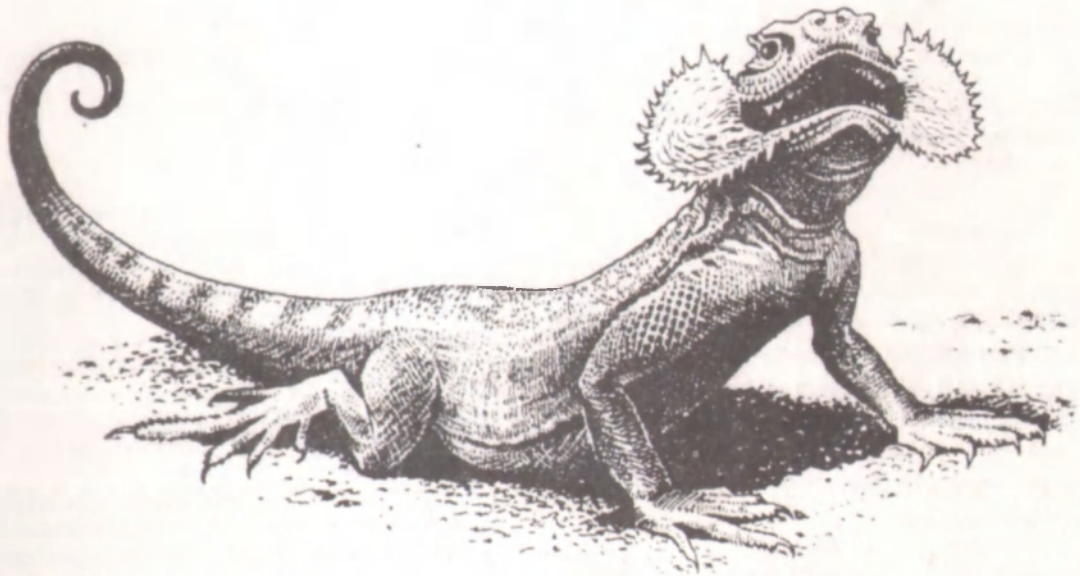


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SOME ASPECTS OF HISTORICAL BIOGEOGRAPHY OF ASIAN ROCK AGAMIDS

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The genesis of areals of Asian rock agamids belonging to the genus *Laudakia* Gray, 1845 is considered. The hypothesis about two routes of radiation of these lizards endemic for arid mountain regions of Palearctic is offered. The southern route from the hypothetical center of origin in the area of mountain systems of Hindukush and Himalayas passed in the conditions of southern subtropics with well developed belt of sclerophilous forests. This evolutionary line with "caucasia" complex remains the relic areas in forest regions. Northern group of species with "himalayana" complex had its speciation in northern subtropic area with more severe climatic situation determined by strong continental and arid conditions. Altitudinal and biotopic differences of *Laudakia* species under their sympatric distribution are specially discussed.

Key words: Reptilia, Sauria, Agamidae, *Laudakia*, Palearctic Asia, systematics, biogeography, distribution, evolution

The Asian rock agamids of the genus *Laudakia* Gray, 1845 includes 16 species distributed in mountain rock landscapes of arid zone from Greece and Nile river delta on the west through Middle East and Central Asia to Gobi Altai on the north-east and Bramaputra river on the east. The mountain ring-tailed agamas belonging to this genus have been considered for a long time as a part of the genus *Agama* Daudin, 1802 (Boulenger 1885; Wermuth 1967). After Moody's revision (1980) they were referred to a distinct genus *Stellio* Laurenti, 1768. The subsequent study of the whole complex of mountain ring-tailed agamas showed that it is a paraphyletic group (Joger and Arano 1987; Ananjeva et al. 1990; Joger 1991). Taking into consideration these data and some nomenclature remarks some authors (Leviton et al. 1992) offer to use the generic name *Laudakia* Gray, 1845 for Asian rock agamids and for Afro-Arabian group of species — the generic name *Acanthocercus* Fitzinger, 1843.

The analysis of phylogenetic relations of *Laudakia* species was accomplished on the basis of both morphological and biochemical data (Joger and Arano 1987; Ananjeva et al. 1990; Anan'eva and Sokolova 1990; Joger 1991). These results are partly contradictory and can be considered only as preliminary ideas. They can not definitely determine the relations within this groups of lizards. The construction of more clear

phylogenetic scheme is impeded by the difficulty obtaining material for genetic analysis for several groups of species and by the obvious existence of parallel trends in different developmental lines within *Laudakia* genus.

We collected data on geographic and biotopic distribution of rock agamas for their discussion in context of notions on the climate and genesis of landscapes and vegetation. A comparison of recent arealographic patterns of the studied species with known data on paleogeography and paleobotany of the region of their distribution may be used as additional method of research for understanding the trends of reptiles radiation (Ananjeva and Tuniyev 1992). It might be especially fruitful for *Laudakia* because of the unique chorological isolation of this genus (Anan'eva and Peters 1990).

We gathered data on geographic and biotopic distribution of *Laudakia caucasia*, *L. chernovi*, *L. erythrogastra*, *L. himalayana*, *L. lehmanni*, *L. stoliczkanana* in 1975 — 1992 during field work in Armenia, Georgia, Dagestan, Turkmenistan, Tadzhikistan, Uzbekistan and Mongolia. We also used all the available published information on the history of landscape formation typical for *Laudakia* areal and biotopical distribution of these lizards in Iran, Afghanistan, Pakistan, Turkey, Greece, Israel, and China.

