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C-band variability and phylogeny of Lacertidae

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Abstract

The karyology of various species from the family Lacertidae (Reptilia, Sauria) has been studied with conventional and C-banding techniques.

The study shows that this family is not so conservative from a karyological viewpoint as considered till now. In fact a higher diploid number than that generally observed in most species of Lacertidae and supernumerary chromosomes have been observed in three of the species investigated. Moreover an evident inter- and intraspecific variability has been found in the C-banding pattern of the various species studied. The situation found in *Podarcis sicula* is particularly remarkable. Different C-banding patterns have been observed in three different subspecies and in two populations of the same subspecies. These variations do not show a well defined trend and their role in the evolution of lacertid lizards is discussed.

The C-banding analysis evidences also the existence in two of the species studied of a female sex heteromorphism, in which the W chromosome has the same shape and size as the Z, but differs from it in being completely heterochromatic. This situation reminds that observed in some snakes and suggests that in lacertid lizards the evolution of sex chromosomes might have followed the same steps previously hypothesized for ophidians.

Introduction

The Lacertidae are a very successful group of lizards including about 160 species (Dowling & Duellman, 1978) widespread in the palearctic and paleotropic regions and adapted to various lifestyles (Klemmer, 1971). Consequently species characterized by considerable polymorphism are frequently found (Darevsky, 1967; Arnold, 1973).

In contrast to this pronounced ecological and morphological variability, the chromosome complements of the 'old world runners' show great uniformity. The greater number of species possess karyotypes with 36 acrocentric macrochromosomes and 2 microchromosomes which are practically indistinguishable by means of conventional cytological techniques (Gorman, 1973; Bickham, 1984). Karyotypes with a lower diploid number have been found only in a few species. Two of these may be derived from the 36 + 2 one by Robertsonian mechanisms, a third lacks microchromosomes (Gorman, 1969, 1973; Kupriyanova, 1980). A 2n = 40 karyotype with an additional pair of small macrochromosomes has recently been reported in the three species of *Gallotia* (Cano *et al.*, 1984; Lopez-Jurado *et al.*, 1985) and in a specimen of *Psammodromus algirus* (De Smet, 1981).

In a preliminary study using C-banding techniques, we observed clear and marked differences among the C-banding patterns of four species, all of them having a typical 36 + 2 chromosome set (Odierna *et al.*, 1985). On this basis, we have extended our investigation to a greater number of species and to several taxonomic levels, in order to assess the extent of the variation in C-banding pattern and its possible role in the karyological evolu-

tion of the Lacertidae. Our investigation is essentially concerned with the *Lacerta*-complex, which is the most speciose in the family and whose phyletic relationships and taxonomy have been recently reexamined by Arnold (1973), who has divided it into four new genera: *Gallotia; Lacerta* part I; *Lacerta* part II and *Podarcis*. In addition we studied the chromosomes of *Psammodromus algirus*, which is considered by Arnold related to the *Lacerta*-complex, and those of *Takydromus sexlineatus*, a species belonging to a genus widespread in Asia and which is supposed to share some features with *Gallotia* (Camp, 1923).

Material and methods

Table 1 summarizes the species studied, the number of specimens examined for each species and their source. Except for *Podarcis sicula sicula, Podarcis sicula klemmeri* and *Podarcis tiliguerta*, all animals were obtained from a commercial dealer and their exact source of origin is not known. The animals were injected with Phytohemagglutinin M (DIFCO) according to the method of Baker *et al.* (1971) for obtaining an adequate number of mitoses. After three days of this treatment the animals were injected with colchicine at a concentration of 0.5 mg/ml (0.01 ml/g body weight) and, 3 h later, anaesthesized with ether or tricainemetasulphonate and then dissected.

Mitotic metaphase cells were obtained from bone marrow, intestine or testis using the air drying spreading (Schmid, 1978) or the air-drying scraping techniques (King & Rofe, 1976).

C-banding was performed by Sumner's method (1972), treating the slides with a saturated aqueous $Ba(OH)_2$ solution for 5 min at temperatures ranging from 45° to 60°C. The slides were then stained with 2% Giemsa in 0.1 M phosphate buffer at pH 7, for 10′ (Olmo *et al.*, 1984; Odierna *et al.*, 1985, for further details).

At least 20 banded plates were examined for each species and 5 banded karyotypes reconstructed, the haploid idiograms of which are depicted in Figure 5, so as to facilitate a comparison among the various taxa. As the chromosome length changes only slightly from one pair to another, the arrangement of the chromosomes in the idiograms is approximate and their numeration arbitrary.

Results

Takydromus sexlineatus (Fig. 1a, b, c)

In the female and male specimens previously investigated (Olmo *et al.*, 1984; Odierna *et al.*, 1985) we reported a typical lacertid karyotype with 36 acrocentric macrochromosomes and 2 microchromosomes, consistent with previous findings in other species of the same genus (Gorman, 1973). In the additional specimens examined in the present study we found mitotic plates with 38, 40 and 42 chromosomes, including respectively 2, 4 and 6 microchromosomes (Fig.1b, c). At diplotene of male meiosis, however, only 20 or 21 bivalents were present.

