Morphological Variation and Distribution of the Unisexual-Bisexual Complex of the Gecko, Lepidodactylus lugubris, in French Polynesia and Easter Island

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Morphological Variation and Distribution of the Unisexual-Bisexual Complex of the Gecko, *Lepidodactylus lugubris*, in French Polynesia and Easter Island[1)]

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Abstract

This paper reviews the distribution and variation of each of the six clonal and one bisexual lineages and their hybrids of *Lepidodactylus lugubris* in French Polynesia and Easter Island. All 20 animals collected from Easter Island were identified as endemic clone F. In French Polynesia, the other five clones (*i.e.*, clones A, B, C, D, and E) were found, of which clone A was most abundant on almost all surveyed islands. Bisexual populations were found only on Scilly, Tupai, Takapoto, and Ua Pou Islands. Hybrid individuals were characterized by the significantly greater body size, whereas clone C showed smaller body when compared with other clones. In the number of postmental scales contacting the first four right infralabials, clone A was most distinctly differentiated from others. Clone F and bisexual lineage, on the other hand, had statistically significantly greater and smaller numbers of fourth toe subdigital lamellae, respectively, than those of the others.

Introduction

The mourning gecko, *Lepidodactylus lugubris* (Duméril and Bibron, 1836), is widely distributed in the tropical and subtropical regions almost around the world except Africa (e.g., Wermuth, 1965; Ineich and Blanc, 1987; Ota, 1989). This lizard has been well known as a parthenogenetic species, characterized by the rarity or complete absence of males in each population (Cuellar and Kluge, 1972; Brown and Parker, 1977). Based on literature information (Makino and Momma, 1949; Cuellar and Kluge, 1972), Kluge (1982) pointed out the probability that *L. lugubris* actually consists of diploid and triploid clones. This prediction was confirmed by Moritz and King (1985), who reported karyomorphs having $2n=2x=44$ and $2n=3x=66$ chromosomes. Further polyclony in Pacific island populations, especially those in French Polynesian islands, was reported by Pasteur *et al.* (1987) and Ineich (1987, 1988). Recent chromosomal studies have revealed that the diploid clones are of hybrid origins (Volobouev et al., 1993). Ineich (1987, 1988), on the other hand, first confirmed the occurrence of bisexual populations in French Polynesia, as well as of hybrids between the bisexual and clonal individuals that are characterized by more or less degenerated gonads and associated organs [see Saint Girons and Ineich (1992) for further details].

As to the distribution and morphological variation of each genetically characterized

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[1)] Major contents of this paper constitute a part of Ineich's (1987) Ph. D. dissertation submitted to Montpellier University.

group within *L. lugubris*, data were compiled in Ineich's (1987) unpublished Ph. D. dissertation, but have not yet been published in a comprehensive format: some analyses were made but only for the population on Takapoto Atoll, Tuamotu Archipelago, where four clonal and one bisexual lineages and their hybrids occur (Ineich and Ota, 1992). In the present paper, we extend our previous work, and review the distribution of each intraspecific group of this gecko within French Polynesia and Easter Island. We also attempt to make preliminary analyses of morphological variation among these groups in eastern Polynesian area.

Materials and Methods

A total of 1520 specimens were examined. These specimens are deposited in, and loaned from, Museum of Zoology, University of Concepcion, Chile (MZUC), or have been newly collected and will be deposited in Muséum national d'Histoire naturelle, Paris (MNHN). Of these, 20 specimens were collected from Easter Island, whereas the remainder from 25 islands belonging to all the five French Polynesian archipelagos by Ch. P. and F. Blanc, I. Ineich, and others [Table 1, Fig. 1; see Ineich (1987) and Ineich and Blanc (1988) for further details on materials examined].

