Additional Remarks on the Unisexual-Bisexual Complex of the Gecko, Lepidodactylus lugubris, in Takapoto Atoll, French Polynesia

Bull. Coll. Sci., Univ. Ryukyus, No. 53 : 31－39 (1992)

Additional Remarks on the Unisexual-Bisexual Complex of the Gecko, *Lepidodactylus lugubris*, in Takapoto Atoll, French Polynesia

Ivan INEICH* and Hidetoshi OTA**

*Museum national d'Histoire naturelle, Laboratoire des Reptiles et Amphibiens, 25, rue Cuvier 75005 Paris, France, and Centre de l'Environnement, Antenne Museum ／E.P.H.E., B.P. 1013, Papetoai, Moorea, French Polynesia.

**Department of Biology, University of the Ryukyus, Nishihara, Okinawa, 903-01 Japan.

Abstract

Intensive survey over a large series of specimens of the mourning gecko, *Lepidodactylus lugubris*, from Takapoto Atoll, Tuamotu Archipelago, French Polynesia, revealed that the population consists of unisexual and bisexual lineages, and their hybrids. Results of observations on the distribution, external characters, and reproductive traits are presented and compared among clones, bisexuals and hybrids.

Introduction

Parthenogenesis in the mourning gecko, *Lepidodactylus lugubris* (Dumeril and Bibron, 1836), was first demonstrated by Cuellar and Kluge (1972). While assuming the unisexual mode of reproduction in this lizard, they noted the presence of a few males (four *versus* 669 females) in the collection from the Solomons and Hawaii Islands. Several subsequent authors also reported the occurrence of rare males with preanal and femoral pores and／or more or less developed testes. In most of these works, however, males proved to be sterile in reality and have been regarded as resulting from genetic and／or developmental anormality within primarily all-female populations, whereas some other records seem to be attributable to misidentification of specimens actually belonging to other species of the genus *Lepidodactylus* (see Ineich and Blanc, 1987, for review). Recently, however, Ineich (1987, 1988) discovered a bisexual population of *L. lugubris* occurring sympatrically with several unisexual clones on Takapoto Atoll of the Tuamotu Archipelago, French Polynesia (Fig. 1). This discovery seems to have great taxonomic significances because type locality of this species (*i.e.*, Tahiti) is close to the atoll. Ineich (1987, 1988) further reported the presence of individuals characterized by degenerated genital tracts on this atoll, and assumed them to have resulted from the hybridization between males from the bisexual population and females belonging to unisexual clones (Ineich, 1988). However, despite its possible significance for the understandings of evolutional aspects of unisexuality and polyploidy in squamate reptiles (Darevsky *et al.*, 1985), biological information on the unisexual-bisexual complex of *L. lugubris* from Takapoto Atoll or other French Polynesian islands is still quite meager.

In the present paper, we provide additional data on the distributional, morphological and ecological features of the bisexual population, and compare them with those of unisexual lineages and the hybrids within Takapoto Atoll.

Materials and Methods

The survey on Takapoto Atoll (an emerged round-shaped landstrip on the reef consisting

