Chromosoma (Berl.) 54, 75—87 (1976)

Karyotypic Variation in the Australian Gekko *Phyllodactylus marmoratus* (Gray) (Gekkonidae: Reptilia)

Max King and Ruth Rofe

Department of Genetics, University of Adelaide, Adelaide, S.A., 5001, Australia

Abstract. The gekko *Phyllodactylus marmoratus* has at least three distinct chromosome races; 2n=36, 2n=36 ZZ/ZW and 2n=34. Specimens from these races are morphologically distinguishable, have a degree of habitat specialization and occur in a defined distribution. The 2n=36 race found in Eastern Australia is the presumed primordial type. The 2n=34 race occurs in Western Australia and is regarded as a fusion derivative. The 2n=36 ZZ/ZW race, which is only found on the Murray River system in Eastern Australia has a heteromorphic sex chromosome system present in the female. Giemsa banding suggests that this heteromorphism is the result of a pericentric inversion.

Introduction

There are only a very few published chromosomal studies on the Gekkonidae, a family of lizards with over 650 described species. The current data suggest a range in chromosome numbers from 2n=28 (King, 1973) to 2n=46 (Makino and Momma, 1949), although numbers up to 70 have been reported in a parthenogenetic species (Kluge and Eckardt, 1969).

The genus *Phyllodactylus* is very widely dispersed and is described as having comparatively few species. They are found in North, Central and South America, Africa, Madagascar, the Galapagos Archipelago, and Australia (Dixon and Kroll, 1974). There are two Australian species. *P. guentheri*, occurs on three islands in the Tasman Sea between Australia, New Caledonia and New Zealand. A second species, *P. marmoratus*, the organism investigated in the present study, is found in a diversity of habitats across southern Australia.

Chromosomally, *P. marmoratus* falls into two areas of interest. Firstly, this species possesses a number of lifestyle characteristics (low vagility, interpopulation isolation and regional habitat specialization) often correlated with chromosome race formation (see White, 1973). Secondly, sex chromosomes have not been identified in any Gekkonid species, whereas, both male and female heterogamety have been reported in other lizard taxa (see Wright, 1973; King and King, 1975).

The present study describes three distinct chromosome races in *P. marmoratus*, one of which is based upon a female sex chromosome heteromorphism.

Materials and Methods

129 live specimens of *P. marmoratus* were collected from 30 localities throughout the species range and analysed chromosomally (see Table 1). Snout to vent lengths were recorded for all specimens captured. Lists of museum locality records were obtained from Australian state museums to provide a species distribution (see Figs. 2 and 3). Museum specimens were not examined morphometrically.

Both female and male mitotic and male meiotic preparations were analysed in the specimens obtained.

1. Mitotic Preparations. Mitotic metaphase cells were obtained from the intestinal lining of the duodenum by using a modified air drying technique (J. Bull, pers. comm.). Specimens were injected with 0.2 ml of 0.02% Colcemid (Ciba) solution 2 hours before killing. A one centimeter length of duodenum was removed from the animal and split down one side to form a sheet of tissue. This was placed in a petri dish containing 5 ml of 0.9% Sodium Citrate solution for 15 minutes and then transferred to a second dish containing freshly mixed 3.1 methanol/acetic acid fixative. The epithelial cells were vigorously scraped from the internal intestinal lining and suspended in the fixative with a pasteur pipette. After 5 minutes in fixative the cell suspension was centrifuged at 500 r.p.m. for 5 minutes, the supernatant was discarded and the pellet of cells resuspended in 3 ml of fresh fixative. Four drops of the suspension were placed on a freshly cleaned slide and were rapidly dried. The slides were stained in 10% Giemsa Solution (Gurr R66) in pH 7 phosphate buffer for 2 minutes, washed in distilled water, dried and mounted in Xam.

2. Meiotic Preparations. Male meiotic preparations were made from both testes of each animal killed. An air drying technique similar to that used by Gorman *et al.* (1967) produced well spread meiotic metaphase cells.

3. Giemsa Banding. The trypsin technique as described by Seabright (1971) was applied to male and female specimens of the 2n=36 sex chromosome race. High cell density, air dried, intestinal epithelial preparations were used.

4. Chromosomal Morphology. The chromosome number was ascertained for each species by counts on all well-spread mitotic and meiotic metaphase cells. Good cells were photographed with Kodak Recordak high contrast 35 mm film. Chromosome measurements were made on cut-out photographic karyotypes of at least 5 well-spread mitotic metaphase cells per race at a magnification of ×3,000. The mean per cent total chromosome length (% T.C.L.) of each chromosome arm, the arm ratios (A.R.) (L.Arm/S.Arm) and their standard errors were calculated.

All specimens examined in this study have been lodged with the South Australian Museum collection.

