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Variable and Invariable DNA Repeat Characters Revealed by Taxonprint Approach Are Useful for Molecular Systematics

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Abstract. A specially optimized restriction analysis of highly repetitive DNA elements, called DNA taxonprint, was applied for phylogenetic study of primates and lizards. It was shown that electrophoretic bands of DNA repeats revealed by the taxonprint technique have valuable properties for molecular systematics. Approximately half of taxonprint bands (TB) are invariable and do not disappear from the genomes during evolution or change spontaneously. Presumably these invariable bands are restriction fragments of dispersed DNA repeats. Another group represents variable taxonprint bands that differ even between closely related species. These variable bands are probably represented by tandem DNA repeats and could be used as species-specific markers. It was shown that taxonprint bands are independent characters since the appearance of a new taxonprint band does not change the previous band pattern. Phylogenetic reconstruction carried out on taxonprint data demonstrated that this approach could be of general utility for molecular systematics and species identification.

Key words: DNA repeats — DNA restriction fragment analysis — Taxonprint — Molecular systematics — Lacertidae — Primates

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Introduction

Since the development of DNA sequencing technology, nucleotide sequence data have been successfully used to reconstruct phylogenetic relationships among and within almost all the main taxa and phyla. These investigations have resolved many evolutionary enigmas. Nevertheless, reconstructing phylogenetic relationships from DNA sequences has produced some controversial data (Pilbeam 1996; Doolittle 1997; Naylor and Brown 1997). It appears that inside gene regions there are no particular sequences that can be used to identify species. At the same time, a large body of data on genomic structure indicates that DNA repeats can be much more helpful as molecular markers of species and higher taxa (Elder and Turner 1995). For tandem DNA repeats the high similarity within a species compared to considerable divergence even among closely related species is due to the phenomenon of concerted evolution (Dover 1982). In the case of dispersed DNA repeats some data support the assumption that emergence of new repeat sequences correlates in time with the appearance of new taxa (Singer 1982; Weiner et al. 1986; Jurka et al. 1995). So at least some types of repeats can be used as taxon markers. The application of DNA repeat analysis to molecular systematics has been limited becuse only a small number of different types of repeats can be simply resolved.

Using routine molecular biological techniques we op-

timized the method of DNA repeat detection (Fedorov et al. 1992). This is achieved by digestion of genomic DNA with short-cutting restriction endonucleases followed by isotopic end labeling of the restriction fragments and their separation on nondenaturing polyacrylamide gels. This approach enables us to detect wide patterns of DNA repeat bands in a 20- to 300-nucleotide range. The band patterns obtained for individual genomic DNA we call a ''taxonprint.'' The application of short-cutting restriction endonucleases for taxonprint generates a very high level of smear from single copied regions of the genome on the autoradiographs, so the detected bands represent only highly copied DNA repeats. Our preliminary studies of broad taxon sampling of more than 60 species, including lizards, hedgehogs, shrews, moles, mice, fishes, bovids, and silkworms (Grechko et al. 1997), have allowed us to conclude that taxonprints for all studied taxonomic groups have the following properties: (1) all individuals from the same species have identical taxonprints; and (2) taxonprint bands (TB) can be subdivided into those specific to individual species, as well as those specific to groups of closely related species, genera, and even families.

In the present paper we used the taxonprint approach to study phylogenetic relationships among some representatives of the Primate order and Old World lizards from the family Lacertidae. We showed that TB can be divided into groups of variable or invariable bands with different characteristics. We have also shown how taxonprint data can be better applied to current systematics.

