

CYTOGENETIC STUDY OF SEVERAL SPECIES OF LACERTA (LACERTIDAE, REPTILIA) WITH PARTICULAR REFERENCE TO SEX CHROMOSOMES

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The karyotypes of 4 european species of Lacertidae were determined in hepatic tissue cultures. The chromosomal formula typical of the Lacertidae ($2n = 36M + 2m$) was found in *L. muralis*, *L. sicula campestris* and *L. viridis*; no morphologically differentiated sex chromosomes were identified in these 3 species.

A population of *L. vivipara* caught in the Massif Central (France) shows the following diploid number: $2n♀ = 32 A + Z_1 Z_2 W$, $2n♂ = 32 A + Z_1 Z_1 Z_2 Z_2$. The existence of the submetacentric W in the female karyotype can be explained by centric fusion between two non homologous telocentric chromosomes. It is possible that only some populations show this rearrangement.

The finding of two types of heterogamety, XY and ZW, in the same Order contributes to our knowledge of the evolution of sex chromosomes among Vertebrates.

Introduction

The presence of sex chromosomes is now well established in several species of Reptiles including Saurians but among the Lacertidae it is an exception. The first interesting studies are those of Oguma (1934), who counted 35 chromosomes in the female and 36 in the male of *Lacerta vivipara*, and concluded that a ZO/ZZ mechanism existed. Makino & Asana (1948) found the same type of heterogamety in two Agamidae, *Calotes versicolor* ($2n♀ = 33$, $2n♂ = 34$) and *Sitana ponticeriana* ($2n♀ = 46$, $2n♂ = 45$).

Matthey (1931, 1934) reported results concerning

heterogamety which disagree with those of the Japanese authors, especially in *Lacerta vivipara*. Margot (1946) did not find any difference between the karyotypes of the two sexes in *Anguis fragilis* ($2n = 44$) et *L. vivipara* ($2n = 36$). Matthey and Van Brink (1956) and Van Brink (1959) studied *L. vivipara* and different species of chameleons; in no case did they observe morphologically differentiated sex chromosomes, and they concluded that there is no cytological proof of the existence of sex chromosomes in Saurians.

Sex chromosomes were identified for the first time in Saurians by Gorman and Atkins (1966) in species of *Anolis*: *A. gingivinus*, *A. marmoratus fereus* and *A. biporcatus*). These species have quite similar karyotypes ($2n♀ = 30$, $2n♂ = 29$); the presence in the male of three chromosomes of different length points to male heterogamety of the $X_1 X_2 Y$ type, the female formula being $X_1 X_1 X_2 X_2$.

Male heterogamety (XY-XX) has been observed in *Cupriganus achalensis* (Gorman et al., 1967), two species of *Anolis*: *A. conspersus* and *A. evermanni* (Gorman & Atkins, 1968), *Uta stansburiana* (Pennock et al., 1969); *Cnemidophorus* (Cole et al., 1969), and *Sceloporus* (Cole 1970, 1971).

Male heterogamety with multiple sex chromosomes ($X_1 X_2 Y$) is present in Iguanas belonging to *Sceloporus* (Cole et al., 1967), *Polychrus marmoratus* (Gorman et al., 1967), *P. peruvianus* (Gorman et al., 1967); in a Pygopod, *Lialis burtonis* (Gorman & Gress, 1970) and a Scincid, *Scincella laterale*, (Wright, 1973).

However, in *Lacerta strigata*, Ivanov & Fedorova

(1970) have shown a heteromorphic pair in the females, W being a small element.

In several species of Lacertidae, including 14 species of *Lacerta*, no sex chromosomes have been demonstrated (Matthey, 1931, 1945; Dallai & Baroni-Urbani, 1967; Arronet, 1968; Kupriyanova, 1968; Kupriyanova & Arronet, 1968; Orlova & Orlov, 1969). Cytogenetic studies made with numerous species of snakes have shown, at least in Colubridae and Viperidae, cytologically recognizable sex chromosomes (Kobel, 1967; Shing et al., 1969; Beçak & Beçak, 1969).