Asian rock agamids endemic for Palearctic have the distribution looking like a integral unit (Fig. 1, Table 1). Within their diversity we can distinguish at least two complexes of species with a number of morphological and ecological differences: "caucasia"

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complex and "himalayana" complex. The first one includes *L. caucasia*, *L. microlepis*, *L. nuristanica*, *L. tuberculata*, and probably *L. sacra*, *L. lehmanni*, and *L. erythrogastra*. "Himalayana" complex consists of related species *L. himalayana*, *L. chernovi*, *L. badakhshana*, *L. stoliczkana* (Peters 1971; Anan'eva et al. 1981; Anan'eva and Peters 1990). It is possible, that *L. pakistanica* that is most closely related to *L. agrorensis* and *L. melanura* (Baig 1989) can be attributed to this complex. We realize that it is a speculative scheme, and probably future genetic examination will permit to distinguish more groups and complexes of species within *Laudakia*.

It was already noted (Anan'eva and Peters 1990), that long limbs, presence of a small gular sac and nuchal crest, the polyannular structure of the caudal segments, juvenile color patterns should be considered as plesiomorphic characters. But the interpretation of separate morphological characters (including scalation) as indication of species relationships is unacceptable, and we use here such notions on plesiomorphic characters of scalation only in context of arealographic patterns of *Laudakia*. As it was noted above, the parallel trends occur in different developmental lines within *Laudakia* genus, expressed for example in parallel changing of the number of annuli in caudal segments in *L. stellio*, *L. stoliczkana*, and *L. caucasia* (Peters 1971; Anan'eva and Ataev 1984).

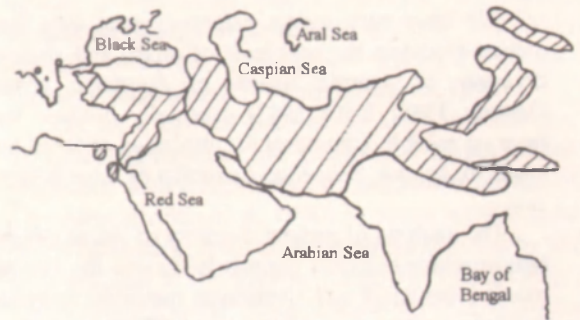


Fig. 1. General distribution of Asiatic rock agamids of *Laudakia* genus in Palearctic.

Despite the absence of clear phylogenetic hypothesis for *Laudakia* all the herpetologists who studied their taxonomy and ecology are unanimous in the opinion, that speciation of these lizards has been connected in the past and at present with Hindukush, Pamir and Himalayas mountains (Peters 1971; Anan'eva et al. 1981; Anan'eva and Peters 1990; Baig 1992). Strong heterogeneity of dissected mountain relief probably promoted the isolation of populations, an ecological differentiation of these lizards is now normally expressed in different altitudinal distribution. In this context it seems to be useful to discuss our hypothesis for geographic distribution of the two complexes of Asian mountain agamas and formation of their contemporary ranges.

TABLE 1. The distribution of the species of *Laudakia* genus.

Species	Distribution
<i>Laudakia agrorensis</i> (Stoliczka 1872)	Afghanistan, Pakistan, India
<i>Laudakia badakhshana</i> (Anderson and Leviton 1969)	Afghanistan
<i>Laudakia caucasia</i> (Eichwald 1831)	Armenia, Georgia, Azerbaijan, Tajikistan, Turkmenistan, Turkey, Iraq, Iran, Afghanistan, Pakistan
<i>Laudakia chernovi</i> (Ananjeva et al. 1981)	Tajikistan, Turkmenistan, Uzbekistan
<i>Laudakia erythrogastra</i> (Nikolskyi 1896)	Iran, Turkmenistan, Afghanistan
<i>Laudakia himalayana</i> (Steindachner 1869)	Tajikistan, Uzbekistan, Kirgizstan, Afghanistan, Pakistan, India
<i>Laudakia lehmanni</i> (Nikolskyi 1896)	Tajikistan, Uzbekistan, Kirgizstan, Turkmenistan, Afghanistan
<i>Laudakia melanura</i> (Blyth 1854)	Iran, Pakistan
<i>Laudakia microlepis</i> (Blanford 1874)	Iran, Pakistan, Afghanistan
<i>Laudakia nupta</i> (De Filippi 1843)	Iraq, Iran, Afghanistan, Pakistan
<i>Laudakia nuristanica</i> (Anderson and Leviton 1969)	Afghanistan, Pakistan
<i>Laudakia sacra</i> (Smith 1935)	Tibet (China)
<i>Laudakia stellio</i> (Linnaeus 1758)	Greece, Southwest Asia, Northern Egypt
<i>Laudakia stoliczkana</i> (Blanford 1875)	Mongolia, China
<i>Laudakia tuberculata</i> (Hardwicke and Gray 1827)	India, Nepal, Afghanistan, Pakistan
<i>Laudakia pakistanica</i> (Baig 1989)	Pakistan

We have very scanty paleontological data that cannot elucidate the problems of origin and ancient diversity of agamid lizards of *Laudakia* genus (Moody 1980; Estes 1983) especially because we have no reliable arguments for allocation of fossil records to *Agama*, *Trapelus*, *Laudakia* or *Acanthocercus*.

The analysis of present diversity of Asian mountain ring-tailed agamas permits to assume the area of recent Hindukush and Himalayas mountain systems to be the center of *Laudakia* origin. Their speciation was influenced by aridization of the southern part of Asian continent and Alpic orogenesis. The allozyme based phylogenetic hypothesis for agamid genus *Phrynocephalus* (Macey et al. 1991, 1992) argues for ancient divergence of agamids of Afro-Asian radiation group including Asian mountain agamas (*Laudakia*). It is possible to think that the first stages of this radiation took place in Miocene on the present territory of Afghanistan, Pakistan, and Tadzhikistan. The patterns of current distribution of *Laudakia* were formed as a result of a number of geological events in Middle East and Central Asia. The established fact concerning the continuous subsistence of mountain belt of arid climate with corresponding subtropical vegetation beginning with the Cretaceous on the territory of ancient Mediterranean geosynclinal is of special importance (Kolakovskii 1974a, 1974b). Theoretically it could serve as a basis for the wide radiation of the ancestor of mountain agamas.