Results

Sampling of *P. marmoratus* populations over their continental and island range has shown that there are two chromosome number races present (2n=36 Eastern Australia and 2n=34 Western Australia). In Eastern Australia there is also a 2n=36 race which has a ZZ♂/ZW♀ sex chromosome system. The specimens from each of these chromosome races exhibit characteristic back patterns. Significant size differences were also observed between the races, and between the sexes within each race (see King, 1975).

a) 2n=36. The chromosome morphology of this race was characterised by a largely acrocentric complement grading from large to small elements with a gradual size diminution (see Fig. 1 and Table 2). The following features were evident: Chromosome pair 1 was noticeably larger than the other acrocentric elements present. Chromosome pair 4 had a longer short arm than other acrocentric elements. The only metacentric chromosomes observed were pairs 7 and 18. The smallest chromosomes are less than 1 μ in length at metaphase. There were no differences in chromosome morphology observed between the sexes in this race.

This chromosome race is widely distributed in Eastern Australia and was collected from localities in both South Australia and Victoria (see Figs. 2 and 3). Specimens were also found on a number of South Australian coastal islands. The animals occur in a wide range of habitats, i.e. under rocks and rock exfoliations, in debris and under the bark of trees.

Table 1. The number, sex and locality of specimens collected and information on chromosome number and morphology

Locality	2n	Presence of female heterogamety	No. of specimens	
			Males	Females
Loxton, S. A.	36	+	1	2
5 ml. W. Loxton, S. A.	36	+	1	1
Morgan, S. A.	36	+	4	1
Blanchetown,. S. A.	36	+	4	1
Robinvale, Vic.	36	+	1	1
Mildura, Vic.	36	+	2	3
Balranald, N. S. W.	36	+	1	2
5 ml. N. of Balranald, N. S. W.	36	+	—	1
25 ml. E. Moulamein, N. S. W.	36	+	3	1
Mannum, S. A.	36	—	—	1
3 ml. S. W. Cambrai, S. A.	36	?	2	—
Marne R, Eden Valley, Bridge, S.A.	36	+	1	2
Somme R, Sedan Rd., Bridge, S.A.	36	?	1	—
Pearson Island, S.A.	36	—	—	1
Greenly Island, S.A.	36	?	1	—
Stenhouse Bay, S.A.	36	—	30	6
Edithburgh, S.A.	36	—	3	1
Port Vincent, S.A.	36	?	1	—
Curramulka, S.A.	36	?	1	—
Adelaide, S.A.	36	—	2	2
2 ml. W. Clarendon, S.A.	36	—	1	1
Kangaroo Island, S.A.	36	—	1	1
Bunjil's Caves, Stawell, Vic.	36	—	20	1
Clare, S.A.	36	—	—	1
Mambray Creek, S.A.	36	—	9	2
Albany, W.A.	34	?	1	—
Ravensthorpe, W.A.	34	?	1	—
Cape Leeuwin, W.A.	34	—	1	2
15 ml. N. Yanchep, W.A.	34	?	1	—
Chidlows, W.A.	34	?	1	—
			95	34
			129	

b) 2n=36 ZZ/ZW. Eighteen males sampled from this race had the 2n=36 karyotype described above. All of the fifteen female specimens collected from the same ten localities had a marked chromosome pair 4 heteromorphism. One element in pair 4 was acrocentric, the other was clearly metacentric (see Figs. 4 and 5 and Table 2). Specimens possessing this heteromorphism are found on the Murray, Murrumbidgee, Marne and Edward Rivers in Eastern Australia. They were also found beneath the bark of live specimens of the Murray River Red Gum tree *Eucalyptus camaldulensis.*

Although there is no evidence for a sex determining capacity, this sex correlated heteromorphism is regarded as a ZZ/ZW sex chromosome system. Since specimens possessing this karyotype morphology have a widespread and apparently exclusive distribution, they were regarded as members of a sex chromosome race.