Acceped : January 16, 1992

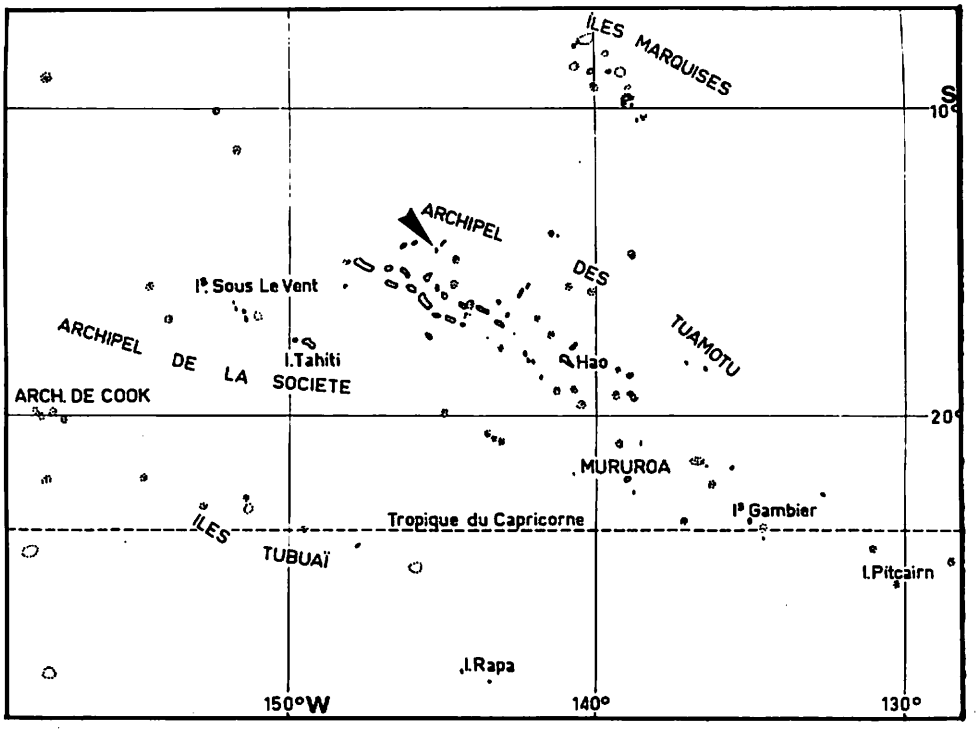

Fig. 1. Map of French Polynesia showing the location of Takapoto Atoll (indicated with an arrow).

of two major arcs and several islets; 17.7 km and 5.7 km in major and minor axes, respectively; less than 5 m above sea level even at the highest point; see Sachet, 1983, for further details) was made in February 1986 by the senior author and Ch. P. Blanc. Specimens of *L. lugubris* were collected by hand at 11 stations as follows (Fig. 2). (1): Northeastern end of the southern branch of the south arc; (2): 1.5 km east of the Fakatopatere Village; (3): Vegetation and inhabited house near the airstrip (collections made only during the night); (4): Inside and outside the Etablissement pour la Valorisation des Activites Aquatiques et Maritimes (E.V.A.A.M., local fisheries service) station; (5): Cemetery of the Fakatopatere Village; (6): ca. 500 m north of the Fakatopatere Village; (7): ca. 1 km north of the Fakatopatere Village; (8): ca. 3 km west of the Fakatopatere Village; (9): Vairua; (10): Northeastern end of the south arc; (11): Gnake (around the middle of the north arc).

Unpublished distributional data and specimens obtained from the south arc of Takapoto Atoll by F. and C. P. Blanc in July 1981 were also incorporated. All materials will be deposited in the Paris Natural History Museum (see Ineich and Blanc, 1988, for detailed sampling data for these specimens).

Snout to vent length (SVL), and the numbers of fourth toe scansors (TIVSD: counted on right side) and preanal and femoral pores (PFP) were measured and counted, respectively, after fixation in 95% ethanol and preservation in 70% ethanol. The sex and maturity were determined for each specimen by the abdominal dissection and direct observation on gonads. As was reported by the senior author (Ineich, 1988), the sample from Takapoto Atoll consists of unisexual and bisexual animals and their hybrids. Further-

more, four of the five French Polynesian clonal lineages were recognizedin the all-female assemblage on this atoll. Each lineage is characterized by the ploidy and the dorsal color pattern as follows (Fig. 3; see Ineich, 1988, for further details). Clone A: diploid, with two longitudinal rows of six to eight (mostly seven) dark dots from the neck to the base of the tail, dorsal ground color light gray or ivory in ethanol; clone B: triploid, with numerous dark spots, especially enlarged and mostly paired on the neck and the base of the tail, dorsal ground color light gray or ivory in ethanol; clone C: triploid, dorsal pattern similar to clone A, but with two longitudinal thin stripes on the neck, dorsal ground color often reddish brown in ethanol; clone E: unknown ploidy, dorsal ground color reddish brown without fixed dark patterns. Specimens belonging to the bisexual lineage are characterized by numerous dark spots on the upper surface of the head, and light gray and dark gray