We suggest here the following hypothesis for the radiation of Asian mountain agamas that could occur by two ways. The first route probably passed from the area of the supposed center of origin to the regions of Eastern Pamir from where further radiation round Takla-Makan along the southern periphery of Altai and Tien Shan was possible. The radiation of Asian mountain agamas could go both in the eastern and north-eastern directions to Mongolian Altai and in south-western direction along the northern foot-hills of Central Asian mountains. The use of natural corridors between Altai and Saur-Tar bagatai (Saissan depression area), "Dzhungar Gates" between Tarbagatai and Dzhunggar Alatau (Alakol depression), and Ili river valley between Dzhunggar Alatau and Tien Shan seems to be very probable for this radiation. The fossil records of agamids were found in Zaisan depression and Balkhash lake area (Chkhikvadze et al. 1983).

The second route of radiation of the Asian mountain agamas probably passed round Transhimalayas mountains. Under the conditions of "rainy shade"

there arose acceptable arid areas as distinct from luxuriant tropical vegetation of the Himalayas proper in appropriate for colonization by these arid lizards. Quickly rising and reaching already cold desert conditions Tibet could not serve as a conductor for the radiation of Asian mountain agamas which retain even now the main recently the chorological patterns in subtropical area of Asia, Europe, and northern Africa (*L. stellio*).

We shall consider two complexes of species of *Laudakia* genus in the framework of this hypothesis.

Our observations are based mainly on the field work results in the areas of distribution of *L. caucasia*, *L. himalayana*, *L. chernovi*, *L. lehmanni*, *L. erythrogastra*, *L. stoliczkana*. These observations and ecological data from literature show that species of "caucasia" complex retain (to a certain extent) the tendency to a semiarbooreal mode of life. Unlike "himalayana" complex species these lizards are closely associated in their distribution with xerophilous forests and their derivatives. Thus *L. caucasia* in Caucasus is rather common in the afforested gorges along Kura river (Borzomsky gorge and others), in the oak forests of northern Armenia (Sevkar), in Juniperetum, Pistacio-Juniperetum light forests of eastern Georgia (Vashlovani) and southern and eastern Armenia (Chosrov, Megri district), etc. *L. caucasia* is mostly common in shibliak belt in western Kopet-Dagh, it can reach also Juniperetum and Aceretum forests.

L. erythrogastra can occupy a considerably wide spectrum of biotops, but reaches its highest density of populations in the gorges with *Pistacia vera*.

L. lehmanni is associated in the most of localities with "blackwood" forests of *Platanus orientalis*, *Juglans regia*, and others. It is necessary to note that the arboreal patterns of behavior for *L. caucasia* in Caucasus and Kopet-Dagh and for *L. erythrogastra* in Badkhyz are observed considerably often. But in comparison with these species *L. lehmanni* uses trees and bushes permanently and it can be referred to both petrophilous and semiarbooreal species. All the adult and juvenile specimens of *L. lehmanni* except for gravid females during and just before egg-laying were observed only on the trees (Gissar and Peter the Great mountain ranges). They can climb up to the height of 8 — 15 m on the trees, where they find places for basking, rest and feeding. One male, three-four females, and young specimens were observed in one arboreal microgroup.

Habitats of *L. tuberculata* and *L. nuristanica* are also correlated with typical forest biotops. Hassinger

(cit. after Anderson and Leviton 1969) notes coniferous and evergreen oak forests and moist habitats among the main biotopes for *L. nuristanica*. Baig (1988) also gives a similar information about the habitat of *L. nuristanica* in Pakistan (Ziarat, District Chitral of N.W.F.P.): "wet, temperate, mountain, coniferous forest along a water courses", p. 200. According to Menitskii (1984) the dense oak forests of evergreen *Quercus baloot* and thick underwood of *Fraxinus xanthoxyloides*, *Lonicera nummularifolia*, *Cotoneaster insignis* are typical for the narrow mountain valleys of mountain rivers at the elevations of 1200 — 1700 m in Nuristan. In the higher areas forests are replaced by coniferous forests of *Cedrus deodara*, *Pinus gerardiana*, *Abies webbiana*, *Picea morinda*. In Pakhtia (Kunar province, Gardez region) *Quercus baloot* oak forests are replaced at an elevation above 2200 m by forests of *Cedrus deodara* and more mesophilous oak forests of *Quercus dilitata* and also *Acer turkestanicum*, *Celtis caucasica*, *Juglans regia*, *Pyrus pashia*, etc.

The area *L. tuberculata* is defined by more luxuriant subtropical and temperate forests. Thus in the forests widely distributed from Penjab to Western Nepal evergreen oak *Quercus incana* dominates with its usual satellites *Rhododendron arboreum*, *Mallotus philippiensis*, *Woodfordia fruticosa*, *Rhamnus triquetra*, and *Ilex dipyrrena*.

