NATURAL PARTHENOGENESIS IN THE GEKKONID LIZARD *LEPIDODACTYLUS LUGUBRIS*

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INTRODUCTION

Parthenogenesis is so different from the usual type of reproduction in vertebrates that it is not surprising the first documented case was so strongly denied. Referring to this discovery by Hubbs and Hubbs (1932), Howell (1933) stated: " It is unwise to intrude the suggestion of parthenogenesis, even of a modified sort, into vertebrate literature. This phenomenon is so at variance with what is known and believed about vertebrate development that I am sure no vertebrate morphologist would admit for a moment that the natural development from an egg to sexual maturity of an individual vertebrate without direct inclusion of the male element is within the realms of probability." Since the initial discovery the list of known or suspected cases of parthenogenetic vertebrates has grown considerably (see Table 1 for a review), and it is now clear that this peculiar form of reproduction cannot be denied nor is it as rare among vertebrates as was once suspected.

With few exceptions, the first clue to the existence of parthenogenesis was provided by observing the absence of males; experimental evidence later confirmed the uniparental nature of these species. Such confirming data were obtained from (1) mating tests demonstrating a purely matroclinous inheritance (Clanton, 1934; Haskins, 1960; Hubbs and Hubbs, 1932; Hubbs, 1964; Meyer, 1938; Schultz, 1967; Uzzell, 1964), (2) determinations of sex in newly hatched young (Darevsky and Kulikova, 1961; Maslin, 1966), (3) the production of successive female generations in the absence of males (Darevsky and Kulikova, 1961; Maslin, 1971), (4) the possession of polyploid chromosome numbers (Fritts, 1969; Hall, 1970; Kluge and Eckardt, 1969; Lowe and Wright, 1966 a, 1966 b; Pennock, 1965; Schultz, 1967; Uzzell, 1964), (5) absence of courtship evidence (Cuellar, 1968; Darevsky and Kulikova, 1961), (6) absence of tissue homograft rejections (Darnell, Lamb and Abramoff, 1967; Eckardt and Whimster, 1971; Kallman, 1962 a; Maslin, 1967), and (7) the mechanism of meiotic restitution (see Cuellar, 1971 for a review).

During a study of the systematics of the gekkonid lizard genus *Lepidodactylus*, one of us (AGK) noted the absence of males in the species *lugubris* from various islands in the Pacific and Indian Oceans. This observation was later corroborated by Allen Greer of Harvard University for populations from the Solomon Islands and Jean M. Vinson of Mauritius for populations from islands in the Indian Ocean pers. comm.). These preliminary findings of a disparate sex ratio led us to hypo-

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thesize the existence of yet another all-female species of vertebrate. This paper is devoted to testing the hypothesis that *lugubris* is parthenogenetic, and collating other data that might provide insight into the kind of reproduction involved.