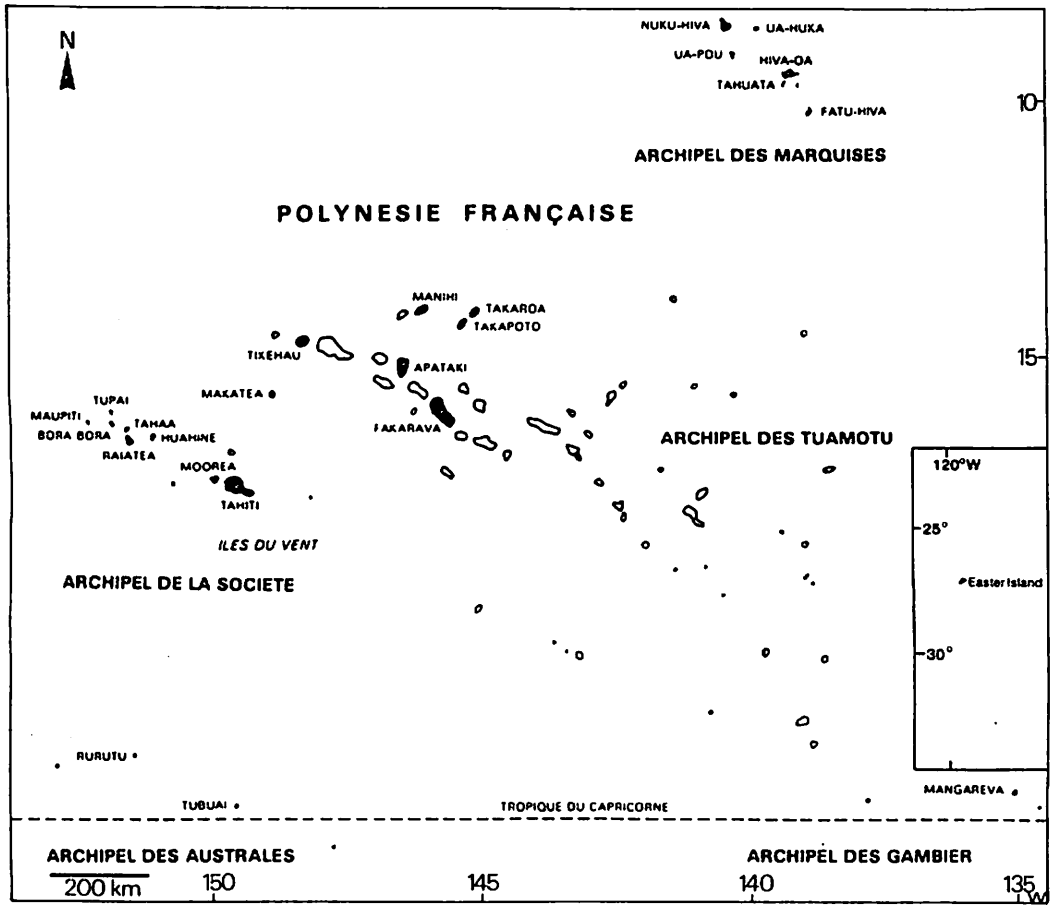

Fig. 1. Maps of French Polynesia and Easter Island (inset) showing locations of islands surveyed in the present study.

Table 1. Localities and sample sizes of clones, bisexuals, and hybrids used in the present study. Sample sizes of adults are given in parentheses. The ratio (in %) of each clone in each locality is given in brackets.