Unlike "caucasia" complex species of "himalayana" complex inhabit open areas without forests, as a rule, with semidesert vegetation, or herbaceous associations on rocks and screes. *L. chernovi* living in refugia of subtropical vegetation (that permits to suppose its relict origin) prefers open rocks. *L. agrorensis* having most southern distribution inhabits the transitory climatic zone (from Mediterranean to monsoon). The arid semidesert subtropical vegetation is distributed here in the lower and middle belts of mountains (Penjab region of the Himalayas). It is replaced at higher elevations altitudes by scleropholous trees and bushes (Menitskii, 1984). It is interesting to note that the southern distribution of *L. himalayana* is limited by the area of inner dry valleys of western Himalayas. *L. pakistanica* described recently from Gilgit (Pakistan) (Baig 1989) inhabits Gilgit river valley near massif Nangaparbat in the area of disjunction of humid monsoon forests that are distributed to the west in Hindukush and to the east in Himalayas. *L. pakistanica* "was usually found in dry, barren rocky mountains" (Baig 1989, p. 120). In this area deserts and arid open woodlands with *Pistacia*, *Capparis*, *Tamarix* are

typical at elevation below 2000 m, wormwood steppes are typical at elevations of 2000 — 2700 m and arid *Junipereto* — *Querceto* — *Pinetum* light forests are typical above 2700 m (Menitskii 1984).

The most eastern distribution has *L. stoliczkana*. Its preferred biotopes are gorges and slopes of the mountains with screes, crevices and thorny bushes of *Caragana* (Borkin et al. 1990). *L. sacra* according to recent knowledge is restricted in its distribution by the river drainage of the Yarlung Zangbo in Lhasa valley, Tibet (Ananjeva et al. 1990). They were observed only on slopes covered with large boulders at elevations from 3000 to 4000 m. This area referred to *Tibet Australis* district of *Provincia Tibetica* of Central Asian subregion of Mediterranean region (Grubov, 1959) is the warmest region of Tibet. This is a considerably arid region in spite of 500 mm of average annual precipitation. The precipitation is brought by the summer monsoon that enters to the Himalayas from the south and breaks through the valley of Zangpo (Brachmaputra) river from the east. Precipitation is of a stormy nature. The average annual temperature of Lhasa is + 9°C at an altitude of 3650 m. The average winter temperature is slightly below 0°C and the average temperature of the warmest month is only about + 15°C. The climatic situation is characterized also by an absolute maximum of temperature + 30°C and an absolute minimum of temperature - 17°C. Open woodland of xerophilous bushes with dominating *Sophora vicifolia*, *Berberis*, *Lonicera spinosa*, *Ceratostigma griffitii*, *Buddleia tibetica* and precipitation of *Rosa sericea*, *Cotoneaster acutifolia*, *Dasiphora fruticosa*, and *Caragana* species predominate in the vegetation of *L. sacra* biotopes. There is overgrowth of *Juniperus pseudosabina* in the upper belts of mountain slopes (Grubov 1959).

We suggest here our hypothesis for possible distribution ways of two complexes of *Laudakia* taking into consideration their differences in ecology and arealographical patterns associated with climate and vegetation.

Radiation of *Laudakia* probably occurred in two ways under the modifications of landscapes and Asian biotic as a whole. The southern route through outlying districts of recent Tibet and Transhimalayas to the Western Himalayas passed in southern subtropics with a strongly developed belt of sclerophilous forests. The relative aridity and the annual amplitude of temperatures were different from these indexes of tropical belt, but they were important for the development of thermophilous and hemixerophilous flora and

fauna. At the same time the northern route of radiation passed in the area of northern subtropics of Kun Lun and Tien Shan with more severe arid and continental climatic conditions. Probably the speciation of Asian mountain agamas could be divided into two trends correlated with environmental conditions. The southern group of the diverse "caucasia" complex retained the relict areas in the forest belt of western Himalayas and Hindukush, and the northern group of species of the "himalayana" complex developed in the conditions of increasing aridization.

The active adaptive radiation could occur probably on the border of Miocene and Pliocene, and later in Pliocene. Pliocene was the time of raising of mountains and orogenic movements of "block-type", i.e., different parts of mountains raised irregularly (Gvozdetskii and Mikhailov 1987). Ecological conditions had different trends of changing during this orogenesis. Species of "caucasia" complex were preserved in the least modified forest conditions of subtropical climate and phytolandscapes. Species of "himalayana" complex distributed in Pamir and Hindukush probably extended their areas under increasing aridization further to the south right up to the interior regions of Kashmir. The numerous disjunctions of formerly continuous areas of species belonging to both complexes took place probably also in Pliocene. The rapid raising of Tibet determined the conditions of a cold desert that could not be suitable for the radiation of mountain agamas. An exception in this area is the warmer Lhasa valley and maybe some refugia of Kun Lun that have different microclimatic conditions. It seems that the glaciation and rapid raising of mountains made impossible the survival of these lizards in the Eastern Pamir and in most high parts of the Central Tien Shan.

The vertical segregation of the species might have been important for evolution of "himalayana" complex in Pliocene. *L. chernovi* was probably common in the belt of deciduous and shibliak vegetation, and *L. himalayana* was distributed in open meadow and rock biotopes above the forest belt. The mountain raising in Central Asia separated the species of "himalayana" complex to a number of populations that must have been important for the speciation of *L. stoliczkana* and probably of another species.

Pliocene was also an important period for the species of "caucasia" complex. At that time Iranian plateau and other high plateaus of South-Western Asia that arised at the site of the Sarmat Sea became a new center of speciation in xerophilous fauna and flora.