The C-banding pattern of *T. sexlineatus* has already been examined (Olmo *et al.*, 1984, Odierna *et al.*, 1985). Almost all the macrochromosomes have small centromeric bands; some pairs show also faint telomeric bands (Figs. 1a, b). The microchromosomes appear completely heterochromatic in some plates, whereas in others they have only a centromeric C-band.

The most striking aspect of *T. sexlineatus* is the presence in the female of heteromorphic sex chromosomes, where the W has the same size and gross morphology as the Z, but differs from it in being completely heterochromatic (Fig. 1a, Olmo *et al.*, 1984).

Psammodromus algirus (Fig. 1d)

All the specimens showed metaphase plates with 36 macrochromosomes and 2 microchromosomes, and in all of the males diplotene meiocytes had 19 bivalents (Fig. 1d). This contrasts with the $2n = 40$ reported for a single specimen by De Smet (1981) and agrees with the karyotype described by Matthey (1939) in *Psammodromus hispanicus*. A similar result has been obtained by Cano and coworkers (Lopez-Jurado *et al.*, 1985; Cano, pers. comm.). We have not yet obtained a satisfactory C-banding pattern for this species.

Gallotia galloti

Here all the specimens had a karyotype with 38 acrocentric macrochromosomes and 2 microchromosomes in agreement with the report of Cano *et al.* (1984). In several metaphase plates some macrochromosomes showed very small short arms, often C-band positive (Fig. 1e). Additionally