Localities		Clones						Bisex.	Hyb.	Total
Archipelago	Island/Atoll	A	B	C	D	E	F			
Society	BoraBora	5 (4) [62.5]	2 (1) [25.0]	1 (1) [12.5]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	8 (6)
	Huahine	14 (12) [82.4]	2 (2) [11.8]	1 (0) [5.9]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	17 (14)
	Maupiti	3 (2) [50.0]	2 (1) [33.3]	1 (1) [16.7]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	6 (4)
	Moorea	553 (362) [70.4]	151 (95) [19.2]	52 (36) [6.6]	23 (13) [2.9]	7 (3) [0.8]	0 [0.0]	0 [0.0]	0 [0.0]	786 (509)
	Raiatea	16 (13) [76.2]	0 [0.0]	4 (2) [19.0]	1 (1) [4.8]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	21 (16)
	Scilly	1 (1) [20.0]	0 [0.0]	1 (1) [20.0]	0 [0.0]	0 [0.0]	0 [0.0]	3 (3) [60.0]	0 [0.0]	5 (5)
	Tahaa	0 [0.0]	2 (1) [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	2 (1)
	Tahiti	7 (5) [53.8]	5 (3) [38.5]	1 (0) [7.7]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	13 (8)
	Tupai	5 (5) [62.5]	1 (1) [12.5]	1 (0) [12.5]	0 [0.0]	0 [0.0]	0 [0.0]	1 (1) [12.5]	0 [0.0]	8 (7)
Tuamotu	Apataki	2 (2) [66.7]	1 (1) [33.3]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	3 (3)
	Fakarava	0 [0.0]	1 (1) [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	1 (1)
	Makatea	2 (2) [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	2 (2)
	Manihi	1 (1) [50.0]	1 (1) [50.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	2 (2)
	Takapoto	219 (163) [50.5]	98 (78) [22.6]	16 (8) [3.7]	0 [0.0]	1 (1) [0.2]	0 [0.0]	78 (51) [18.0]	22 [5.1]	434 (301)
	Takaroa	0 [0.0]	2 (2) [66.7]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	1 [33.3]	3 (2)
	Tikehau	1 (0) [33.3]	2 (1) [66.7]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	3 (1)
Gambier	Mangareva	2 (1) [16.7]	9 (8) [75.0]	1 (1) [8.3]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	12 (10)
Australs	Rurutu	33 (28) [80.5]	4 (3) [9.8]	3 (2) [7.3]	1 (1) [2.4]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	41 (34)
	Tubuai	13 (9) [92.9]	1 (1) [7.1]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	14 (10)
Marquesas	Fatu Hiva	12 (7) [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	12 (7)
	Hiva Oa	12 (11) [92.3]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	1 [7.7]	13 (11)
	Nuku Hiva	22 (17) [73.3]	4 (4) [13.3]	4 (3) [13.3]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	30 (24)

Table 1. (extended)

	Tahuata	2 (2)	0	1 (0)	0	0	0	0	0	0	3 (2)
		[66.7]	[0.0]	[33.3]	[0.0]	[0.0]	[0.0]	[0.0]	[0.0]		
	Ua Huka	21 (20)	0	0	1 (1)	0	0	0	0	0	22 (21)
		[95.5]	[0.0]	[0.0]	[4.5]	[0.0]	[0.0]	[0.0]	[0.0]		
	Ua Pou	4 (4)	0	0	0	0	0	1 (1)	0	0	5 (5)
		[80.0]	[0.0]	[0.0]	[0.0]	[0.0]	[0.0]	[20.0]	[0.0]		
Easter	Easter	0	0	0	0	0	20 (17)	0	0	20 (17)
		[0.0]	[0.0]	[0.0]	[0.0]	[0.0]	[100.0]	[0.0]	[0.0]		
Details unknown		25 (19)	5 (5)	5 (5)	0	0	0	0	0	35 (29)
(French Polynesia)		[71.4]	[14.3]	[14.3]	[0.0]	[0.0]	[0.0]	[0.0]	[0.0]		
Total		975 (690)	293 (209)	92 (60)	26 (16)	8 (4)	20 (17)	83 (56)	24	1521 (1052)
		[64.1]	[19.3]	[6.0]	[1.7]	[0.5]	[1.3]	[5.5]	[1.6]		

Each of these specimens was first determined its allocation to certain intraspecific group [*i.e.*, one of the six clonal lineages defined in Ineich (1988) or below, bisexual lineage, or hybrid assemblage], and then was examined for the sex and maturity status on the basis of gonadal morphology after Ineich and Ota (1992). Following characters were measured and counted for comparisons: snout to vent length (SVL), measured to the nearest 1mm; the number of postmental scales contacting the first four right infralabials (RPMCIL); and the number of subdigital lamellae on the fourth toe (TIVSD).

Results and Discussion

Geographical distribution. -- Distributions of clones, bisexuals and hybrids are presented in Table 1. All specimens collected from Easter Island showed dorsal black pattern, adult SVL and RPMCIL count similar to those of clone D (*sensu* Ineich, 1988) (Fig. 2; Table 2), but seem to be slightly different from the latter in having somewhat prominent dark spots in the posterior part of the body and slightly greater TIVSD count (see below).