Among Reptiles, there is not, as in Eutherian Mammals, a unique type of heterogamety; our knowledge favours female heterogamety in snakes and male heterogamety in saurians. In saurians, the coexistence in the genus *Anolis* of the formulae X_1X_2Y et XY permits us to imagine that the divergence between the results of Matthey and those of Japanese authors could be explained by the variety of chromosomal formulae in the Saurians. Only one species, *Lacerta vivipara*, is the basis of this controversy.

For this reason, we have studied again the karyotype of *L. vivipara* (Chevalier, 1969) and compared it with three other european lizards, *L. muralis*, *L. sicula campestris* and *L. viridis*.

Material and methods

L. muralis and *L. viridis* were caught in several regions of France; *L. vivipara* only in the Massif Central; specimens of *L. sicula campestris* come from Italy.

Cytogenetic studies were made on hepatic tissue cultures in monocellular layers according to the technique of Lejeune et al. (1960).

Freshly sampled tissue is placed on slides and covered with plasma film. The culture medium is made by addition of foal serum to Hanks solution with antibiotics, and chicken embryo extract (2:2:1). The culture tubes are maintained at 30°C for 4 days; 24 hours prior to harvesting, explants are removed and the medium is renewed. Colcemid is added to cultures to accumulate cells in metaphase. After hypotonic shock, 10 min in bidistilled water, the cells are fixed for 40 min in Carnoy and stained with Unna blue.

In addition, small pieces of testes are minced in distilled water for 20 min, the cell suspension is cen-

trifuged, the supernatant removed, and the cells fixed for 30 min in Carnoy, then stained 3-4h in lacto pro-picnic orcein.

Observations

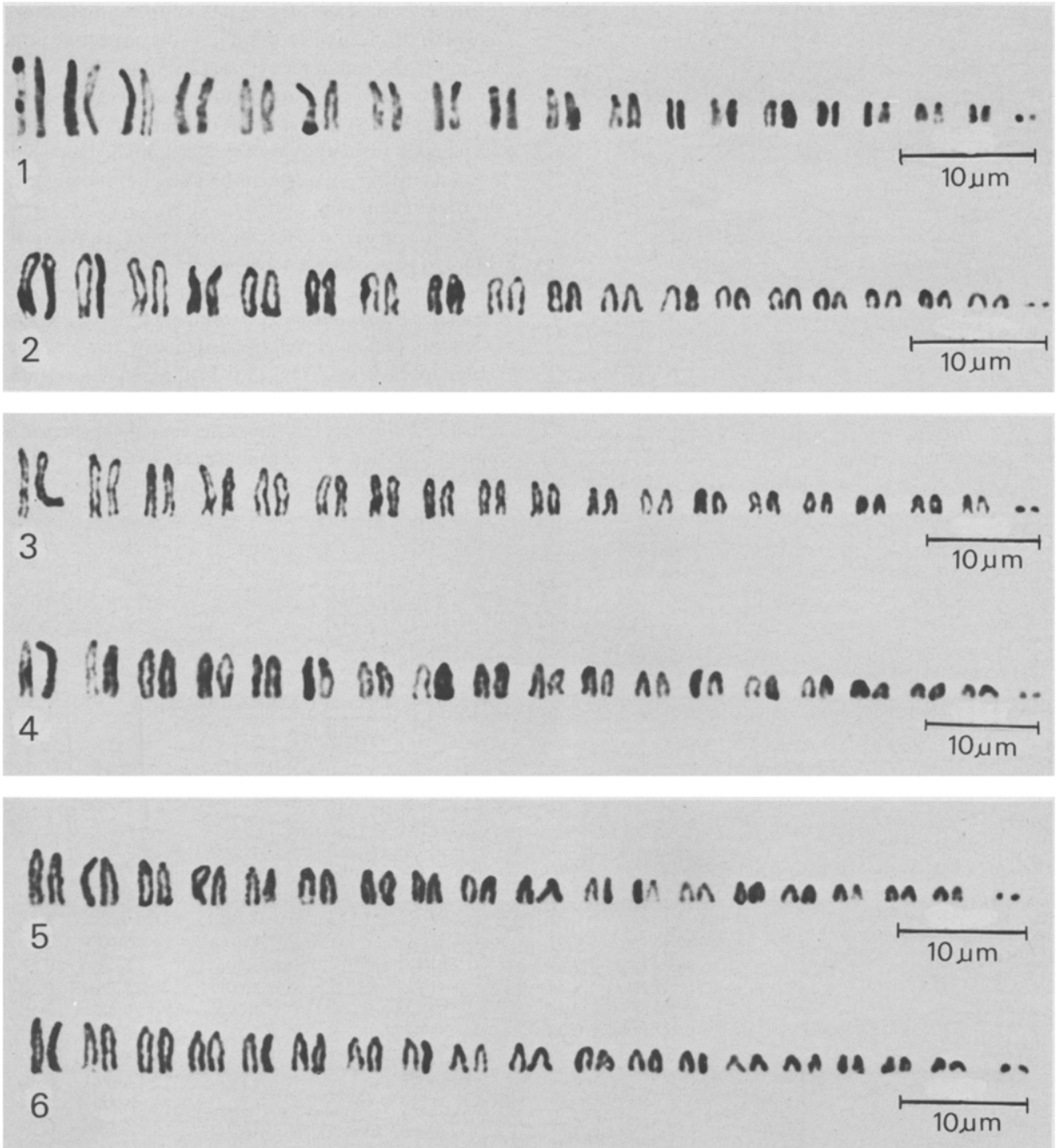
L. muralis in both sexes possesses 36 telocentric macrochromosomes and two microchromosomes ($2n = 38$). As a general rule, when techniques are standardized, the chromosomes of the male (ranging from 5,93 μm to 0,62 μm) are longer than those of the female (ranging from 4,37 μm to 0,62 μm).