Materials and Methods

Species Characterization and Sources of Genomic DNA. DNA samples of primates were prepared from ethanol-preserved tissues. All 29 human placenta samples were collected in remote areas and represent six human races—Mongoloids—5 Vietnamese, 5 Evenks, 5 Koriaks, and 2 Malagasies; Negroid—6 Equatorial Africans and 2 Malagasies; and Caucasians—4 Georgians. DNA from primates was obtained from livers of three chimpanzees *Pan trogloydytes*, two pig-tailed macaques *Macaca nemestrina*, three baboons *Papio gamadryas*, and one vervet monkey *Cercopithecus aethiops.* Lizard DNA was prepared from fresh blood samples of one to five representatives of each species. Lizards from the family Lacertidae were represented mainly by the genera *Lacerta* and *Podarcis.* The genus *Lacerta* consists of primitive paleoarctic lizards of different geological ages (Arnold 1989). Our study included green lizards from the *Lacerta agilis* group (*L. agilis, L. strigata, L. viridis);* the *Lacerta saxicola* group [*L. mixta, L. valentini, L. portschinskii, L. rudis, L. saxicola lindholmi, L. saxicola darevskii, L. raddei* (Eghegnadzor and Gosh populations). *L.nairensis, L. caucasica, L. derjugini, L. practicola*]; and *L. vivipara. L. vivipara* has many unique features and differs considerably from all other lacertas lizards. The *L. saxicola* group—Caucasian rocky and forest archaeolacertas—is composed of closely related species which diverged about 10,000 years ago (Darevsky 1993). This group of species inhabits Caucasian regions only. Other studied lacertas are ancient species that inhabit East European and Asian areas. The genus *Podarcis* is closely related to the genus *Lacerta* and is represented by two species in our study. *Eremias velox* and *Ohpiops elegans* were taken for our study as outgroups (their taxonprints are not shown here). *E. velox* and *O. elegans* are desert lizards and have the most complicated morphology within the whole family. The habitat of *E. velox* overlaps with that of some lacertas. *O. elegans* inhabits North Africa, Middle Eastern, and Indian deserts.

Genomic DNA. Genomic DNA was purified from placenta, liver, and blood tissues by proteinase K digestion followed by phenol/chloroform extraction and ethanol precipitation.

Taxonprint Analysis. One-half microgram genomic DNA was incubated with 5 U of restriction endonuclease (MBI, Lithuania) in 20 μl of its specific buffer for 4–5 h. Labeling the recessed 3′ termini of DNA restriction fragments (0.1 μg) was carried out in 10 μl of buffer [10 m*M* Tris–HCl (pH 7.5), 10 m*M* $MgCl_2$, 50 m*M* NaCl] in the presence of 1 μCi of appropriate [α^{32}P] dNTP (Obninsk Russia), a 20 μ*M* concentration of each of the three remaining cold dNTPs, and 0.1 U of Klenow fragment (Biomaster, Russia) for 15 min at 20°C. Then 1 μl of a 0.5 m*M* concentration of each of the four cold dNTPs was added, and the reaction was continued for an additional 10 min. The reaction was stopped by the addition of EDTA to 10 m*M.* Samples (2–3 μl) were electrophoresed on the same day or were stored for up to several days at −20°C. Electrophoresis was carried out in 0.3 × 300 × 500-mm nondenaturing 8–10% polyacrylamide gels with 1× TBE buffer at 700–900 V and 10 W for 4–5 h. After electrophoresis the gel was dried and autoradiographed for 16–48 h.

Single-Strand Conformation Polymorphism (*SSCP*) *Analysis of Taxonprint Bands.* For preparative band purification 0.5 μg of *Taq*I-digested DNA was labeled in 20 μl of buffer [10 m*M* tris–HCl (pH 7.5), 10 m*M* $MgCl_2$, 50 m*M* NaCl] contained 10 μCi of [α-^{32}P]dCTP; a 30 μ*M* concentration of each of cold dATP, dTTP, and dGTP; and 1 U of Klenow fragment for 20 min at 20°C. Whole samples were preparatively electrophoresed under standard taxonprint conditions for 4 h on a 1 × 200 × 400-mm 8% nondenaturing polyacrylamide gel with 1× TBE. After electrophoresis the gel was covered with Saran Wrap film and autoradiographed for 3 h at 20°C. The autoradiograph was used to localize bands on the gel. Pieces of gel containing bands were excised and transferred into microfuge tubes with 150 μl 2× TE buffer (20 m*M* Tris, pH 7.5, and 2 m*M* EDTA) and left overnight on a shaker (100 rpm) at 20°C. The next morning, after 1 min of centrifugation the supernatant was purified twice on a Sephadex G-50 microcolumn and concentrated to 10 μl by evaporation. The purified bands were subjected to standard SSCP analysis (Orita et al. 1989).

