

Phylogenetic Relationships and Subgeneric Taxonomy of Toad-Headed Agamas *Phrynocephalus* (Reptilia, Squamata, Agamidae) as Determined by Mitochondrial DNA Sequencing

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Toad-headed agamas (*Phrynocephalus*) is an essential element of arid biotopes throughout the vast area spanning the countries of Middle East and Central Asia. They constitute one of the most diverse genera of the agama family (Agamidae), variously estimated to comprise 26 to 40 species [1]. The subgeneric *Phrynocephalus* taxonomy is poorly studied: recent taxonomic revision have been conducted without analysis of the entire genus diversity [1]; therefore, its phylogenetic position within Agamidae family remains unclear [2–5]. There were several attempts to reconstruct the phylogeny of this genus [4–10]. Reconstruction on the basis of the morphological traits is difficult because of high intraspecific morphological variation of the toad-headed agamas and because of prevalence of substrate races, the morphs confined to specific substrates [11]. At the same time, the phylogenetic schemes on the basis of molecular data [4, 5, 10] are incomplete: they have been obtained on a small sample of species, and the genetic markers used were insufficiently informative.

To clarify the main patterns of herpetofauna differentiation in arid Eurasian areas, we studied phylogenetic relationships between 37 agama taxa encompassing about 80% of the known *Phrynocephalus* species and all the main species groups. The resultant scheme makes it possible to revise the subgeneric taxonomy of toad-headed agamas and to clarify the positions of some morphs.

Tissue samples of 52 *Phrynocephalus* specimens and eight closely related agamas from the Agaminae subfamily (the genera *Laudakia*, *Paralaudakia*,

Trapelus, and *Stellagama*) were used in molecular genetic analysis. In total, 69 sequences from the GenBank were studied, 28 of which served as outgroups (the members of Agamidae, Chamaeleonidae, Iguanidae, and Lacertidae).

The fragment sequences of the following four mitochondrial DNA genes were used in phylogenetic analysis: the genes of subunit I of cytochrome *c* oxidase (*COI*), of subunits II and IV of NADH-dehydrogenase (*ND2* and *ND4*), and of cytochrome *b* (*cyt b*). The overall length of alignment was 2703 bp (GenBank numbers HQ919083; HM915020; and KF691616–KF691738, see table). The algorithms of the maximum likelihood (ML), maximum parsimony (MP), and Bayesian analysis (UBA) for the concatenated sequences of the four genes were used in analysis. To assess the level of genetic differentiation between taxa, the average uncorrected *p*-distances were calculated. The figure shows the dendrograms obtained. There is considerable topological similarity between the phylogenetic schemes for nucleotide and amino acid sequences; the differences concern the nodes with low values of support.

