488, 70490 to 70491, 70496 to 70497, 70499 to 70500, OMNH R3065.

Emended diagnosis. An *Ateuchosaurus* species characterized by the following: usually fused FrNa and frontal; a pair of frontoparietals that do not contact each other; eight SuCis; anteroposteriorly reduced parietals separated from SuO and pretemporal by EcP; no distinct nuchals; usually six InLas; body size medium (SVL ca. 42–70 mm); widely separated forelimb and hindlimb when appressed; usually 26 or 28 MSRs (mode = 28, 25–28); 54–64 (mode = 59) and 55–67 DMSs (mode = 58) in male and female, respectively; 10–16 TIVs (mode = 13); 10 preanals not enlarged; usually no black stripe on dorsal scale row or one pair of DSRBS; a karyotype of $2n = 28$ (Ota et al. 1998).

Comparison. *Ateuchosaurus okinavensis*, together with *A. pellopleurus*, is distinguished from *A. chinensis* by having the following characters (Nguyen et al. 2008): usually six InLas (vs. seven InLas); smaller body size (SVL ca. 42–70 mm vs. 70.0–83.8 mm; see also Okamoto and Kurita 2021); usually 26 or 28 MSRs (vs. 30 scale rows); usually 10–14 TIVs (vs. usually 16–18 TIVs); 10 preanals (vs. usually six preanals); blackish line on dorsolateral surface from snout to midbody (vs. no such line). This species also is distinguished from *A. chinensis* by the karyotype of $2n = 28$ (vs. $2n = 26$; no information about the karyotype of *A. pellopleurus*; Ota et al. 1998). *Ateuchosaurus okinavensis* resembles *A. pellopleurus* in MSR and body size but differs in almost having a fused FrNa and frontal (vs. separated ones), 54–64 and 55–67 DMSs in male and female (vs. 53–70 and 56–69 DMSs in male and female), 10–16 TIVs (vs. 8–14 TIVs), usually 0–1 pair of DSRBS (vs. usually 2–3 pairs).

The mean K2P distance ± standard deviation (range in parenthesis) based on cytochrome *b* sequences between *A. okinavensis* and *A. chinensis* was 24.7% ± 0.3% (23.9%–25.5%); the value between *A. okinavensis* and *A. pellopleurus*, see Comparison of *A. pellopleurus.*

Description. Mainly based on a specimen (KUZ R77462), an adult male collected from Ogimi Village in Okinawajima Island (26°41'44.88"N, 128°07'31.14"E, 111 m above sea level) (followed by ranges of several morphometric and meristic characters in parenthesis; $N = 13$ collected from Ogimi Village, KUZ R70673–70674, 77446, 77451–77454, 77458–77462, 77464); SVL 54.4 mm (55.0 ± 4.4, 49.8–64.8); HL 6.7 mm (6.3 ± 0.4, 5.7–7.0); HW 5.4 mm (5.5 ± 0.4, 5.1–6.1); HH 3.8 mm (3.8 ± 0.3, 3.3–4.4); SEyL 3.2 mm (3.1 ± 0.2, 2.8–3.4); EyL 2.3 mm (2.3 ± 0.2, 2.0–2.6); EyEaL 3.3 mm (3.0 ± 0.3, 2.6–3.3); EaD 1.0 mm (1.1 ± 0.1, 0.9–1.4); SAL 19.3 mm (19.2 ± 1.5, 16.7–21.8); AGL 31.1 mm (31.8 ± 2.8, 27.5–37.5); TaL 38.8 mm (the tip of tail lost; the remaining tail original; 61.4 ± 3.5, 57.6–64.5, $N = 3$ with undamaged original tail); FlL 8.5 mm (8.9 ± 0.9, 7.5–10.2, $N = 12$); HlL 14.3 mm (14.2 ± 1.0, 12.3–15.5); FIIIL 2.0 mm (1.9 ± 0.2, 1.6–2.3, $N = 12$); TIVL 4.4 mm (4.3 ± 0.4, 3.5–5.1).