Phylogenic Reconstruction. The maximum parsimony method was used for phylogenetic reconstruction. Variation in band intensity among different species has not been taken into account, and taxonprint bands have been treated as independent binary characters. The programs Mix (Wagner maximal economy), Seqboot, and Consense from the PHYLIP (Version 3.5) package (Felsenstein 1993) were used for inferring the topology of phylogenetic trees. From the VOSTORG package (Zharkikh and Rzhetsky 1990) we used the programs MATDIS and MATTRE for dendrogram construction, followed by modification of tree structure in accordance with given topology and for tree branch length calculation based on the Fitch approach.

Results

Populational Studies

Twenty-nine human DNA samples from six races were tested by the taxonprint approach with five restriction endonucleases (*Msp*I, *Csp6*I, *Taq*I, *Sau*3AI, *Hin*fI). No

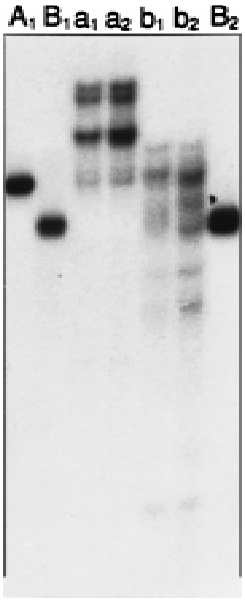


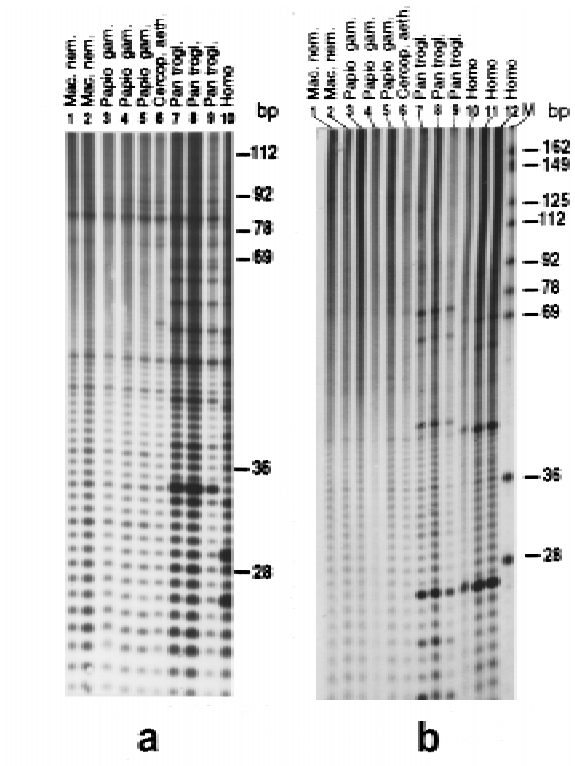
Fig. 1. SSCP analysis of human *Taq*I taxonprint bands. **A, B** Electrophoretically purified double-strand DNA from *Taq*I taxonprint bands of 105 and 123 bp, respectively. **a, b** SSCP analysis of DNA repeats from A and B bands. Analyzed human Negroid and Caucasian DNAs are indexed 1 and 2, respectively.

difference among more than 100 bands of human individuals was found (results not shown).

To examine further the nature of taxonprint bands we applied single-strand conformation polymorphism (SSCP) analysis (Orita et al. 1989). The SSCP study of human genomic DNA digested with restriction endonucleases provided little additional information because of the high background (data not shown). To improve this approach, we purified DNA from individual taxonprint bands and then subjected them to SSCP analysis. We studied DNA from 10 *Taq*I taxonprint bands in the 30- to 110-bp range from Caucasian and Negroid human individuals (Fig. 1). Every taxonprint band tested yielded from 4 to 10 thinner bands on the SSCP gel. As both DNA strands of restriction fragments were labeled, these thinner bands correspond to the detection of two to five subfamilies of DNA repeats in each taxonprint band. No difference in 56 SSCP bands was found between Caucasian and Negroid individuals.

