

Historical Biogeography of the *Phrynocephalus* Species of the USSR

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Abstract. -There are 22 species and subspecies of *Phrynocephalus* in the USSR. Some species inhabit sandy deserts, while others occur in hard soil and gravel deserts. Speciation and present day distributions are a result of geologic events such as mountain building causing the isolation of valleys and basins and changes in the direction of river courses.

Key words: Reptilia, Sauria, Agamidae, *Phrynocephalus*, Armenia, Azerbaijan, Kazakhstan, Kirgizistan, Russia, Tadzhikistan, Turkmenistan, Uzbekistan, USSR, biogeography, distribution, evolution.

Introduction

The reconstruction of the genesis of *Phrynocephalus* species can not be based on the paleontological evidence since data in this field are extremely poor. The only fossil locality is from the Pliocene of Turkey (Zerova and Chkhikvadze, 1984). However, a comparison of recent arealographic patterns of species studied with known ideas about the historical geography and paleogeography of the region where the species occur may be used as one method of research. The data about climate and the genesis of landscapes and vegetation are of great importance.

According to recent ideas, 22 species and subspecies of the genus *Phrynocephalus* live in the USSR (Bannikov et al., 1977; Borkin and Darevsky, 1987). We use here the last list and do not try to reflect more recent and often opposing ideas about *Phrynocephalus* taxonomy (Golubev, 1989a, 1989b; Mezherin and Golubev, 1989; Semenov, 1987; Semenov and Dunayev, 1989; Semenov and Shenbrot, 1982, 1990; Shenbrot and Semenov, 1987), and about the status of some populations, subspecies, and species. This paper does not consider problematic nomenclature problems that need special research. We try here to understand the present complicated distribution of *Phrynocephalus* in the USSR. This includes their disjunct populations. We also try to explain the

possible ways of the development and formation of the distributions of different forms independently from the disagreement on the opinion about their taxonomic status. We discuss here the information about the ranges of these lizards and although the status of some of them may be problematic, this does not so strongly influence our speculations about historical biogeography. Most *Phrynocephalus* species inhabit Middle Asia and Kazakhstan territories. Only a few species penetrate to the eastern part of the northern Caucasus and eastern Transcaucasia. *Phrynocephalus versicolor kulagini* extends to the southern regions of Tuva Autonomous Republic, Russia (Fig. 1).

Discussion

As is well known, it is impossible to understand the history of the fauna without knowing the history of the flora and climatic and geological evolution. The history of the flora in the Caspian region is known from the Upper Cretaceous-Paleogene (Korovin, 1961) when the Tethys transgression flooded most of Middle Asia and central Kazakhstan. In this region a continental regime was retained only in the Tien Shan area and in the eastern part of the Kazakh hummock topography (Gvozdezky and Mikhailov, 1987), (Fig. 1). At that time the Central Asian land already had an arid regime (Agakhanyanz, 1981). The middle of the Gobi was probably real desert surrounded by steppe landscapes (Serebrovsky, 1936).



FIG. 1. Sea basin and land (hatched) in Middle Asia and Kazakhstan in Upper Eocene - beginning of the Oligocene. 1- the Lower Cretaceous records of plants in Er-Oliian-Duz Depression (Serebrovsky, 1936); 2- Eocene - Oligocene records of reptiles and amphibians in Zaissan Depression (Bakradze and Chkhikvadze, 1988).

A warm tropical and subtropical climate, humid, but from time to time with seasonal aridity and probably with seasonal falls of temperature, was dominant on the continental parts of Middle Asia (Gvozdezky and Mikhailov, 1987).

It may have promoted the growth of such species as *Taxodium distichum*, *Populus balsamifera*, *Juglans acuminata*, *Fagus antiposii*, *Liquidambar europaeum*, *Diospiros sp.*, *Ginkgo biloba*, and *Liriodendron tulipifera*. The analogous flora was distributed throughout all of the Siberian territory (Serebrovsky 1936).

Luxuriant thermophilous flora of Middle Asia was accompanied by a highly rich and diverse fauna of the Late Cretaceous such as salamanders and frogs from the families Scapherpetontidae, Batrachosauroidae, Prosirenidae and Pelobatidae (Bakradze and Chliikvadze, 1988). Lizards of the families Parasaniwidae, Teiidae, Anguidae, Agamidae, Saniwidae, Gekkonidae, and Varanidae were also present (Nesov, 1981a, 1981b).

From data about the Cretaceous flora in southern Middle Asia, we hypothesize the presence of a more dry and hot climate

(Korovin, 1961).

The Lower Tertiary findings in the Er-Oilan-Duz Depression in Badkhyz contains *Dryandra schrenkii*, *Celastrorhynchus turcomenicus* and other typical xerophilous plants which also indicates adaptation of these plants to the survival during the hot and dry periods during the vegetation period (Serebrovsky, 1936), (Fig. 1).

From the Eocene fossils of the family Agamidae were found in some localities in Kazakhstan including the Zaisan Basin (Bakradze and Chkhikvadze, 1988).

In the Oligocene the sea retreated and the formation of a continental landscape began. However, the development of relief took place in different ways. In the Kara-Kum and Kyzil-Kum deserts and the Ustyurt Plateau, anticlinal and synclinal structures were formed in the Neogene. In spite of their platformal type of structure, they are sufficiently sharp with an angle of declination of more than 10°. The Turgai Plateau and western Betpak-Dala were slightly touched by the most recent orogenic movements on these small territories. This not only resulted in the formation of different geomorphological structures which will be discussed below, but also in the difference of the amplitude of the raising and sinking of whole territorial divisions. These differences in the amplitude of movements have resulted in the isolation and formation of the specific relief in each of the plains in Middle Asia (Voskresensky, 1968).

In the middle Oligocene there was a sharp change in the composition of the herpetofauna of the Zaisan Depression. The early Oligocene giant salamanders (*Zaisanurus*), giant snakes (Boidae), Glyptosaurinae, etc. were replaced by amphibians of the families Pelobabidae, Ranidae, and Bufonidae and by boids of the genus *Bransaterix* (Bakradze and Chkhikvadze, 1988).

The formation of two centers of speciation of the genus *Phrynocephalus* probably began on the boundary of the

Paleogene-Neogene time in arid regions of Central Asia and in the southern part of Middle Asia (Fig. 2). Until middle or late Pliocene the herpetofauna of Central Asia and Turan represented, more or less, a single unit (Chkhikvadze et al., 1983). The independent formation of Central Asian and Middle Asian centers of different fauna began readily after their separation by mountain structures of Alpic orogenesis (Ananjeva, 1986; Chernov, 1959; Geptner, 1938; Peters, 1984).

In discussing the center of origin of the genus *Phrynocephalus*, Moody's (1980) opinion should be noted. He suggested that the most primitive *Phrynocephalus* species is *P. vlangalii* inhabiting north-eastern Tibet and Qinghai. The validity of this conclusion is problematic because he studied only two species of this genus in his phylogenetic and biogeographic study of agamids.

Of special interest for understanding the origin of *Phrynocephalus* is the finding of a new species, *Phrynocephalus langwalaensis* (Sharma, 1970), from the Radjastan Desert, in western India.