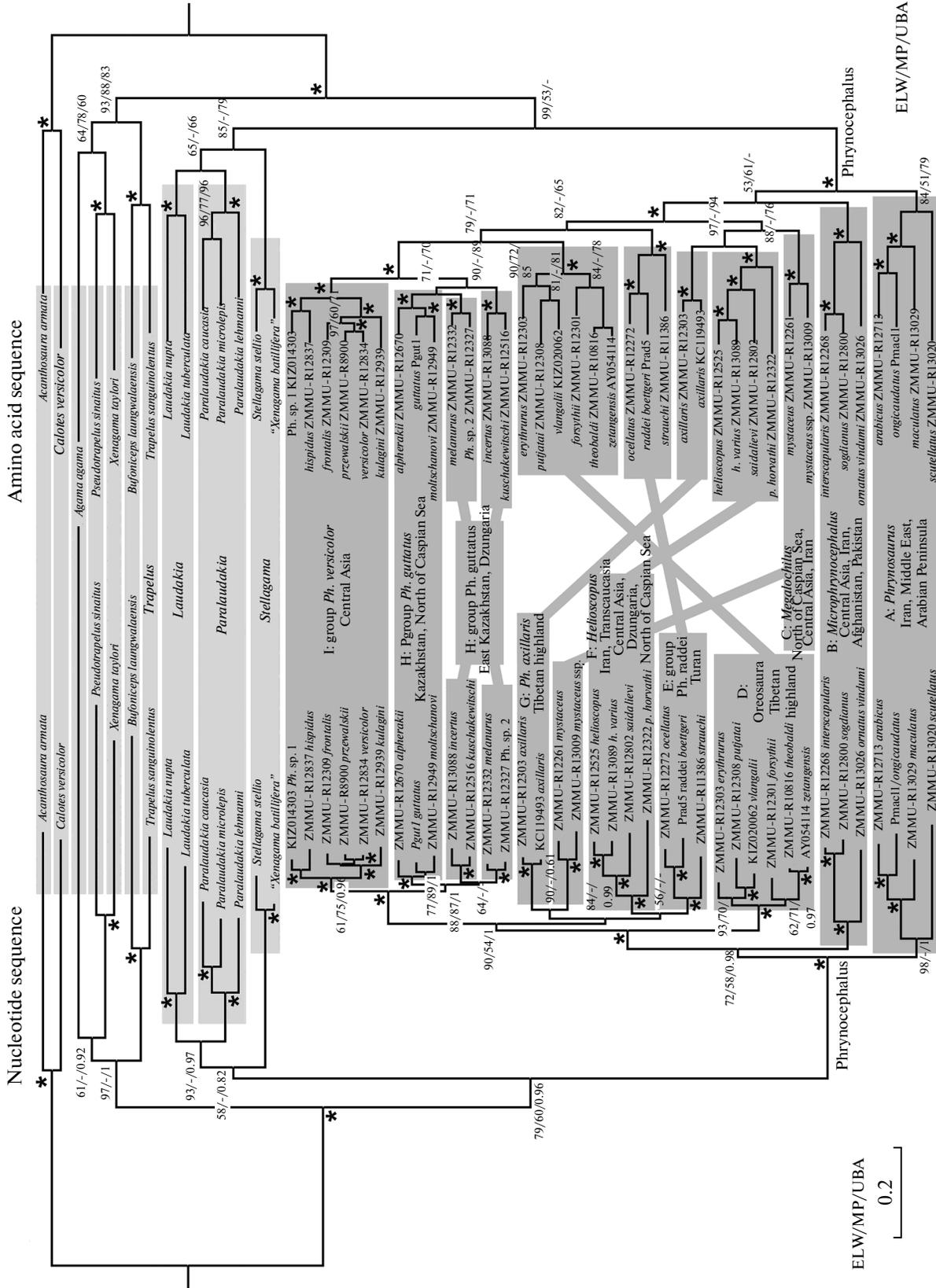
All kinds of phylogenetic analysis reliably confirm monophyly of Agaminae subfamily, which splits into two clades. The first clade combines Afro-Arabian genera (*Agama*, *Xenagama*, *Pseudotrapelus*), as well as the steppe (*Trapelus*; Central Asia and Middle East) and toad-headed (*Bufoinceps*; Rajasthan, India) agamas. The *Bufoinceps* genus was believed to be a part of *Phrynocephalus* because of similarity in outer morphology. Our data confirm the earlier data suggesting that it is close to *Trapelus* [3, 5]. The second clade of Agaminae combines the genus *Phrynocephalus* (Middle East, Central Asia) and the members of mountain agamas (*Laudakia* s. lato). Paraphyly of this genus relative to *Phrynocephalus* has been suggested in some reports [2, 3]; therefore, it was recently divided into the genera *Laudakia* s. stricto (Iran, east of Himala-

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The list of samples of the members of Agaminae subfamily. The inventory and field numbers of individual specimens and samples are indicated, as well as the accession numbers of GenBank (underlined) and the sequences used