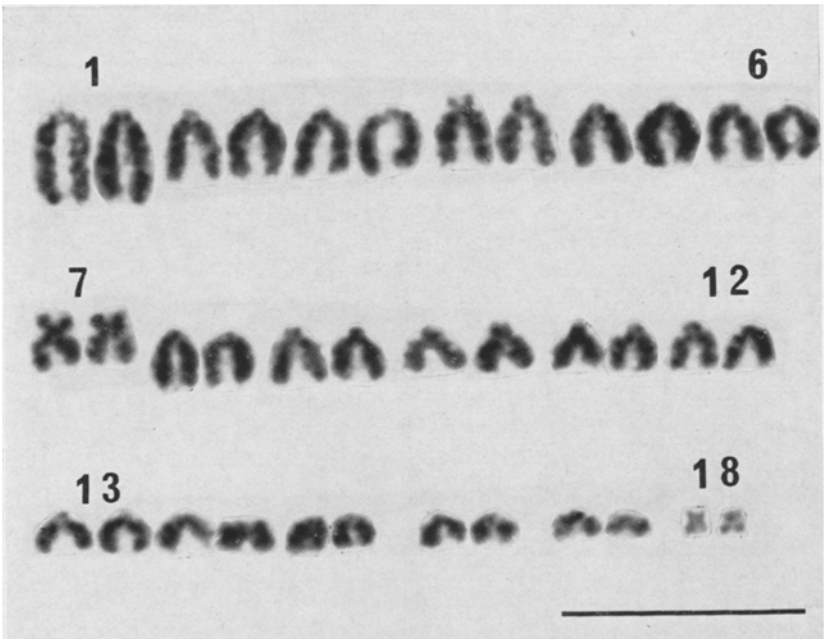

Fig. 1. The karyotype from a female of the 2n=36 race collected at Stenhouse Bay, S. Australia. The bar scale is equivalent to 10 μm

A single female specimen from Mannum, South Australia (on the Murray River) was found to have the homomorphic 2n=36 karyotype. This raises the possibility that the abovementioned heteromorphism is not a sex chromosome system. There are a number of reasons why such an hypothesis is unacceptable. First, only heterozygous females and homozygous males of one chromosome form were encountered at all other localities, and no females of the theoretical WW type were observed. This is a most unlikely distribution of phenotypes for an autosomal polymorphism. Secondly, the single homomorphic female was found at the southern most extreme of the known distribution of the postulated sex chromosome race, and is possibly a member of the 2n=36 race. The specimen could not be unambiguously classified on morphometric characters into either race.

The trypsin banding technique (Seabright, 1971) was applied to males and females of the 2n=36 ZZ/ZW race in an attempt to determine the internal chromosome morphology and possible origin of this heteromorphism.

Two features of the internal chromosome morphology are apparent. Firstly, in most chromosomes, banding is restricted to the body of the elements, *i.e.* both telomeric and centromeric ends are interband areas (Figs. 6 and 7). Secondly, the banding pattern of the heteromorphic W chromosome in pair 4 appears to have been reorganized and could be interpreted as the result of a pericentric inversion. That is, there appears to have been a break through the interband in the short arm of pair 4, accompanied by a second break through the middle of a third major band in the long arm of this pair (see Fig. 8). If the segment

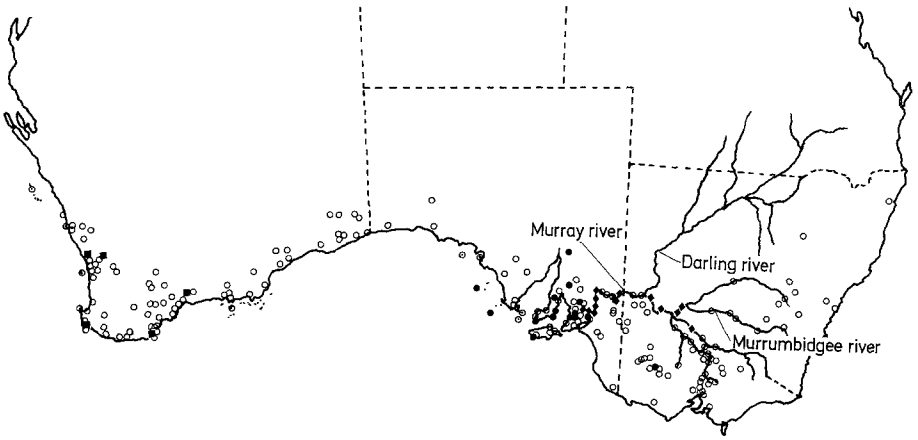

Fig. 2. The Australian distribution of *P. marmoratus* chromosome races: 2n=36 (•), 2n=36 ZZ/ZW (◆), 2n=34 (■) and museum localities (○)

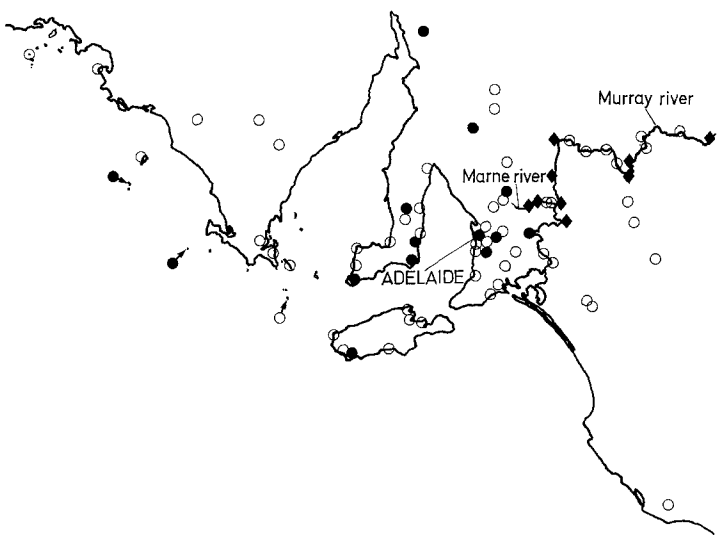

Fig. 3. The South Australian chromosome race distribution: 2n=36 (●), 2n=36 ZZ/ZW (◆), museum localities (○). Note the distribution of the 2n=36 ZZ/ZW race along the Murray River

between these breaks was inverted, the submetacentric W chromosome produced would have an additional "half" band on its short arm and two and a "half" bands in a more distal position on the long arm. It is assumed that the difference in the intensity of staining between bands on the heteromorphic chromosomes is due to the vagaries of the trypsin technique.