Whiteman (1978) suggested that *Phrynocephalus* probably originated in the early Miocene in Central Asia. On Whiteman's map (Whiteman, 1978: his figure 12) illustrating the hypothesized dispersal of *Phrynocephalus*, he showed this point in southern Middle Asia. The reason of such term confusion is connected with the absence of separating, in English, the terms Central Asia and Middle Asia traditionally used in German and Russian geographical and zoological literature.

Middle Asia is the part of Asian territory of the USSR from the Caspian Sea in the west to the Chinese border in the east, and also from the Aral-Irtysh drainage divide in the north to the border of Iran and Afghanistan in the south.

Central Asia is defined as the desert and semidesert plains, tableland and high plateaus which are limited to the east by the southern part of Great Khingan and



FIG. 2. Sea basin and land (hatched) during the Lower - middle Miocene. Hypothesized centers of *Phrynocephalus* speciation: A- Middle Asian center; B- western edge of the Central Asian center. Lower - middle Miocene records (Bakradze and Chkhikvadze, 1988): 1- northern Aral Sea region; 2- Turgai; 3- Zaisan Depression. The arrow shows the hypothesized direction of movement of ancestral forms of the *Phrynocephalus guttatus* complex.

Taikhanshan ridge and to the south by the longitudinal tectonic basin of the upper Indus River and Brahmaputra (Tsangpa). In the west and in the north the border of Central Asia corresponds to the mountain ridges of eastern Kazakhstan, Altai, western and eastern Sayan, approximately coinciding with the state border between the USSR on the one hand, and China and Mongolia on the other hand.

Eremias sp., *Varanus*, *Ophisaurus*, *Eryx*, and *Protestudo* were found in the late Miocene deposits in eastern Kazakhstan

(Bakradze and Chkhikvadze, 1988). The ancestor of *Phrynocephalus maculatus* may have already existed during the Neogene in Middle Asia in the condition of southern savannas and xerophytous vegetation of the southern and southeastern Transcaspien region. The ancestral form of *P. raddei* (Fig. 3) may have already been distributed along all the southern part of the Thetys geosyncline from the Caspian Sea to the Pamir. We can hypothesize this because fossil remains of giant land tortoises and monitors are known from the Pliocene in Tadzhikistan. Some lizards, *Trapelus*

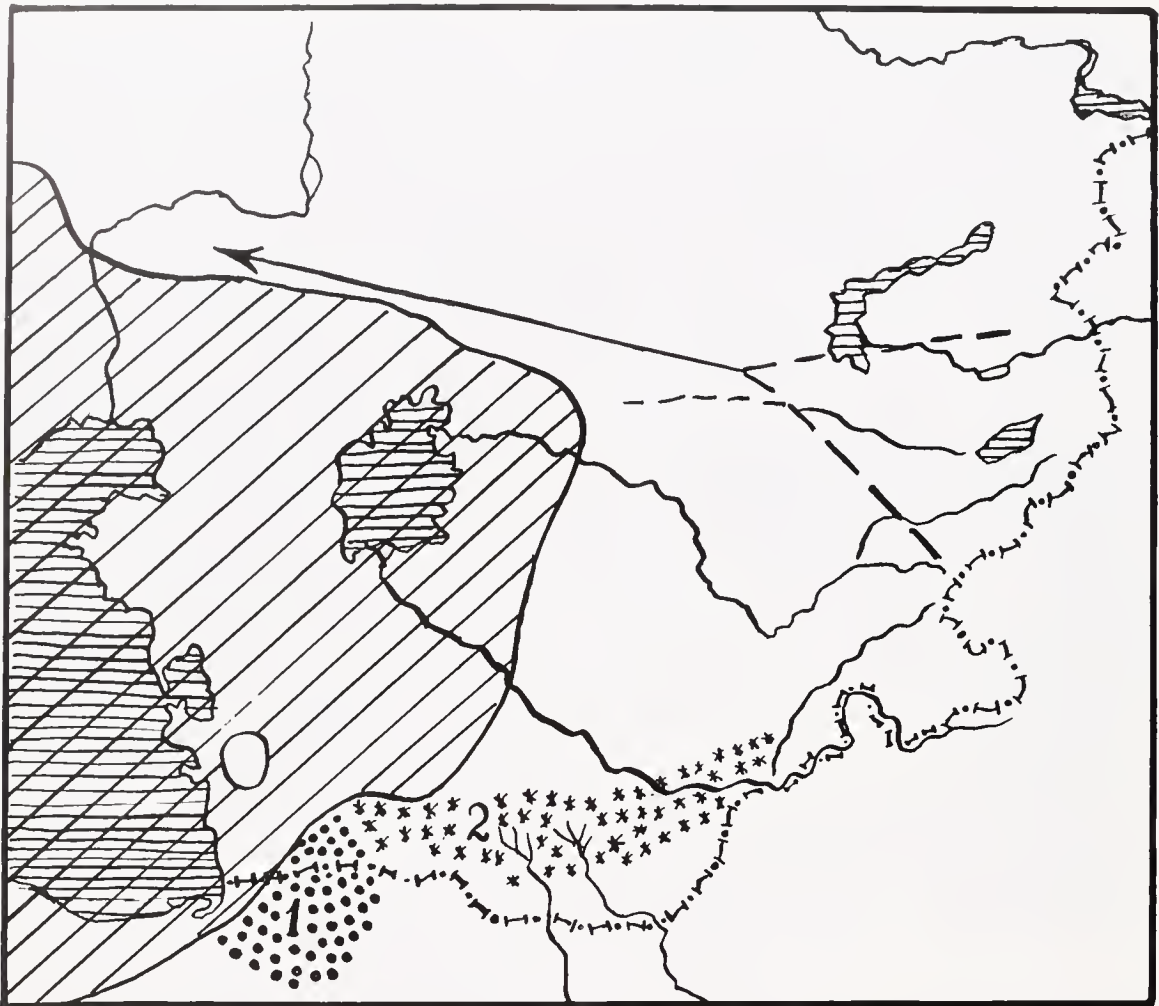


FIG. 3. Sea basin and land during the Upper Miocene (Sarmat Sea is hatched). 1- Hypothesized distribution of *Phrynocephalus maculatus* ancestor; 2- Hypothesized distribution of *Phrynocephalus raddei* ancestor. The arrow shows the direction of continuing dispersal of the forms of the *Phrynocephalus guttatus* complex.

sanguinolentus, *Eremias* sp., and *Varanus cf. griseus* are known from the Pliocene in Turkmenia (Ananjeva and Gorelov, 1981; Bakradze and Chkhikvadze, 1988)

In the Pliocene, the genus *Phrynocephalus* could have divided into species complexes or into the genera *Phrynocephalus* and *Megalochilus* (Ananjeva, 1986) on the territory of the southern Kara-Kum Desert. Federovitch (1946) assumes that one should look for the origin of typical recent sandy desert vegetation associations in the Neogene in the Kara-Kum (Fig. 4).