Taxon	The voucher specimen number	Accession number of sequences in Genbank (COI, cyt b, ND2, ND4)
<i>Agama agama</i>	—	NC014175; AB263940; AF128504; AF443225
<i>Pseudotrapelus sinaitus</i>	—	NC013603
<i>Xenagama taylori</i>	—	DQ008215
“ <i>Xenagama batillifera</i> ”*	—	AB113825
<i>Bufoinceps laungwalaensis</i>	—	DQ008214
<i>Trapelus sanguinolentus</i>	ZMMU R-12709; R-12732	— ; AY053997; GQ242223; <u>KF691668</u>
<i>Paralaudakia caucasia</i>	ZMMU R-12465; Lca	<u>KF691701</u> ; <u>KF691617</u> ; AF028687; <u>HQ919083</u>
<i>Paralaudakia microlepis</i>	Lmi	<u>KF691703</u> ; <u>KF691647</u> ; — ; <u>KF691699</u>
<i>Paralaudakia lehmanni</i>	ZMMU R-12248	<u>KF691702</u> ; <u>KF691618</u> ; <u>KF691670</u> ; AF028677
<i>Stellagama stellio</i>	ZMMU R-11324	<u>KF691700</u> ; <u>KF691616</u> ; AF128516; <u>KF691669</u>
<i>Laudakia nupta</i>	ZMMU R-12711	<u>HM915020</u> ; — ; AF128513; <u>KF691667</u>
<i>Laudakia tuberculata</i>	ZMMU R-11749	— ; — ; AF128514; —
<i>Phrynocephalus alpherakii</i>	ZMMU R-12670	<u>KF691729</u> ; <u>KF691639</u> ; GQ242221; <u>KF691692</u>
<i>Ph. arabicus</i>	ZMMU R-12713	<u>KF691708</u> ; — ; <u>KF691675</u> ; <u>KF691651</u>
<i>Ph. axillaris</i>	ZMMU R-12302; R-13087	<u>KF691724</u> ; <u>KF691635</u> ; AY396570; AY054012
<i>Ph. erythrurus</i>	ZMMU R-12303	<u>KF691718</u> ; <u>KF691632</u> ; GQ141231; <u>KF691684</u>
<i>Ph. forsythii</i>	ZMMU R-12301	<u>KF691720</u> ; <u>KF691633</u> ; AY054017; <u>KF691661</u>
<i>Ph. frontalis</i>	ZMMU R-12309	<u>KF691695</u> ; AY053909; AY396592; <u>KF691733</u>
<i>Ph. g. guttatus</i>	Pgut1; RuHF 080-3	<u>KF691731</u> ; <u>KF691640</u> ; GQ242203; <u>KF691693</u>
<i>Ph. h. helioscopus</i>	Phel11; ZMMU R-12525	<u>KF691716</u> ; <u>KF691630</u> ; <u>KF691658</u> ; <u>KF691683</u>
<i>Ph. helioscopus varius</i>	ZMMU R-13089; R-12524	<u>HQ543966</u> ; <u>KF691628</u> ; GQ242183; AY054050
<i>Ph. hispidus</i>	ZMMU R-12837	<u>KF691732</u> ; <u>KF691644</u> ; <u>KF691663</u> ; <u>KF691694</u>
<i>Ph. incertus</i>	ZMMU R-13088	<u>KF691728</u> ; <u>KF691637</u> ; GQ242206; <u>KF691690</u>
<i>Ph. interscapularis</i>	Uz-10-05; ZMMU R-12268	<u>KF691704</u> ; <u>KF691620</u> ; AF128517; <u>KF691671</u>
<i>Ph. kulagini</i>	ZMMU R-12939	<u>KF691735</u> ; <u>KF691641</u> ; <u>KF691664</u> ; <u>KF691696</u>