MATERIALS AND METHODS

All live *L. lugubris* used in the experimental part of our investigation were obtained from Oahu, Hawaii; they represent most of the individuals from that island listed in Table 2. The *Hemidactylus turcicus* were collected in New Orleans, Louisiana. All experimental animals were permanently referenced by amputating specific digits from their feet. The individuals used in the skin graft experiment were divided into two groups. Group I consisted of nine pairs of *L. lugubris*, while Group II was made up of six pairs, each consisting of a *L. lugubris* and a *H. turcicus*. Reciprocal grafts were made between the members of each pair in the two groups. Transplantation in the first group was performed to document the large degree of genetic similarity expected between members of a parthenogenetic form. Transplantation in the second group was performed to demonstrate the presence of an immune response in *L. lugubris*. Animals undergoing transplant surgery were anesthetized in a sealed jar containing the vapor of the liquid anesthetic trichlorethylene. The jar was partitioned with a screen to prevent the lizard from contacting the residual liquid at the bottom of the jar. Apparently, this anesthetic is readily absorbed through their skins since even slight contact was lethal. About 90 seconds was adequate to anesthetize *L. lugubris*, and about 45 seconds for *H. turcicus*. Recovery times were about 20 and ten minutes, respectively. A preliminary set of skin transplants between dorsal, ventral, and dorsoventral sites revealed that the amount of subcutaneous area exposed (due to stretching of the surrounding skin) following excision of equal-sized grafts was greater on the dorsal than on the ventral side. Thus, while dorsal grafts transplanted to the ventral side filled most of the evacuated recipient space, the reciprocal transplants did not. Even the same piece of skin excised from the dorsal side did not fit its original space completely. Since ventral skin does not stretch appreciably in *L. lugubris*, the ventral to ventral combination was performed in most of the transplants. A single square measuring about $2 \cdot 5 \times 2 \cdot 5$ mm was cut from the venter of each animal. Prior to surgery the skin area to be excised was coated with a layer of nobecutane measuring the same dimensions as the graft. After the nobecutane hardened, the skin was cut along the edge of the coat, and the stiffened graft was transplanted without losing its original shape. Transplantation was not attempted until both the recipient and donor skins had been cut and were ready to be excised, then both grafts were exchanged simultaneously. A drop of saline perfused on the wound margin allowed the transplant to float and be positioned with ease. After the saline dried, the adjoining skin was temporarily adhered to the graft by pincing their sticky borders together. Finally the entire area was sealed with a coat of nobecutane.

At least 10 specimens of *L. lugubris* were analyzed for karyological data. The somatic chromosome number was determined from 3–10 cells in each specimen,

Table 1. *Known or suspected vertebrate species reproducing naturally by parthenogenesis*

Species	Source	Chromosome			Probable Method of cleavage initiation
		Ploidy	Number	Authority	
FISH					
Family Poeciliidae					
Poecilia formosa	Hubbs et al., 1932	2N	46	Drewry, 1964	Gynogenetic
Poeciliopsis lucida	Schultz, 1967	3N	72	Schultz, 1967	,,
Poeciliopsis monacha	Schultz, 1967	3N	72	Schultz, 1967	,,
Poeciliopsis viriosa	Schultz, 1971	3N	72	Schultz, 1971	,,
Family Cyprinidae					
Carassus auratus	Golovinskaya, 1947	3N	141	Cherfas, 1966	,,
Family Comephoridae					
Comephorus baicalensis	Taliev, 1949	..	..	..	,,
Family Pleuronectidae					
Atheresthes stomias	Novikov, 1962	..	..	..	,,
Family Salmonidae					
Coregonus lavaretus	Melander et al., 1950	..	..	..	?
Family Clupeidae					
Paralosa lacustris	Astaurov, 1962	..	..	..	?
AMPHIBIANS					
Family Bufonidae					
Nectophrynoides occidentalis	Angel et al., 1944	..	..	..	?
Family Ambystomidae					
Ambystoma laterale	Uzzell, 1963	3N	42	Uzzell, 1963	Gynogenetic
Ambystoma tremblayi	Uzzell, 1963	3N	42	Uzzell, 1963	,,

TABLE 1 (Contd.)