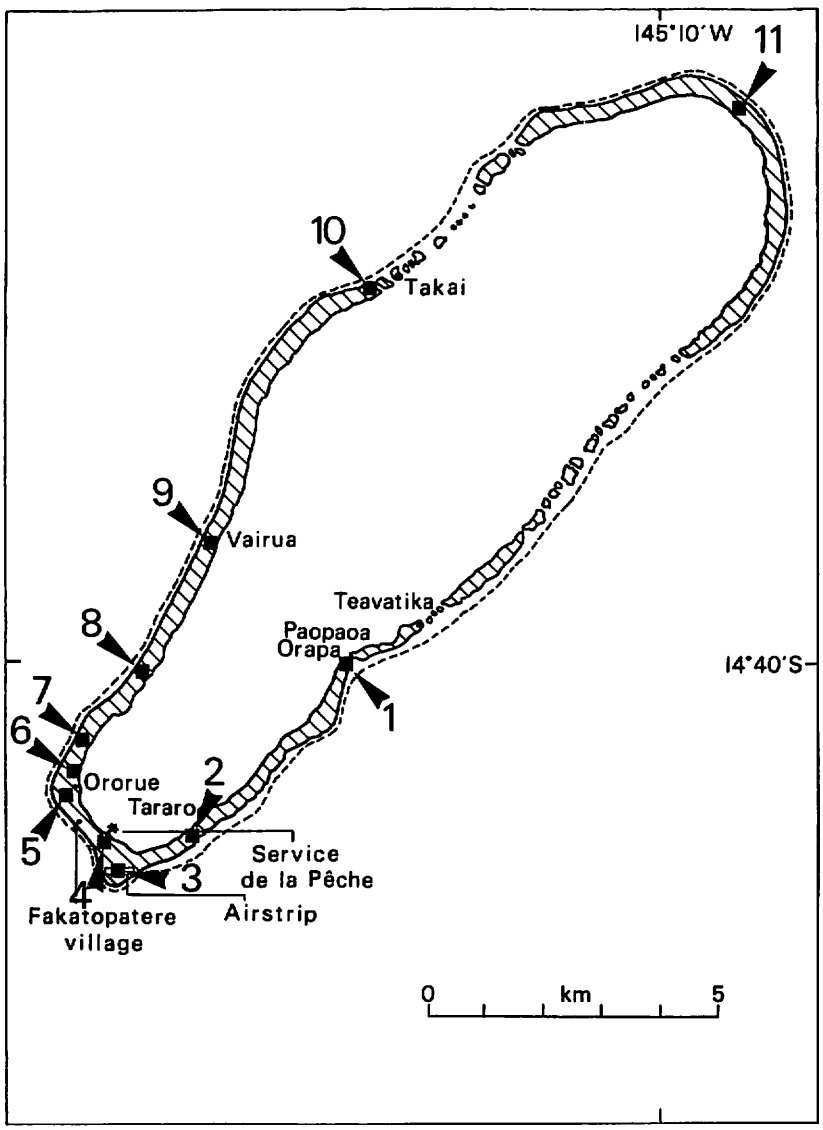

Fig. 2. Map of Takapoto Atoll showing the location of 11 sampling stations (see the text).

ground color in middorsal and flank regions, respectively. Furthermore, bisexual lineage has males with preanal and femoral pores and enlarged cloacal spurs (*sensu* Ota and Hikida, 1988); pores are lacking and cloacal spurs are much smaller in females. Besides these, several hybrids characterized by degenerated gonads were also found. They resemble clone A in dorsal coloration, but differ from the latter by having a pair of enlarged dark spots on the neck, as well as by the occasional appearance of femoral and preanal pores. Hybrids are further divided into male and female phenotypes on the basis of the presence and absence of pores and relative size of cloacal spurs.

A total of 439 specimens were examined, of which 219, 98, 16, 1, 78, and 22 were assigned to clones A, B, C, E, bisexual lineage, and hybrids, respectively. Allocations of the remaining five specimens were not determined because of the poor state of preservation, or apparent color anormality such as distinctly asymmetrical dorsal pattern.