<i>Ph. kuschakewitschi</i>	ZMMU R-12516; RuHF 082	<u>KF691727</u> ; <u>KF691643</u> ; GQ242210; <u>KF691689</u>
<i>Ph. longicaudatus</i>	Pmaclong1	<u>KF691737</u> ; <u>KF691645</u> ; <u>KF691666</u> ; <u>KF691698</u>
<i>Ph. maculatus</i>	ZMMU R-12501; R-13029	<u>KF691707</u> ; <u>KF691623</u> ; <u>KF691650</u> ; <u>KF691674</u>
<i>Ph. melanurus</i>	ZMMU R-12332	<u>KF691725</u> ; <u>KF691636</u> ; GQ242197; <u>KF691687</u>
<i>Ph. moltschanovi</i>	ZMMU R-12942	<u>KF691730</u> ; <u>KF691638</u> ; <u>KF691662</u> ; <u>KF691691</u>
<i>Ph. m. mystaceus</i>	ZMMU R-12261; Pmy2	<u>KF691713</u> ; <u>KF691626</u> ; AF128518; AY054055
<i>Ph. mystaceus</i> ssp.	ZMMU R-13009-2	<u>KF691714</u> ; <u>KF691627</u> ; <u>KF691656</u> ; <u>KF691680</u>
<i>Ph. ocellatus</i>	Uz-10-9-1; ZMMU R-12272	<u>KF691709</u> ; <u>KF691624</u> ; <u>KF691652</u> ; <u>KF691676</u>
<i>Ph. ornatus vindumi</i>	ZMMU R-13026	<u>KF691706</u> ; <u>KF691622</u> ; <u>KF691649</u> ; <u>KF691673</u>
<i>Ph. persicus horvathi</i>	ZMMU R-13243-1-3; R-12322	<u>KF691715</u> ; <u>KF691631</u> ; <u>KF691657</u> ; <u>KF691681</u>
<i>Ph. przewalskii</i>	ZMMU R-8900	<u>KF691734</u> ; AY053941; AY396586; AY054061
<i>Ph. putjatai</i>	ZMMU R-12308-1; KIZ20238	<u>KF691722</u> ; <u>KF691634</u> ; <u>HM629331</u> ; <u>KF691686</u>
<i>Ph. raddei boettgeri</i>	Pra5; IZIP-998	<u>KF691710</u> ; <u>KF691625</u> ; <u>KF691653</u> ; <u>KF691678</u>
<i>Ph. saidalievi</i>	ZMMU R-12802	<u>KF691717</u> ; <u>KF691629</u> ; <u>KF691659</u> ; <u>KF691682</u>
<i>Ph. scutellatus</i>	ZMMU R-13020	<u>KF691712</u> ; <u>KF691619</u> ; <u>KF691655</u> ; <u>KF691677</u>
<i>Ph. sogdianus</i>	T-11-18; T-11-13; R-12800	<u>KF691705</u> ; <u>KF691621</u> ; <u>KF691648</u> ; <u>KF691672</u>
<i>Ph. strauchi</i>	Uz-10-15-4; ZMMU R-11386	<u>KF691711</u> ; — ; <u>KF691654</u> ; <u>KF691679</u>
<i>Ph. theobaldi</i>	ZMMU R-10816	<u>KF691721</u> ; AY053965; EU275226; AY054089
<i>Ph. versicolor</i>	ZMMU R-12834; RuHF-048-2	<u>KF691736</u> ; AY053968; <u>KF691665</u> ; <u>KF691697</u>
<i>Ph. vlangalii</i>	KIZ20062	<u>KF691719</u> ; <u>KF691642</u> ; <u>KF691660</u> ; <u>KF691685</u>
<i>Ph. zetangensis</i>	RuHF 086-2	<u>KF691723</u> ; AY053992; EU275228; AY054114
<i>Phrynocephalus</i> sp. 1	KIZ14303	<u>KF691738</u> ; <u>KF691646</u> ; — ; —
<i>Phrynocephalus</i> sp. 2	ZMMU R-12327	<u>KF691726</u> ; AY053919; AY396572; <u>KF691688</u>