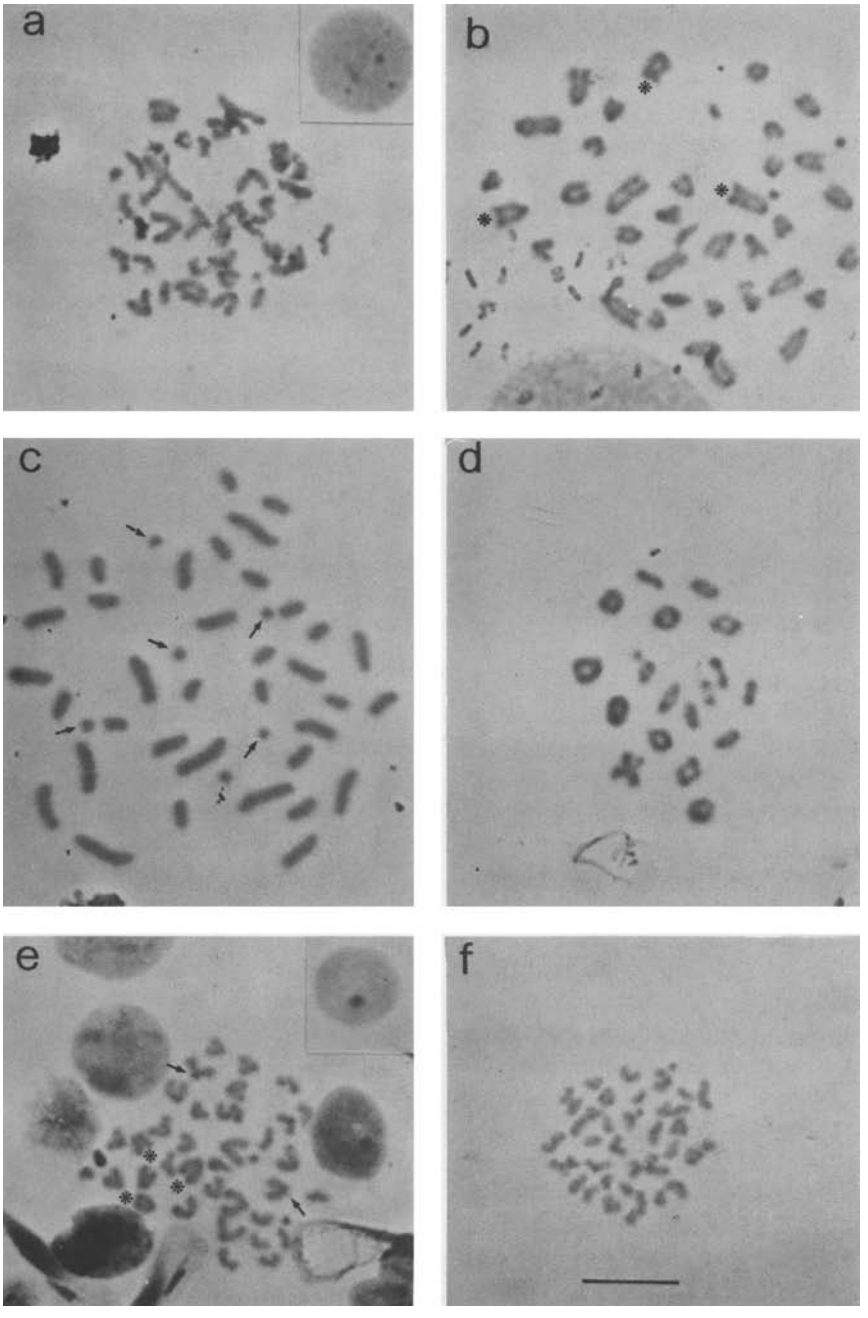

Fig. 1. Chromosomes of Lacertidae, conventionally stained (c, d) and C-banded (others): (a) *Takydromus sexlineatus*, female, metaphase, note completely heterochromatic W chromosome but absence of a corresponding heterochromatic block in interphase nucleus (inset); – (b) *T. sexlineatus*, male, metaphase, no chromosome completely banded, faint telomeric bands in some macrochromosomes (asterisks); – (c) *T. sexlineatus*, female, four additional microchromosomes (arrows); – (d) *Psammodromus algirus*, male meiotic metaphase; – (e) *Gallotia galloti*, female metaphase with completely heterochromatic W chromosome and corresponding heterochromatic mass in interphase (inset); some chromosomes with minute short arm (arrows), faint telomeric bands visible in some chromosomes (asterisks); – (f) *G. galloti*, male, no chromosome completely heterochromatic. Bar, 10 μm.

(Fig. 1e, f) all but 5 pairs of the smallest macrochromosomes, had small centromeric bands, and some of them showed faint telomeric bands too. The two microchromosomes are completely heterochromatic (Fig. 5). In *Gallotia* a sex heteromorphism is also present in the 13th pair with one of the homologs being completely C-band positive (Fig. 1e). Heteromorphism was also observed in female interphase nuclei, in the form of a single large heterochromatic C-band positive mass (Fig. 1e). This is lacking in males of *Gallotia* and is not evident in either sex of *Takydromus* (Fig. 1a) despite the fact that the W chromosome is similar in both species.

Lacerta part I

Lacerta lepida. The male mitotic plates examined all had two metacentric macrochromosomes, 32 acrocentric macrochromosomes and two microchromosomes (Fig. 2b). At male diplotene we mostly found 18 bivalents but some meiocytes had an additional univalent microchromosome (Fig. 2d). In females most mitotic plates lacked one of the acrocentric macrochromosomes but had an additional microchromosome (Fig. 2a). This situation suggests the existence of a sex chromosome heteromorphism similar to that observed in many other lacertid species. In addition we also found some plates with 2n = 37, having 33 macrochromosomes and 4 microchromosomes (Fig. 2c). Yet a third situation has been observed by Cano (pers. comm.) where in females, from a population in Galicia (Northern Spain), the karyotype included 24 macrochromosomes and 3 microchromosomes

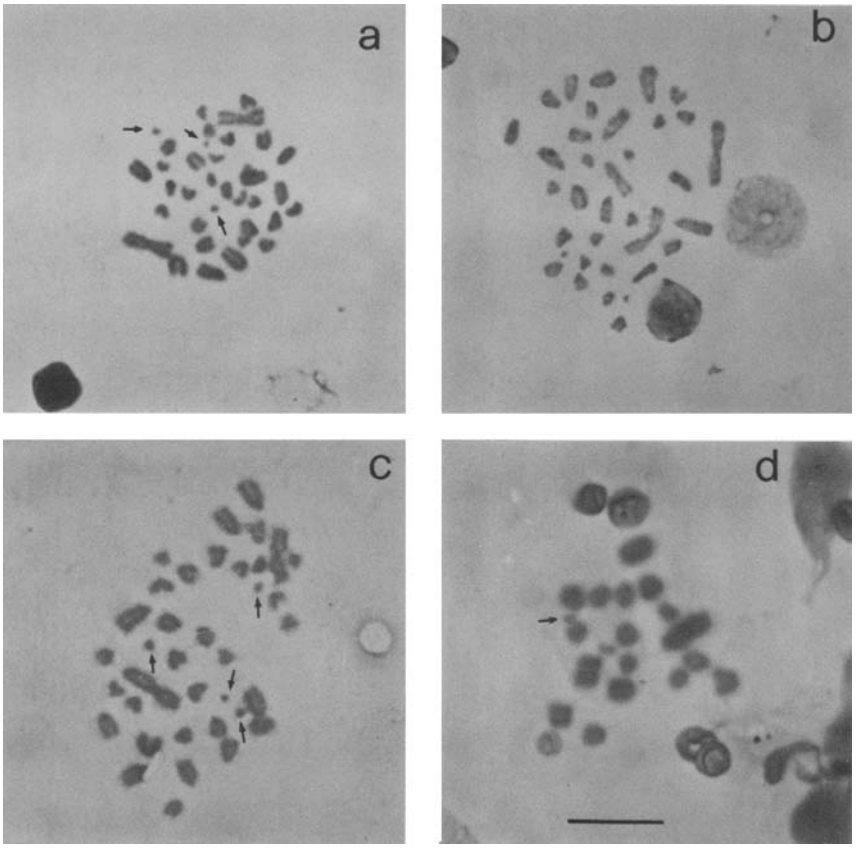

Fig. 2. Conventionally stained (a, c, d,) and C-banded (b) chromosomes of *Lacerta lepida*: (a) Female metaphase, 33 macro- and 3 microchromosomes (arrows); – (b) Male metaphase, 34 macro- and 2 microchromosomes, centromeres of biarmed macrochromosomes unstained; – (c) Female metaphase, 33 macro- and 4 microchromosomes (arrows); – (d) Male meiosis, 18 bivalents and one microchromosome (arrow). Bar, 10 μm.