c) 2n=34. Specimens obtained from a series of diverse localities in Western Australia had 2n=34 chromosomes present (see Fig. 2). The largest chromosome pair was distinctly metacentric and measurements indicate that it was probably derived from the fusion of pairs 2 and 7 in the 2n=36 race (see Fig. 9 and Table 2).

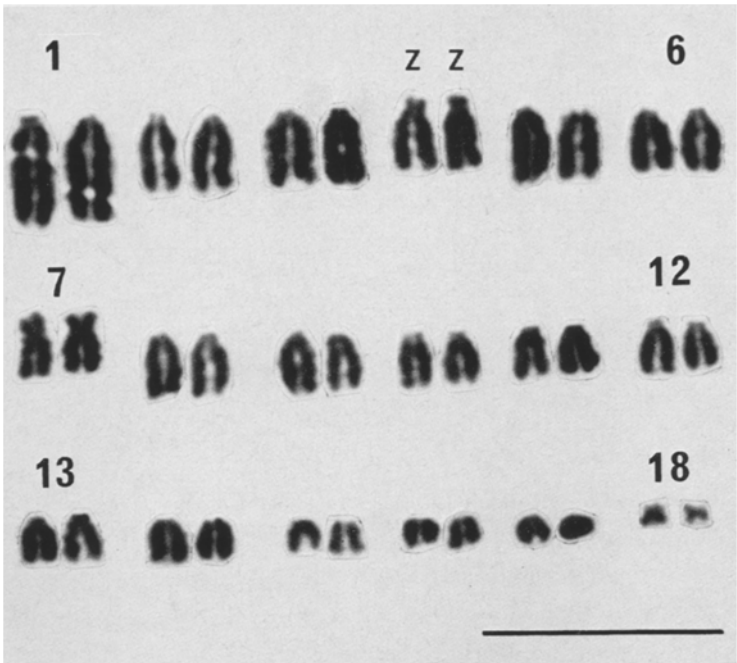

Fig. 4. A karyotype constructed from a male specimen from Loxton, S. Australia. The bar scale is equivalent to 10 μm

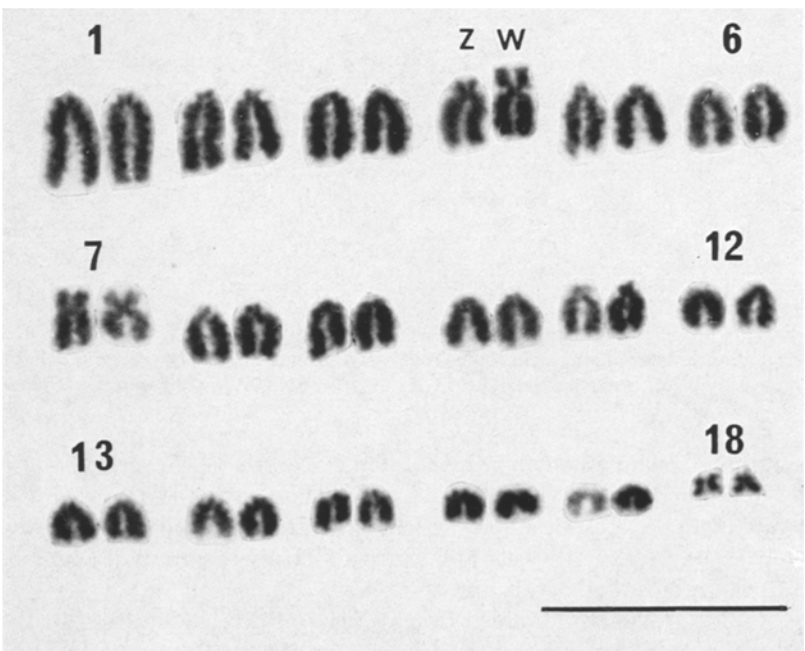

Fig. 5. A karyotype constructed from a female specimen from Loxton, S. Australia. The bar scale is equivalent to 10 μm