The Miocene may be considered as the time when the ancestral form of the *Phrynocephalus guttatus* complex (Figs. 5 and 6) from the Central Asian center penetrated as far as the eastern boundaries of the Tethys (recent regions of Pamir-Alai and Gissar-Darvaz mountains), (Fig. 2). This territory, now occupied by mountains and intermountain depressions, resembled low mountain relief now present northwest of Samarkand and Djizak (Voskresensky, 1968). The subsequent dispersion of this group to the west was along the northern shore of the Thetys (later the Sarmat Sea, Fig. 3). Further spreading to the north was

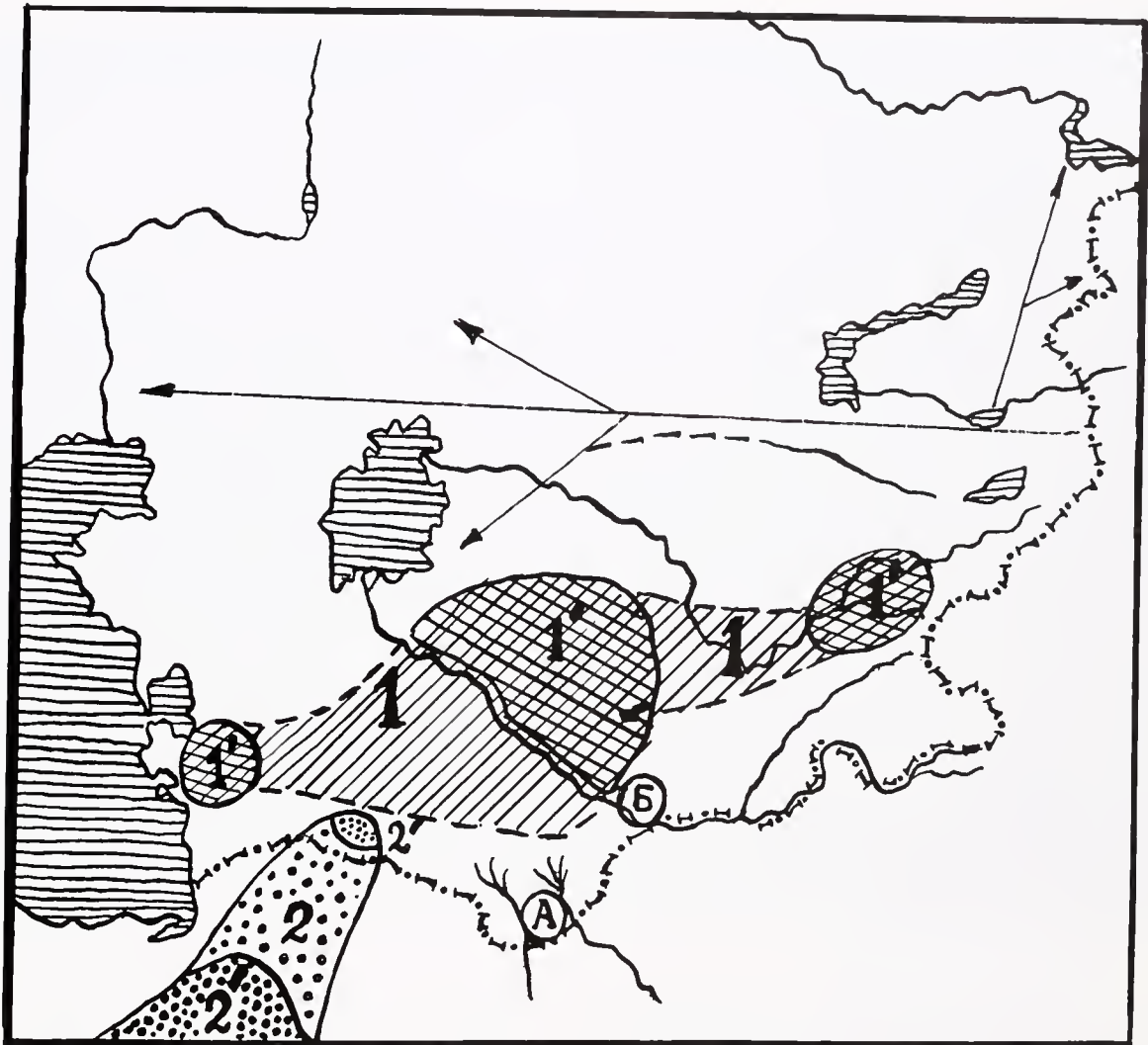


FIG. 4. The middle Pliocene changes of *Phrynocephalus*. 1- Lower Pliocene distribution of *Phrynocephalus reticulatus*; 1'- middle Pliocene populations of *Phrynocephalus reticulatus* on emerged land; 2- Lower Pliocene distribution of *Phrynocephalus maculatus*; 2'- middle Pliocene populations separated by alpic orogenesis of the Kopeth-Dag. The arrows show the direction of dispersal of the species of the *Phrynocephalus guttatus* complex. A- hypothesized place for divergence of *Phrynocephalus* and *Megalochilus*; B- hypothesized place of origin for *Phrynocephalus rossikowi*.

prevented by phytogeographical conditions since the plains of central Kazakhstan were covered by deciduous forests of *Populus sp.*, *Salix sp.*, *Alnus sp.*, *Zelkova sp.*, *Ulmus sp.*, *Acer sp.*, i.e. the vegetation was intermediate between the Turgai and recent types. The xerophilous formations were only beginning to develop in this territory (Gvozdezky and Mikhailov, 1987).

During the first half of the Neogene, a lake regime was predominate on the

elevated plains of Middle Asia such as the Turgai tableland and western Betpak-Dala. The southwestern branch of the *P. guttatus* complex dispersion could have penetrated this area. The process of uplifting took place across the entire plains of Middle Asia towards the end of Sarmatian time and to the beginning of the Pliocene. The sea basins disappeared and erosional division of the region took place (Voskresensky, 1968). During this period, *Phrynocephalus reticulatus* could have dispersed widely over the entire plain area from the Caspian



FIG. 5. *Phrynocephalus guttatus* from the west side of the Caspian Sea in Chechen-Ingush, Russia.

Sea in the west to the Fergan Depression in the east. This species apparently did not reach beyond the limits of the dry subtropic climatic belt. The same is observed at the present (Fig. 4). In such context, the opinion of Golubev (1989b) on the unity of the origin of *P. moltschanovi* and *P. reticulatus* from the forms penetrating here from the north in the middle Pleistocene seems to us doubtful.