* Position of *Xenagama batillifera* is unclear because the sequence AB113825 published in Genbank under the name *Xenagama batillifera* seems to refer to an incorrectly defined specimen of *Stellagama stellio* ($p = 7.56\%$) [12].



Phylogenetic ML-dendrograms of *Phrynocephalus* genus as constructed on the basis of nucleotide and amino acid sequences (to the left and right, respectively). Bootstrap supports in MP analysis, the values of Expected Likelihood Weights (ELW) in ML analysis and posterior probabilities (PP) in Bayesian analysis (UBA) are presented in the order indicated in the figure. Asterisk (*) marks the nodes with high support (BS > 95%; PP = 1.0). The species groups of *Phrynocephalus* genus are indicated (A–I). Available designations of the generic and subgeneric rank are underlined.

yas), *Paralaudakia* (Central Asia, Caucasus), and *Stellagama* (SE Europe, NE Africa, Middle East, and Asia Minor) [12]. Our results do not make it possible to define unambiguously phylogenetic relationships between *Phrynocephalus* and the mountain agamas; nevertheless, there is a clear-cut tendency of *Laudakia* s. lato to monophyly, as well as monophyly of the combination *Laudakia* s. stricto and *Paralaudakia*.

All kinds of phylogenetic analysis confirm significantly monophyly of the genus *Phrynocephalus*. Phylogenetic relationships within the genus are not unambiguously defined: some nodes that reflect the earlier stages of *Phrynocephalus* differentiation are poorly supported. Nevertheless, the clades corresponding to the level of species and species groups have high values of bootstrap support and posterior probabilities (BS/PP 98–100%/1.0). In total, we have identified the following nine clades within the genus *Phrynocephalus*, which correspond to the main species groups of *Phrynocephalus* (groups A–I in the figure).

Group A includes species rather different in morphology and ecology that inhabit Iran, Middle East, and the Arabian Peninsula. This group forms a clade that is a sister-clade in relation to all other species of the genus *Phrynocephalus*. The members of this clade have been earlier demonstrated to be significantly distant in morphology, especially *Ph. arabicus* [7]. The group with moderate support includes the Iranian species *Ph. scutellatus*, which was earlier assumed to be close to *Ph. ocellatus* (cited from [7]) and belong to *Phrynosaurus* [1]. Our data testify to paraphyly of *Ph. maculatus* s. lato relative to *Ph. arabicus*: *Ph. m. longicaudatus* from Oman forms a strongly supported group with *Ph. arabicus*. The morphological and ecological features of this form enable us to assume that it is an independent species *Ph. longicaudatus* Haas, 1957 comb. et stat. nov.

Group B. Small psammophilous species of the southern Central Asia, Turan, and Middle East (Iran, Afghanistan, Pakistan): *Ph. interscapularis*, *Ph. sogdianus*, and *Ph. ornatus*. This group forms at high significance a sister-clade in relation to the remaining *Phrynocephalus* of the Middle and Central Asia. Because of significant morphological isolation, this group of the smallest *Phrynocephalus*, along with *Ph. clarckorum* and *Ph. luteoguttatus* [13, 14], has been earlier referred to as Microphrynocephalidae, though no subgeneric designation has been proposed. Only insignificant differentiation ($p = 3.80\%$) has been found between *Ph. interscapularis* and *Ph. sogdianus*; the status of *Ph. sogdianus* should be verified.

Group C. The eared toad-headed agamas *Ph. mystaceus*. These are the biggest *Phrynocephalus* inhabiting the sands of Central Asia up to northern Iran. Analysis of nucleotide sequences suggests that *Ph. mystaceus* are close to the Tibet species *Ph. axillaris* (G); the amino acid analysis suggests that they are grouped into

a poorly supported clade together with *Ph. axillaris* and *Phrynocephalus helioscopus* (F). Because of uncommon morphology, *Ph. mystaceus* are often considered an independent subgenus *Megalochilus* [1]. The Central Asian *Ph. m. mystaceus* was found to be considerably isolated from the northern Iranian population ($p = 7.36\%$), which we regard as a new taxon of an undefined rank.

Group D. Tibetan toad agamas (*Ph. erythrurus*, *Ph. putjatai*, *Ph. vlangalii*, *Ph. forsythii*, *Ph. theobaldi*, and *Ph. zetangensis*) assigned to the *Oreosaura* subgenus [1]. This monophyletic [4] group of species from the highlands of the Tibetan Plateau differs from all other toad-headed agamas in the live birth, specific morphology, and behavior [7, 9]. Phylogenetic position of group D is ambiguous: according to nucleotide sequence analysis, it forms a sister-clade at moderate support with the toad-headed agamas of groups (C + E–I); the amino acid analysis suggests with low values of support that it forms a sister-clade with a combination of *Ph. guttatus* (H) and *Ph. versicolor* (I) groups. Within group D, two subclades are distinguishable, which correspond to the Tibetan–Himalayan Qinghai species (*Ph. forsythii*, *Ph. theobaldi*, *Ph. zetangensis* and *Ph. erythrurus*, *Ph. putjatai*, *Ph. vlangalii*, respectively).