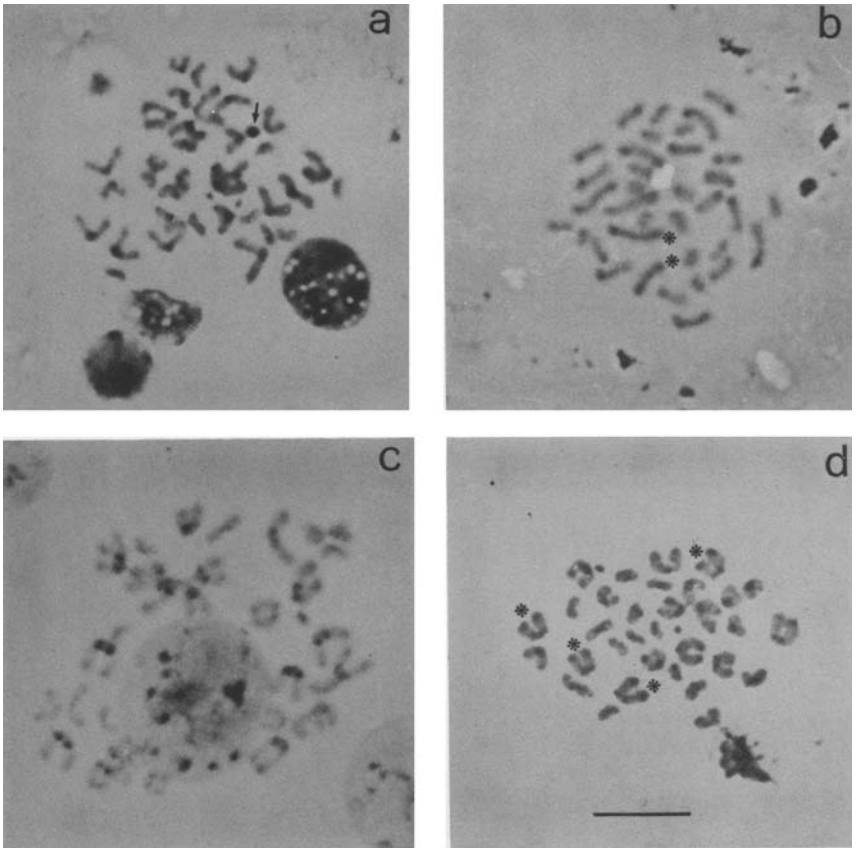

Fig. 3. C-banded metaphase plates of *Lacerta* species: (a) *L. viridis*, female, completely heterochromatic W chromosome (arrow); – (b) *L. viridis*, male, no chromosome completely heterochromatic, some with faint telomeric bands (asterisks); – (c) *L. trilineata*; – (d) *L. dugesii*, telomeric bands in some of the largest macrochromosomes (asterisks). Bar, 10 μm.

but was devoid of sex chromosome heteromorphism.

From a preliminary C-banding study it is evident that, in this species, several acrocentric macrochromosomes have more or less markedly banded centromeres, whereas the metacentrics show only telomeric bands (Fig. 2b).

Lacerta trilineata. As previously reported (Odierna *et al.*, 1985) this species has the smallest amount of heterochromatin. Only 8 pairs of macrochromosomes show C-bands, which are essentially paracentromeric. Microchromosomes are not always banded (Figs. 3c, 5).

Lacerta viridis. All the specimens show a typical 36 + 2 chromosome set. In C-band preparations many macrochromosomes show clearly stained centromeres, and some of them also faint telomeric bands (Fig. 3a). The microchromosomes are generally, but not always, heterochromatic (Fig. 5).

Female heterogamety is evident and as in *Takydromus* and *Gallotia*, the W-chromosome is completely C-banded (Fig. 3a). It also differs from the Z, however, in having a smaller size, intermediate between that of the macro- and of the microchromosomes (Fig. 5). De Smet (1981) has also reported sex-chromosomes with a clearly different morphology in this species, though he describes the W-chromosome as a microchromosome.

Lacerta part II

Lacerta dugesii. Details of this species have been reported previously (Odierna *et al.*, 1985). Some chromosomes show centromeric bands, and others

paracentromeric bands. Most of the largest homologues possess telomeric bands. The microchromosomes are intensely banded.

Podarcis

All of the species investigated have a typical 36 + 2 chromosome set.

Podarcis melisellensis (Fig. 4a). In this species all but five pairs of the chromosomes show centromeric bands. The first and the 10th pairs also show telomeric bands (Fig. 5); microchromosomes are completely labelled. In contrast to De Smet's obser-