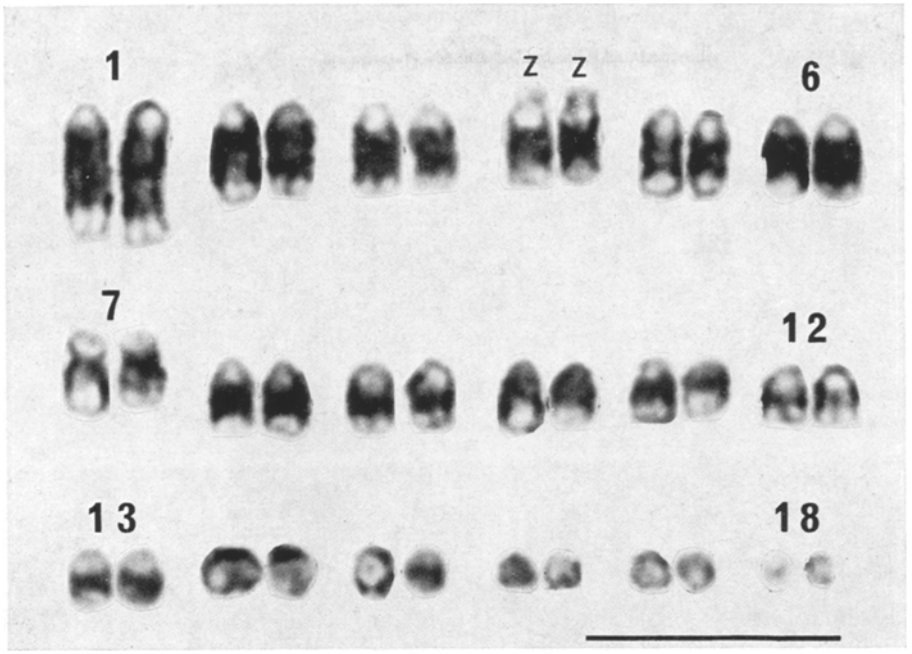

Fig. 6. A G-banded karyotype of a male from the 2n=36 ZZ/ZW race. The bar scale is equivalent to 10 μm

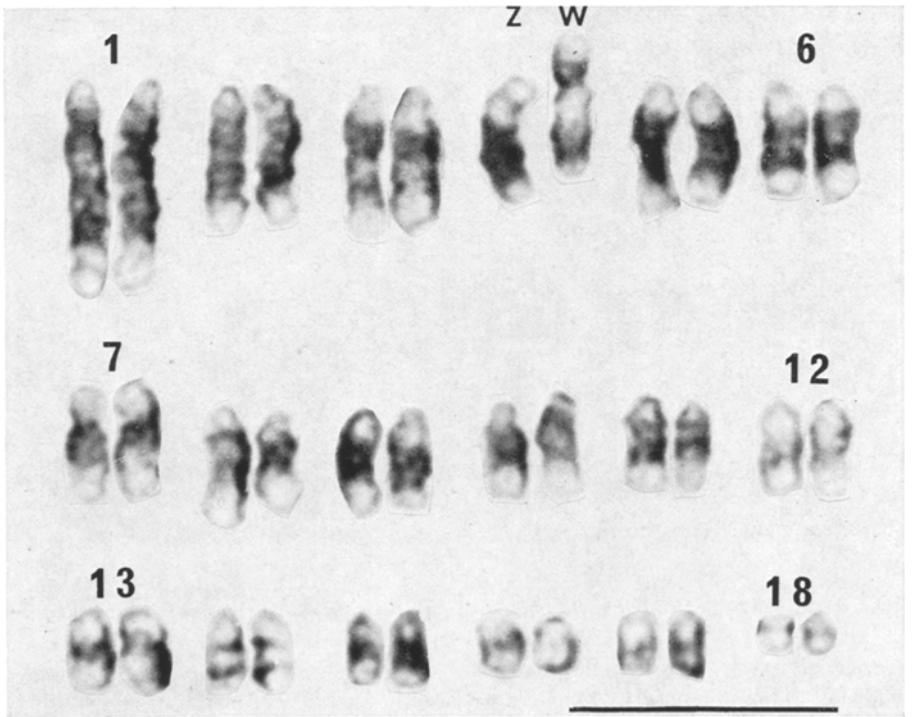

Fig. 7. A G-banded karyotype of a female from the 2n=36 ZZ/ZW race. Note the heteromorphic W chromosome. The bar scale is equivalent to 10 μm