Study of Primates

We examined Old World monkeys from the guenon subgroup, pig-tailed macaque, baboon, and vervet monkey; and from hominoids, chimpanzee and human (Fig. 2). The *Taq*I taxonprint (Fig. 2d) is characterized by multiple bands; approximately half of them are common for all studied primates. Guenon bands on the *Taq*I taxonprint are identical among all studied species in this group, while human and chimpanzee also have bands identical to each others, some of which differ in inten-



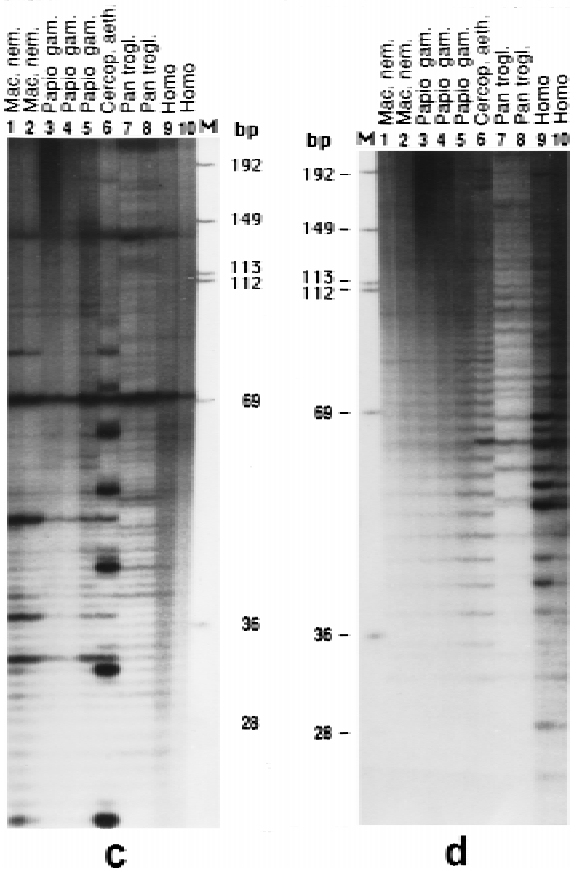


Fig. 2. **(a)** *Hin*fI, **(b)** *Csp*6I, **(c)** *Msp*I, and **(d)** *Taq*I taxonprints of primates.

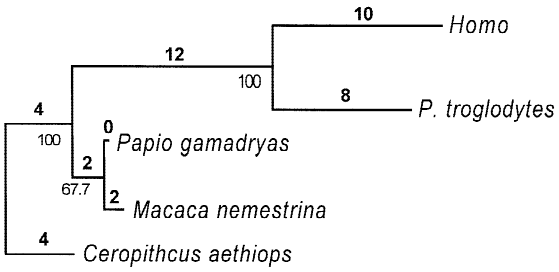


Fig. 3. The phylogenetic relationships among studied primates based upon taxonprint data. The *numbers under the lines* show the percentage bootstrap support at each node. The *numbers above the lines* are genetic distances.

sity. We consider the *Taq*I taxonprint not suitable for phylogenetic analysis since a vast number of bands causes a high possibility of occasional coincidence of nonhomologous bands (see Discussion). On four other taxonprints [*Msp*I, *Sau*3AI (not shown), *Csp*6I, and *Hin*fI restriction endonucleases], there are eight bands common for all studied primates (48- and 82-bp bands on the *Hin*fI taxonprint; 70 and 136 bp on the *Msp*I taxonprint; and 20, 26, 43, and 178 bp on the *Sau*3AI taxonprint). In addition, there are 11 bands identified only in studied hominoids and 2 bands specific only for all studied species from the guenon subgroup (33 and 48 bp on the *Msp*I taxonprint).