The karyotype in both sexes is composed of 18 pairs of telocentric macrochromosomes and one pair of microchromosomes (Figs. 1 and 2). Measurements show that the relative lengths of male and female chromosomes are very similar for each pair and progressively decrease from the 1st to the 18th pair, the latter being clearly smaller than the others. The comparison between the karyotypes of both sexes does not show morphologically recognizable heteromorphic sex chromosomes.

In *L. sicula campestris*, there are in both sexes 18 pairs of telocentric macrochromosomes and one pair of microchromosomes ($2n = 38$) (Figs. 3 and 4). The length of the chromosomes ranges from 6,25 μm to 0,93 μm in the male and from 6,41 μm to 0,93 μm in the female. The relative lengths of the chromosomes of both sexes are very similar for each pair. In no case have we found well differentiated sex chromosomes in this species.

In *L. viridis*, both sexes have 36 telocentric chromosomes and two microchromosomes forming 18 pairs of regularly decreasing length, and one very much smaller pair (Figs. 5 and 6). The lengths of the chromosomes range from 5.15 μm to 0.62 μm in the male and from 5.93 μm to 0.62 μm in the female; for each pair the relative lengths in the male and in the female are quite similar. The differences between the karyotypes of the male and the female are not sufficient to signify the presence of a heterogamety recognizable by LM observation.

In the population of *L. vivipara* studied, male mitotic metaphases show 36 telocentric chromosomes; female mitotic metaphases show 34 telocentrics and one submetacentric (Fig. 7). This observation agrees with our previous results (Chevalier, 1969). The fundamental number (N.F.) defined by Matthey (1949)



Figs. 1-6. Karyotypes of species of *Lacerta*: (1-2) *L. muralis*, x 2000, (1) ♂; (2) ♀; - (3-4) *L. sicula campestris*, x 1700, (3) ♂, (4) ♀. - (5-6) *L. viridis*, x 1900, (5) ♂, (6) ♀.