Results and Discussion

Geographical distribution and habitats. ——Among the four unisexual lineages, clones A and B were most dominant in this order, and were observed throughout the Takapoto Atoll. Clone C was much rare, and was not found in the north arc and most portion of the northern branch of the south arch. Clone E on the atoll was represented only by a single specimen collected from Station 3 (Fig. 2, Table 1). This clone is more abundant in some other French Polynesian islands, but never exceeds 5% of total sample in any locality (Ineich, 1988).

During the present survey, the bisexual form was relatively abundant in the northern branch of the south arc between Stations 4 and 9 (*i.e.*, Stations 4, 5, 7 and 9), whereas they were rare or not found at all in the remaining parts (Table 1). Likewise, bisexuals were found only between the cemetery (Station 5) and the northeastern end of the northern branch (Station 10) during the survey in 1981, although the north arc was not surveyed in that occasion.

Records of hybrids are scattered throughout the atoll. But their density seems to be low in most, if not all, portions of the atoll (Table 1).

On Takapoto Atoll, the majority of collection of *L. lugubris* was obtained from live and dead wood-plants of several species such as *Pandanus* sp., *Guettarda speciosa, Casuarina equisetifolia*, and *Cocos nucifera*. This gecko was also found abundant in artificial constructions, and under fallen leaves on the ground.

Animals belonging to more than one clone, bisexual lineage and/or hybrids were found to occur syntopically in various microhabitats. At Station 5, for example, 28 individuals were obtained from a dead tree (*Casuarina equisetifolia*), of which 12 animals were clone A, four were clone B, 11 were bisexuals, and the other was a hybrid individual.

It seems unlikely that climatological and/or vegetational factors are responsible to the distributional bias of the bisexual. For, the atoll shows low variability in these aspects due to its small size and low elevation (see "Materials and Methods" section). Environments under which bisexual animals were found are rather variable: some animals were collected from dead trees, others from live trees, and others from beneath dead palm leaves on the ground. This also makes the circumstantial evidences to reject the probability that the patchy distribution of the bisexual merely resulted from that of available habitats. Thus, it is likely that the distribution and frequency of the bisexual reflect the