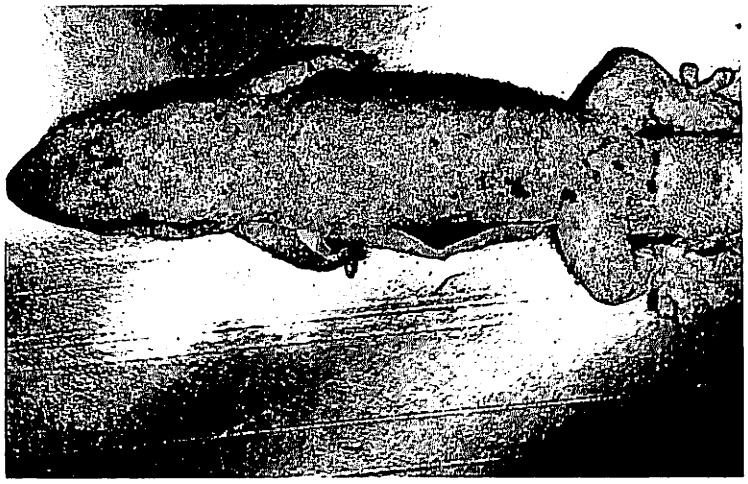

Fig. 2. Dorsal view of a specimen of clone F from Easter Island (specimen deposited in MNHN collection).

Table 2. Meristic characters of clones, bisexuals and hybrids of *Lepidodactylus lugubris* from French Polynesia and Easter Island. SVL: snout-vent length (in mm); RPMCIL: postmental scales contacting the first four right infralabials; TIVSD: subdigital lamellae on the fourth toe.

Lineage	Adult SVL				RPMCIL				TIVSD			
	N	$\bar{x}$	SD	range	N	$\bar{x}$	SD	range	N	$\bar{x}$	SD	range
Clone A	680	39.4	3.21	33-49	950	6.82	0.78	5-9	956	11.67	0.72	9-16
Clone B	209	39.3	2.81	33-45	288	7.41	0.84	5-10	291	11.94	0.73	10-14
Clone C	60	37.2	2.46	33-43	91	7.75	0.68	6-9	89	11.81	0.69	10-13
Clone D	12	39.0	3.13	33-44	22	7.36	0.73	6-9	22	12.14	0.71	11-14
Clone E	4	37.3	3.30	34-41	8	7.75	0.46	7-8	8	12.13	0.84	11-13
Clone F	17	39.4	1.80	35-41	20	7.30	0.80	6-9	11	12.63	0.68	12-14
Bisexuals	55	38.2	2.62	33-44	81	7.58	0.97	5-10	80	10.63	0.68	9-12
Hybrids	20	41.7	3.05	34-46	24	6.88	1.04	5-9	24	11.96	0.86	9-13

Since this colormorph was not found in the collection from French Polynesian islands, we tentatively refer them here as clone F. Considering such similarities, it seems likely that the two clones have a common parental species or share an ancestral clone with each other exclusively.

It has been pointed out that *L. lugubris* is a succecssful colonizer, having spread its range of distribution presumably by use of artificial transportation media on many occasions (e.g., Cuellar and Kluge, 1972; Ota, 1986; Zug, 1991). If this is the case for eastern Polynesian populations, absence of clone F in French Polynesia and of the others in Easter Island may reflect the low frequency of traffics jointing these two regions. This speculation seems to be circumstantially supported by the ethnological view that Easter Island was colonized by Polynesians only one time at about A.D. 400 (*e.g.*, Conniff, 1993).

Within French Polynesia, clone A seems to be dominant, followed by clones B and C in this order, on most islands surveyed (Table 1). Clones D and E are relatively rare, although absence of their records on several islands may simply be attributable to the insufficent sample size. Clone D is found only on Moorea and Raiatea of the Society Archipelago, Rurutu of the Australs Archipelago, and Ua Huka of the Marquesas Archipelago, whereas clone E on Moorea, and Takapoto of the Tuamotu Archipelago.