In the case of monkeys, the band patterns are mostly similar between macaque and baboon. These species differ only in two bands on the *Msp*I taxonprint (macaque has a unique band at 37 bp, while an 80-bp band is specific for macaque and green monkey only). Two bands are specific only for baboon and macaque (50 and ~300 bp on the *Sau*3AI taxonprint; not shown). The *Msp*I taxonprint is informative for the guenon subgroup, whereas on this taxonprint bands characterizing human and chimpanzee are absent. At the same time the *Hin*fI and *Csp*6I taxonprints are informative for hominoids (there are 10 *Homo*-specific and 7 chimpanzee-specific bands), but monkey-specific bands are not detectable with these restriction enzymes.

Forty-nine bands from four taxonprints (the *Taq*I taxonprint was not considered) were summarized and used as binary characters for reconstructing phylogenetic relationships. The pattern of the inferred tree (Fig. 3) is in complete accordance with the widely accepted phylogeny of primates (Martin 1990).

The nature of the TB has been analyzed by examining nucleotide consensus sequences of DNA repeats of primates' genome. Very intense bands of 70 and 136 bp on the *Msp*I taxonprint (Fig. 2c) and of 178 bp on the *Sau*3AI taxonprint were found for all primates examined. In the summarized consensus sequence of *Alu* repeats (Batzer et al. 1996) we found three *Msp*I sites, at 3–6, 137–140, and 205–208 bp, and two *Sau*3AI sites, at 59–62 and 233–236 bp. Thus, the three bands of 70, 136, and 178 bp shown above to be common to all primates are likely to represent restriction fragments of *Alu* repeats.

Another example of taxonprint band characterization is a tandem deca-satellite repeat, which is dispersed within α-repeats of the green monkey genome (Maresca and Singer 1983). These satellites have an approximate length of 1000 nucleotides and consist of 10-nucleotide-long, tandem repetitive elements with consensus sequence AAACCGGNTC. There is an *Msp*I restriction site (underlined) in approximately half of the characterized core elements. The estimated quantity of this repeat is 10^5. The intensive bands of 12, 22, 32, 42, 52, and 62 bp seen on the green monkey *Msp*I taxonprint (Fig. 2c) are likely to represent the described deca-satellite repeat.

Study of Lacertidae

Using taxonprint approach we studied relationships within lizards of the family Lacertidae. Nine taxonprints [restriction endonucleases *Msp*I, *Hin*fI, *Csp*6I, *Hin*6I, *Taq*I, *Sty*I, *Asu*I, *Tru*9I, (*Eco*RI + *Hind*III)] were obtained for all species (four of them are shown in Figs. 4a–d). In total, 211 taxonprint bands were analyzed. Among these bands there are 14 bands common to all studied lizards. Thirteen bands are common to all representatives of the genera *Lacerta*, *Podarcis*, and *E. velox.* Nineteen bands are common to all *Lacerta* and *Podarcis* (among them, two bands coincide with *O. elegans* bands). Twenty-four bands are specific only for *Podarcis* species. The *L. agilis* group and *L. vivipara* have two common bands. Seven bands are specific only for the *L. agilis* group. Seven bands common to all studied archaeolacertas are revealed. The bands described are specific to particular groups of related species and are remarkable in the sense that all representatives of a group of species have these group-specific bands without exception. So we assume that these specific bands have a common origin and cannot disappear spontaneously from the genome.

Besides group-specific bands, there are many bands unique to a single species or to a few species in a genus. Only between the two species *L. nairensis* and *L. valentini* was no difference found. At the same time, differences in one to three bands between two subspecies of *L. saxicola* (*lindholmi* and *darevskii*), two populations of *L. agilis*, and two populations of *L. raddei* were found. These differences are interpopulational but not intrapopulational.

The phylogenetic tree inferred from the taxonprint data is shown in Fig. 5. High bootstrap indexes and genetic distance values support the existence of three monophyletic clusters among the studied species: (1) genus *Podarcis*, which has diverged from all investigated *Lacerta;* (2) the *L. agilis* group with *L. vivipara;* and (3) Caucasian rocky and forest archaeolacertas. For archaeolacertas divergence patterns moderate bootstrap support was obtained for most branches.