Snout obtusely pointed; rostral visible from above, overlapping supranasal and nasal; nasal fused with first supralabial, with no groove on boundary between nasal and labial parts; nostril at center of nasal part of nasal; supranasal unpaired with posterior edge concaved, overlapped by nasal; supraloreal overlapped by supranasal and anterior and posterior loreals, overlapping frontonasal part and first supraciliary; frontonasal and frontal fused, frontonasal part overlapped by supranasal, overlapping first supraocular, frontal part overlapping frontoparietals and interparietal; no prefrontal; four supraoculars (no variation, $N = 12$), anterior ones overlapping posterior ones, first one overlapped by first, second and third supraciliaries, first and second ones overlapping frontal part, third and fourth ones overlapping frontoparietal; a pair of frontoparietals as long as width, separated from each other by interparietal, overlapping interparietal, parietal and ectoparietal;

Figure 5. Dorsal (**a**) and ventral (**b**) views of the holotype of *Ateuchosaurus okinavensis* (CAS 21537).

interparietal with short arrowhead-like tetragonal shape, a little longer and narrower than frontoparietal, overlapping parietals; ectoparietal pentagonal, shorter than and as wide as fourth supraocular, overlapped by fourth supraocular and upper pretemporal, overlapping parietal; parietals shorter and almost 1.2 times wider than interparietal, separated from each other by interparietal; no distinct nuchal.

Two loreals with a half length and similar height of second supralabial, anterior one overlapped by nasal, overlapping supranasal, posterior one and second supralabial, posterior one overlapped by second supralabial, overlapping first supraciliary and upper and lower preoculars; eight supraciliaries (mode = 8, 8–9), anterior ones overlapping posterior ones, first one overlapped by upper preocular, third and fourth ones overlapping second supraocular, fifth and sixth ones overlapping third supraocular, seventh one overlapping fourth supraocular, eighth one overlapping upper pretemporal and upper postocular; two preoculars, upper one similar size to first supraciliary, overlapped by lower one, lower one larger than upper one, overlapped by second supralabial, overlapping third supralabial; two presuboculars, anterior one overlapped by lower preocular in left side (overlapped by third supralabial and lower preocular in right side), overlapping third supralabial and posterior one in left side (overlapping posterior one in right side), posterior one overlapped by third supralabial, overlapping fourth supralabial; three postsuboculars, lower ones overlapping upper ones, lowermost one largest, overlapped by fourth supralabial, lowermost and middle ones overlapping fifth supralabial, middle and uppermost ones overlapping primary temporal, uppermost one overlapping anterior and lower postoculars; three postoculars, anterior one overlapping upper and lower ones, upper one overlapping lower one; two pretemporals, upper one overlapped by fourth supraocular and upper postocular, overlapping lower one and uppermost secondary temporal, lower one smaller than upper one, overlapped by upper and lower postoculars, overlapping first to third secondary temporals; temporals with similar shape and size of body scale; single primary temporal overlapped by lower postocular and fifth supralabial, overlapping sixth supralabial; four secondary temporals, uppermost one overlapped by ectoparietal, second one overlapped by uppermost one, third one overlapped by primary temporal and second one on left side (overlapped by primary temporal, overlapping second one on right side), lowermost one overlapped by primary temporal, third one and sixth supralabial, overlapping upper postlabial; six supralabials (no variation), anterior ones overlapping posterior ones, fourth and fifth ones largely interrupted by lower-anterior postsubocular, fifth one longest, third to fifth ones under eye; two postlabials overlapped by sixth supralabial, upper one overlapping lower one.

Mental as wide as and lower than rostral, overlapping postmental and first infralabial; single postmental as long as and narrower than mental, overlapped by first infralabial, overlapping chinshields; six infralabials on left side (five on right side, mode = 6, 4–7), anterior ones overlapping posterior ones, first one overlapping chinshield, sixth one smallest; a pair of chinshields, separated from each other, smaller than postmental, overlapped by second infralabial, overlapping postgenial; a pair of postgenials, smaller than chinshields, overlapped by second and third infralabials.