Bisexual populations were found only from Scilly and Tupai of the Society Archipelago, Takapoto of the Tuamotu Archipelago, and Ua Pou of the Marquesas Archipelago. Recent surveys have revealed that bisexual populations also occur on Maiao of the Society Archipelago and Rangiroa of the Tuamotu Archipelago (Ineich, unpublished data). Furthermore, because animals having degenerated gonads and presumably originating from hybridizations between parthenogenetic females and bisexual males (Ineich, 1988; Ineich and Ota, 1992; Saint Girons and Ineich, 1992) were found from Takaroa of the Tuamotu Archipelago and Hiva Oa of the Marquesas Archipelago, it is highly probable that future intensive surveys will reveal the occurrences of gonochoristic populations on these islands as well.

Morphological variation. — Meristic characters of clonal and bisexual lineages of *L. lugubris* and their hybrids are presented in Table 2, and compared with each other in Tables 3 and 4. In both clonal and bisexual lineages, individuals exhibiting SVL as great

Table 3. Comparisons of adult snout-vent length among clones, bisexuals, and hybrids of *Lepidodactylus lugubris* from French Polynesia and Easter Island by Student's (for equal variance) and Aspin-Welch's *t*-tests (for unequal variance:*). NS: $P > 0.05$, +: $P < 0.05$, ++: $P < 0.01$, +++: $P < 0.001$.

	Clone A	Clone B	Clone C	Clone D	Clone E	Clone F	Bisexuals	Hybrids
Clone A	---	NS*	++++*	NS	NS	NS*	+	++
Clone B		---	+++	NS	NS	NS*	+	+++
Clone C			---	+	NS	++	+	+++
Clone D				---	NS	NS*	NS	+
Clone E					---	NS	NS	+
Clone F						---	NS	++*
Bisexuals							---	+++

Table 4. Comparisons of the numbers of postmental scales contacting the first four right infralabials (upper diagonal) and subdigital lamellae on the fourth toe (lower diagonal) among clones, bisexuals, and hybrids of *Lepidodactylus lugubris* from French Polynesia and Easter Island by Wilcoxon's 2-sample test. NS: $P > 0.05$, +: $P < 0.05$, ++: $P < 0.01$, +++: $P < 0.001$.

	Clone A	Clone B	Clone C	Clone D	Clone E	Clone F	Bisexuals	Hybrids
Clone A	---	+++	+++	++	+++	++	+++	NS
Clone B	+++	—	+++	NS	NS	NS	NS	++
Clone C	NS	NS	—	+	NS	+	NS	+++
Clone D	++	NS	+	—	NS	NS	NS	NS
Clone E	NS	NS	NS	NS	—	NS	NS	++
Clone F	+++	+++	+++	+	NS	—	NS	NS
Bisexuals	+++	+++	+++	+++	+++	+++	---	++
Hybrids	NS	NS	+++	NS	+++	++	+++	—

as or greater than 33 mm possessed more or less developed gonads, and hence are regarded as adults: comparisons of SVL were made only among adult samples. No significant differences were recognized in adult SVL between males and females of the bisexual lineage ($P > 0.05$: Student's *t*-test). So, data for both sexes were combined for further analyses. Because hybrid individuals are characterized by degenerated reproductive organs, there are no criteria to divide them into adult and juvenile categories. We thus used SVLs of hybrids greater than 33 mm for comparisons.

SVL of the hybrid assemblage is significantly greater than those of clonal and bisexual lineages. On the other hand, SVL of clone C (triploid: Ineich, 1988) is significantly smaller than those of the other clones and bisexuals excepting clone E. This is presumably due to the small sample size for the latter. These results well coincide with those in previous reports (Ineich, 1988; Ineich and Ota, 1992), confirming the presence of heterosis in hybrid individuals.

In RPMCIL, clone A is significantly smaller than other groups except for the hybrid assemblage. This seems to support the previous assumption that hybrids have resulted from mating between the gonochoristic males and females belonging to clone A (Ineich, 1988;

Ineich and Ota, 1992).