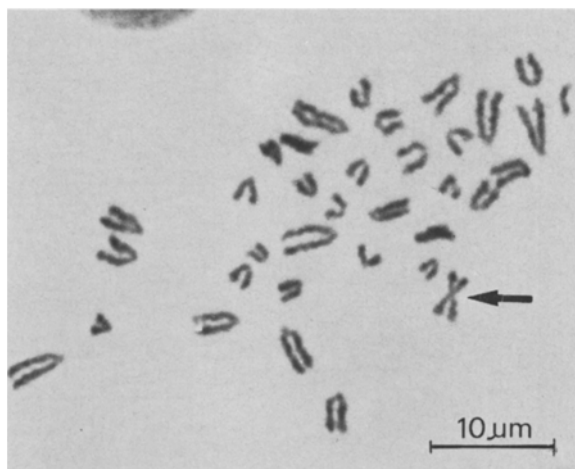


Fig. 7. *L. vivipara*, mitotic metaphase, x 1700. Arrow indicates submetacentric element.

is 36 for both sexes. The length of the chromosomes ranges from 3,2 μm to 0.8 μm in the male and from 4,2 μm to 0.2 μm in the female (Tab. 1).

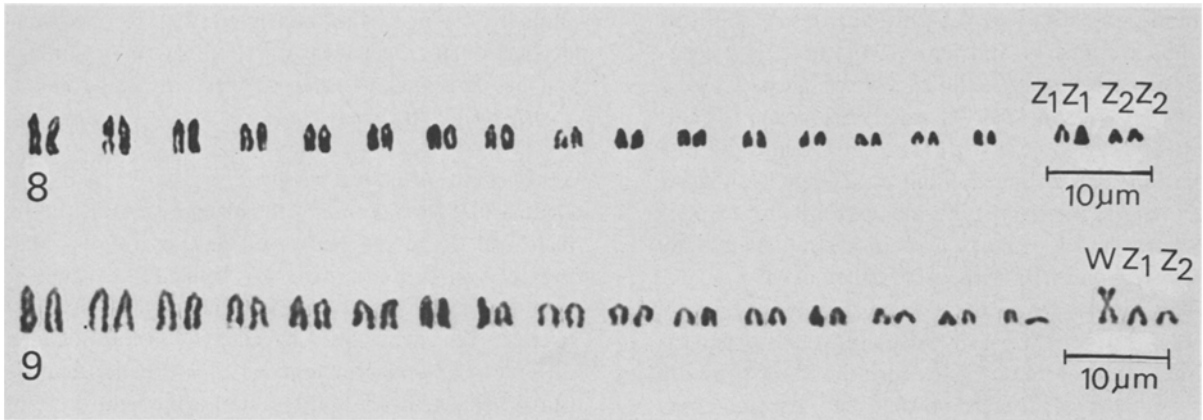
In the male 36 chromosomes can be grouped in 18 pairs (Fig. 8) but in the female we observed only 16 pairs, 3 chromosomes always remaining unpaired: two telocentrics of different lengths and the submetacentric element (Fig. 9).

During male meiosis one can count 18 bivalents (Fig. 10). In order to determine in the male the pairs of chromosomes corresponding to the unpaired telocentrics of the female, we compared the idiograms based on the mean relative lengths of the chromosomes of each sex (Fig. 11). In the female idiogram unpaired elements are the 11th and 15th; hence, we can conclude that in the male sex, these elements represented the sex chromosomes, or more exactly

Table 1

Comparison of the lengths of the chromosomes in both sexes in *L. vivipara*; $L = \frac{\text{length of the chromosome}}{\text{length of } 16A + X}$; $X = Z_1 + Z_2$ in the female; $X = \frac{Z_1 + Z_1 + Z_2 + Z_2}{2}$ in the male.