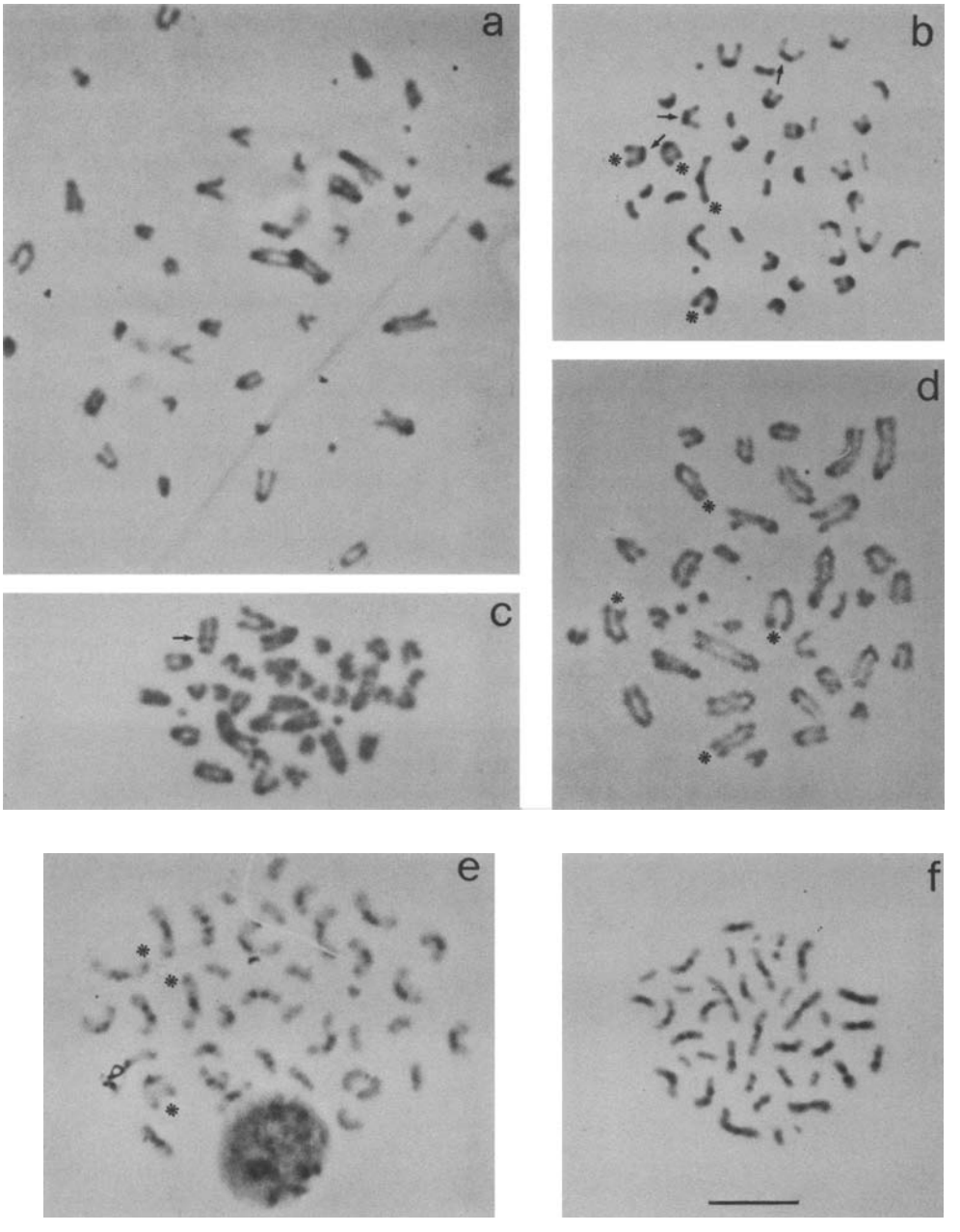

Fig. 4. C-banded metaphase plates of *Podarcis* species: (a) *P. melisellensis*; – (b) *P. tiliguerta*, arrows indicate paracentromeric bands, asterisks faint telomeric bands; – (c) *P. sicula campestris*, intercalary bands on two chromosomes (arrows); – (d) *P. sicula sicula* from Scafati; – (e) *P. sicula klemmeri*, faint telomeric bands (asterisks); – (f) *P. sicula sicula* from Punta Licosa. Bar, 10 μm.