REPTILES					Spontaneous
Family Lacertidae					
Lacerta armeniaca	Darevsky et al., 1961	2N	38	Darevsky, 1966	"
Lacerta dahli	Darevsky, 1966	2N	38	Darevsky, 1966	"
Lacerta rostrombekovi	Darevsky, 1966	2N	38	Darevsky, 1966	"
Lacerta unisexualis	Darevasky, 1966	2N	38	Darevsky, 1966	"
Family Teiidae					
Cnemidophorus velox	Maslin, 1962	3N	69	Pennock, 1965	"
C. neomexicanus	Maslin, 1962	2N	46	Pennock, 1965	"
C. exsanguis	Maslin, 1962	3N	69	Pennock, 1965	"
C. tesselatus	Maslin, 1962	2N	69	Pennock, 1965	"
C. tesselatus	Maslin, 1962	3N	46	Lowe et al., 1966 b	"
C. cozumela	Maslin, 1962	2N	50	Wright et al., 1968	"
C. uniparens	Wright et al., 1965	3N	69	Lowe et al., 1166 b	"
C. flagellicauda	Lowe et al., 1964	3N	69	Lowe et al., 1966 b	"
C. sonorae	Lowe et al., 1964	3N	69	Lowe et al., 1966 b	"
C. opatae	Wright, 1967	3N	69	Wright, pers. com.	"
C. rodecki	Fritts, 1969	2N	50	Fritts, 1969	"
C. lemniscatus	Vanzolini, 1970	2N	48	Peccinini, 1971	"
Gymnophthalmus underwoodi	Thomas, 1965	..	..	..	
Family Gekkonidae					
Hemidactylus garnoti	Kluge et al., 1969	3N	70	Kluge et al., 1969	"
Gehyra variegata	Hall, 1970	3N	63	Makino et al., 1949	"
Family Xantusidae					
Lepidophyna flavinaculatum	Telford et al., 1970	..	..	..	"
Family Agamidae					
Leiolepis belliana	Hall, 1970	3N	54	Hall, 1960	"
Family Chameleontidae					
Brookesia spectrum	Hall, 1970	..	..	..	"

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Table 2. *Localities and numbers of males and females of* Lepidodactylus lugubris *examined*

Geographic source	Institutions in possession of samples	Number of females	Number of males	Sex examined by
Guam	Department of Bioscience, University of Guam	120	..	M.V.C. Falanruw (Pers. Comm.)
Solomon Islands	Museum of Comparative Zoology, Harvard	217	3	Z. Greer (Pers. Comm.)
Panama	Museum of Natural History	1	..	Smith et al., 1961
Ecuador	Museum of Comparative Zoology, Harvard	3	..	Fugler, 1966
Panama, Colombia and Diverse Islands from the Pacific and Indian Oceans	Museum of Zoology, University of Michigan	58	..	Authors
Diverse Pacific Islands	Natural History Museum, University of Kansas	49	..	Authors
Oahu, Hawaii	Authors possession	221	1	Authors

Each *L. lugubris* was injected intraperitoneally with 0·2 cc of a 0·05 aqueous solution of velban. The intestine was excised 3–4 hours later, placed in distilled water, and divided into several small pieces each of which was severed longitudinally. The severed tubular sections automatically curled outward exposing the mucosal lining. These were then washed free of any intestinal debris, and stained in ·05–1·0 aceto-orcein for 15–30 minutes. The chromosomes were spread by gently smearing the tissue on a slide, and squashing the dividing cells sloughed from the mucosal lining. Healthy animals gave the best results; emaciated or otherwise inactive individuals showed few dividing cells. The use of intestinal mucosa as a source of chromosome data has considerable advantages over the current techniques employing in vitro culture of bone marrow leucoblasts and other tissues. Not only does it provide an instant and abundant source of dividing cells, but it also eliminates the practice of subjecting the animals to injury ("stressing the animal") in order to obtain an adequate number of dividing cells.