Ear opening with oval shape, no ear lobule; forelimbs with five short but distinct fingers, third one longest; third finger with supradigital scales of single row at tip and two rows at base and eight subdigital scales (mode = 7, 7–8, $N = 12$); 25 scale rows around midbody (mode = 26, 25–28); 59 pairs of dorsal median scales from posterior side of parietal to position of posterior margin of preanal (mode = 56, 55–61); usually three keels on a dorsal scale; hindlimbs with five distinct toes, fourth one longest; fourth toe with three rows of supradigital scales at base and 14 subdigital scales (mode = 14, 13–16); 10 preanals, central ones with shorter length and similar width of midbody scales, overlapped by outer ones, right-central one overlapped by left-central one, outermost ones small; subcaudal not enlarged; 18 scale rows around tail at 10th subcaudal position.

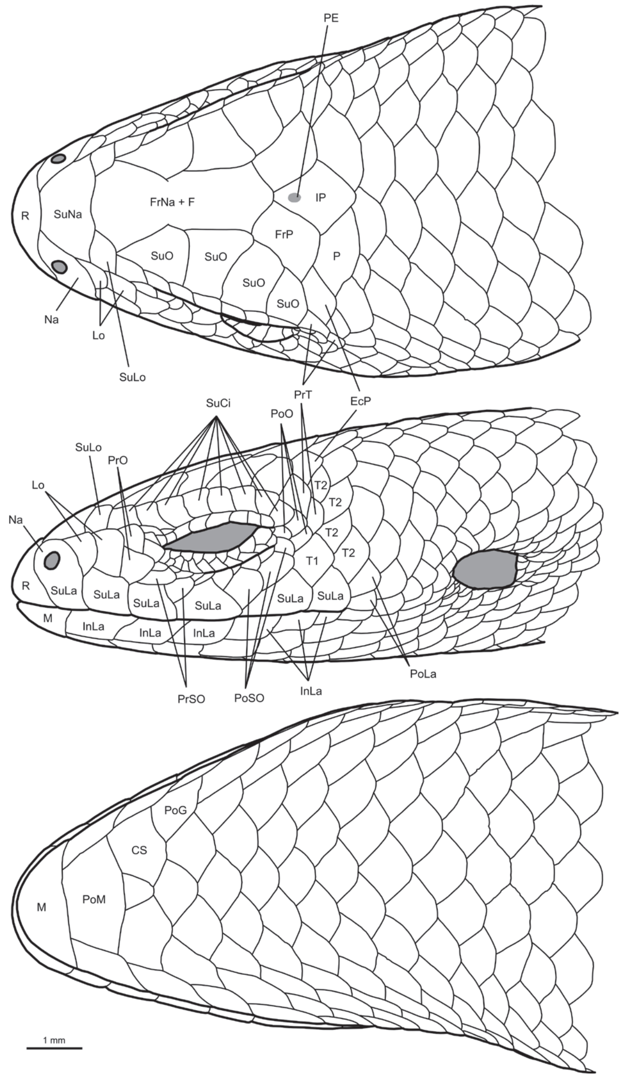

Figure 6. Dorsal, lateral, and ventral views of head scalation of *Ateuchosaurus okinavensis* (KUZ R77462). See Fig. 4 legend for abbreviations of scale names.

In alcohol, dorsal surface of head to tail light brown, first scale row from dorsal median line on midbody marginally darker with small blackish spots; no distinct blackish stripe on dorsal scale row (mode = 0, 0–1); first scale row from dorsal median line on original tail with a pale blackish stripe; upper and lower eyelids whitish with blackish edge; blackish line on dorsolateral surface from snout to midbody interrupting dorsal and lateral sides, with narrower width of second supralabial on snout, interrupted by eye, with similar width of dorsolateral scale from eye to neck, 1.0–1.5 times wider than dorsolateral scale at position above forelimb, obscure from that position to midbody; upper margin of blackish line distinct from posterior corner of eye to midbody, located on middle position of scales on fourth scale row from dorsal median line; lateral surface of head to neck brownish white with many black spots; lateral surface of upper and lower jaws with several black spots; lateral surface around forelimb to tail dark brown; ventral surface pale yellow from head to tail, with many short stripes and spots irregularly scattered in head, black spots