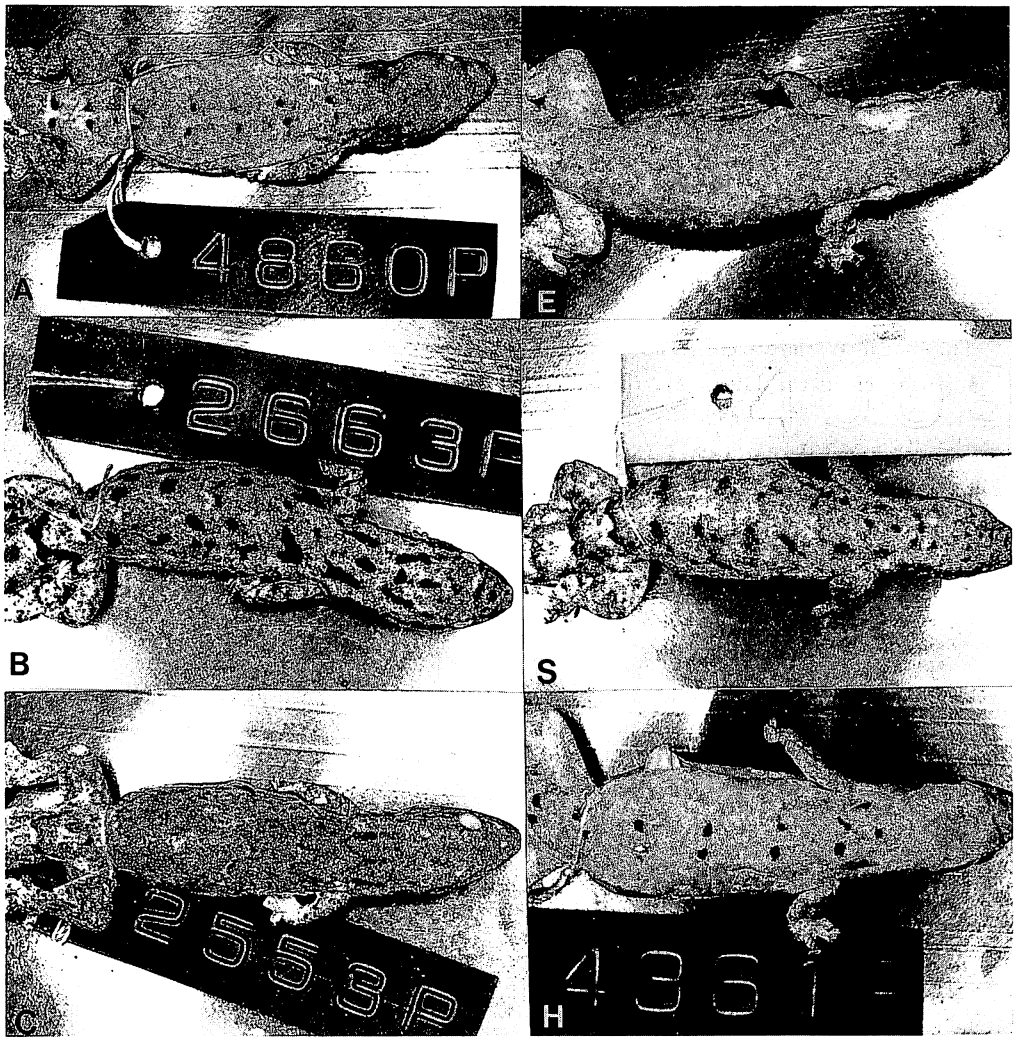

Fig. 3. Dorsal patterns of clones, bisexual, and the hybrid of *Lepidodactylus lugubris* from French Polynesia.
A: Clone A. B : Clone B. C: Clone C. E: Clone E. S: Bisexual. H: Hybrid.

history of its entry or emergence on the atoll and subsequent competitive interaction with the clones that have lead to the decrease of the bisexual.

Size of adults. --Specimens of both unisexual and bisexual *L. lugubris* from Takapoto Atoll that are as large as or greater than 33.0 mm in SVL possess well-developed gonads, and thus are regarded as adults. Minimum size of the mature individual is close to those for populations from American Samoa (35 mm: Schwaner, 1980), Guam of the Mariana Islands (34 mm: Sabath, 1981) and Fiji (35 mm: Zug, 1991), and greater than that for Philippine population (29.9 mm: Brown and Alcala, 1978).

No significant differences are recognizable in the adult SVL between the sexes belonging to the bisexual lineage ($p > 0.05$, Student's t-test). Clone C is smaller than the other clones ($p < 0.01$) or bisexuals ($P < 0.05$, Student's t-test). On the other hand, adult SVL in the hybrid is, as was briefly noted by Ineich (1988), significantly greater

than those in clones and bisexuals ($p<0.001$, Student's t-test; Tables 2 and 3). This seems to be attributable to the heterosis resulting from the hybridization between genetically diverged lineages.

Number of fourth toe scansors.--The number of scansors beneath the fourth toe (TIVSD) is highly variable in *Lepidodactylus lugubris* on Takapoto Atoll, ranging nine to 16 (Table 2), but there are no significant differences among means of this value in the clones and hybrids, or between those in males and females of the bisexual lineage ($p>0.05$, Wilcoxon's 2-sample test). On the other hand, the scansor count in the bisexual is significantly smaller than those of clones and hybrids ($p<0.001$, Wilcoxon's 2-sample test; Tables 2 and 3).

This suggests the larger genetic differences between the bisexual lineage and the clones than those among the latter. On the other hand, the data could be indicative of the close genetic similarity of hybrids to clones rather than to bisexuals. Ineich (1988), on the basis of anatomical features of the genital tract, assumed animals with degenerated gonads from the Takapoto Atoll (here treated as hybrids) to be triploid and have resulted from the hybridization between males of the bisexual lineage and females of Clone A, the only diploid clone of French Polynesia. Present data seem to fit well to this assumption in that these imply the predominance of diploid genom sets from the Clone A over haploid genom from the bisexual male in hybrids.