TESTS OF THE HYPOTHESIS OF PARTHENOGENESIS IN *lugubris*

Absence of Males.—Sex was determined in 673 individuals, four of which exhibited male characteristics (Table 2). Only those individuals were listed in Table 2 whose identification we could positively verify as *L. lugubris*. We did not include all of the very many literature references to this species, wherein sex was given, because of its overall similarity to other species in the genus *Lepidodactylus* which are known to be bisexual (Kluge, 1968). In our experience taxonomic misidentification has been very common in the literature, and this can obscure the occurrence of parthenogenesis (see Kluge and Eckardt, 1969). A single male from Oahu possessed normal appearing testes and associated sperm ducts and the typical secondary sexual character of well developed preanal pores. In bisexual gekkonids the typical preanal pore condition consists of a well developed waxy plug protruding from a large aperture in each of several scales. In the Solomon Islands collection located in the Museum of Comparative Zoology there are three males (65861-Turubei Is., 17471-Busa, and 17367-Botaala, Malaita Is.). In the Turubei specimen the testes were elongate, rather than the normal oval shape. The testes in all three appeared to be abnormally granular. Among the 217 females in the Museum of Comparative Zoology Solomon Island collection, a few adults exhibited slight indentations in the preanal scales. This condition is similar to the poorly developed one found in juvenile males of related species, but is by no means as well developed as in adult males of the related bisexual species. In addition, some of the adult Solomon Island females had abnormal ovaries (poorly differentiated, of elongate shape, and granular appearance). Moreover, in three individuals normal oviducts were present while both ovaries could not be located; a fourth specimen from Botaala (17426) did not appear to have any reproductive organs or preanal pores.

The seemingly anomalous shape and surface texture of the testes in most of the *L. lugubris* males suggests that spermatogenesis could not have proceeded normally. This is supported by the fact that males found in other parthenogenetic vertebrates (Maslin, 1962; Schultz and Kallman, 1968; Taylor et al., 1967; Taylor and

Medica, 1966) are known to be triploid hybrids (Cuellar and McKinney unpubl; Rasch et al., 1965; Schultz and Kallman, 1968; Lowe and Wright 1966 a) characterized by histologically abnormal testes (Christiansen and Ladman, 1968), anomalous meiotic divisions (Rasch et al., 1965) and probable sterility (Kallman, 1964). However in the case of *L. lugubris* there are some circumstantial data indicating that the males may not be of hybrid origin. In the first place hybrid individuals usually exhibit phenotypes deviating from the normal condition of either parent species. The four males that we found were not obviously different from the typical female *L. lugubris* phenotype. Secondly at least in the Hawaiian Islands there are no known bisexual congeners that would be the likely candidates to involve in hybridization. This is not true of the Solomon Islands where as many as four bisexual *Lepidodactylus* species are recognized (Kluge, 1968).

Absence of Sperm in Oviducts.—A reliable method for detecting recent courtship in female lizards is to examine their oviducts for the presence of sperm (see Cuellar, 1968 for details of procedure). Absence of sperm at the approximate moment of ovulation provides reasonable proof of a parthenogenetic mode of reproduction. For example, Cuellar (1968) showed that females of a bisexual lizard species examined during this phase of the reproductive cycle contained large quantities of sperm while the females of several suspected parthenogenetic species at the same state in the reproductive cycle did not. Similar evidence was presented by Darevsky and Kulikova (1961) for other lizards. In our investigation, 19 live adult female *L. lugubris* failed to reveal any traces of spermatozoa throughout their oviducts. These females were examined shortly after capture and they exhibited the critical reproductive stages cited above. In addition to supporting a purely thelytokous mode of reproduction these results rule out the possibility of the type of parthenogenesis requiring insemination (gynogenesis) which appears to be restricted to fish and amphibians (Table 1).

Absence of Homograft Rejection.—Permanent acceptance of tissue grafts among members of a species excluding the members of highly inbred strains (Kallman, 1962 b) provides evidence for parthenogenesis (Kallman, 1962 a; Maslin, 1967). Generally, individuals of bisexual species reject tissues transplanted among themselves presumably because few individuals possess the same antigenic or immunologic properties. Parthenogenetic species, however, having dispensed with fertilization and its consequent panmictic influence on the genetic structure of the population, tend to produce progeny possessing identical or nearly identical genotypes to their mothers. Consequently, parthenoforms do not recognize the homografts transplanted among themselves as immunologically foreign. In some parthenogenetic species, however, genetic similarity, at least for certain histocompatibility genes may be confined to the descendents of a clone (Healy et al., 1962; Kallman, 1962 b; Maslin, 1967) whereas in others it may be widespread, between different local populations (Maslin, 1967). Table 3 provides ample evidence for the presence of histocompatibility genes in *lugubris* (see *Lepidodactylus* × *Hemidactylus* control crosses).