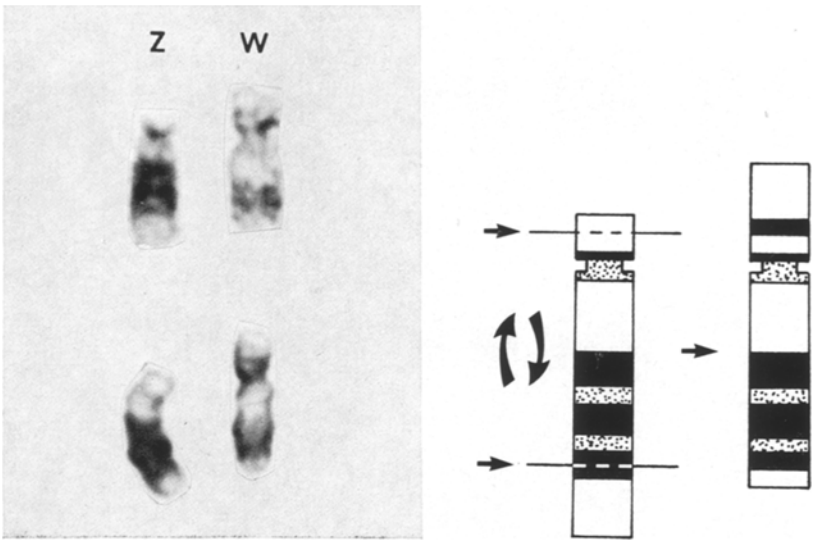

Fig. 8. A model for the origin of the ZW heteromorphism by pericentric inversion. The postulated break points are represented by dotted lines

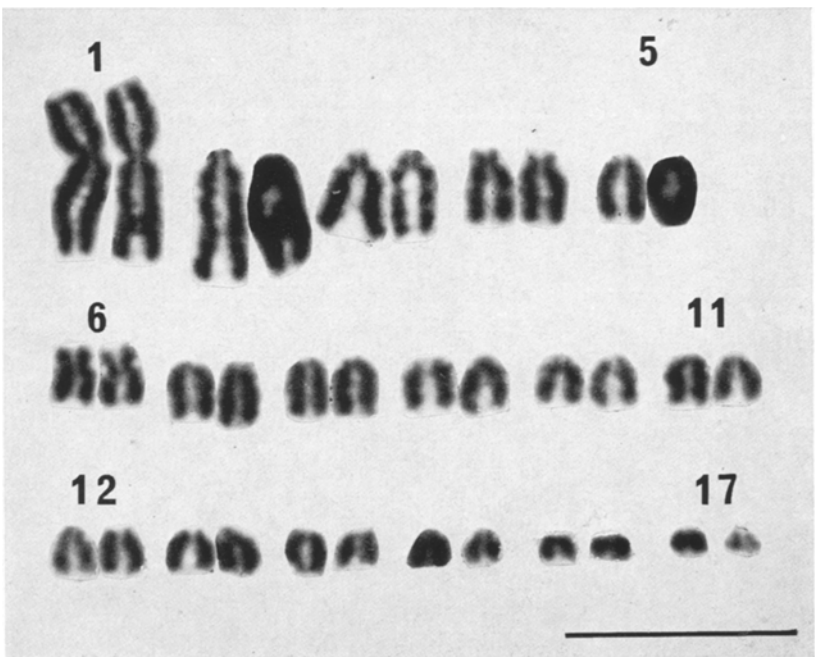

Fig. 9. The karyotype from a female of the 2n=34 race collected at Cape Leeuwin, W. Australia. The bar scale is equivalent to 10 μm

The remaining elements had the characteristic 2n=36 chromosome morphology, and in no case was any form of sex chromosome heteromorphism observed. Animals from this race were found in a variety of habitat types.

Table 2. Chromosomal measurements for the different chromosome races

Chromosome pair		2n = 36	2n = 36 ZZ/ZW	2n = 34
1	% T.C.L.[a]	10.19	10.61	14.81
	AR ± SE[b]	21.15 ± 2.3	22.58 ± 1.24	1.28 ± 0.13
2	% T.C.L.	7.95	7.90	9.84
	AR ± SE	9.32 ± 0.84	13.91 ± 1.94	8.94 ± 0.93
3	% T.C.L.	7.27	7.44	8.19
	AR ± SE	16.73 ± 1.01	23.80 ± 1.64	8.00 ± 0.82
4	% T.C.L.	7.81	7.27 (Z) 7.44 (W)	7.87
	AR ± SE	4.54 ± 0.55	4.51 ± 1.59 1.82 ± 0.20	3.77 ± 0.29
5	% T.C.L.	6.78	6.72	6.91
	AR ± SE	22.38 ± 3.30	13.00 ± 2.01	27.79 ± 2.61
6	% T.C.L.	5.95	6.10	6.68
	AR ± SE	34.00 ± 5.71	45.92 ± 6.75	1.64 ± 0.10
7	% T.C.L.	6.61	6.37	5.83
	AR ± SE	1.86 ± 0.09	1.86 ± 0.06	57.30 ± 7.61
8	% T.C.L.	5.94	5.77	5.98
	AR ± SE	16.47 ± 2.10	18.23 ± 2.50	32.22 ± 2.43
9	% T.C.L.	5.48	5.48	5.20
	AR ± SE	10.91 ± 0.80	41.15 ± 4.23	22.64 ± 3.81
10	% T.C.L.	5.07	5.33	4.60
	AR ± SE	12.34 ± 1.01	13.81 ± 2.21	—
11	% T.C.L.	5.08	5.10	4.42
	AR ± SE	7.69 ± 0.60	8.44 ± 1.70	—
12	% T.C.L.	4.91	4.77	4.40
	AR ± SE	8.82 ± 0.73	20.68 ± 3.31	—
13	% T.C.L.	4.51	4.65	4.41
	AR ± SE	27.19 ± 2.73	11.24 ± 2.25	—
14	% T.C.L.	4.12	4.10	3.36
	AR ± SE	33.33 ± 4.90	—	—
15	% T.C.L.	3.61	3.67	3.14
	AR ± SE	18.00 ± 3.68	21.94 ± 2.71	—
16	% T.C.L.	3.34	3.09	2.67
	AR ± SE	—	—	23.27 ± 2.00
17	% T.C.L.	2.95	2.83	2.20
	AR ± SE	—	24.73 ± 6.70	5.88 ± 0.43
18	% T.C.L.	2.27	2.37	
	AR ± SE	1.99 ± 0.60	1.86 ± 0.40	