The eastern branch of the *P. guttatus* complex, i. e. *Phrynocephalus versicolor* was widespread north and northeast of the Tien Shan (Mountains), (Fig. 4). Isolation of *Phrynocephalus rossikowi* (Fig. 4) could have taken place on the dense river sediments of the Amu Darya (River) which flowed into the Caspian Sea at that time. The Pliocene raising of Asia Minor and the Iranian Plateau had apparently already led to disjunction of the area inhabited by the

ancestor of *Phrynocephalus helioscopus* and also by some species of the genus *Trapelus* with similar ecological requirements. The diverged populations of *P. helioscopus*, *P. helioscopus persicus* (*P. persicus*, Meszserin and Golubev, 1989; Nikolsky, 1915), could probably have separated in the Pliocene. In the middle of the Pliocene a sinking process occurred in the sand deserts of Middle Asia to the slightly elevated Zaunguz Plateau. However, on the Turgai Plateau in western Betpak-Dala and on the Ustyrt Plateau the raising of the Kysil-Kum and Mangyshlak was no longer restored by the regime of accumulation. The relief continued to develop slowly by an erosion and denudation process (Voskresensky, 1968). It was in the middle of the Pliocene that the disjunction of the continuous range of *Phrynocephalus reticulatus* took place. That led to isolation of three relict



FIG. 6. Habitat of *Phrynocephalus guttatus* on the west side of the Caspian Sea in Chechen-Ingush, Russia.

populations on the plateau islands not covered by sea: South Ustyurt Krasnovodsk, Kiysil-Kum and Fergana Depression (Fig. 4).

The formation of the *Phrynocephalus mystaceus* complex (or genus *Megalochilus*), (Figs. 7 and 8), and of the parallel sand inhabiting *P. interscapularis* complex, continued in the extreme southern portion of Middle Asia under conditions of sandy desert formation. The adaptive radiation of *Phrynocephalus* in sympatry, according to Peters (1984), could have been accompanied by increasing differences in the body size. This seems to have been important in the evolution of *P. mystaceus*. On quick moving sand dunes with steep slopes, the largest specimens could survive. They were able to dig uncrumbling deep holes protecting them from summer heat and low winter temperatures. They were also able to

release themselves from the captivity of the sand during movement of sand dunes. It should be noted that ridges formed from the stabilized aeolian landforms in the Pleistocene when mountain structures, which mainly determine the direction of the air streams, were formed. It is assumed that the direction of sand movement remained the same at least to the Upper Neogene (Voskresensky, 1968). The plains with newly formed meso- and microrelief created before the Quarternary drying and cooling by wind activity were alluvial plains with all the typical features (Voskresensky, 1968).

P. mystaceus evolved under the conditions of blowing sand. The decreasing of body size of *P. mystaceus mystaceus* in comparison with *P. mystaceus galli* may be indirect evidence in favour of this hypothesis. There may be correlations between this change of body



FIG. 7. *Phrynocephalus mystaceus* from Repetek (38° 34' N 63° 11' E), Turkmenistan.

size and the inhabiting of *P. mystaceus* in the comparatively stabilized Terek-Kuma rivers sands on the west side of the Caspian Sea in Russia. Smaller sizes of specimens of *P. mystaceus* are typical of the populations from the Sari-Kum Sand

Dune, Dagestan, Russia. This form developed under the conditions of a unique isolated sand dune with a special wind regime (Khonyakina, 1962).

The restricted distribution of *P.*



FIG. 8. Habitat of *Phrynocephalus mystaceus* (large sand dunes), *Phrynocephalus interscapularis* (sand dune edges), *Phrynocephalus raddei* (hard packed soil to the left) from the Kara Kum Desert 80 km north of Ashkabad (37° 57' N 58° 23' E), Turkmenistan.

mystaceus and relatively poor food availability of the sand dunes could have driven the small *P. interscapularis* back to the dune valleys. This species, sharing a common southern origin with *P. mystaceus*, could not spread beyond the limit of the subtropical climatic belt during the next geological epoch. Its present distribution almost completely lies in the climatic zone of the continental southern Turanian region with a small penetration to the extreme southern part of the continental north Turanian region (after Alisov, 1969). These species occur where the temperature during January -3°C in the north, up to 2°C in the south and annual precipitation from 100 to 200 mm. According to Kashkarov and Korovin (1936) *P. interscapularis* inhabits Mediterranean deserts with a winter-spring period of precipitation and vegetation of the ephemeral type (Table 1). The relatively restricted range of *P.*

interscapularis may be explained by some ecological peculiarities. This lizard is very small. It is not capable of digging deep into the sand, and it also has a greater tolerance to high temperatures. The temperature preference of *P. interscapularis* may fluctuate only 3°C , whereas in *P. mystaceus* it may fluctuate 4°C and in *Eremias grammica* up to 5°C (Cherlin and Muzicenko, 1983).

The mode of preference of temperatures in *P. mystaceus* and *Eremias grammica* is 39°C which may be comparable with the very high level of tolerance known for *Dipsosaurus dorsalis*. However, for *P. interscapularis* this index is still higher (41.3°C). This may be considered an outstanding example of adaptation of a small lizard to extremely arid conditions.

In the north and northwestern deserts, *P.*

TABLE 1. Distributional characteristics of *Phrynocephalus* species in the USSR.

Name	Climatic Belt	Geo-morphology	Desert Type	Climatic Region	Ecological Type	Recent Area	Age of Recent Area	Center of Origin
<i>P. raddei raddei</i>	Subtropical	Accumulation plains with aeolian landforms	Mediterranean clay soil or sandy soil	Continental southern Turanian	Sclerobiont	Turkmenia	Pliocene-Pleistocene	Middle Asia
<i>P. raddei boettgeri</i>	Subtropical	Accumulation plains with aeolian landforms	Mediterranean clay soil or solonchaks desert	Continental southern Turanian	Sclerobiont	Kukhistan valleys	Miocene-Pleistocene	Middle Asia
<i>P. maculatus</i>	Subtropical	Accumulation plains with aeolian landforms	Mediterranean solonchaks desert	Continental southern Turanian	Sclerobiont	Turkmenia, Bami region	Neogene	Middle Asia
<i>P. rossikowi rossikowi</i>	Temperate	Plains of river valley origin	Mediterranean loess-clay soil	Continental northern Turanian	Sclerobiont	Lower course of Amu Darya (River) and southern coast of Aral Sea	Pleistocene	Middle Asia
<i>P. rossikowi schammakowi</i>	Temperate	Plains of river valley origin	Mediterranean loess-clay soil	Continental northern Turanian	Sclerobiont	Lower course of Amu Darya (River) and southern coast of Aral Sea	Pleistocene	Middle Asia
<i>P. reticulatus reticulatus</i>	Subtropical-temperate	Plateau with superimposed aeolian landforms	Mediterranean sand and gypsum desert	Border between continental northern Turanian and continental southern Turanian	Sclerobiont	Kysil Kum Plateau	Pliocene	Middle Asia
<i>P. reticulatus bannikowi</i>	Subtropical	Plains covered with superimposed aeolian landforms	Mediterranean sand and gypsum desert	Continental southern Turanian	Sclerobiont	Southern Ustyrt and Krasno-vodskoye Plateau	Pliocene	Middle Asia

TABLE 1. Continued.