In general, inferred by taxonprint data, phylogenetic

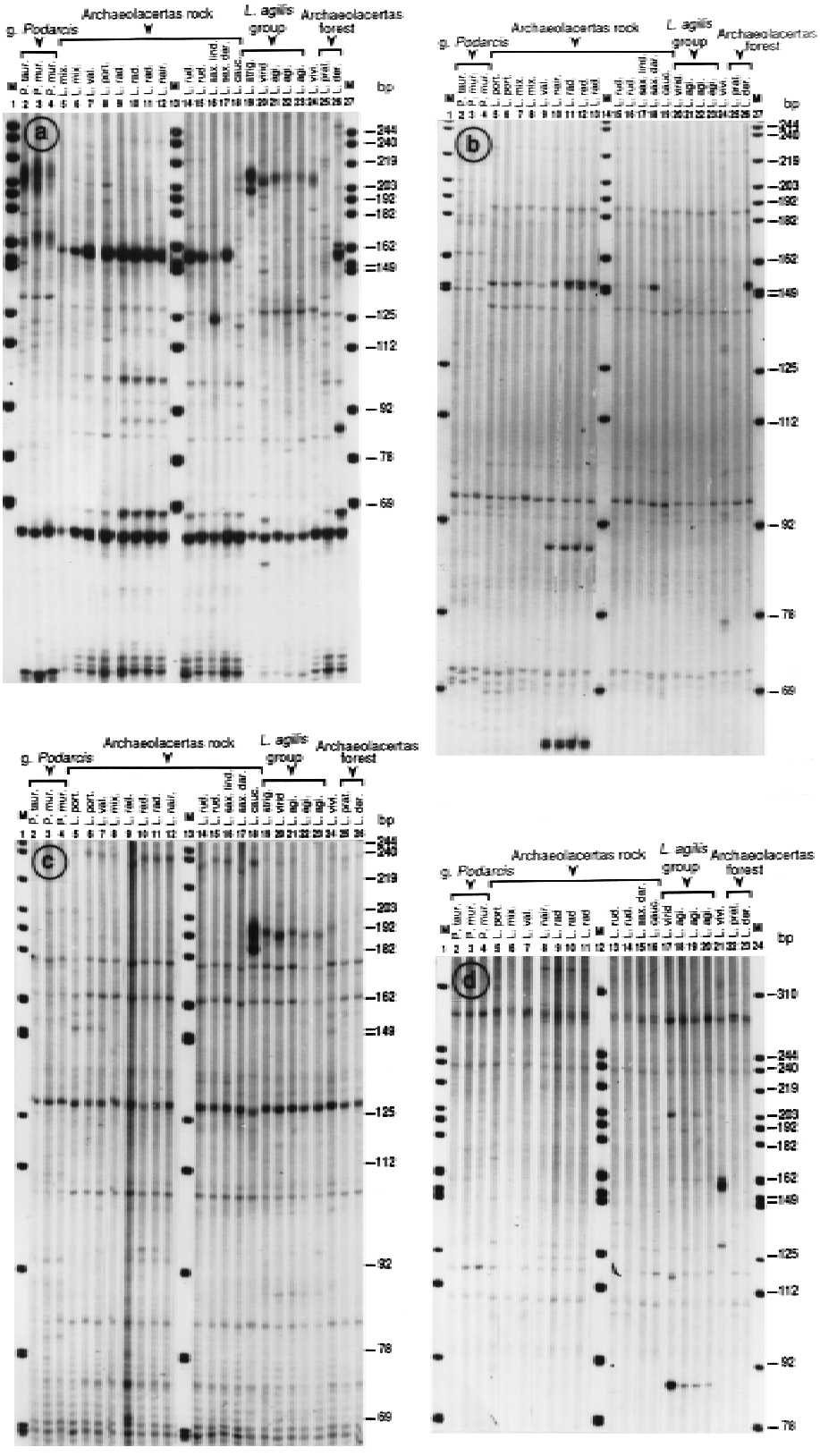


Fig. 4. **(a)** *Taq*I, **(b)** *Csp*6I, **(c)** *Hin*fI, and **(d)** *Sty*I taxonprints of lizards from family Lacertidae.