Group E. Turanian species of *Phrynocephalus*, which inhabit sands (*Ph. strauchi*), mixed (*Ph. ocellatus* [= *Ph. reticulatus*]), and dense substrates (*Ph. raddei*) of the southern area of Central Asia. Phylogenetic position of this clade is not completely clear: according to data on amino acid sequences, it tends with moderate supports to be in the group that includes *Oreosaura* (D), *Ph. guttatus* (H), and *Ph. versicolor* (I).

Group F. A complex of sunwatcher toad-headed agamas includes sclerobiont species from Central Asia, Transcaucasia and Iran that inhabit only dense soils and which were earlier assigned to the species *Ph. helioscopus* s. lato of the genus *Helioscopus* [1]. The group is divided into two subclades: Persian (here, *Ph. persicus horvathi*) and *Phrynocephalus helioscopus* proper (here, *Ph. h. helioscopus*, *Ph. h. varius*, *Ph. h. saidalievi*). Phylogeny of this group is described in detail in [15].

The phylogenetic position of the complex is ambiguous, but, according to the amino acid sequence analysis, *Phrynocephalus helioscopus* is associated with *Ph. axillaris* (G). Genetic isolation of *Ph. h. saidalievi* from other subspecies is considerable ($p = 9.53\%–10.29\%$) and comparable with the species level of differentiation.

Group G includes the only species *Ph. axillaris* inhabiting the highland stony deserts of Tibet and Kashgar; unlike other Tibetan agama, this is an oviparous species. According to mtDNA data, it is probably related to the *Ph. helioscopus* complex (F).

Groups H and I are close to each other and form monophyly with high support.

Group H comprises *Phrynocephalus guttatus*, which inhabit various types of deserts from the Caspian Sea to western China. There are three subclades within this area, two of which includes the species of Semirechye (*Ph. kuschakewitschi*, *Ph. incertus*) and Dzungaria (*Ph. melanurus*, *Phrynocephalus* sp. 2), while the third subclade includes species from the western part of the area (*Ph. guttatus*, *Ph. moltschanovi*) and Ili valley (*Ph. alpherakii*). We have confirmed isolation of *Ph. moltschanovi* from *Ph. guttatus* ($p = 4.58\%$), as well as differentiation of the Trans-Balkhash forms *Ph. incertus* and *Ph. kuschakewitschi* ($p = 4.69\%$) (their diagnosing on the basis of the morphological traits is difficult). The form from Dzungarian Gate (*Ph.* sp. 2) proved to be close to *Ph. melanurus* from Zaisan ($p = 2.67\%$); the morphological distinctions between them are probably due to the confinement of *Ph.* sp. 2 to dense soils [11].

Group I comprises the species of the *Ph. versicolor* complex encountered on different substrates. There are two subclades in this group: the first of them includes a species from Dzungarian Gobi, we have identified it as *Ph. hispidus*, and a related form of uncertain status from Gansu *Phrynocephalus* sp. 1 ($p = 4.90\%$). The second subclade includes the related species from northern China and central Mongolia, *Ph. frontalis*, *Ph. przewalskii*, and *Ph. v. versicolor*, as well as the more distant form *Ph. v. kulagini* from Tuva. Paraphyly of *Ph. versicolor* s. lato and isolation of Tuvian toad agama ($p = 5.18\%–5.37\%$) suggest that it is an independent species *Ph. kulagini* Bedriaga, 1909 comb. et stat. nov.

