Studies in Herpetology, Roček Z. (ed.) | pp. 85 - 88 | Prague 1986

# On Karyotype Evolution in Lizards

Larissa A. KUPRIYANOVA

Zoological Institute, USSR Academy of Sciences, Department of Herpetology,
199034 Leningrad, USSR

Recent karyological data reveal that the reptilian karyotypes are not uniform. This would suggest speciation, however, chromosomal changes do not always accomplish this process. To explain karyotype evolution, "canalization model" was proposed for rodents, bats and turtles /Bickham and Baker, 1979/, but it has also often been applied to other vertebrates. The aim of present paper is to test the applicability of the model to lizard families Lacertidae and Scincidae and briefly to some other ones, too.

The major assuption of the model is that the karyotype is of adaptive value for the organism and that for each "adaptive zone" there is an "optimal karyotype". A highly adaptive /optimum/ karyotype has been evolved in higher categories within a "new adaptive zone" via intrachromosomal rearrangements /stage I/. At stage II, an adaptive zone due to the restriction /canalization/ of the chromosomal rearrangements has persisted within the family. This occurs primarily because of the Robertsonian changes, which do not markedly alter the gene arrangements. Further speciation might have proceeded without chromosomal changes in karyotype stability /stage III/. This means that the longer the taxon occupies the "adaptive zone" the higher is the taxonomic level and its karyotypic stability. Thus, one of the main tests of the model is a direct relationship between the age of the group and chromosomal uniformity within it.

Returning to lizards, the Lacertidae /180 recognized species and subspecies/ display a great chromosomal uniformity: 62 of 69 species studied karyologically /representing 10 genera/ have uniformly, in number and morphology, 38 acrocentrics /e.g. Lacerta portschinskii, 2n = 38A, N.F. = 38; Fig. 1a/. However, 6 species belonging to 3 genera /Gallotia, Psammodromus, Lacerta/ have somewhat different karyotypes /2n = 40A or 34 - 37A + 1 - 2V, SV/. The karyotype of L. parva is very different from those of all other lacertid lizards /2n = 24: 14V + 10A; N.F. = 38/, which testifies to a special position of this species. As the N.F. is the same within the genus the differences can be accounted for by 14 centric fusions or fissions. This indicates that despite the fact that insignificant non-Robertsonian changes are usually associated with speciation in the Lacertidae, the Robertsonian mechanisms also occur. From the principle of karyotype orthoselection, it can be assumed that within the family Lacertidae a group of species with biarmed karyotypes may exist. The rates of chromosomal changes within the genus Lacerta as well as the genus Eumeces seem to be different.

There have been a lot of data in the literature showing that the most common karyotype for the Lacertidae is 12 MV + 24m, which may indicate its primitive and initial character or convergence. This karyotype has often been observed in 7 other families of different phylogenetic branches. There is a similar karyotype structure with a size break on the chromosome pairs 12 - 14 in some skinks and lacertids. The modified karyotype has also been shown in four families. A "lacertid" karyotype structure with a graded series of acrocentrics has been found in the phylogenetically related Teiidae and in both the remote Gekkonidae and the Agamidae.

One possible interpretation of this phenomenon may be that of Bennett /1982/ who suggested "a relatively invariant spatial arrangement of the chromosomal limbs in the nucleus", which leads to restricted rearrangements in the karyotype, and that of White /1982/ who considered the "primitive" karyotype in morabine /grass-hoppers/ to be "an efficient and functionally harmonious arrangement of chromosome arms". During the last few years, a relationship has been shown between speciation and system reorganization of the chromosomal apparatus which involves both the structure and function of the nucleus /Stegnii, 1979/, indeed.

Judging by their rough chromosomal morphology, the lacertid karyotype evolution seems to have been proceeded by insignificant non-Robertsonian rearrangements that preserve both the karyotype and its structure. Thus speciation within the Lacertidae is not accompanied by chromosomal changes /the last stage in the model/. However, there are some exceptions which were discussed above.

