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Satellite DNA and phylogeny of Lacertid Lizards

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Abstract: Satellite DNA located on heterochromatic areas are of particular interest, since they may be used as a probe to estimate phyletic distances between species. In this review, four different satellite DNA families so far isolated from the lacertid genome are described. Though conservativeness and divergence rate are not the same for all satellite DNAs, they appear as a useful tool for phylogenetic and taxonomic investigations. In fact, the results obtained agree quite well with those from morphological and immunological studies.

Key words: Satellite DNA, Reptiles, Phylogeny.

INTRODUCTION

The occurrence and evolution of highly repeated DNAs, also called satellite DNAs, is being increasingly studied as a means of investigating phylogeny and taxonomy. The significance of this kind of investigations is supported by the numerous observations showing that these DNAs are free to evolve, and their divergence is directly proportional to the increase in the phyletic distance between species (MIKLOS, 1985; LIMA DE FARIA *et al.*, 1984).

However, the rate of variation and the turn-over of satellite DNAs are not always the same. In fact, some of them can be found in a single species or in closely related species (BARSACCHI, 1991; MACGREGOR, 1991; CAPRIGLIONE *et al.*, 1989), others show a wider distribution in species belonging to different genera or even different families (CAPRIGLIONE *et al.*, 1993; MACGREGOR, 1991; BARSACCHI, 1991).

I have been carrying out an investigation on the characterization of the lacertid genome for some years. It has provided interesting results, and is a good example of how studies of satellite DNAs can provide significant information on the existing phylogenetic relationships at various taxonomic ranks.

SATELLITE DNAS IN LACERTIDS

Four different satellite DNAs have so far been isolated from lacertid genomes. They show quite a wide distribution.

Two of these sequences have been isolated from the genome of *Podarcis sicula*. One, called pLCS, has been isolated by the Taq1 restriction enzyme; it is rich in adenine-thymine and is localized at the level of centromeric heterochromatin (CAPRIGLIONE *et al.*, 1989, 91). It is found with few variations in all of the species examined belonging to the genus *Podarcis* (Tab.1), in two species of *Algyroides* (*fitzingeri* and *moreoticus*), in *Lacerta graeca* and *dugesii*. pLCS sequences of *Algyroides* and *L.graeca* show little divergence from those of *P.sicula*, unlike that of *L.dugesii*, which diverges much more. Finally, no pLCS sequence has been found in species ascribed to other genera of the family, such as *Zootoca*, *Lacerta s.str.* and *Archaeolacerta*.

This distribution and evolution of pLCS indicates that *Podarcis* is quite a homogeneous natural group, and that *Algyroides*, *L.graeca* and, to a lesser extent, *L.dugesii* are related to *Podarcis*. This is in good agreement with similar results obtained from morphological, immunological, isoenzymatic and karyological studies (LUTZ & MAYER, 1985; ARNOLD, 1973, 89; ODIERNA *et al.*, 1987; OLMO *et al.*, 1989).

The other sequence, called pLHS, has been isolated by the HindIII restriction enzyme, and is found almost exclusively in the genus Podarcis. This DNA, too, is rich in adenine-thymine, and its sequence differs from that of pLCS only by 20%. It is, however, localized at pericentromeric and telomeric levels. This has suggested that pLHS is derived from the differentiation, translocation and subsequent reamplification of some pairs of pLCS by a mechanism also observed in other organisms (FLAVELL *et al.*, 1980; DOVER, 1982; MIKLOS, 1985; BOSTOCK, 1986).

The occurrence of this DNA only in *Podarcis* suggests that it might have a more recent origin. It would have appeared only after the divergence of this genus from other lacertids belonging to the same lineage.

Though being restricted to *Podarcis*, pLHS, however, shows a more rapid evolutionary rate. In fact, pLCS displays very little or no variation in all the *Podarcis* species; pLHS, instead, is practically the same in *P.sicula* and *P.muralis*,

but shows marked differences in *P.taurica* and *P.tiliguerta*. This observation is also interesting from the systematic standpoint, since it confirms that *P.sicula* and *P.muralis* are closely related, and the two other species belong to lineages other than *P.sicula*, as indicated by immunological and genetic studies (LUTZ & MAYER, 1985).