Results of comparisons of TIVSD are similar to those using samples from Takapoto (Ineich and Ota, 1992) in emphasizing the distinct diversification of the bisexual lineage from the others. It is also interesting to note that the value in clone F is slightly, but significantly, greater than that in clone D ($P < 0.05$; Wilcoxon's 2-sample test), because this seems to support the presumption that these two groups are genetically differentiated from each other to warrant the separation in clonal level (see above). Further cytogenetic and molecular studies are definitely needed to clarify the actual status and relationship of the unique Easter Island clone.

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References

Brown, W. C. & F. Parker. 1977. Lizards of the genus *Lepidodactylus* (Gekkonidae) from the Indo-Australian Archipelago and the islands of the Pacific, with descriptions of new species. *Proc. Calif. Acad. Sci.*, 41: 253-265.

Conniff, R. 1993. Easter Island unveiled. *Nat. Geogr.*, 183(3): 54-79.

Cuellar, O. & A. G. Kluge. 1972. Natural parthenogenesis in the gekkonid lizard *Lepidodactylus lugubris*. *J. Genet.*, 61: 14-26.

Ineich, I. 1987. Recherches sur le peuplement et l'éveloution des Reptiles terrestres de Polynèsic française. 515 pp., Ph.D. dissertation, Univ. Montpellier.

Ineich, I. 1988. Mise en évidence d'un complexe unisexué -bisexuée chez le gecko *Lepidodactylus lugubris* (Sauria, Lacertilia) en Polynèsic française. *C. R. Acad. Sci. Paris, sèr III*, 307: 271-277.

Ineich, I. & C. P. Blanc. 1989 [1988]. Distribution des Reptiles terrestres en Polynèsic orientale. *Atoll Res. Bull.*, (318): 1-75.

Ineich, I. & H. Ota. 1992. Additional remarks on the unisexual-bisexual complex of the gecko, *Lepidodactylus lugubris*, in Takapoto Atoll, French Polynesia. *Bull. Coll. Sci., Univ. Ryukyus*, (53): 31-39.

Kluge, A. G. 1982. The status of the parthenogenetic gekkonid lizard *Gehyra variegata ogasawarasimae*. *J. Herpetol.*, 16: 86-87.

Makino, S. & E. Momma. 1949. An idiogram study of the chromosomes in some species of reptiles. *Cytologia* 15: 96-108.

Moritz, C. & D. King. 1985. Cytogenetic perspectives on parthenogenesis in the Gekkonidae. *In*: Grigg, G., R. Shine & H. Ehmann, eds. Biology of Australasian Frogs and Reptiles, Surrey Beatty & Sons, Sydney, 327-337.

Ota, H. 1986. The mourning gecko *Lepidodactylus lugubris* (Duméril and Bibron, 1836); an addition to the herpetofauna of Taiwan. *J. Taiwan Mus.*, 39: 55-58.

Ota, H. 1989. A review of the geckos (Lacertilia: Reptilia) of the Ryukyu Archipelago and Taiwan. *In:* Matsui, M., T. Hikida & R. C. Goris, eds. Current Herpetology in East Asia, Herpetological Society of Japan, Kyoto, 222-261.

Pasteur, G., J.-F. Agnese, Ch. P. Blanc & N. Pasteur. 1987. Polyclony and low relative heterozygosity in a widespread unisexual vertebrate, *Lepidodactylus lugubris* (Sauria). *Genetica*, 75: 71-79.

Saint Girons, H. & I. Ineich. 1992. Histology of the reproductive tract of hybrids between gonochoristic males and parthenogenetic females of *Lepidodactylus lugubris* in French Polynesia (Reptilia, Gekkonidae). *J. Morphol.*, 212: 55-64.

Volobouev, V., G. Pasteur, I. Ineich & B. Dutrillaux. 1993. Chromosomal evidence for a hybrid origin of diploid parthenogenetic females from the unisexual-bisexual *Lepidodactylus lugubris* complex (Reptilia, Gekkonidae). *Cytogenet. Cell Genet.*, 63: 194-199.

Wermuth, H. 1965. Liste der rezenten Amphibien und Reptilien: Gekkonidae, Pygopodidae, Xantusiidae. *Tierreich*, 80: 1-246.

Zug, G. R. 1991. The lizards of Fiji: Natural history and systematics. *Bishop Mus. Bull. Zool.*, 2: 1-136.