Unlike the Lacertidae, the Scincidae show greater karyotypic diversity /2n = 26 - 36/. As an illustration, karyotypes of following species are mentioned: Eumeces taeniolatus (2n = 28: 4V + 24V, SV, ST; N.F. = 56); E. schneiderii princeps (2n = 32: 4V + 18SV, ST 1 10A; N.F. = 54); E. latiscutatus (2n = 26: 12V + 14 /10V, SV + 4A/; N.F. = 48 ); Asymblepharus (formerly Ablepharus) alaicus (2n = 30: 12V, SV + 18 /6V, SV + 12A/; N.F. = 48) /Fig. 1b-f, respectively/. However, less than 100 of 1200 species have been studied karyologically. They include less than 20 of 94 genera. Variability has often been observed between and within primitive and ancestor genera of the subfamilies Scincinae and Lygosominae, e.g. Scincus /2n = 32 - 36/, Eumeces /26 - 32/, Mabuya /26 - 34/, Sphenomorphus /28 - 30/. This diversity cannot be accounted for by Robertsonian changes only, which is not quite consistent with the above model. At the same time, more advanced genera like Scincella /2n = 30/ and Ablepharus /30/ show karyotype stability.

The chromosomal data principally support the phylogenetic interpretations of the relationships between different groups within the family /Greer, 1970, 1974/ and within the ancient primitive stem genus Eumeces /Taylor, 1935; Greer, 1974; Estes, 1983/. The karyotype of E. taeniolatus /section I of Taylor, 1935/ sharply differs from those of the schneiderii group of Taylor´s same section and resembles those of some Chalcides and Mabuya. The significant differences suggest that Taylor´s section I may be a heterogeneous group whose taxonomic status should be checked.

E. latiscutatus has the same karyotype as 20 other species belonging to 11 groups of Taylor´s advanced section III. Thus, chromosomal changes are not associated with speciation in section III, which corresponds to the last stage of the model. At the same time, within the schneiderii group /E. s. prineps, E. s. algeriensis; cf. Talluri, 1968/ as well as within both the ancient section I and the genus itself, speciation is accompanied by multiple /inter- and intrachromosomal/ changes, which disagrees with the model. The rate of chromosomal changes in the genus Eumeces may vary. The fact that the chromosomal /preferably Robertsonian/ changes and speciation processes are intricately involved with colonizing radiation has been shown in organisms such as rodents and Gehyra /cf. King, 1984/.

Asymblepharus alaicus was derived from a Scincella-like ancestor /Greer, 1974/

and its karyotype resembles that of some Scinecella species in the number, structure and sex heteromorphism of chromosomes. One should emphasize the similarity of the general karyotype structure in A. alaicus and in the advanced species of Eumeces /Fig. 1d, e/.

Thus, in the Lacertidae and the Scincidae, chromosomal evolution occurs by different mechanisms, which lead to a karyotype uniformity in the former and to karyotypic variability in the latter family.

Regarded in terms of the main test of the model, the karyological data suggest that the Lacertidae should be older than the Scincidae. However, the recent paleontological review by Estes /1983/ has shown that the fossil record of the Scincidae goes back farther than that of the Lacertidae. The antiquity of the Scincidae seems to be testified by their cosmopolitan distribution.

Analysis of the available karyological data on the Lacertilia indicates that nearly none of the lizard families demonstrate a strong karyotype uniformity. The number and morpohology of chromosomes vary between and within genera due to multiple, often non-Robertsonian changes. With some reservation, one may speak about a maintenance of a certain karyotype structure in some groups within the families, which might be due to an orthoselection principle /White, 1975/. This means that in the course of evolution lizard karyotypes have not undergone a common type of canalization.

All the above somewhat decreases the applicability of the model and shows that this challenging scheme does not seem to be universal. However, this suggestion should be regarded as preliminary because the available karyological data on lizards are far from being complete. The "primitive" karyotype structure may often be an "optimal" one with a highly adaptive nature. This idea may help to explain the frequent occurrence of similar structures in different families. Further detailed comparative studies of these karyotypes may lead to a better understanding.

I thank Ch. Ataev and F. Danielyan for field assistance and L. Borkin and V. Jeriomtschenko for providing me lizards. I thank also M. Morales for correcting my manuscript.