relationships are in keeping with modern ideas about Lacertidae phylogeny based upon morphological data, with some exceptions. We did not confirm the assumption that genus *Podarcis* is more closely related to the arhaeolacertas group than to the genus *Lacerta* (Arnold 1989). Two subspecies of *L. saxicola* seem to represent two different species. They inhabit remote areas—*L. saxicola lindholmi* is strictly a Crimean lizard and *L.*

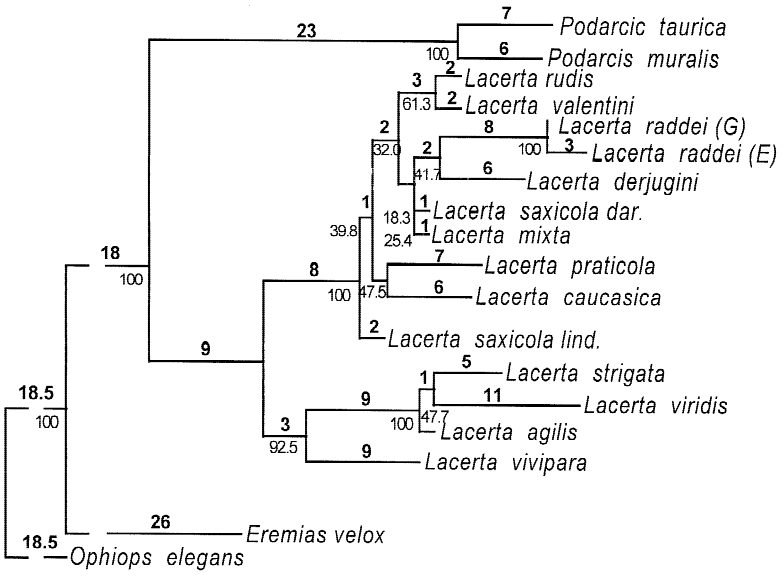


Fig. 5. The phylogenetic relationships among studied lizards based upon taxonprint data. The *numbers under the lines* show the percentage bootstrap support at each node. The *numbers above the lines* are genetic distances.

saxicola darevskii is strictly a Caucasian lizard (Darevsky 1993). The Eghegnadzor population of *L. raddei* has some differences from other populations of this species, which was also confirmed by other biochemical investigations (Bobin et al. 1996). This study demonstrates that the molecular genetic features of taxa, detected by taxonprints, not only correlate well with the current phylogeny, but also allow additional information to be gained.

Discussion

The advantage of using taxonprint analysis for molecular systematics relies on its integral characterization of the genome. The detection of DNA repeats as an electrophoretic band is dependent on the presence of restriction sites at identical positions in many thousands of repeat elements, whereas multiple point mutations in the repetitive elements do not influence the electrophoretic mobility of these restriction fragments. As we demonstrated, TB are identical within any population and, most commonly, within a species (Bannikova et al. 1995, 1996; Grechko et al. 1997). Moreover, SSCP analysis of some of the taxonprint bands showed their fine structure identity within a species.

A hierarchic order of TB organization is frequently seen on a higher taxonomical level: bands can be common for a group of closely related species or common for larger taxa such as genus and family. This hierarchic organization of band patterns reflects a common evolutionary origin of DNA repeats revealed by the taxonprint approach and allows us to consider each TB as a ''character'' for phylogenetic reconstruction (Vogler and DeSalle 1994).