Although not all of the homografts transplanted among *L. lugubris* were retained (Table 3) the fact remains that in six of the nine crosses the grafts healed perma-

Table 3. *Results of skin homograft and heterograft transplants among* Lepidodactylus lugubris *and between* Lepidodactylus lugubris *and* Hemidactylus turcicus

Cross Number	Animal pairs cross Grafted	Number of post-transplant days animals Survived	Number of days to graft loss or rejection	Number of days graft retained
1	*L 7	?		?
	L 17	69	56	
2	L 8	151	1	
	L 9	147		147
3	L 11	3	..	3
	L 19	167		167
4	L 37	?	..	?
	L 38	167		167
5	L 1–9	71	9	..
	L 1–12	150	16	
6	L 1–13	88	..	88
	L 2–7	?		?
7	L 1–17	137	11	
	L 2–9	157		157
8	L 2–12	101	14	..
	L 2–14	14	10	
9	L 3–8	22	..	22
	L 3–10	91		91
10	L 2–15	..	19	..
	†H 1–6		15	
11	L 2–17		19	
	H 1–7	9	Undergoing rejection	9
12	L 2–20	..	19	..
	H 1–8		15	
13	L 3–18	?	Rejected	?
	H 1–9		20	
14	L 3–9	..	12	..
	H 1–10		18	
15	L 3–14	6		6
	H 1–12		15	

* L = *Lepidodactylus lugubris,* † H = *Hemidactylus turcicus,* ? = fate of animal unknown. In cross 13, animal 3–18 rejected graft, but exact time of rejection and fate of animal unknown.

nently (Fig. 1 a). These observations demonstrate the genetic similarity expected among the members of *L. lugubris* given the hypothesis of its being parthenogenetic. Grafts were rejected (Fig. 1 b) or became detached, in crosses 1, 2, 5, 7, and 8, but with the exception of individual L 17 in cross 1 the grafts became detached so soon after transplantation that these losses may not be accurately explained on the basis of rejection. We know that in cross 2 the graft on individual L 8 detached by the following day because it had not been covered with nobecutane. On the other hand, the reciprocal, which was coated with nobecutane survived permanently. We also know that in cross 5 both individuals ecdysed during the early stages of healing and lost their grafts with the shedded skin. The loss of the graft in L 17 of cross 7 also seems to have been accidental since the reciprocal graft was retained until the death of its host 157 days later. We cannot easily account for the early loss of both grafts in the individuals of cross 8. However, the longer time required for the actual rejection of heterografts among the controls (*Lepidodactylus* × *Hemidactylus*) than among homografts between parthenogenetic individuals suggests that this was not due to rejection.

Actual graft rejection in a parthenoform might be expected to proceed at a slower rate than in those grafts between individuals of different species. In general, one should expect the rate of rejection to be proportionately related to phylogenetic (genetic) divergence. The one loss of a graft in *L. lugubris*, which we interpret as an actual rejection, may be an example of the hypothesized slower rate of rejection. For example, eighteen days after transplantation the homograft of L 17 of cross 1 appeared normal, but 38 days later it had been reduced to a small, round scab, which eventually was shed. Unfortunately, the fate of L 7, possessing the reciprocal graft, could not be traced beyond the 7th day after transplantation.

Not all of the experimental animals were obtained from the same locality on Oahu. Most were collected at Kahalua, but a few were from Kailua, and we have no way of knowing which individuals came from what locality. If the graft loss in L 17 was not accidental, but due to a slight immune response, then several genetically different populations may occur on the island of Oahu.