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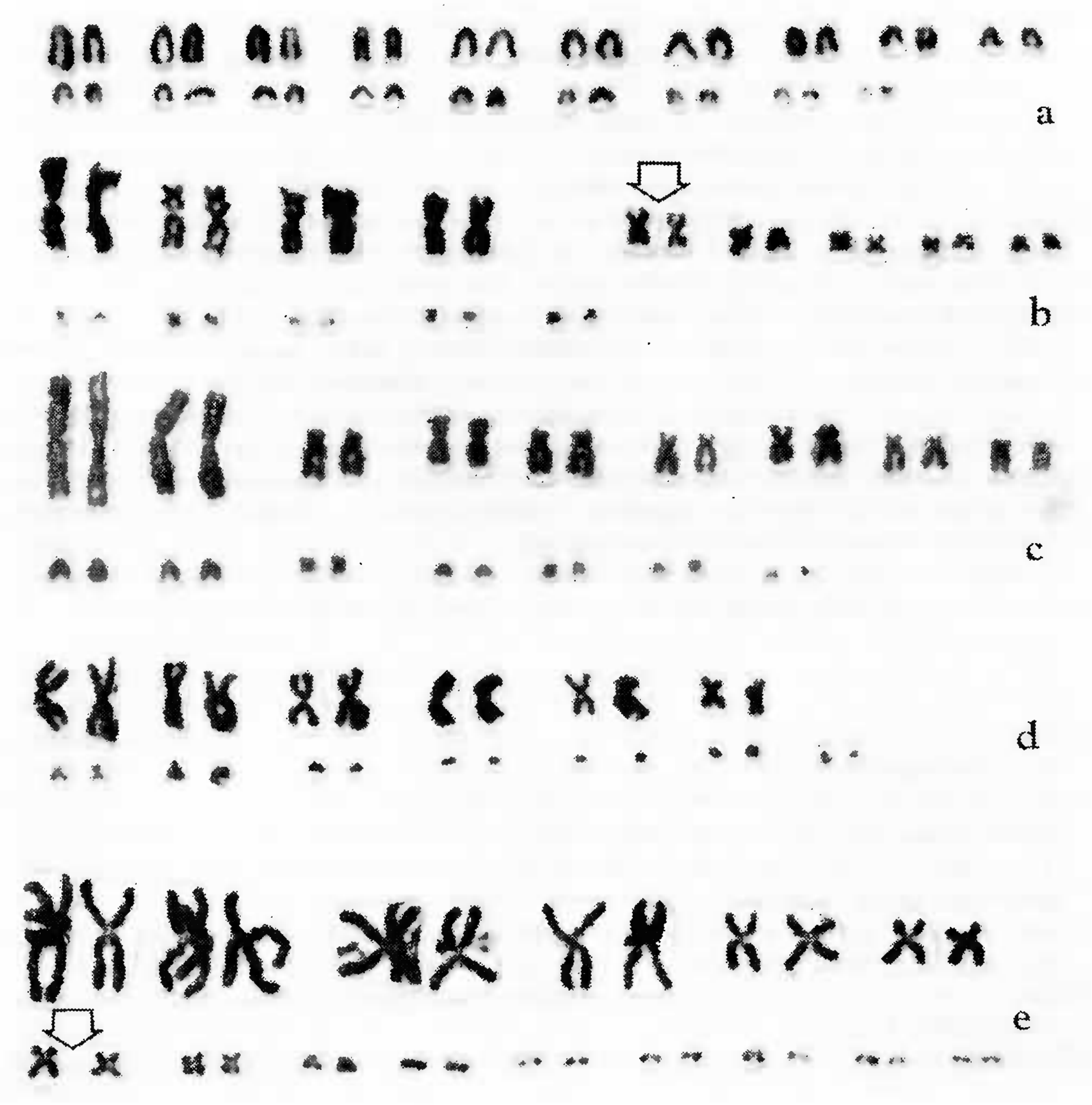

Fig. 1: Karyotypes of selected lizard species. /a/ Lacerta portschinskii Kess, ♂, Armenia, near Gosh; /b/ Eumeces taeniolatus Blyth, ♂, south and southwest of Turkmenia; /c/ E. schneiderii /Daud./, ♀, western Turkmenia; /d/ E. latiscutatus Hallowell, ♂, island Kunashir; /e/ Asymblepharus alaicus Jeriomtschenko et Szczerbak, ♂, northern Kirgizia. Arrows point to heteromorphic pairs /XY/ 4 and 7.