Figure 7. Photograph of a live individual of *Ateuchosaurus okinavensis* collected at Urasoe Park in Urasoe City, Okinawajima Island (26°15'17.37"N, 127°43'41.25"E, 38 m above sea level).

between hindlimb, and a pale black spot on each scale in tail; dorsal surface of forelimb dark brown with a rough blackish line on each scale row; ventral surface of forelimb pale yellow without blackish line; dorsal surface of hindlimb dark brown with a blackish line on each scale row; ventral surface of hindlimb pale yellow with a blackish dotted line on each scale row.

Variation. For SuNa, this species usually shows a single scale with a concave posterior edge (84/104 specimens), and sometimes two laterally separated scales (1/104 specimens) or a single scale with an almost straight posterior edge (19/104 specimens).

This species usually has a long fused FrNa and frontal scale, but sometimes FrNa and frontal are distinct (Table 1; Ota et al. 1999).

In the Tokashikijima population, males have smaller DMSs (mode = 57, 54–61) than females (mode = 60, 56–62).

Mitochondrial DNA sequences differ among the four groups of Iheyajima and Izenajima Islands (site 14 and the adjacent island), the northern part of Okinawajima Island (site 15) and the adjacent islets (including site 16), the southern part of Okinawajima Island and the islands of the Kerama Group (site 19 and the adjacent islets), and Agunijima, Tonakijima, and Kumejima Islands (sites 20–22) (Makino et al. 2020). The populations in the northern and southern parts of Okinawajima Island have different *RAG1* allele compositions (Makino et al. 2020).

Distribution. Okinawa Group (sites 14–22 and surrounding islets in Fig. 1) of the Ryukyu Archipelago.

Natural history. *Ateuchosaurus okinavensis* exhibits similar microhabitat use to *A. pellopleurus*. On Iheyajima, Okinawajima, Minnajima, Tokashikijima, Agunijima and Kumejima Islands (sites 14–16, 19, 20, and 22 in Fig. 1), *A. okinavensis* is usually seen in the daytime (6:53–17:54, 62/72 specimens) in spring to autumn (T.M., personal observation); however, it is sometimes also seen at night (18:06–23:18, 10/72 specimens). This species is found in warm microhabitats (28.6 ± 2.1 °C, 25.1–33.2 °C, 72 specimens), and is more frequently seen on sunny days (47/72 specimens) than on cloudy (15/72 specimens) or rainy days (10/72 specimens).

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Appendix 1. Institutional acronym

CAS, California Academy of Sciences; KUZ, Zoological Collection of Kyoto University; NMNH, National Museum of Natural History; OMNH, Osaka Museum of Natural History; USNM, United States National Museum.

Supplementary material 1

List of the examined specimens

Authors: Tomohisa Makino, Takafumi Nakano, Taku Okamoto, Tsutomu Hikida

Data type: excel file

Explanation note: List of the examined specimens of *Ateuchosaurus pellopleurus*, *A. okinavensis*, and *A. chinensis*. Site numbers correspond to fig. 1, tables 1, 2, and Suppl. materials 2, 3.

Link: https://doi.org/10.3897/zse.99.95923.suppl1

Supplementary material 2

Variation of the number of midbody scale rows (MSR)

Authors: Tomohisa Makino, Takafumi Nakano, Taku Okamoto, Tsutomu Hikida

Data type: excel file

Explanation note: Variation of the number of midbody scale rows (MSR) in males and females of *Ateuchosaurus pellopleurus* and *A. okinavensis*.

Link: https://doi.org/10.3897/zse.99.95923.suppl2

Supplementary material 3

Variation of the number of dorsal median scales (DMS)

Authors: Tomohisa Makino, Takafumi Nakano, Taku Okamoto, Tsutomu Hikida

Data type: excel file

Explanation note: Variation of the number of dorsal median scales (DMS) in males and females of *Ateuchosaurus pellopleurus* and *A. okinavensis*.

Link: https://doi.org/10.3897/zse.99.95923.suppl3