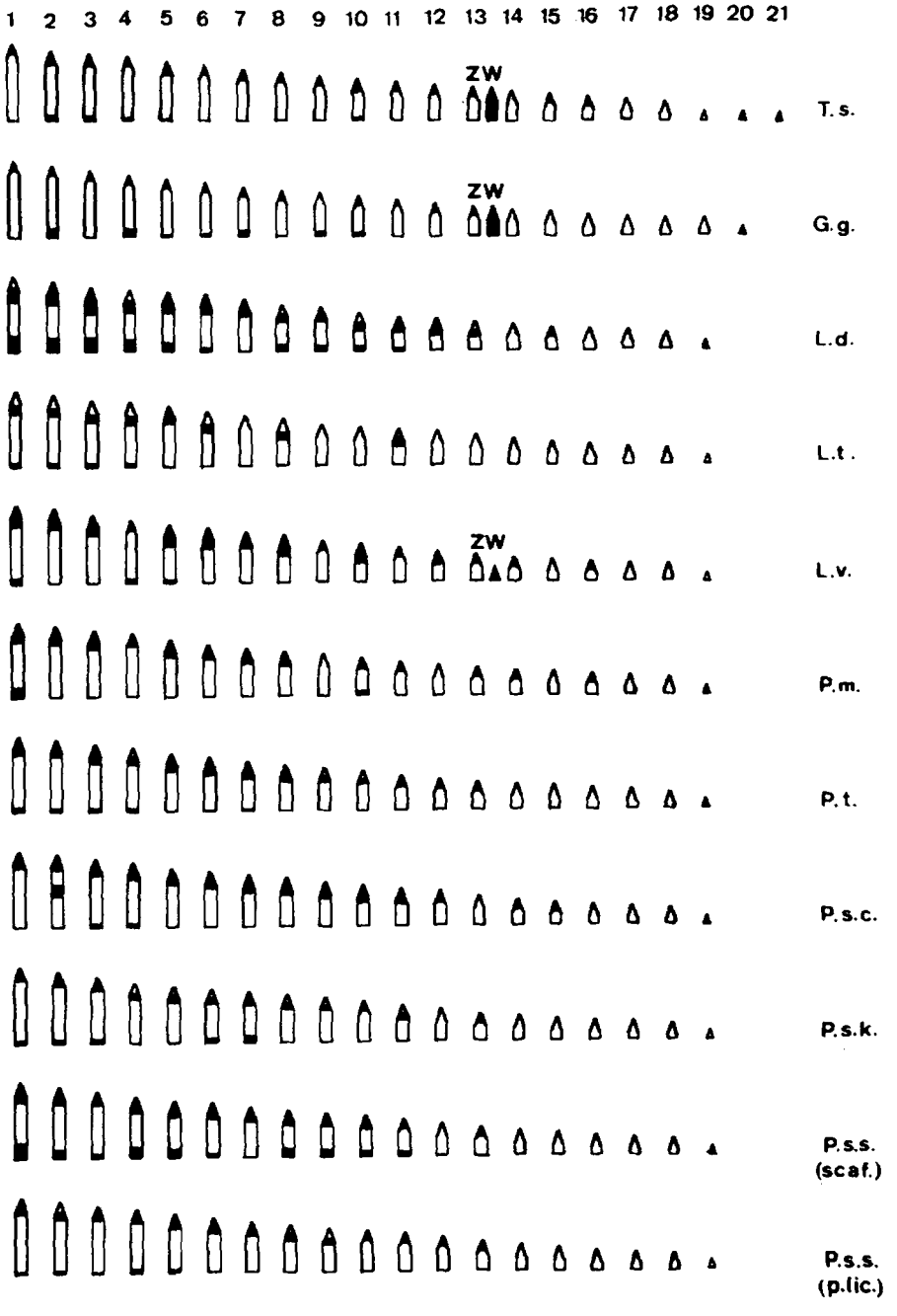

Fig. 5. Haploid idiograms showing variations in C-banding pattern in the species and subspecies of lacertid lizards investigated. T.s.: *Takydromus sexlineatus*; G.g.: *Gallotia galloti*; L.d.: *Lacerta dugesii*; L.t.: *Lacerta trilineata*; L.v.: *L. viridis*, P.m.: *Podarcis melisellensis*; P. t.: *P. tiliguerta*; P.s.c.: *P. sicula campestris*; P.s.k.: *P. sicula klemmeri*; P.s.s.: *P. sicula sicula*, (scaf.) specimens from Scafati, (p.lic.) specimens from Punta Licosa.

Table 1. Material studied and provenience.

Genus	Species	Specimens No.	Source
Gallotia	*G. galloti*	8m; 8f	Canary Islands
Lacerta part I	*L. lepida*	5m; 3f	Spain
	L. trilineata	2m	The Balkans
	L. viridis	3m; 2f	Hungary
	L. viridis	3m	Northern Italy
Lacerta part II	*L. dugesii*	5m; 5f	Madeira
Podarcis	*P. melisellensis*	4m; 4f	Islet of Mclisello (YU)
	P. sicula campestris	2m; 2f	Northern Italy
	P. sicula sicula	5m; 5f	Scafati (Salerno, Italy)
	P. sicula sicula	3m; 3f	Punta Licosa (Salerno, Italy)
	P. sicula klemmeri	3m; 3f	Islet of Licosa (Salerno, Italy)
	P. tiliguerta	1f	Island of La Maddalena (Sassari, Italy)
Psammodromus	*P. algirus*	4m; 4f	Spain
Takydromus	*T. sexlineatus*	10m; 10f	Thailand

vations (1981), we failed to find any heterochromosomes.

Podarcis tiliguerta (Fig. 4b). Almost all the macrochromosomes show labelled centromeres, except those of the 4th, 9th and 10th pairs, which have paracentromeric bands, very close to the centromeres (Figs. 4b, 5). Telomeric bands are found in the first 4 pairs of macrochromosomes, and the microchromosomes are completely labelled.

Podarcis sicula. We have studied three subspecies from this species. In one of them, specimens from two different populations have been examined.

P. sicula campestris (Fig. 4c). Most chromosomes show centromeric bands and two pairs have faint telomeric bands. The chromosomes of the second pair are characterized by an intercalary band (Figs. 4c, 5). Microchromosomes are usually banded. De smet (1981) reports the presence of sex chromosomes in a specimen of this species. However, there was no chromosome heteromorphism in the specimens we examined, and this is consistent with the observations of Dallai and Baroni-Urbani (1967).