Name	Climatic Belt	Geo-morphology	Desert Type	Climatic Region	Ecological Type	Recent Area	Age of Recent Area	Center of Origin
<i>P. strauchi</i>	Subtropical	Accumulative Aeolian landform on the synclorium	Mediterranean sand and gypsum desert	Continental southern Turanian	Sclerobiont	Fergan Valley	Pleistocene	Middle Asia
<i>P. helioscopus helioscopus</i>	Subtropical	Plains of different origins	Intrazonal takyrt	Continental southern Turanian	Sclerobiont	Plains of Middle Asia Kazakhstan Volga region	Pleistocene	Middle Asia
<i>P. helioscopus persicus</i>	Subtropical	Relief of the graben (trough) synclorium	Mediterranean clay soil and sand desert	Continental southern Turanian	Sclerobiont	Valley of the Middle Araks River	Pliocene	Middle Asia
<i>P. guttatus guttatus</i>	Temperate	Plains of different origins	Central Asian clay soil and sand desert	Continental northern Turanian	Psammobiont	Northern Caspian region and Aral region	Miocene-Pleistocene	Central Asia
<i>P. guttatus kuschakewitchi</i>	Temperate	Plains with accumulative aeolian relief	Central Asian sand desert	Continental northern Turanian	Psammobiont	Sary Ischik Otrau	Pleistocene	Central Asia
<i>P. moltischanowi</i>	Temperate	Plains of river and lake origin	Mediterranean loess-clay desert	Continental northern Turanian	Sclerobiont	Delta of Amu Darya (River)	Pleistocene	Central Asia
<i>P. versicolor kulagini</i>	Temperate	erosion accumulative relief on the bottoms of intermontane depressions	Central Asian clay and sand desert	Continental northern Turanian	Sclerobiont	Ubsu Nur Depression	Pleistocene	Central Asia
<i>P. versicolor paraskiivi</i>	Temperate	Accumulative Aeolian relief on the synclorium	Central Asian clay and sand desert	Continental northern Turanian	Mesobiont	Ili River depression	Pliocene	Central Asia

TABLE 1. Continued.

<i>P. melanurus</i>	Temperate	Lake alluvial plain	Central Asian clay and sand desert	Continental northern Turanian	Psammobiont	Zaissan Depression	Pliocene	Central Asia
<i>P. interscapularis</i>	Subtropical	Accumulative plains with aeolian landform	Mediterranean sand desert	Continental southern Turanian	Psammobiont	Deserts of the south of Middle Asia	Pliocene	Middle Asia
<i>P. sogdianus</i>	Subtropical	Accumulative plains with aeolian landform	Mediterranean sand desert	Continental southern Turanian	Psammobiont	Kukhistan valleys	Pleistocene	Middle Asia
<i>P. mystaceus galli</i>	Subtropical-temperate	Plains of different genesis with aeolian landform	Mediterranean and Central Asian sand deserts	Continental southern Turanian	Psammobiont	Middle Asia and Kazakhstan	Pliocene-Pleistocene	Middle Asia
<i>P. mystaceus mystaceus</i>	Temperate	Plains of different genesis with aeolian landform	Central Asian sand desert	Continental southern Turanian	Psammobiont	Southeastern part of European USSR	Pleistocene	Middle Asia

mystaceus occurs on steep slopes of sand dunes were as the sympatric *P. guttatus* occurs in the valleys between sand dunes.

Large mountain ranges were formed in the place of residual plains and low mountain relief with a Paleozoic folded structure. The peneplain was subjected to folded deformations (Gvozdesky and Mikhailov, 1987). In this context it is difficult to share Golubev's (1989b) opinion that the conditions of the early Pleistocene were favorable for the penetration of *Phrynocephalus* from Central Asia to eastern Kazakhstan. However, Golubev (1989b) noted that owing to active alpic orogenetic processes in the Junggar Alatau and the Tian Shan, the contact of the reptiles between the Balkhash-Alakol and the Junggar Depression became gradually more difficult or was interrupted. This period was probably characterized by disjunction of continuous ranges and by the isolation in the intermountain depressions of the central branch of the *P. guttatus* complex. Further history of the speciation of each population seems to have resulted in the formation, during the Pleistocene, of more clearly isolated taxonomical forms in different depressions: Ili- (*P. alpherakii* according to Peters, 1984; Golubev, 1989b, or *P. versicolor paraskivi* according to Semenov, 1987); Alakol Depression- (*P. versicolor* ssp.), and Zaissan Depression- (*P. salenskyi* according to Peters, 1984; Golubev, 1989b, or *P. melanurus* according to Semenov, 1987). Definitive formation of eastern populations of the *P. reticulatus* complex, which subsequently led to the isolation of *P. strauchi*, may have taken place at the same time. Its speciation occurred because of the isolation of the Fergana Valley. Retaining of isolated populations in intermountain depressions was possible due to the absence of repeated leveling of the relief in Neotectonic time. This is supported by geological evidence such as the composition and thickness of sediments in the Ili and Fergana depressions (Voskresensky, 1968).

Most of the distribution of *P. mystaceus* seems to have been formed during the end of the Neogene when these lizards could

have occupied all of Middle Asia, from the Caspian Sea in the west to Balkhash Lake in the east, and from the plains near the slopes of Kopeth-Dagh and Hindu Kush in the south up to the Naryn Sands in the north. Its primary Aralo-Caspian (Turanian) origin and distribution is supported by all zoogeographers (Anderson, 1968; Chernov, 1954; Rustamov and Sczcerbak, 1985; Vereshagin, 1966). The penetration to the deserts north of the Caucasus Mountains probably took place around the northern Caspian Sea (Chernov, 1954; Darevsky, 1957).

In the Pleistocene, the Central Asian elements of the flora dispersed from the east to the north of Middle Asia and central Kazakhstan. The other important center which influenced the development of Middle Asian vegetation was the eastern Mediterranean center (Gvosdezky and Mikhailov, 1987). All the plains of this extensive region are classified by vegetation type into two kinds of deserts: Mediterranean (after Kashkarov and Korovin, 1936), and subtropical deserts of the northern zone (after Gvosdezky and Mikhailov, 1987), or accordingly, the deserts of the northern zone (after Gvosdezky and Mikhailov, 1987). The present boundary between the two zones approximately corresponds to the boundary distinguished by Alisov (1969) for the climatic regions of continental northern Turanian and continental southern Turanian.

In the Pleistocene, speciation of the *P. guttatus* complex occurred in the northern deserts of the Caspian and Aral Regions. During the Upper Pleistocene, river beds of the Amu-Darya and Syr-Darya rivers turned to the Aral Sea (Voskresensky, 1968). This resulted in a change from sand massive on the southern coast of the Aral Sea to loess and clay plains of river origin. Under these conditions of hard soils, the formation of the isolated southwestern population of the *P. guttatus* group, considered now as a separate species, *P. moltschanowi* (Semenov and Shenbrot, 1982) took place (Fig. 9). The taxonomic