We can suppose that it was the time of the widest distribution of polymorphic species *L. caucasia*. According to the general idea of "forest" development of "caucasia" group the populations from the north of Suleiman mountains, (the southern slope of Hindukush) are likely to be the most ancient. This area presents also the limit of the Asian summer monsoon influence and development of evergreen oak forests. The taxonomic status of these populations and *L. caucasia* from southern Tadzhikistan and regions adjacent to Afghanistan (where *L. reticulata* (*Agama reticulata* Chernov, 1935) was discovered) and Southern Afghanistan — Western Pakistan (between Kandagar and Quetta) is of special interest for following research. The origin of *L. caucasia* distributed from Turkmen — Khorassan mountains to Transcaucasus seems to be more recent. Probably in Pliocene *L. caucasia* reached the northern slope of Great Caucasus. The South-Eastern part of Iranian high plateau might be considered as the place of formation of *L. microlepis* in this period. The problem of relationships of this species (or subspecies *L. c. microlepis*) needs further examination (Anan'eva and Ataev 1984). Further dispersion of the species of *L. caucasia* complex both to the west and to the east was possibly stopped by climatic situation and probably by competition with other related species: *L. nupta* in the southern regions of Iranian high plateau and *L. melanura* on the east. *L. caucasia* occupied at that time the widest area including not only the majority of the Eastern Kopet-Dagh, all the Central and the Western Kopet-Dagh, but also reached Lesser and Bigger Balkhan mountains on the North-West of Turkmenistan along the canyons of small rivers from Kopet-Dagh to the coast of the ancient Amu-Darya river flowing at that time into Caspian Sea. It reached also the regions of upland of Kjujuki and Meshed-Messerian inclined plain on the south-west along the incised valley of Atrek river. It's interesting to note, that now a similar dispersion of *L. caucasia* along the steep banks of rivers to the plains in the Eastern Transcaucasus and in the South-Western Kopet-Dagh in Sumbar river valley (Makeev 1985) is observed.

We would like to discuss the possible ways of the formation of *L. erythrogastra* areal. If we share the view that *L. erythrogastra* and *L. melanura* are related species it is possible to propose the way of penetration of their ancestors from the south of Iranian high plateau. This way could pass along the depressions of Mash-kef, Sabari, Dagi-Tundi, Namaksar to the basin of Geri-Rud (Tejen) river. *L. erythrogastra* dispersed

to the east and to the west from this area to Meshed, on the south to the regions of Kopet-Dagh, Badkhyz, Karabil and to Central Hindukush along its northern foot-hills. It inhabited the biotopes that were not occupied by *L. caucasia*, a species with similar ecological requirements. In rare cases of sympatry of *L. caucasia* and *L. erythrogastra* they have altitudinal differences: biotopes more xerophilous and thermophilous *L. erythrogastra* are characterized everywhere by lower hypsometric indexes. This is also typical for *L. nupta*, *L. melanura*, *L. stellio*. On the northern slope of Eastern Kopet-Dagh *L. erythrogastra* inhabits the elevations of 600 — 900 m and *L. caucasia* inhabits the biotopes at the elevations 800 — 1500 m. According to Anderson's (1968) data, on the southern slope of Eastern Kopet-Dagh the elevations of 800 — 1600 m are typical for *L. erythrogastra* and 960 — 2575 m are typical for *L. caucasia*. In the area of sympatry in Hindukush *L. erythrogastra* is distributed at an elevation of 915 — 2440 m (Anderson and Leviton 1969) and *L. caucasia* has a higher altitudinal distribution — 2440 — 2745 (Clark et al. 1969; Anderson and Leviton 1969; Leviton and Anderson 1970). *L. erythrogastra* penetrated into the northern slope of Kopet-Dagh (Tuniev et al. 1991) probably in Pliocene by the Tejen river valley. A distinct subspecies, *L. e. nurgeldievi* is known from some localities between the Chaacha and Layensuv rivers (Tuniyev et al. in press). *L. erythrogastra* is petrophilous lizard, but it inhabits areas with burrows of rodents normally used as shelters. That was also noted for *L. stellio* (Clark and Clark 1973).

Quaternary period was characterized over the whole Euroasiatic continent by the global alteration of climate and landscapes connected with Pleistocene glaciations on the north of the continent and its mountain regions and periods of hot arid climate during interglacial periods and Postglacial epoch. It was Pleistocene that probably determined the current patterns of distribution of Asian mountain agamas.

It seems possible to assume the trends of speciation in "*himalayana*" complex during this time. The area of *L. himalayana* desintegrated into a number of populations isolated by high mountain ranges (5000 — 7000 m elevation) of Gissaro-Darvaz, Western Pamir, etc. This Pleistocene isolation seems to be a definite factor of speciation for such species as *L. pakistanica* or *L. badakhshara*.

In Pleistocene the refugia of subtropical microclimate were reduced to small territories on the western outskirts of Pamir-Altai mountains; in all the other parts of this mountain system the subtropics totally

disappeared. As a result three localities of *L. chernovi* were preserve: 1. Tupolang river valley on the southern slope of Gissar mountain range (Uzbekistan) at an elevation of 800 — 1000 m; 2. Surkhu ridge (Tadjikistan) — elevation of 900 — 1400 m, and 3. on the crest of the southern part of Kugi-Tang mountain ridge (the border between Turkmenistan and Uzbekistan) — elevation of 2400 — 3000 m (Ataev 1985; Khabibulov 1990). It is important to note the increase of hypsometric marks of biotops of *L. chernovi* in the southern direction from Tupolang to Kugi-Tang. It is a result of both Holocene altitudinal displacement of vegetation upwards along the slopes and of the general recent alterations of temperature and solar radiation in the southern direction. This regularity is observed for most mountain Asian agamas with relatively extensive areals. The altitudinal displacements of biotopes of *L. erythrogastra* from the northern slope of Eastern Kopet-Dagh to Hindukush was already noted. The altitudinal differences in biotops was noted also for *L. caucasia*: elevation of 600 m in the north of its range (Great Caucasus, Dagestan) to 1000 m on the north of Lesser Caucasus (Georgia, gorge in the middle stream of Kura river); 900 — 2000 m in Armenian highland; 950 — 2575 m in Kopet-Dagh (Ataev 1985; Anderson 1968) and 2745 m in South-Eastern limit of the *L. caucasia* distribution in Hindukush (Leviton and Anderson 1970).