P. sicula klemmeri (Fig. 4e). The C-banding pattern of this subspecies is remarkably different from that of the other subspecies of *P. sicula.* All but few chromosomes have paracentromeric bands (Figs. 4e, 5). Faint telomeric bands can be observed on some among the largest chromosomes. Microchromosomes are generally free of C-bands.

P. sicula sicula. We examined specimens from two different areas of Campania, and have observed clear differences between their C-banding pattern. In specimens from the more northern area (Scafati), whose banding pattern has already been described (Odierna *et al.*, 1985), the distribution of C-bands is very similar to that observed in *P. s. campestris* (Fig. 4d). Thus, the first nine pairs of homologues show marked centromeric bands and some have more or less marked telomeric bands (Fig. 5). As in *P. s. klemmeri* and in *P. tiliguerta* the 5 pairs of smallest macrochromosomes have no C-bands (Fig. 5). The microchromosomes are completely labelled.

The specimens from Punta Licosa, however, show a C-banding pattern more similar to that of *P. s. klemmeri* (Fig. 4f). In them most chromosomes have paracentromeric bands, while telomeric bands are very rare and not always present in all of the plates examined. The smallest macrochromosomes do not C-band while the microchromosomes appear faintly stained in some plates and devoid of heterochromatin in others (Figs. 4f, 5).

Discussion

Sex chromosomes

Several cases of sex chromosomes have been reported in lacertid lizards. In all but one of these, female heterogamety of the ZW type is present. Here the Z is one of the smallest macrochromosomes while the W is a microchromosome (Kupriyanova, 1968; Gorman, 1969; Ivanov *et al.*, 1973; Ivanov & Fedorova, 1973; Bhatnagar &

Yoniss, 1976; Darevsky & Kupriyanova, 1982). *Lacerta vivipara*, however, has sex chromosomes of the Z_1Z_2W type, where the W is metacentric and the two Z chromosomes are small acrocentrics (Chevalier, 1969; Chevalier *et al.*, 1979).

The sex chromosomes found in *Gallotia galloti* and *Takydromus sexlineatus* are identical with those found in some colubrids and considered to be an early stage in the differentiation of sex-chromosomes (Ray-Chaudhuri *et al.*, 1971; Singh *et al.*, 1976, 1980). Singh and co-workers have suggested that in snakes, and presumably also in other vertebrates, sex-chromosome differentiation starts with the selective accumulation on either homologue of a specific satellite DNA, accompanied by heterochromatinization. This may subsequently be followed by structural rearrangement of the heterochromatic homologue (Singh *et al.*, 1980).

This model may not apply to all the types of heterochromosomes observed in reptiles (King, 1977) and it has been clearly shown that in the snake *Acrantophis dumereli* (Mengden, 1981) and in the lizard *Gehyra purpurascens* (Moritz, 1984b) the primary step in the differentiation of sex chromosomes involves inversion and not variation in heterochromatin. However the resemblance between the sex-chromosomes of the lizards studied by us and those observed in colubrids, seems to suggest that, at least in lacertids, sex chromosome differentiation might go through the same evolutionary steps as in some snakes. It is also possible that the sex chromosomes of *Takydromus* and *Gallotia* are not exactly at the same stage of differentiation, since, in the latter, interphase nuclei show a single heterochromatic C-band mass, which has the same size as the whole W chromosome, whereas in *Takydromus* no sex heterochromatin is present in interphase (Fig. 1a).

A more differentiated sex-chromosome system, similar to that reported by other workers in other lacertid species is present in *L. viridis* and *L. lepida*. Here the W is smaller than the Z, suggesting that it might have been derived from a heterochromatic chromosome like that of *Gallotia* and *Takydromus*, by deletion. The differences between our observations, those of Cano in *L. lepida* and those of De Smet (1981) in *L. viridis*, suggest that there might be intraspecific variability in both the occurrence and the morphology of the sex chromosomes. A similar situation has been already described in some lizards (King & Rofe, 1976; Moritz, 1984b) and snakes (Singh *et al.*, 1979; Mengden, 1982). In lacertids this variability might be explained assuming that the transition from the condition observed by us in *Gallotia* and *Takydromus* to a more differentiated state, in which the two heterochromosomes differ markedly in size, may have occurred several times independently in different species.

The presence of similar genetic sex determining systems suggests a relationship between *T. sexlineatus* and the *Lacerta*-complex, and especially with *Gallotia*. This is consistent with other karyological analogies between *Takydromus* and *Gallotia*, such as the relatively small amount of constitutive heterochromatin, appearing essentially as small centromeric bands, and a diploid number in excess of 38. These karyological similarities agree well with analogies observed between these two genera at the morphological level (Camp, 1923).

Supernumerary chromosomes

In two of the species studied, *Lacerta lepida* and *Takydromus sexlineatus* · supernumerary microchromosomes were present. It is known that the chromosome number of a mitotic plate, and especially that of microchromosomes, can be affected by the method of preparation used (Shields, 1982). In our case, however, we can confidently rule out that the differences in microchromosomes number depend on the technique employed, since we have used methods that are considered among the most suitable for studying lizard karyology (Baker *et al.*, 1971; Peccinini-Seale, 1981).