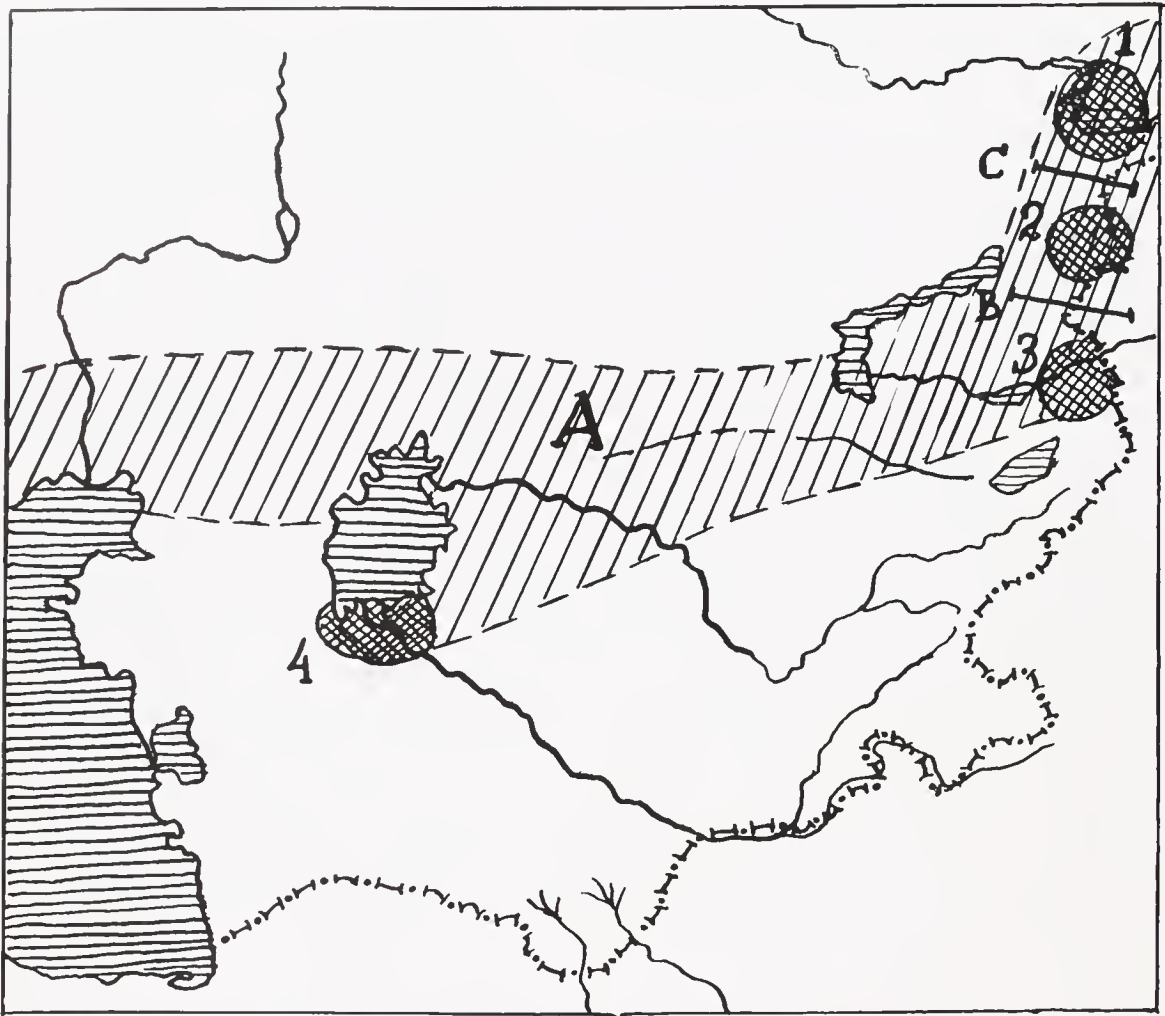


FIG. 9. Upper Pliocene changes of *Phrynocephalus*. A- middle Pliocene distribution of the species of the *Phrynocephalus guttatus* complex. The disjunction of the continuous distribution of this complex occurred in the Upper Pliocene by: B- Junggar Alatau (Altai mountains); C- Saur and Tarbagatai mountain ridges. 1- *Phrynocephalus melanurus*; 2- *Phrynocephalus versicolor* ssp.; 3- *Phrynocephalus versicolor paraskivi*; 4- the place of speciation of the southwestern branch of the *Phrynocephalus guttatus* complex and *Phrynocephalus moltschanovi*.

status of this species was discussed recently by Golubev (1989b).

It should be noted that the flow of Middle Asian rivers to the Caspian Sea changed to the Aral Sea, as a result of the downwarp of the region (Voskresensky, 1968). This was of crucial importance for the reconstruction of the ranges of most sclerobiont *Phrynocephalus* species. Probably before the Amu-Darya River (Uzboi), changed its course *P. raddei* was distributed on the clay and loess areas from the Caspian Sea to Kukhistan. Its range

decreased considerably from the north and from the south owing to orogenesis (Fig. 9). In the south this species remained on the incline plain of the Kopeth Dagh and in the loess regions in the estuaries of the Murgab and Tedjen rivers.

After the Amu Darya changed its flow to the Aral Sea, which coincided in time with the maximal development of the sand deserts, the area inhabited by *P. raddei* was divided into a number of isolated populations. These include the piedmont plains in Kukhistan and the Kopeth Dagh,