[a] % T.C.L. = The percentage total chromosome length of each chromosome pair.
[b] AR ± SE = The arm ratio with standard error.

Discussion

1. Chromosome Race Evolution

The present study has shown that there are three distinct chromosome races of *P. marmoratus*; two in Eastern Australia (2n=36 and 2n=36 ZZ/ZW) and

one in Western Australia (2n=34). Each race has an extensive distribution, a constant chromosome morphology throughout its range, a distinct external morphology and a degree of habitat specialization.

A number of characteristics of this species' lifestyle (a very low vagility, considerable interpopulation isolation and restriction to areas of a habitat type) parallel its diversification into a series of chromosome races. Studies on a number of organisms have shown a similar correlation of lifestyle with karyotypic differentiation: flightless morabine grasshoppers (White, 1973), some Phasmatodea (Craddock, 1972), fossorial rodents (Patton, 1972) and Sceloperine lizards (Cole, 1970). All are low vagility species with a degree of interpopulation isolation; presumably ideal criteria for the fixation of newly arisen chromosomal rearrangements.

On the basis of earlier studies on the Gekkonidae (see White, 1973) and after karyotyping numerous Australian species (King, 1975), it is probable that the "primitive" Gekkonid karyotype is all acrocentric with a gradual size diminution from the largest to the smallest elements. It is also likely that the primordial chromosome number is 2n=38, the number most often encountered in the primitive Diplodactylinae.

In *P. marmoratus* the 2n=36 race is closest in chromosome morphology to the "primitive" karyotype and is regarded as the extant primordial form. The modified karyotypes of the remaining races, the nature of the karyotypic changes, and the fact that each karyomorph is exclusive to that race, suggests that both the 2n=34 and 2n=36 ZZ/ZW races evolved independently from the 2n=36 race.

The distinctive karyotype morphology of the 2n=34 race (having one very large metacentric pair) suggests that evolution has been by centric fusion rather than fission. Chromosome measurements indicate that a fusion has occurred between pairs 2 and 7 in the 2n=36 karyotype.

The two most likely hypotheses for the evolution of the 2n=34 race from the 2n=36 race are; firstly, that a fusion was established within a primordial 2n=36 population in Western Australia and displaced it forming a 2n=34 race. Secondly, that the 2n=34 race was the result of a westward radiation from eastern Australia (inhabited by the primordial 2n=36 race) during which the fusion was established.

The very low vagility of *P. marmoratus* and the improbability of effective gene flow occurring over its vast range, suggests that it is unlikely that a chromosomal rearrangement could have become established within a theoretical primordial 2n=36 race range in Western Australia and then spread throughout that range. This would be the "stasipatric" interpretation of chromosome race evolution (see White, 1968). If this had occurred, one might expect to find isolated populations of the 2n=36 race in Western Australia which had been missed by the "advancing front" of the new rearrangement.

An allopatric interpretation, would propose that the 2n=34 fusion race was founded on the periphery of the 2n=36 race range in Eastern Australia, and formed the core of a successful radiation into Western Australia. As a consequence of this model, there should be no 2n=36 race forms in Western Australia. Clearly, additional samples from Western Australia are needed to test between

the models; however, the present evidence suggests that the allopatric interpretation is the most likely.

The apparently continuous distribution of the 2n=36 and 2n=34 chromosome races of *P. marmoratus* along the coastline of the Great Australian Bight suggests that an area of population contact exists. However, a detailed investigation of the race distributions in this area is required to determine whether they are parapatrically or allopatrically distributed.