δ				φ			
Chromosome No.	Length in μm	L	σ	Chromosome No.	Length in μm	L	σ
I	3,2	10,13	0,57	I	4,20	10,38	0,58
II	2,8	9,13	0,34	II	4	9,62	0,39
III	2,7	8,33	0,23	III	3,38	8,71	0,22
IV	2,3	7,63	0,34	IV	2,87	7,73	0,40
V	2,1	7,18	0,32	V	2,77	7,06	0,24
VI	2	6,68	0,33	VI	2,56	6,69	0,37
VII	2	6,39	0,23	VII	2,46	6,46	0,37
VIII	1,8	5,94	0,26	VIII	2,26	6,09	0,39
IX	1,6	5,38	0,27	IX	2,26	5,16	0,33
X	1,5	4,86	0,19	X	2,05	4,55	0,33
Z ₁	1,4	4,60	0,31	Z ₁	1,85	4,44	0,63
XI	1,3	4,27	0,31	XI	1,64	4,15	0,24
XII	1,2	3,96	0,32	XII	1,44	3,69	0,22
XIII	1,1	3,63	0,27	XIII	1,44	3,49	0,20
Z ₂	1	3,33	0,22	Z ₂	1,23	3,17	0,33
XIV	1	3,12	0,27	XIV	1,02	3,13	0,29
XV	1	3,02	0,28	XV	1,02	2,90	0,20
XVI	0,8	2,52	0,23	XVI	1,02	2,60	0,16
				W	2,67	7,34	0,66



Figs. 8-9. *L. vivipara*, $\times 1400$, (8) male karyotype with 18 pairs of telocentrics; - (9) female karyotype with 16 pairs of autosomes and three sex chromosomes including a submetacentric element.

the pairs of chromosomes which are involved in the rearrangement.

Discussion

General considerations on the karyotypes

In *L. muralis* the karyogram consists of 18 pairs of telocentric macrochromosomes and a pair of micro-

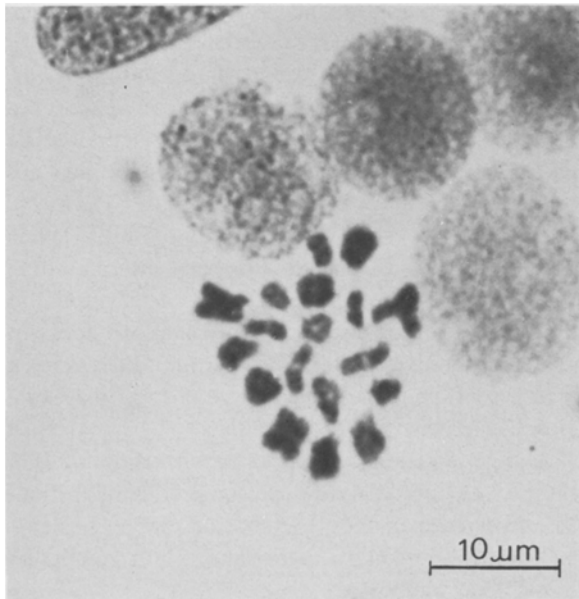


Fig. 10. *L. vivipara*, male diakinesis, $\times 1800$.

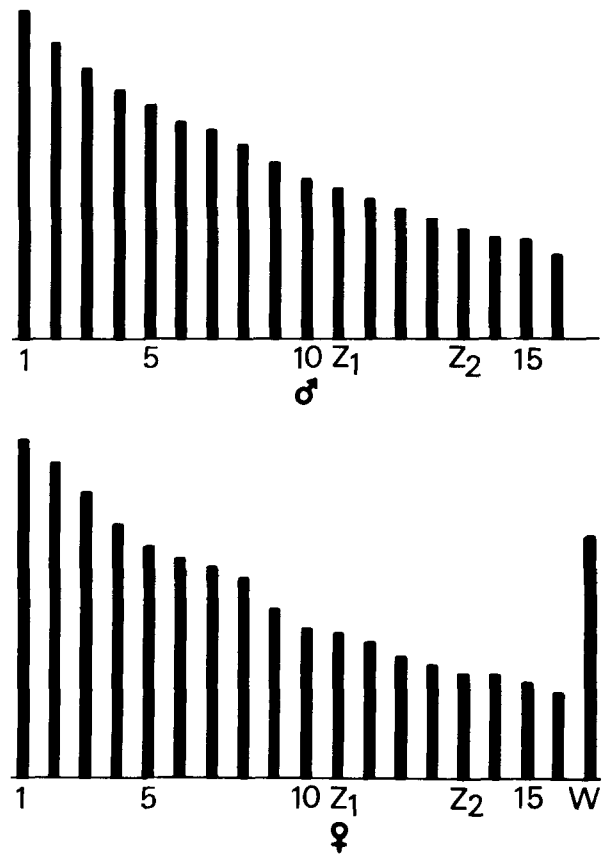


Fig. 11. Idiograms of *L. vivipara* ♂ and ♀.