Table 1. The numbers and ratios (in %) of specimens belonging to the four clones, bisexual lineage, and hybrids between unisexual females and bisexual males of *Lepidodactylus lugubris* collected from 11 sampling stations within Takapoto Atoll.
See Fig. 2 and text for locations of the stations.

Station	Number (ratio)							
	Clone A	Clone B	Clone C	Clone E	Bisexual	Hybrids	Unidentified	Total
1	10 (45.5)	10 (45.5)	1 (4.5)	0 (0.0)	0 (0.0)	1 (4.5)	0 (0.0)	22
2	5 (50.0)	4 (40.0)	1 (10.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	10
3	50 (78.1)	8 (12.5)	2 (3.1)	1 (1.6)	0 (0.0)	3 (4.7)	0 (0.0)	64
4	8 (40.0)	5 (25.0)	3 (15.0)	0 (0.0)	3 (15.0)	0 (0.0)	1 (5.0)	20
5	41 (30.6)	20 (14.9)	3 (2.2)	0 (0.0)	59 (44.0)	9 (6.7)	2 (1.5)	134
6	24 (61.5)	9 (23.1)	2 (5.1)	0 (0.0)	1 (2.6)	3 (7.7)	0 (0.0)	39
7	5 (38.5)	5 (38.5)	0 (0.0)	0 (0.0)	1 (7.7)	2 (15.4)	0 (0.0)	13
8	10 (45.5)	3 (13.6)	0 (0.0)	0 (0.0)	7 (31.8)	2 (9.1)	0 (0.0)	22
9	9 (37.5)	10 (41.7)	0 (0.0)	0 (0.0)	5 (20.8)	0 (0.0)	0 (0.0)	24
10	11 (45.8)	11 (45.8)	1 (4.2)	0 (0.0)	0 (0.0)	1 (4.2)	0 (0.0)	24
11	34 (75.6)	7 (15.6)	0 (0.0)	0 (0.0)	2 (4.4)	1 (2.2)	1 (2.2)	45
Total	207 (49.6)	92 (22.1)	13 (3.1)	1 (0.2)	78 (18.7)	22 (5.3)	4 (1.0)	417

Number of preanal and femoral pores. --Preanal and femoral pores were present in adult males of the bisexual lineage ($N=17$; Fig. 4), as well as the male phenotypes of the hybrid of 42 to 46 mm in SVL ($N=8$; $x=43.8$). In the former, the number of pores (PFP) varied from 11 to 27 ($x=22.0$, $SE=1.05$), and is statistically significantly correlated with SVL ($p<0.01$; Fig. 5). The regression equation, obtained by the least squares method are:

$$PFP = 0.955SVL - 13.019.$$

Significant correlation between SVL and PFP implies that the pore number increases with the growth of the male even after its attainment to the sexual maturity. PFP in hybrids varied from 22 to 28 ($x=24.9$, $SE=0.77$), and is significantly greater than that of the bisexual ($p<0.01$; Wilcoxon's 2-sample test). No significant correlations are recognizable between PEP and SVL ($p>0.05$; Fig. 5).

Table 2. Adult SVL (in mm) and the numbers of fourth toe scansors (TIVSD) of the four clones, bisexual lineage, and hybrids between unisexual females and bisexual males of *Lepidodactylus lugubris* collected from Takapoto Atoll.

Lineage	Sex	N (Adults)	SVL			TIVSD		
			x	SE	range	x	SE	range
Clone A	f	219(163)	38.9	0.22	33-47	12.0	0.05	9-16
Clone B	f	98(78)	38.7	0.27	33-44	12.1	0.08	10-13
Clone C	f	16(8)	36.0	0.46	33-37	12.1	0.17	11-13
Clone E	f	1(1)	39.0	----	-----	12.0	----	-----
Bisexual	f	35(29) *	38.5	0.52	33-44	10.7	0.09	10-12
	m	28(22) *	37.6	0.52	33-42	10.5	0.16	9-12
	combined	78(51) *	38.1	0.37	33-44	10.6	0.08	9-12
Hybrids	-	22(18)	41.7	0.74	34-46	11.9	0.19	9-13
Unidentified	f	5(1)	39.0	----	-----	11.8	0.37	11-13

* Many juveniles of the bisexual lineage (identified on the basis of the dorsal color pattern) were not sexed.