Moreover, as has been already mentioned, our observations on *L. lepida* are consistent with those of Cano (pers. comm.). Some doubts might be raised as to the mitotic counts of $2n = 38$ seen in *Takydromus*, since we never found less than 20 bivalents in male meiosis of this species. Therefore it is possible that the normal karyotype of this species consists of 36 acrocentric macrochromosomes and 4 microchromosomes, though in other species from the same genus a typical 36 + 2 complement has been described (Gorman, 1973).

The only case of supernumerary chromosomes previously described in lacertid lizards is in *Lacerta parva*, where Kupriyanova (1980) found specimens with 2, 4 or 6 additional microchromosomes, sug-

gesting that they originated '*de novo*' as a consequence of centric fusions, which would have characterized the origin of the karyotype of this species since it includes 14 biarmed macrochromosomes. This hypothesis could also explain the situation in *L. lepida*, which has a pair of metacentrics, but obviously cannot account for the condition observed in *Takydromus*, which possesses an all acrocentric complement. An alternative hypothesis may be that these additional chromosomes are the remnants of an ancestral condition characterized by a karyotype with a greater diploid number than 40 and numerous microchromosomes. In fact, in *T. sexlineatus* there are specimens with 42 chromosomes while in one male of *L. parva* a karyotype with 44 arms has been reported (Kupriyanova, 1980). Such a hypothesis has been already put forward by Lopez-Jurado *et al.* (1985), who assume that *Gallotia* has a constant 40-chromosome karyotype.

Starting from an ancestral karyotype similar to that hypothesized by us, subsequent karyological evolution in lacertid lizards would have taken place by a reduction in number, due essentially to a loss of microchromosomes or to their translocation to macrochromosomes, a mechanism which is supposed to be shared by several groups of saurians (Gorman, 1973; Cobror, 1985). In some species this would result in the presence of unstable supernumerary elements.

The condition of *Gallotia*, which has an additional pair of macrochromosomes and is confined to the Canaries, suggests that this genus diverged very early from others in the family, and hence before the reduction in diploid number had reached the present level. Lopez-Jurado *et al.* (1985) moreover, hold that the fixation of the *Gallotia* karyotype may stem from its insular habitat.

If supernumerary chromosomes in lizards prove to be more widespread than so far observed, this might explain some of the divergences which different authors have reported for the diploid number in some species, for example *Psammodromus algirus*.

C-band variability

Relatively few studies on the C-banding pattern of saurians have been performed so far (Kasahara *et al.*, 1982; Moritz, 1984a, b; Princée & De Boer, 1983; King, 1984; Solleder & Schmid, 1984).

They are generally limited to only one or few species, but seem to clearly show that the C-bands are fairly variable in this order. Thus the C-banding patterns of the saurian species studied so far show both interspecific (King, 1984) and intraspecific (Kasahara *et al.*, 1982; Moritz, 1984a, b) variations.

This may be true also for lacertid lizards in which, in contrast with the relatively stable chromosome morphology, the C-banding pattern displays greater variability. In fact each of the species studied has its own characteristic C-banding pattern and variations occur not only among species from the same genus, but at the intraspecific level too (Figs. 4, 5).

These variations, which may be due to differences in the amount and distribution of given highly repetitive DNA fractions (Odierna *et al.*, 1985), do not follow any well defined trend in either a taxonomic or a phylogenetic sense. Some species, such as *Podarcis sicula*, show variations among different subspecies or even among populations belonging to a single subspecies. In other species, such as *Lacerta viridis*, the same C-banding pattern occurs in specimens from as far apart as Hungary and Northern Italy. Moreover, greater similarities may be found between the banding patterns of species from different genera than between subspecies of the same species (see for instance *Lacerta trilineata* and *P. sicula klemmeri*, *L. viridis* and *P. sicula sicula* from Scafati).

Some authors have hypothesized that variations in C-banding are correlated with speciation processes (Deaven *et al.*, 1977; Fry & Salser, 1977). The situation observed by us in lacertids and especially the intraspecific variability seen in *P. sicula*, might be consistent with this idea; however our investigation is not sufficiently exhaustive at the population level. Thus the evolution and distribution of the various subspecies of *P. sicula* is as yet unclear and undefined (Bruno, 1982). For this reason it is not possible to establish whether in Lacertidae the variations in C-banding are correlated with speciation or are a simple case of polymorphism.

Another function in which the C-band variations can be involved is the control of some chromosome mutations (Hatch *et al.*, 1976; Mengden & Stock, 1980; Kasahara *et al.*, 1982). At this regard of particular interest is the presence in some chromosomes of *G. galloti* of short arms, which are clearly

C-band positive. These might represent an initial stage in the transformation of uniarmed into biarmed chromosomes through heterochromatin amplification similar to that observed in some rodents (Hatch *et al.*, 1976) and snakes (Mengden & Stock, 1980). Alternatively they result from the translocation of microchromosomes to macrochromosomes.

In conclusion, although the data collected by us on the C-banding of lacertid lizards are only preliminary, there are good grounds for extending our investigations in the C-banding patterns to a greater number of species as well as to characteristics and variations of the highly repetitive DNA fractions, which are presumably related to the C-bands. The results obtained so far certainly support the idea that the variations in distribution and amount of C-bands may have played a significant role in the evolution of lacertid lizards.

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