chromosomes ($2n = 36 M + 2m$); this result confirms the observations of Matthey (1949) for this species. In *L. sicula campestris*, the karyotype shows 18 pairs of macro- and one pair of microchromosomes. This result is in agreement with those of Dallai & Baroni-Urbani (1967) obtained using a different technique. In *L. viridis*, the karyotype is constituted by 18 pairs of macro- and a pair of microchromosomes; this observation agrees with those of Matthey (1949).

The karyotypes of these three species appear very similar: $2n = 36 M + 2m$. Also, the relative lengths of the chromosomes of the corresponding pairs are very similar; no heteromorphic sex chromosomes have been detected in any case.

The great majority of Lacertidae has a karyotype of 36 macro- and two microchromosomes (Matthey, 1931, 1945; Darevsky, 1966; Dallai & Baroni-Urbani, 1967; Arronet, 1968; Kupriyanova, 1968; Kupriyanova & Arronet, 1968; Orlova & Orlov, 1969); this karyotype corresponds both to a diploid number and a N.F. of 38. The two known exceptions are *L. ocellata*: $2n = 36$ (Matthey, 1939) and *L. strigata*: $2n = 36$ (Orlova & Orlov, 1969) but the presence of 2 macrochromosomes, metacentric in the first species, submetacentric in the second, does not introduce any change in the N.F.

L. vivipara ($2n = 36$) is an exception also. While the opinions of several authors diverge on sex determination, they agree on the presence in the male sex of 36 telocentric chromosomes (Oguma, 1934; Matthey, 1943; Margot, 1946; Matthey & Van Brink, 1956; Orlova & Orlov, 1969; Chevalier, 1969). In this species, the absence of two microchromosomes reduces the N.F. to 36. This absence could be the result of a loss, or of an incorporation of the microchromosomes in the large elements of the karyotype as a result of a non-Robertsonian rearrangement.

Although the comparative studies of karyograms of closely related species give interesting results, the interpretation often remains difficult. The general opinion is: a karyotype constituted of telocentric chromosomes (Lacertidae) is more primitive than a karyotype with numerous metacentric chromosomes (Iguanidae); but a karyotype with few microchromosomes (Lacertidae) is considered as less primitive than a karyotype with many (Iguanidae); these interpretations seem conflicting.

The following hypothesis can be proposed: among Lacertidae, the first step was the diminution of the

number of microchromosomes, the second step (Robertsonian mechanisms) is still in its beginning, and has appeared in three species only (*L. ocellata*, *L. strigata*, *L. vivipara*).

Sex chromosomes in L. vivipara

Oguma (1934) has found 35 chromosomes in the female and 36 in the male; but Matthey (1949), Matthey & Van Brink (1956), Van Brink (1959) and Orlova & Orlov (1969) did not find any dissimilarity between the two sexes. Chevalier (1969) has shown a difference between the female ($2n = 35$) and the male ($2n = 36$). As these results do not agree with those of Matthey et al., and those of Orlova & Orlov, this species has been reinvestigated.

In the male, during meiosis, 18 bivalents are present, without ambiguity, and at mitotic metaphase 36 chromosomes are visible. In the female, at mitotic metaphase one can count 36 chromosomes, one submetacentric, all the others telocentric.

It is very likely that the submetacentric of the female results from a centric fusion (Robertsonian mechanism); this hypothesis is supported by the fact that the male possesses 36 telocentrics and the female 34 telocentrics and a submetacentric, the N.F. being the same in both sexes. The comparison of the karyogram of both sexes shows that the unpaired telocentric elements of the female correspond to the chromosomes of the 11th and 15th pairs; one can conclude that these pairs in the male represent the original sex chromosomes plus a pair of autosomes attached to the heterosomes as a consequence of a Robertsonian mechanism. In *L. vivipara*, the female sex is heterogametic and sex determination depends on a complex mechanism: ♀ $Z_1 Z_2 W$, ♂ $Z_1 Z_1 Z_2 Z_2$. The results published here resemble those of Oguma (1934) but do not lead to the same interpretation. This author gives for the female a ZO mechanism, but the observation of histological preparations does not reveal morphological details of chromosomes, so, the presence of a submetacentric chromosome may have escaped the attention of Oguma.