Table 3. Statistical comparisons of adult SVL (upper right matrix, tested by Student's t-test) and the number of toe IV scansors (TIVS: lower left matrix, tested by Wilcoxon's 2-sample test) among the four clones, bisexual lineage, and hybrids between unisexual females and bisexual males of *Lepidodactylus lugubris* collected from Takapoto Atoll.

	Clone A	Clone B	Clone C	Bisexual	Hybrids
Clone A	-------	NS	$p<0.01$	NS	$p<0.001$
Clone B	NS	-------	$p<0.01$	NS	$p<0.001$
Clone C	NS	NS	-------	$p<0.05$	$p<0.001$
Bisexual	$p<0.001$	$p<0.001$	$p<0.001$	-------	$p<0.001$
Hybrids	NS	NS	NS	$p<0.001$	-------

Several authors have reported that pores are rarely present in *L. lugubris* (*e.g.*, Cuellar and Kluge, 1972; Brown and Alcala, 1978). Absence of reproductive females having pores in the present sample suggests that some of those observations have based on male phenotype hybrids, others are indicative of the presence of bisexual populations, and others have derived from the misidentifications of specimens actually belonging to other species.

Clutch size. --A total of 60 females, captured both in February and July, had one or two eggs in oviducts, and thus were regarded as gravid. Of these, 16 animals belonging

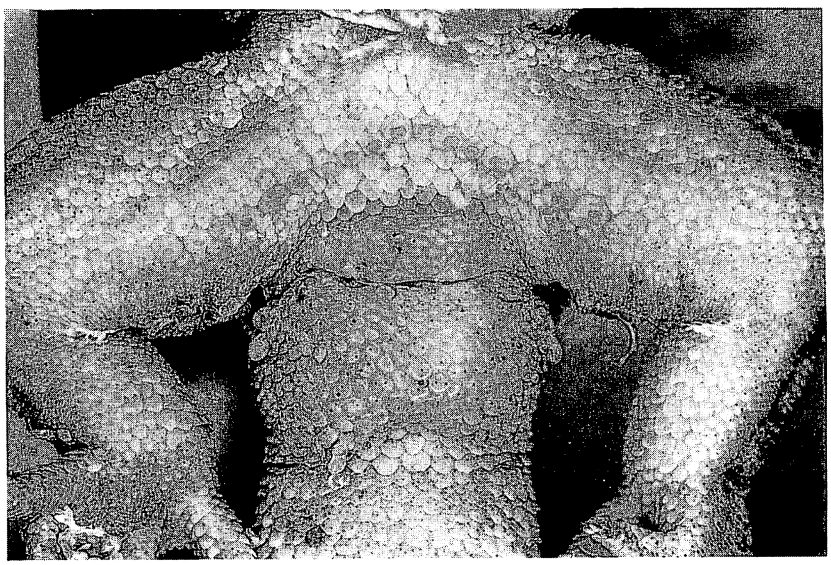

Fig. 4. Ventral view of cloacal-femoral region of a male *Lepidodactylus lugubris* showing pore series and enlarged spurs.