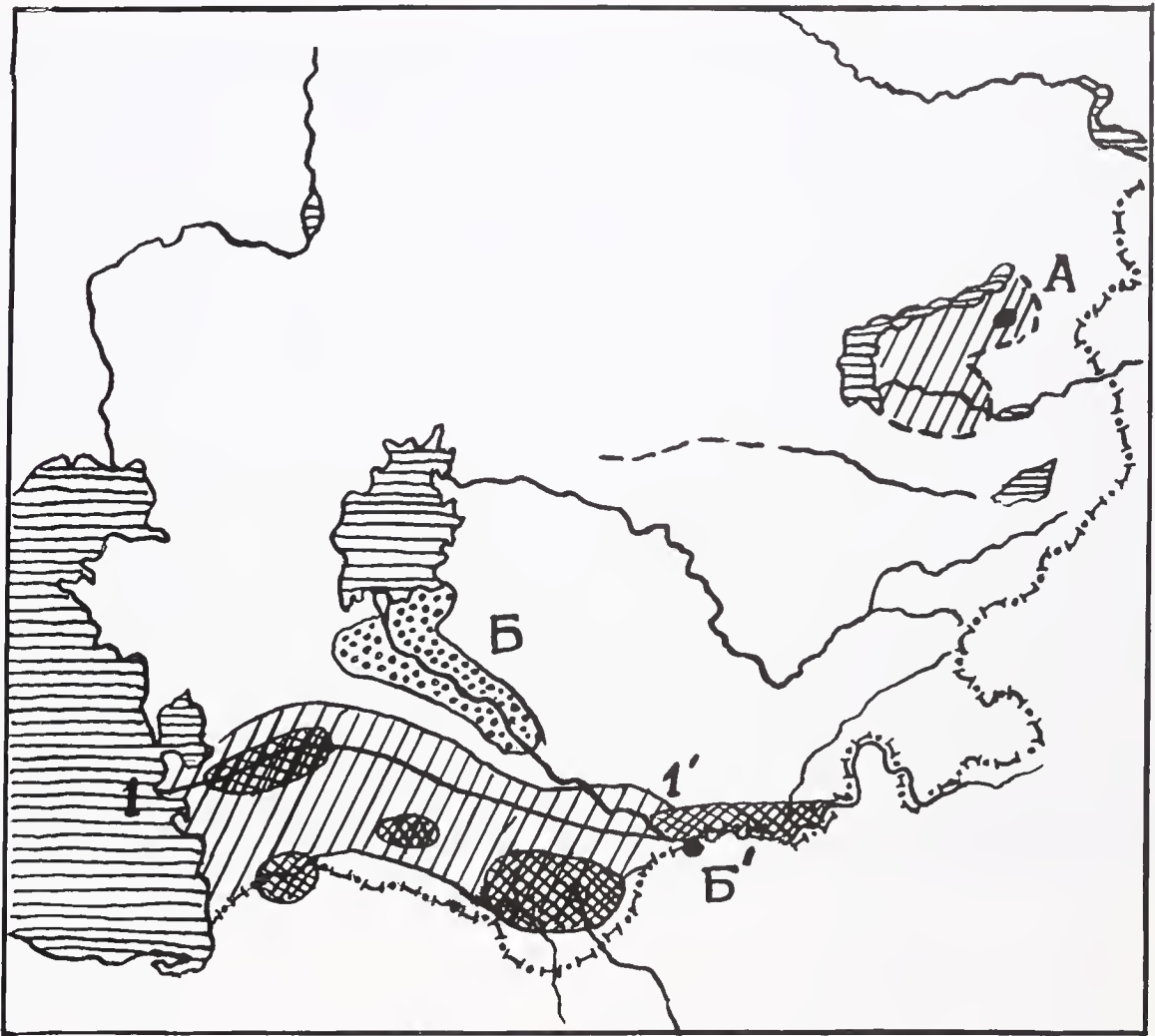


FIG. 10. Pleistocene changes of *Phrynocephalus*. 1 to 1'- the river course of the Amu Darya River (Kelif Uzboi and Uzboi) flowing in to the Caspian Sea before the Lower Pliocene. The distribution of *Phrynocephalus raddei* before the change of the Amu Darya River course to the Aral Sea is hatched. The relictual populations (Upper Pliocene to present) after the change of the Amu Darya River course to the Aral Sea are depicted by cross hatching. A- present distribution of *Phrynocephalus guttatus kushakewichi*; B- the transformed distribution of *Phrynocephalus rossikowi* during the Upper Pleistocene from pre-Pleistocene center of speciation (B').

remaining loess and other valley originated forms of the mouth of the Murgab and Tedjen rivers, and the dry bed of the Uzboi. *P. raddei boettgeri* was formed in the eastern isolated part and it is possible that the western populations also present combinations of different forms (now the nominative subspecies *P. raddei raddei*, (Fig. 10).

The genesis of the area inhabited by *P. rossikowi* (Figs. 11 and 12) is also

correlated with the change of course of the Amu Darya River. This area decreased in the south and reached the southern coast of the Aral Sea in the north (Fig. 10). Owing to the constant change of the configuration of the Amu Darya estuary also observed now (Voskresensky, 1968). The northern part of the range of *P. rossikowi* was also changing repeatedly, resulting in the isolation and long existence of this isolated western population. It was described recently as a distinct subspecies, *P.*



FIG. 11. *Phrynocephalus rossikowi* (size x 2) from along the Amu Darya River, 30 km WNW of Deynau (39° 15' N 63° 11' E), Turkmenistan.

rossikowi shammakovi. It is also possible that the extreme northeastern population has been isolated from the main distribution for a long time and represents a distinct taxonomical form.

After the formation of sand ridges and the deepening of the dune valleys slowed, the process of washing away the subtle material from the ridges to the valleys with the formation of the "takyr" landscapes began in the Pleistocene (Voskresensky, 1968). Under such new conditions *P. helioscopus* became widespread in the plains of Middle Asia.

The Pleistocene glaciation in Europe resulted in the sharp displacement of vegetation zones in the southern Russian plains and vegetation belts in the Caucasus Mountains. As a result, the distribution of *P. mystaceus* in the deserts north of the

Caucasus Mountains was separated into a number of isolated parts. Its range increased in the piedmont regions north of the Caucasus Mountains to the westward, probably in the postglacial xerothermic time of the Holocene. At this time *P. mystaceus* reached the present border of Dagestan and Stavropolsky Territory along the Terek-Kuma rivers sands.

During the Pleistocene, *P. mystaceus* and *P. interscapularis* dispersed into mountainous Kukhistan along the sands formed from the alluvial of the Amu Darya (River). *Phrynocephalus sogdianus* evolved as a result of the disjunction of the Kukhistan enclave during the Upper Quaternary from the continuous range of *P. interscapularis*. This species was described by Chernov (1959) as a subspecies, *P. interscapularis sogdianus*. This form was given the status of a distinct species after



FIG. 12. Habitat of *Phrynocephalus rossikowi* (size x 2) from along the Amu Darya River, 30 km WNW of Deynau (39° 15' N 63° 11' E), Turkmenistan.

Sokolowsky (1975) discovered considerable karyotypical differences between *P. sogdianus* and *P. interscapularis*. With the alternations of the Quaternary glacial and interglacial epochs, the pluvial and xero-thermic climatic periods were connected. However, during the whole Quaternary period, the climate was sharply continental. The desert or desert steppe (in pluvial epochs) regime was retained on the plains of Middle Asia (Gvozdezky and Mikhailov, 1987).

During the Quaternary, the last accumulation changing of the relief on the plains in Middle Asia took place. This may explain the present configuration of the ranges of desert animals. The last considerable accumulation (Khvalynskaya) included the Caspian and low land Kara Kum Desert, Muyn Kum and Sary Ishik Otrau. Toad headed agamids completely

disappeared in the middle Quaternary period from the Muyn Kum Desert. After which only *P. mystaceus* could inhabit it.

The Khvalynskaya transgression of the Caspian Sea defined the western part of the range of *P. raddei*. The flooding of the Sary Ishik Otrau sands near the southern coast of Balkhash Lake resulted in the almost total disappearance of *P. guttatus* and *P. mystaceus* in this region. They are retained probably only near the foot of isolated island mountains that have risen recently among the sands in the eastern part of Sary Ishik Otrau (Fig. 10). Subsequently, dispersal from these refugia and isolated areas could have led to the formation of *P. guttatus kuschakevitschi* in the Balkhash sands.

Thus, the history of the formation of *Phrynocephalus* distributions, which is the sclerobionts (hard soils) depressions and

the blooms of psammobionts, is correlated with step wise development of the sand deserts of the Middle Asian plains. It was influenced by geological processes. All this wide belt is correlated with the zone of most recent downwarp along the peripheral part of the mountain massives of Middle Asia with the accumulation in them. This was followed by transformation of river and estuary sediments under arid conditions.

In some *Phrynocephalus* groups, species secondarily inhabiting sands are known, (Semenov, 1987). For example this pattern is observed in the *P. guttatus* complex, apart from typical sclerobiont forms. Chernov (1948, 1959) noted that *P. guttatus* inhabits different types of sandy biotopes from *P. mystaceus* and *P. interscularis*.