We noted that TB characters have some prominent features. Approximately half of the TB is likely to be conservative and cannot disappear spontaneously from the species genome. Such TB we call ''invariable.'' The inference of invariable TB was based on our data on lizards, primates, hedgehogs, and shrews (Bannikova et al. 1995, 1996). We could not find a TB that was presented in a vast majority of species of a taxon but lacking in one or a few species, which, according to other biological data, cannot be an outgroup for the taxon. For instance, if all studied primates have a particular band, then humans should also have the same band. The existence of such an ''invariable'' group of TB is obvious for dispersed repetitive elements, which cannot disappear or change in the same way in thousands of different loci in the genome. So it is most likely that the TB, represented by dispersed repeats, composes this invariable group. In contrast to invariable bands, there are a large number of species-specific bands unique to a single species. Because of the large proportion of such species-specific bands, it appears that they can rapidly change from one species to another. This observation is in good agreement with the phenomenon of concerted evolution of tandem repeats, according to which DNA repeats are conservative within a species but differ considerably even between closely related species (Dover 1982). Thus, presumably ''variable'' species-specific bands are represented by the fraction of tandem DNA repeats subjected to concerted evolution. Both variable and invariable groups of TB can be helpful for molecular systematics. Variable TB are to be applied as species-specific markers for species identification, whereas invariable bands, with their remarkable stability across groups of related species, are especially useful for the study of phylogenetic relationships within a genus or a family. If characters cannot disappear during evolution, there is no need to carry out statistical analysis as in the case of gene sequence data. Only a few invariable group-specific bands can be successfully used to resolve some phylo-

genetic questions, as has been done, for example, in the study of hedgehogs (Bannikova et al. 1995).

There are objections to the use of restriction fragment data for input to phylogenetic analysis because restriction fragment characters are not independent: ''If a new site evolves between two preexisting sites, one (longer) fragment disappears and two new (shorter) ones appear'' (Swofford et al. 1996). This criticism cannot be applied to taxonprint analysis because there is a crucial difference between the properties of single-copy DNA restriction fragments and restriction fragments of highly repetitive DNA elements. From our data, in the vast majority of cases the appearance of new TB did not change the patterns of preexisting TB, presumably because the arrival of new bands is due to the appearance of new types or subtypes of DNA repeats and not to the appearance of new restriction sites in identical positions in thousands of preexisting repetitive elements. Thus, TB characters, in contrast to restriction fragment characters, for single-copy DNA regions are independent of each other. At the same time TB characters can be linked to each other if there are more than two restriction sites inside a DNA repeat element. The most profound example of such linkage among TB characters is the seven bands specific to vervet monkey on the *Msp*I taxonprint (Fig. 2c). All seven bands presumably originated from the same tandem deca-satellite element with *Msp*I restriction sites inside it (Maresca and Singer 1983). For phylogenetic purposes it is more correct to consider such linked TB as one character, but additional experimental efforts are necessary to determine the linkage. Unconsidered linkage in TB characters should change only the branch length, and not the topology, of the inferred phylogenetic tree.

The question of the homology of the same-size bands from different species is very important. The fact that, among all analyzed closely related species, the portion of bands of the same length is much higher than among more distant species indicates that the large majority of the common bands of closely related species is homologous and is a consequence of the descent relationships. The probability of an occasional coincidence of a band from a species A with any nonhomologous band from a species B [$P_{(A/B)}$] is

$$P_{(A/B)} = N_B/M$$

where N_B is the number of bands of species B on the analyzed gel, and M is the total number of bands which can be resolved on the analyzed gel. Under optimal conditions the resolution capacity for a taxonprint gel is approximately the same as for a sequencing gel. According to our estimations about 300 bands can be resolved by the taxonprint technique. So if, for example, 10 bands are observed for species B, then the value of $P_{A/B} = 10/300 = 0.03$. Hence, to improve the trustworthiness of phylogenetic relationships inferred by the taxonprint approach, it is better to use more restriction endonucleases that give a relatively small number of TB. These nonhomologous TB of different species, which occasionally coincide, produce a random nonsystematic error that has no bias to any particular species group. Under optimal conditions this error is relatively small and should not cause any serious deviations for the inferred tree.

In conclusion, we showed that DNA repeat bands, revealed by taxonprint analysis, can be divided into two groups with different properties. One group (invariable), representing parts of DNA repeats, is unable to disappear or change spontaneously during evolution. The other group of bands represents those that are likely to be highly variable and unique to a particular species or to the closest species. The simple procedure of obtaining a large number of variable and invariable bands on the same picture makes the taxonprint approach useful for routine phylogenetic studies. Our data suggest that taxonprint analysis is most appropriate for the characterization of taxa not larger than a family. When comparing more distant taxa, the proportion of TB common to distant species is low and, as a consequence, the error due to nonhomologous band coincidence is high.

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