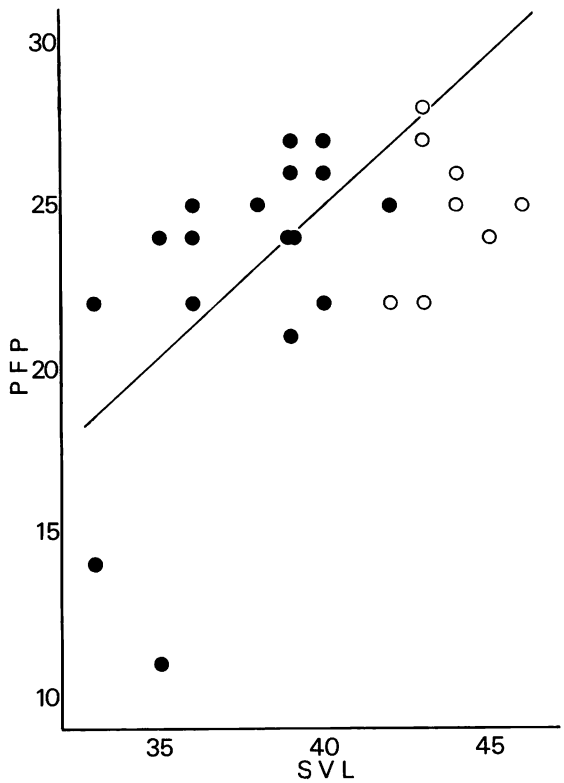

Fig. 5. Relationships between snout to vent length (SVL, in mm) and the number of preanal and femoral pores (PFP) in adult males of the bisexual lineage (represented by closed circles) and hybrids of *Lepidodactylus lugubris* (represented by open circles).

See the text for statistical significance of correlation between the two parameters in each group, and the equation of the regression line for the former.

to clone A, 12 clone B, one clone C, one clone E, and nine bisexual lineage had two oviductal eggs. Two animals belonging to clone A and one clone B had one oviductal egg and one distinctly enlarged ovarian follicle. The remainder (seven animals belonging to clone A and one clone B) had only one oviductal egg and lacked enlarged follicles in ovaries. Therefore, clutch size of *L. lugubris* on Takapoto Atoll seems normally two but sometimes one like those of populations from other French Polynesia and Pacific Islands (*e.g.*, Schwaner, 1980; Sabath, 1981; Ota, 1989; Zug, 1991).

Acknowledgments

We thank Craig Moritz and Alain Dubois for many useful comments. The senior author is also much grateful to George Pasteur and Charles P. Blanc for stimulative and fruitful discussion and continuous encouragements throughout this work. Part of the sample used in the present study was provided by Ch. P. and Françoise Blanc.

Ineich's fieldwork was supported partially by the R.C.P.806 from the C.N.R.S. Ota's laboratory work was financed by a Grant-in-Aid from the Japan Ministry of Education, Science, and Culture (A-63790257).

References

Brown, W. C., & A. C. Alcala, 1978. Philippine lizards of the family Gekkonidae. Silliman Univ. Nat. Sci. Monogr. Ser. 1. 146 pp., Silliman Univ. Press, Dumaguete.

Cuellar, O., & A. G. Kluge, 1972. Natural parthenogenesis in the gekkonid lizard *Lepidodactylus lugubris*. *J. Genet.*, 61(1): 14-26.

Darevsky, I. S., L. A. Kupriyanova & T. Uzzell, 1985. Parthenogenesis in reptiles. *In* : Gans. C., ed. Biology of the Reptilia Vol. 15B, Wiley, New York, 411-526.

Ineich, I., 1987. Recherches sur le peuplement et levolution des Reptiles terrestres de Polynesie française. 515 pp., Ph.D. dissertation, Univ. Montpellier.

Ineich, I., 1988. Mise en evidence d'un complexe unisexue-bisexue chez le gecko *Lepidodactylus lugubris* (Sauria, Lacertilia) en Polynesie française. *C. R. Acad. Sci. Paris, ser. III*, 307: 271-277.

Ineich, I. & C. P. Blanc, 1987. Le peuplement herpetologique de Polynesie française. Adaptations et aleas. *Bull. Soc. Zool. Fr.*, 112(3&4): 381-400.

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

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.

Ota, H. & T. Hikida. 1988. A new species of *Lepidodactylus* (Sauria: Gekkonidae) from Sabah, Malaysia. *Copeia*, 1988(3): 616-621.

Sabath, M. D., 1981. Gekkonid lizards of Guam, Mariana Islands: Reproduction and habitat Preference. *J. Herpetol.*, 15(1):71-75.

Sachet, M.-H. 1983. Takapoto Atoll, Tuamotu Archipelago: Terrestrial vegetation and Flora. *Atoll Res. Bull.*, (277): 1-41.

Schwaner, T. D., 1980. Reproductive biology of lizards on the American Samoan Islands. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*, (86): 1-53.

Zug, G. R., 1991. The lizards of Fiji: Natural history and systematics. Bernice P. Bishop Museum Special Publication.