The 2n=36 ZZ/ZW Eastern Australian race is also regarded as a recently derived form evolving from the 2n=36 race. It appears to have had a sex linked and heterozygous pericentric inversion established (see following subsection). This rearrangement evolved in specimens which have attained considerable geographic and ecological isolation. Specimens from the 2n=36 ZZ/ZW race occur along the Murray, Edward, and Murrumbidgee Rivers. They are not found on the Darling River, where another gekko, *Gehyra variegata*, appears to occupy the same niche. Specimens from this race also differ from the 2n=36 form in habitat preference (living on *Eucalyptus camaldulensis*), back pattern and size. Indeed, the 2n=36 ZZ/ZW race is an ecologically specialized form of the 2n=36 race and is now an effective northern, interior extension of the species range. Since *E. camaldulensis* forms a continuously distributed habitat along these rivers, active migration or forced migration by flooding may have extended the range of this race.

2. Sex Chromosomes

The female heterogamety of the ZW type described in the 2n=36 ZZ/ZW race of *P. marmoratus*, is the first report of any sex chromosome system in the Gekkonidae. Most reports of sex chromosome systems in lizards have come from New World Iguanidae and have shown male heterogamety [Gorman and Atkins (1966) in *Anolis*, Cole *et al.* (1967) in *Sceloporus*, Pennock *et al.* (1969) in *Uta*, and Peccinini *et al.* (1971) in *Polychrus*]. Male heterogamety has also been reported in the Scincidae (Wright, 1973) and the Pygopodidae (Gorman and Gress, 1970). Female heterogamety has been reported in the Lacertidae [by Ivanov and Fedorova (1970) in *Lacerta strigata* and by Oguma (1934) and Chevalier (1969) in *L. vivipara*], the Varanidae [King and King (1975) in the genus *Varanus*] and now in the Gekkonidae.

The mode of origin of these systems is equally diverse. A loss of chromosomal material to form an XY has been reported in the Iguanidae (Peccinini *et al.*, 1971). Additions appear to have produced a ZW heteromorphism in the *Varanus* (King and King, 1975), whilst a pericentric inversion was the most acceptable mechanism for forming an XY system in *Cnemidophorus tigris* (Cole *et al.*, 1969). The simplest hypothesis applicable to *P. marmoratus* is also by pericentric inversion. Both detailed chromosomal analysis and Giemsa banding suggest that there has been an internal rearrangement of the chromatin, apparently induced by two breaks and a centromeric shift. There does not appear to be any heterochromatinisation of the W chromosome.

The development of sex chromosome heteromorphism associated with a structural change and with no alteration in size has been described in snakes

(Beçak *et al.*, 1964) and is considered by Ohno (1967) to be the first stage in sex chromosome heteromorphism.

The great diversity in the type and modes of origin of sex chromosomes in lizards supports the proposition that they had evolved in a number of lineages. The fact that a chromosome race of *P. marmoratus* has differentiated from a homomorphic stock by establishing a sex chromosome system, suggests that such systems may have evolved independently and on a number of occasions in each lineage. This implies that some sex chromosome rearrangements may be as adaptively significant as any other gross chromosomal change involved in chromosome race formation.

3. Giemsa Banding

The trypsin G-banding technique (Seabright, 1971) when applied to *P. marmoratus* reveals a concentration of bands in the body of the acrocentric elements. The centromeric and telomeric regions appear as non-staining areas. Preliminary results with the C-banding technique (Arrighi and Hsu, 1971) have shown a centromeric localization.

Studies on the seasonal variation of chiasma frequency and distribution in *P. marmoratus* (King, 1975; King and Hayman, in preparation) suggests that chiasma localization may be related to the G-banding distribution. A majority of the chiasmata are localized in the large interband areas present on the chromosome ends. A similar correlation of chiasmata with interband areas has been observed in Man (cited by Fox *et al.*, 1973) and in *Schistocerca gregaria* (Fox *et al.*, 1973).

4. Taxonomic Implications

Each of the chromosome races of *P. marmoratus* is characterized by a large and discrete distribution. Specimens from these races exhibit a degree of habitat specialization, have a distinctive race back pattern and differ in size. Even though the distributions appear to be allopatric, it is likely that there are areas of parapatry. The races appear to be functioning as independent biological species.

A detailed taxonomic analysis of the chromosome races of *P. marmoratus* is obviously required.

Acknowledgements. The authors would like to thank Dr. D. L. Hayman for his critical reading of the manuscript and Dr. P. Baverstock for his valuable discussion. We are indebted to Dr. D. King for sending Western Australian specimens, and to P. King, D. Roberts and R. D. Sharrad for their assistance in collecting. Dr. G. Storr (W.A. Museum), Dr. T. Housten (S.A. Museum), A. Coventry (Vic. Museum) and Dr. H. Cogger (N.S.W. Museum) were particularly helpful in providing locality data.

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Received September 19 — October 7, 1975 / Accepted October 7, 1975 by H. Bauer
Ready for press October 8, 1975