Karyological Analysis.—Our karyological analysis indicates that *L. lugubris* is characterized by 44 acrocentric chromosomes, which cannot be divided into obvious macro and micro sets (Fig. 2). Deviations in chromosome number of 42, 43, and 45 were counted frequently, and in some instances as many as twice the number of 44 were observed. However, the chromosomes were either excessively spread and overlapping, or superimposed on the chromosomes of other cells, or not adequately spread, in most of these cells, and we do not consider these counts to be reliable. Moreover, when the spreads were obviously isolated and free of contamination from the chromosomes of neighbouring cells, or when all of the chromosomes from one cell were separate and could be readily discerned, the number was consistently found to be 44. Except for *Gehyra variegata* and *Hemidactylus garnoti*, both of which are considered triploid and parthenogenetic (Hall, 1970; Kluge and Eckardt, 1969) all bisexual gekkonid lizards so far karyotyped exhibit diploid numbers around 40 (range 32–46). The triploid numbers of 63 and 70 reported for these two parthenogenetic species are consistent with the expected increase

(presumably acquired by alloploidy in all other known triploid parthenogenetic vertebrates) of one haploid set from the basic diploid parental condition. Based on the diploid and triploid numbers known in other gekkos, and on the number of 44 established herein, we consider *lugubris* to be diploid.

CONCLUSION

The original hypothesis that *Lepidodactylus lugubris* is parthenogenetic is strongly supported by the following data: disparate sex ratio (only 4 individuals with mae characteristics among a total of 673 examined), absence of courtship in reproductively mature females, and acceptance of skin homografts. The chromosome number of *L. lugubris* is about 44, and very likely a diploid complement. It seems very unlikely that gynogenesis is the mode of parthenogenesis in *L. lugubris* owing to the absence of congeners and even species in closely related genera throughout much of its geographic range. The meiotic mechanism and the origin of the males is being further investigated by us.

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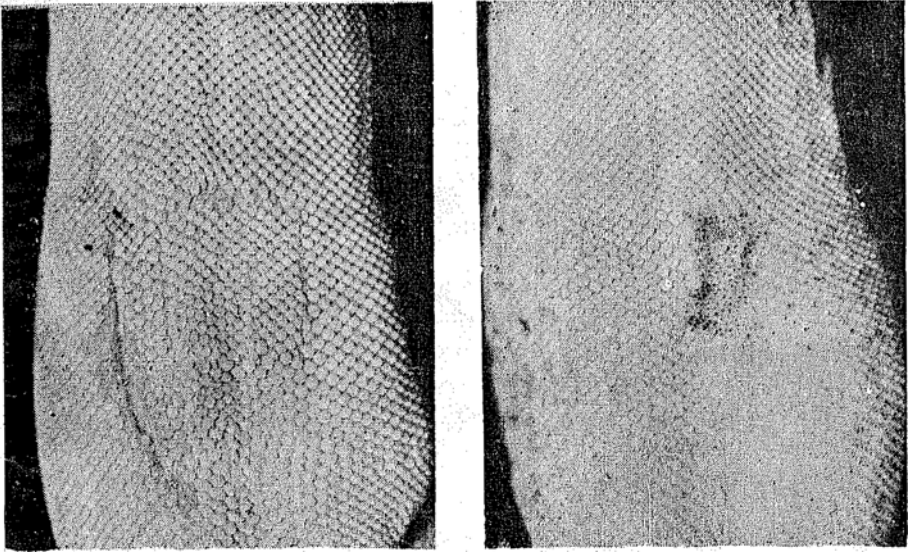
PLATE 1

FIG. 1 a (left). Ventral view of L 2–9 showing permanent homograft transplanted from L 1–17. Graft was 89 days old at the time the photograph was taken. Note the lightly discerniable scar between the graft and the surrounding skin. Longitudinal scar to the left of the graft resulted from previous surgery performed to excise oocytes.