L. himalayana inhabits the elevations of 2400 — 2600 m in the Big offspur of Gissar range, the elevation of 3200 m in Western Pamir (Vanch river valley near glacier of Russian Geographical Society) and the elevations above 3500 m in Southern Pamir.

Pleistocene fluctuation of the Caspian Sea modified the primary distribution of *L. caucasia* along Western and Eastern seashores. The maximal transgression of the Caspian Sea flooded Kura-Araks river lowland and the littoral part of Dagestan in the Caucasian part of the areal of *L. caucasia*. As a result some populations of this species were isolated. In Central Asian part of its range the flow of Amu-Darya river was turned to the north to Aral Sea. Accelerated process of aridization divided the continuous areal of *L. caucasia* into several isolated populations inhabiting Krasnovodsk plateau, Bigger Balkhan, Lesser Balkhan and Western Kopet-Dagh. Khvalyn transgression of Caspian Sea flooded most of the territory of Transcaspian plain including the western part of Meshed sands and residual — mountain Kyuyuki. Its overthrust sheet was later covered additionally by the drift of deposits of the Atrek river (Durdyev 1969).

Only the eastern part of Meshed sands remained, as an island not flooded during all the period. *L. caucasia triannulata* was speciated just in this unique landscape. Meshed sands with the capacity of 25 — 350 m (Durdyev 1969) extends for 50 km from north to south and for 20 — 25 km from west to east (Kalenov 1973). The development of the ravine system in this area is of special interest. This unique phenomenon is absent in all other sandy deserts of Turkmenistan. On the east of Meshed massif a stratum of non stratified Meshed formation was distinguished. Its sands have a more prominent thickness in comparison with the sands of diagonal stratification of Meshed formation. They are characterized by more intensive development of ravine system and by the absence of bush vegetation.

According to Kalenov (1973) Meshed sands are distributed in subtropical region with the average annual temperature of +16.3°C; the average January temperature +4.3°C and the average temperature of the warmest month is +28°C. The absolute maximum of the temperature in this area is +47°C and absolute minimum of the temperature is -23°C. Frost-free period lasts 236 days and annual precipitation is 236 mm.

A special character of sandy substrat in Meshed massif, i.e., fain-grained texture and presence of compressing sandy-clayey crust determine the original composition of plant association (Kalenov 1973). *Haloxylon persicum*, *Haloxylon aphyllum*, *Ephedra strobilacea*, and *Ammodendron conolnyi* which are usually very common in Central Asian sandy deserts are absent within Meshed massif. This is the only sandy massif in Central Asian deserts where the species of *Artemisia* genus absent (Kalenov 1973). *L. c. triannulata* as the subspecies of normally petrophilous species has an interesting biotopical displacement in this area. It inhabits here the holes in the walls of ravines the soils of which are much softer than the rocky soils in the biotopes of *L. caucasia* in other parts of its range. It is possible to suppose a correlation between this factor and subtropical microclimate conditions with the increasing of size of *L. c. triannulata* specimens. It is interesting to note, that Meshed sands also preserved another typical mountain species of reptiles — *Vipera lebetina* (S. Shammakov's personal communication) that is absent in all other sandy desert of Middle Asia.

The Pleistocene fall of temperature in the mountains and increasing aridization prevented the survival of mountain agamas in central part of Iranian high pla-

teau. Their absence is the general regularity for all interior plateaus in the southern part of Asia. For example, they are absent in the lesser territories of Anatolian and Kars plateaus although their northern and eastern outlying districts are inhabited by *L. caucasia*, and *L. stellio* lives on their southern outlying districts. It is also possibly can be explained by the screening effect of the marginal mountain ranges along all the asiatic mountain belt of the Alpic folding.

The survival of *L. sacra* during Pleistocene can be explained also by the climatic peculiarities of the Lhasa valley. The average temperature in this area is even more high than in the adjacent subtropical region of Sichuan at the same latitude. Being measured at the same elevation the average July temperature of Lhasa is by 10°C and the average January temperature is by 14°C exceed the average temperatures in Chunzin city on the eastern outskirts of Sichuan depression (Le Kai Fu 1957).

L. nupta and *L. melanura* which taxonomical position is debatable till now are distributed now along the southern periphery of Iranian high plateau: *L. nupta* is found in Zagross mountains and *L. melanura* is found along the eastern piedmonds of Iranian high plateau to the south of Hindukush.

The wide Euroasian distribution of *L. stellio* is of special interest. It is distributed in Thessaloniki, Corfu, Cyclades (Mykonos, Delos, Paros, Antiparos, Naxos) across the shores of Asia Minor and islands of Turkey to Syria, Northern Iraq, Lebanon, Israel, lower Egypt and Iordania. European distribution has *L. s. stellio* (Mykonos-Archipelago) and *L. s. daani* (Paros-Archipelago, Thessaloniki and its region). Several Asiatic subspecies inhabit Cyprus (*L. s. cypriaca*), Egypt (*L. s. vulgaris*), some areas in Sinai, Negev, Transjordan, Arabia (*L. s. brachydactyla*), islands of Asia Minor and some area in the Middle East (Israel, Iraq) — *L. s. daani* (Beutler 1981; Levinton et al. 1992).