In connection with the problems discussed, it is necessary to mention the problem of *Phrynocephalus* origin. As was already stated above, paleontological data are available for *Phrynocephalus* only from the Pliocene of Turkey. This is not enough significant data about fossil *Phrynocephalus*. The data of present distribution and life history allow us to speculate about the primary character of habitats typical of these lizards. Golubev (1989b) wrote, correctly in our opinion, about the development of the most primitive *Phrynocephalus* in gravel and sand-stone (Gobi) deserts. Most herpetologists (Chernov, 1948; Semenov, 1987; Whitman, 1978) suggest that the primary character is sand biotypes. Thus, Chernov (1948) assumed that *Phrynocephalus* originally adapted to sand habitats and then moved to hard soils. The same opinion is shared by Whiteman (1978) and Semenov (1987). It is interesting that all these herpetologists use as the most serious argument, the number of morphological adaptations shared by all species of *Phrynocephalus* and are typical of many other lizards adapted to life in deserts. Whiteman (1978), referring to Stebbins (1944), names the following morphological characters: 1) dorsoventral depressed body form; 2) protruding labial border; 3) nostrils closed

by special valves; 4) special "scaled" eyelids close the eyes; 5) tympanum absent or hidden under the skin; 6) granular smooth scales; 7) comparatively high speed of locomotion, sometimes bipedal; 8) increased finger surface, "sand ski"; 9) the capacity to bury into the sand; 10) short recurveable tail.

However a more detailed study of these characters refutes the simplified determination of their correlation with a habitat in the sand. It is doubtful that the dorsoventral depression of the body may be an indicator of inhabiting sand biotopes. This character is in the basis of the identification key in the Agamidae family (Boulenger, 1885), separating more specialized tree agamids from all terrestrial, rock and desert forms. It is well known that such form of the body of mountain agamids of the genus *Stellio* is not an indicator of their origin in sand deserts.

Such characters as closed upper lip covering the mouth, nostrils closed by special valves, and special "horny scaled" eyelids closing the eyes undoubtedly may be considered as defensive structures. However they can be developed in different kinds of deserts (not only sand deserts) with a typical windy regime.

Considering the ideas about the origin of *Phrynocephalus* and the so called "primary substratum" one may assume that the terms "desert" in general and sand desert are sometimes confused. Thus, Chernov (1948, p. 132) was absolutely right that *Phrynocephalus* "originated and developed in the conditions of rather sparse vegetation." This, however, does not permit these complexes of landscapes and sand desert to be considered as equal. The latter is only one type of desert and it is the youngest from a geological aspect.

The character, tympanum absent or hidden under the skin, is of special importance. Analysis of the distribution of this character and trends to the reduction of the middle ear among all the agamids, shows that it has arisen independently in some evolutionary lines. The loss of the

tympanum and tympanum cavity is typical of the Australian genus *Tympanocryptis*. Such reduction may arise even in primitive forms like *Ceratophora*, *Cophotis* and *Lyricephalus*. These convergent trends are noted in *Otocryptis*, *Phoxophrys*, *Phrynocephalus*, and *Ptyctolaemus* (Moody, 1980). The enumeration of these genera shows that side by side with the desert lizards (but not psammophilous) there are even forest species. Thus *Otocryptis* is a terrestrial lizard which prefers to inhabit the vicinity of rivers shaded by vegetation in India and Sri Lanka. With this consideration, further examination of the new form, *Phrynocephalus laungwalaensis* from the Radjastan Desert of India may be important.

The granular smooth scales also may be observed not only in psammophilous agamids but also in *Leirolepis*, *Uromastix*, and *Physignathus* (Moody, 1980). Besides, an examination of the correlation of *Phrynocephalus* morphological characters and the type of substrate (Galayeva, 1974) shows that psammophilous species have granular smooth scales. Where as lizards inhabiting hard soil (rock debris desert or arid desert with clay soil) usually have somewhat enlarged, imbricate scales and small protuberances. These data show that there are gradations of morphological characters among *Phrynocephalus* from sclerobionts to psammobionts, and not indisputable psammophilous morphological adaptations of the whole genus. The possible functional importance of small granular scales in the capillary collection and transport of the water in many desert lizards should be noted (Schwenk and Greene, 1987).

The comparatively high speed of locomotion, sometimes bipedal although the limbs may be weak, are typical of many agamids inhabiting open areas (Sukhanov, 1968; Cogger, 1975) and can not be restricted to psammophilous species only.

The increased toe fringes are widely discussed but there are no good

explanations of their function (Chernov, 1948; Fausek, 1906, 1959; Luke, 1986; Werner, 1987). These structures are really typical of many sand lizards, but simple character environment correlation may be misleading (Luke, 1986; Smith, 1935). Toe fringes have arisen independently at least 26 times in seven families of lizards (Luke, 1986) and can be used for locomotion on shifting sand, across water, and for digging in some kinds of soil such as sand and loess (Chernov, 1948; 1959; Luke, 1986).

The original capability of burying into the sand with horizontal movements of the whole body is very well expressed in psammophilous *P. mystaceus* and *P. interscapularis*. There exists an opinion that such behavior may evolve only on large areas of moving sand (Fausek, 1906). But one should not excluded the development of such interesting defensive behavior on the loose sand from the elements of cryptic and or sit and wait behavior with similar patterns observed in *P. helioscopus* on hard soil. This species presses the depressed widening body to the ground with several horizontal movements before standing still.

In general, the idea of Geptner (1933) seems to be fruitful for such considerations. He thought that the animal world of the sand deserts and that of the deserts with hard soils are two formations different in many aspects with their own, to a considerable extent independent, ways of development. The purpose of the adaptations in the two kinds of landscapes is considerably different.

To summarize the review of the recent chorology of *Phrynocephalus* in the USSR fauna, it should be noted that the differences in the outlines of the distributions in general correspond to two main centers of origin. The species of Central Asian origin have the northern most distribution, inhabiting totally a moderate climatic zone and the species of Middle Asian origin mainly did not go beyond the limits of the subtropical climatic zone. The relatively young species (*Phrynocephalus*

helioscopus, and *P. mystaceus*) have the widest distribution. A large portion of their distributions were formed in the Pleistocene in immediate connection with the development of the sand deserts and accompanied takyr.

We can distinguish several types of the present ranges of *Phrynocephalus*:

1. Miocene-Pleistocene range of a northern Thetys origin (*P. guttatus guttatus*).

2. Miocene-Pleistocene disjunct range of a southern Thetys origin (*P. raddei raddei*, and *P. raddei boettgeri*).

3. Pliocene relict range: a) connected with marine transgressions (*P. reticulatus reticulatus*, and *P. reticulatus bannikowi*); b) connected with alpine orogenesis (*P. maculatus*, *P. melanurus*, *P. versicolor parasskiwii*, *P. versicolor ssp.*, *P. helioscopus persicus*, and *P. strauchi*).

4. The Pliocene-Pleistocene ranges: a) wide (*P. helioscopus helioscopus*, and *P. mystaceus*); b) subtropical (*P. interscapularis*, and *P. sogdianus*).

5. Pleistocene transformed area (*P. moltschanowi*, *P. rossikowi rossikowi*, *P. rossikowi shammakowi*, and *P. guttatus kuschakewichi*).

Since the process of continuing aridization of Middle Asia is undoubted, it may be predicted that a reduction in the ranges of the stenotopic sclerobiont *Phrynocephalus* is occurring.

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