FIG. 1 b (right). Ventral view of L 3–18 showing previous location of graft approximately 60 days after rejection. Graft site typically shrinks following loss of graft and becomes filled with small, round, darkly pigmented scales. Oval region below and to the right of the graft is an oviductal egg visible through the transparent skin of *lugubris*.
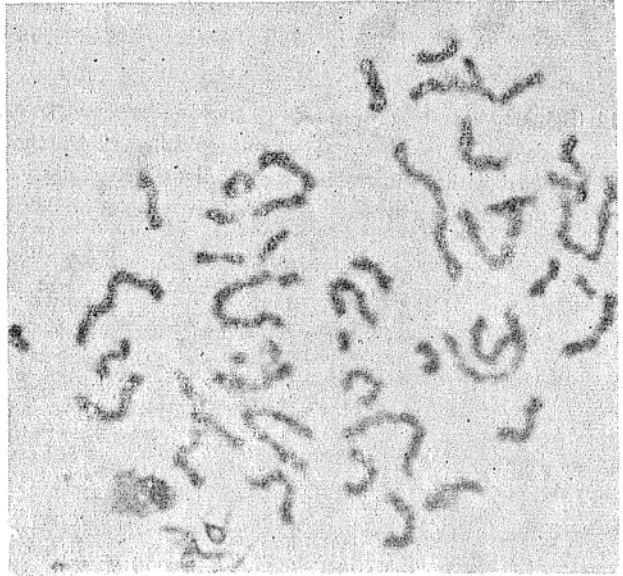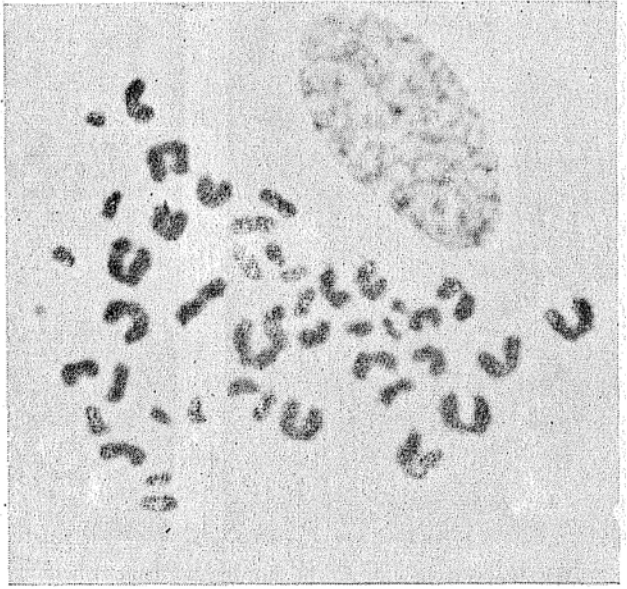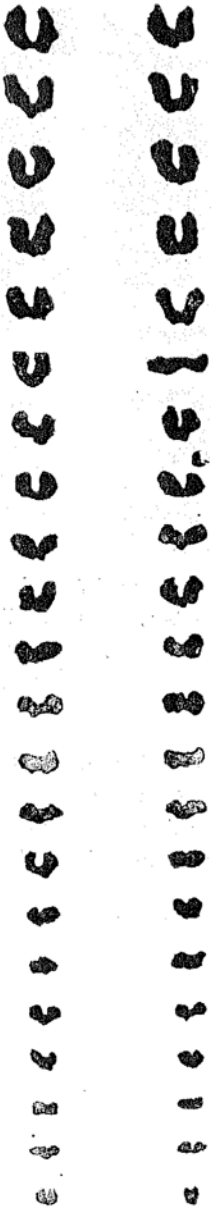
PLATE 2

FIG. 2 a (left). Somatic karyotype of *Lepidodactylus lugubris* prepared from camera lucida drawing of metaphase in Fig. 2 b (top right); 2N = 44.

FIG. 2 c (bottom right). Metaphase showing details of less condensed chromosomes.