On the basis of current configuration of *L. stellio* areal its dispersion along the eastern shore of Mediterranean Sea could be supposed quite easily. However it is necessary to take into consideration the distribution of nominative subspecies in most part of Euroasian area of *L. stellio*, the presence of *L. s. brachydactylus* on the south-east of the range and the absence of *L. stellio* in Cyprus, Crete, Rhodos and Karpatos. We can make an attempt to explain these facts on the basis of new hypothesis of the geological history of Mediterranean area. The abyssal drilling of research ship "Glomar Challenger" has made a sensa-

tional discovery. It showed that 2-km stratum on the bed of Mediterranean Sea was build by the evaporate deposits which were formed owing to the evaporation of water on salty shallows. These are rock salts in the deepest parts of Mediterranean Sea. The gradually less and less soluble substances (i.e., gypsum, anhydrite, dolomite) were formed in the bordering and less deep parts of the sea bed (Monin 1977). Geological age of low and upper limits of this stratum (so called "Reflector M") was estimated as 6 and 5.5 millions years. The most natural hypothesis of the origin of evaporate stratum is the total drying of the Mediterranean Sea in Miocene due to the closing of the straight of Gibraltar. It is possible to suppose that it took only about 1 thousand years for the formation of this stratum of evaporate deposits. At that time the Mediterranean Sea became a vast basin of 2 — 3 km depth with shallow intermittent salty lakes on its bottom. The concretions of anhydrite formed in columnar sections of the drilling were formed under these conditions of drying of the Mediterranean Sea. They can usually arise from the solution only at the temperature above 35°C. Above and under the evaporate deposits and between their layers the usual abyssal oceanic sediments were found. During the periods of the drying of the Mediterranean Sea (hypothetically there were two such periods) the release of the sea bed from the water weight occurred. It resulted in isostatic lifting of sea bed at least by several hundred meters. The deep canyons should come through steep slopes of the sea bed by the rivers flowing from the continent. One of such canyons several hundred meters deep was found under the present delta of the Rhone river. It was traced for 240 km from the delta along the continental slope. The canyon is filled by the sediments of the geological age earlier than lower Pliocene. Another analogous canyon with the length of more than 1200 km was found under the Nile river bed by geologist I. S. Chumakov who offered to explain its formation by the upper Miocene lowering of the level of the Mediterranean Sea for 1 — 1.5 m (the so called Pontian regression). Similar explanation was expressed earlier by geologists of "Oasis Oil" Company for the upper Miocene canyons in Libya, but this idea seemed to be too fantastic. Nowadays, upper Miocene canyons are found practically everywhere around the Mediterranean Sea.

The radiation of *L. stellio* could pass directly from the Near East to the south of Asia Minor (Anatolia) and further to Aegean land along hot canyons under continental connections of the north of Africa with the south of Europe. It was promoted also by climatic con-

ditions established in Europe after the drainage of the Mediterranean Sea. On the contrary after the final filling of the Mediterranean Sea at the beginning of Pliocene the European climate become humid and cool again. These climatic modifications increased until the development of glacial periods in Pleistocene (Monin 1977).

The problem of the genesis of Asian mountain agamas can be supplemented by the data on their sympatric distribution. It is known that *Laudakia* genus contains both species with wide distribution and with restricted areal (*L. chernovi*, *L. nuristanica*, *L. pakistanica*), and only limited overlapping of their ranges is typical (Anan'eva et al. 1981). No more than two species of *Laudakia* may be occasionally found sympatrically in the Asian arid mountains. It is necessary to note, that as many as three species of Asian agamids of *Phrynocephalus* genus (Macey et al. 1991, 1992) may be sympatric. They represent the members of separate clades in the rare cases of sympatric distribution. The limited number of sympatric agamids, especially Asian mountain agamas of *Laudakia* genus seems to be correlated with the strong territoriality of the lizards of this family.

Among sympatric species of *Laudakia* altitudinal and habitat partitioning was revealed. A sympatric couple of species: *L. chernovi* — *L. lehmanni* can be considered in details. These species belonging to different complexes of species were found sympatrically in type locality of *L. chernovi* in Tadjikistan (mountain range Surkh-Ku, near Nurek town). In these mountains *L. chernovi* prefers biotopes at an elevation of 900 — 1400 m: steep slopes and boulders of grey red sandstone massifs with numerous crevices. *L. lehmanni*, as was already noted above, is a semiar-boreal species. It inhabits gardens and bushes in ravines and plane terraces in the foothills. We have found sympatrically in the same altitudinal belt both these species of *Laudakia* having a spatial partitioning. We had the possibility to observe the same couple of species in another part of their areal — in the Tupolang river valley on the southern slope of Gissar mountain range. *L. lehmanni* inhabits the elevations of 500 — 900 m and *L. chernovi* inhabits the elevations 800 — 1000 m. Besides these altitudinal differences these species also have biotopical differences: *L. lehmanni* prefers forested parts of deciduous forests and bushes (*Ampelopsis vitifolia*) on shingly terraces. *L. chernovi* lives on the open rocks near the river. Both species were observed side by side in the ecotopes of these biotops. These species are sympatric also in