Clone	pGPS	pLCS	pLHS	pSHS
Mon.Size	160	180	140	130
Species Chr.Loc.	p	c	p.t.	?
Podarcis sicula	++	X	X	-
Podarcis muralis	++	+++	+++	?
Podarcis tiliguerta	++	+++	++	?
Podarcis taurica	+	+++	++	?
Podarcis hispanica	+	?	?	-
Algyroides fitzingeri	?	+++	-	-
Algyroides moreoticus	++	++	?	-
Lacerta graeca	X	+++	?	?
Lacerta dugesii	?	+	-	?
Lacerta lepida	?	-	-	-
Lacerta viridis	++	-	-	-
Lacerta vivipara	++	?	-	-
Archaeolacerta bedriagae	++	-	-	-
Archaeolacerta saxicola	-	?	-	X
Psammodromus hispanicus	?	?	-	-

Table 1: Presence and distribution of highly repetitive DNAs in lacertid lizards. **Mon.Size** = size of the monomeric unit in base pairs. **Chr.Loc.** = chromosome localization: **p** = pericentromeric, **c** = centromeric, **t** = telomeric, **?** = unknown. **X** = species from which the highly repetitive DNA has been isolated. + = presence of the satellite DNA, the number of + indicates the level of hybridization and then the affinity between the species examined. - absence of the satellite DNA. **?** = the presence of the satellite DNA was not tested.

A third, highly repeated DNA, called pSHS, has been isolated from *Lacerta saxicola* with HindIII. It does not show any similarity to pLHS, but, like the latter, has a limited distribution. In fact, it hybridizes only to the homologous DNA, whereas it fails to hybridize either to that of species belonging to other genera or to that of species ascribed to the genus *Archaeolacerta*, in which some investigators also include *L.saxicola* (ARNOLD, 1973, 89).

A different behaviour is displayed by the fourth satellite sequence (pGPS), which has recently been isolated from *L.graeca* with the PstI restriction enzyme. In fact, this DNA has quite a wide distribution, being found with some differences both in species related to *L.graeca*, such as several *Podarcis* and *Algyroides*, and in species that are not considered related to it, such as *L.viridis*, *L.bedriagae* and *L.vivipara*. Moreover, pGPS is not present in *L.saxicola*, which appears to have a much more differentiated DNA than many other lacertids so far investigated.

Its presence in different genera suggests that pGPS might be a very ancient sequence appearing before the divergence of the main lacertid taxa.

COMMENTS AND CONCLUSIONS

As already mentioned, the study of satellite DNAs has provided interesting contributions to the knowledge of lacertid phylogeny and taxonomy.

The most exhaustive and convincing results concern *Podarcis*, which is the genus most investigated. In fact, the analysis of satellite DNAs has confirmed that this genus is quite a homogeneous natural group; in addition, it has clearly shown its relation with other taxa of the family (*Algyroides*, *L.graeca*, *L.dugesii*), and has contributed to elucidating the relationships existing between some species of the genus, such as *P.sicula*, *P.muralis*, *P.taurica* and *P.tiliguerta*.

The contribution of these studies to other genera of the family is more limited. However, they provide interesting data deserving further investigation, such as the evidence that *Archaeolacerta* is probably a heterogeneous group and *L.saxicola* genome is greatly differentiated compared to that of all the other species studied.

The reliability of the results should also be emphasized. In fact, they agree with morphological, immunological and karyological results.

In conclusion, the study of satellite DNAs appears a useful tool for phylogenetic and taxonomic investigations. However, some remarks should be made.

The effectiveness and reliability of the study of satellite DNAs is more marked when related species are compared; the results of comparisons between more distant species, instead, are sometimes questionable. This depends on the rather complex trend that the evolution of a certain highly repeated sequence can show. Some of them are preserved for a long period, and their sequence can undergo gradual differentiation with time. Some, instead, can be reduced or disappear by deletion processes, or give rise to new sequences by divergence and reamplification of some of their copies, and this is the case of pLCS and pLHS (CAPRIGLIONE *et al.*,1994). Moreover, the rate of divergence is not the same for all satellite DNAs.

Therefore, a joint analysis of more than a sequence should be made, and satellite DNAs from different species should be compared. In this regard, it is significant that, as already

mentioned, the most satisfactory results concern *Podarcis* and its allied, in which we observed three different DNA sequences.

Finally, the results of studies of satellite DNAs should be compared with data from other kinds of investigation.

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