Our observations do not agree with those of Matthey et al., but Matthey (personal communication) has observed a metacentric chromosome in adult females and about half of their embryos in a population of the Alpes vaudoises.

The difference between the first result of Matthey et al. and our results could be explained by the fol-

lowing interpretation: the centric fusion which leads to the formation of the W chromosome is limited to some populations. *L. vivipara* and *L. strigata* (Ivanov & Fedorova, 1970) so far are the only two Lacertidae with heteromorphic sex chromosomes; they are an exception among the saurians where all species with heteromorphic sex chromosomes have male heterogamety (XY or X_1X_2Y). Finally, it must be noted that *L. vivipara* is a rare example among animals of multiple sex chromosomes in female heterogamety.

The differentiation of sex chromosomes has occurred through an evolutionary process (Ohno, 1967); the successive steps of this mechanism have been well reconstituted in snakes by Beçak & Beçak (1969). These authors have shown that in the 'old' family Boidae none of the species studied have heteromorphic sex chromosomes; in several Colubridae the Z and the W differ by a pericentric inversion. Poisonous snakes (Crotalidae and Viperidae), the most advanced, have very different sex chromosomes, W being a minute element. The fact that Z and W differ by a pericentric inversion, which decreases chiasma frequency and reduces crossing over leads Ohno (1967) and Beçak & Beçak (1969) to advance that this phenomenon is at the origin of the evolutionary process which leads to the morphological differentiation of sex chromosomes.

In *L. vivipara* the mechanism which occurs is quite different, and there is no loss of material, but if we compare this species with the other species of the genus *Lacerta*, which have the same N.F., the metacentric W can be considered as the beginning of an evolutionary process.

In Pisces, sex determination is very variable, some species are hermaphrodite, and the two types of heterogamety have been observed in the same species (Ohno, 1967). In Amphibians, Lacroix (1970) has shown differential segments on lampbrush chromosomes in *Pleurodeles poireti*, so the differentiation of Z and W exists but is too small to be observed on metaphasic chromosomes.

Among Reptiles, there is no homogeneity of cytogenetic sex determinism as in Birds and Mammals, and without knowledge of the sex chromosomes of Turtles, Crocodiles and *Sphenodon*, the comparison is limited to Snakes and Saurians.

Snakes show female heterogamety (Beçak & Beçak, 1969), the majority of Saurians male heterogame-

ty (Wright, 1973) but in Saurians male and female heterogamety coexist. The mechanisms which produce heteromorphic sex chromosomes could have occurred:

(1) on the chromosome bearing the genetic units responsible for the determination of the male sex (XY-XX mechanism and derivatives)

(2) on the chromosome bearing the genetic units responsible for the determination of the female sex (ZW-ZZ mechanism and derivatives)

Considering the degree of differentiation of sex chromosomes, Reptiles are very interesting; female heterogamety and male heterogamety coexist, as in Amphibians, but the differentiation of sex chromosomes is more pronounced, several species show heteromorphic chromosomes during metaphase, so from this point of view they resemble Birds and Mammals. It must be noted too, that in Saurians, as in Eutherian Mammals, Y is dominant whatever is the number of X chromosomes; tetraploid hybrids between *Cnemidophorus tigris* and *C. sonorea* bearing XXXY constitution are males (Lowe et al., 1970).

In conclusion, proof of female heterogamety in *L. vivipara*, demonstrated by the presence of heteromorphic sex chromosomes, and the existence of a W in *L. strigata* are of great interest to our understanding of karyotype evolution not only of Reptiles but of the Vertebrates in general.

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Note added in proof:

Cnemidophorus tigris shows male heterogamety with unusual large sex chromosomes; X and Y cross over except in the medial segments where they differ in centric position and heterochromatin; this case probably represents an early stage of differentiation.

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