Kugitang-Tau mountain range (Eastern Turkmenistan). The vertical zoning of this mountain range is clearly expressed (Ataev 1985; Khabibulov 1990). *L. lehmanni* was found here on the elevations of 800 — 1200 m, the upper mark of its distribution is 2600 m. This semiarborescent lizard quite often penetrates to the plain along separate rocky chains. *L. chernovi* in Kugitang-Tau inhabits exceptionally the ridge of the mountain range in the elevation 2700 — 2800 m. It is proved to be a typical petrobiont, preferring bare rocks without vegetation on the edge of eastern scarp. It was observed on the highest middle part of the mountain range, which is the highest, along the upper cornices of the gorge walls near their sources. Khabibulov (1990) determined it as one of the most stenotopic species of lizards in this region. Altitudinal preference of high elevation is typical for *L. chernovi* from Kugitang-Tau (Ataev 1985; Khabibulov 1990) as for the agamas from Baisun-Tau in Uzbekistan. As it was noted above, the populations from Nurek and Tupolang areas inhabit lower vertical belts. It is explained by the landscape and climatic differences in these parts of areal. The reasons of this ecological displacement were considered above. The altitudinal displacement is usual for *Laudakia* species with extensive areals. It relates also to *L. stellio* that shows vertical differences in Turkey (1200 m), Cyprus (1600 m), Lebanon (2000 m). It was found at the Hermon foothills at an elevation of 1650 (Werner and Avital 1980).

With regard to *L. chernovi* Khabibulov (1990) supposed that as far as the relative humidity of the air on the external mountain ranges of this mountain system in the area of the ridge is reduced in comparison with the middle mountains and is close in humidity to the low-mountain regions of interior mountain ranges it can determine strong differences of the altitudinal preferences of lizards from the populations of Kugitang-Tau and Baisun-Tau (high elevations) and southern Gissar and Surkh-Ku (low elevations). Humidity really can be important as a limiting factor for the distribution of arid reptiles. It is especially significant for *L. chernovi* preferring low indexes of the moistening coefficient typical for the regions of interior mountain ranges of Pamir.

Very few data on sympatric distribution of *Laudakia* species and on their altitudinal and biotopical preferences are available. According to Anderson and Leviton's (1969) data *L. lehmanni* and *L. himalayana* are sympatric at an elevation of 457 m near Mazar-i-Sharif in Hindukush. In Paghman area (An-

derson and Laviton 1969) on the southern slope of Hindukush *L. erythrogastra* inhabits the belt up to an elevation of 2440 m, and *L. caucasia* and *L. badakhshana* are distributed at higher elevations up to 2600 — 2650 m.

The case of sympatric distribution of related species from the same complex: *L. chernovi* and *L. himalayana* is of special interest. This information was received from *L. chernovi* specimen 11421 stored in Dresden museum fur Naturkunde. This specimen was collected by German Alpinist G.Schöne in 1974 on Matcha river (upper part of Zeravshan river) near Khudgif village. This collector noted also sympatric *L. himalayana* in the same place. The examination of this specimen and also of another specimen 8513 (Dresden museum fur naturkunde) collected on Kshtut river, Gissar mountain range, elevation of 2900 — 3500 m, show that these *L. chernovi* specimens do not demonstrate such strong differences in scalation with *L. himalayana* as *L. chernovi* from *terra typica* (Anan'eva et al. 1981). This fact of sympatric record of *L. chernovi* and *L. himalayana* seems to be an additional argument for their specific distinctivity.

Another couple of sympatric species: *L. caucasia* and *L. erythrogastra* presumably belongs to one "caucasia" complex. The data on altitudinal preferences of these species were already considered above. In rare cases of their sympatry (for example in Charchinian gorge in the Eastern Kopet-Dagh) these lizards have biotopical differences: *L. caucasia* inhabits steep slopes of canyons and *L. erythrogastra* occupies the gently sloping of hills in the gate of gorge and above the rocks. The conclusion about the possibility of sympatric occurrence of no more than two species in the same altitudinal belt seems to be possible. Normally they belong to different complexes and have microbiotopic differences. The sympatric species of the same complex usually have not only biotopical but also altitudinal differences.

The problem of sympatry of related species from the same complex of *Laudakia* is correlated with ideas of hybridization and hybridogenous origin of some forms of mountain agamas. Panov et al. (1987) expressed interesting hypothesis for hybridogenous origin of the western group of populations of *L. caucasia* in Turkmenistan. They supposed that this area may be considered as the zone of secondary intergradation. Two hypothesis are discussed in this context: a) these populations are a result of *L. caucasia* and *L. c. trianulata* hybridization or b) these populations and also

"triannulata" form are a result of hybridization of *L. caucasia* and *L. microlepis*. Zykova and Panov (1990) were also the authors of a hypothesis for hybridogenous nature of some individuals in sympatric area of *L. caucasia* and *L. erythrogastra*. They suggested that the type specimen of *Laudakia (Agama) erythrogastra pallida* Nikolsky, 1897 considered should be as hybrid from sympatric zone. These ideas about hybridogenous origin of some forms of *Laudakia* may be useful also in elucidation of some debatable problems of taxonomy in "himalayana" complex. This concerns the form *Laudakia (Stellio) bochariensis* Nikolsky, 1899 that was reduced to synonyms of *L. himalayana* by Chernov (1959). This form has a number of characters intermediate for *L. himalayana* and *L. chernovi* that can be treated as an argument for hybridogenous origin of some forms of *Laudakia*.

The hypothesis for *Laudakia* radiation and their arealographic patterns can be modified and corrected after new records and results of using of new methods in taxonomy. One might expect new records and descriptions of new forms from unexplored high mountain areas of Afghanistan, Iran, Western China, and Northern India. The proposed shame of radiation of mountain Asian agamas is typical for speciation in mountain regions. Such type of speciations resulting in polytypic genus (or supergenus) was described before for *Archaeolacerta* from Caucasus and Asia Minor (Darevskii 1967) and Euro-Siberian viperid snakes of *Vipera kaznakovi* complex from Great and Small Caucasus (Orlov and Tuniev 1986).

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