The taxonomic status of many recognizable forms of the *Phrynocephalus* genus is still discussed. In our study, genetic differences between the related species of toad-headed agamas are in general below the level of $p = 5.0\%$. Nevertheless, when determined on the basis of mtDNA genes, the genetic distances cannot serve as a universal marker of species differentiation [15]. For example, the distances between the morphologically discrete species of the group *Ph. guttatus* (H) ($p = 4.58–8.75\%$) [11] are significantly lower than the distances between the lineages of *Ph. helioscopus* (F) [15], which are traditionally considered to be subspecies. The complex *Ph. versicolor–Ph. frontalis–Ph. przewalskii* with its extremely short genetic distances ($p = 2.14\%–3.57\%$) and clinal variation of the morphological traits [11] remains the most troublesome. Further studies could be helpful in determining the status of these forms. In this report, the violated monophyly of a taxon in its traditional sense served as the main criterion of species delimitation.

Our study has confirmed monophyly of the genus *Phrynocephalus* and demonstrated that three main significantly isolated clades constitute its phylogenetic

structure: the Middle East–Arabian and Iranian species (group A), small psammophilic species of the Middle East and Turan (group B), and the clade that unites all the remaining species (groups C–I). Two basic clades of *Phrynocephalus* (A, B) are spread over the Middle East, Arabia, Iran, and Turan; we suggest that the genus has originated from this very area. Probably, the formation of toad-headed agama is related to a gradual closing of Tethys because of collision of the Arabian plate and Iranian land in Miocene, which resulted in formation of the arid climate and desert landscapes in this area [see 6, 7]. Reconstruction of the ancient ecological niche of *Phrynocephalus* is difficult, because basal lines of the genus include both psammophilic and sclerobiont species.

Modern intrageneric structure of *Phrynocephalus* implies isolation of only the Tibetan subgenus *Oreosaura* [1]. Our data testify conclusively to a higher genetic isolation of the Near East and Iranian (group A) and small psammophilic (group B) toad-headed agama species. The same is confirmed by the data of the multilocus analysis of nuDNA genes, which are not discussed in this study and will be reported later. Probably, a separate subgeneric designation can be given to the group A: *Phrynosaurus* Fitzinger, 1843 (type species, *Phrynocephalus Olivieri* Duméril et Bibron [= *Ph. scutellatus*]). However, considerable isolation of *Ph. scutellatus* (Olivier, 1807) from the remaining members of the group (*Ph. arabicus* Anderson, 1894, *Ph. longicaudatus* Haas, 1957, *Ph. maculatus* Anderson, 1872, and *Ph. golubewii* Shenbrot et Semenov, 1990) suggests that further studies are necessary. Isolation of small psammophilic species of the group B (Microphrynocephalidae) [13, 14] has been emphasized by many authors [7, 13]; we propose a new subgenus for this group.

Subgenus Microphrynocephalus subgen. nov.

Type species: *Phrynocephalus interscapularis* Lichtenstein, 1856. Species included: *Ph. interscapularis* Lichtenstein, 1856, *Ph. sogdianus* Chernov, 1948, *Ph. luteoguttatus* Boulenger, 1887, *Ph. ornatus* Boulenger, 1887, *Ph. clarkorum* Anderson et Leviton, 1967. Relation to the group *Ph. euptilopus* Alcock et Finn, 1897 is controversial and should be additionally studied.

Diagnosis. All of the members of the new subgenus differ from other *Phrynocephalus* species in the following combination of traits (our data [7] and the references therein): (1) small psammophilic species; in adults, the maximum body length is 48 mm and tail length is 60 mm; (2) a series of enlarged scales on the gular skin extends from chin to mouth corners; (3) the suborbital and pretemporal scales are enlarged; (4) up to 13 supralabial scales; (5) 22–23 presacral vertebrae; (6) the maxillary outer process underlies the premax-

illa offshoot; (7) there is one tooth on the premaxilla; (8) there is no offshoot of the nasal bone, the dorsal surface of the nasal bone is flat; (9) the middle episternal process is reduced or very short; (10) *m. episternocleidomastoideus* is attached to the occipital bone. The subgeneric taxonomy of *Phrynocephalus* and of *Microphrynocephalus* subgenus will be published in detail later.

Etymology. A Latin masculine noun formed from the Greek generic name *Phrynocephalus* and the root *micro* designating the small size of the members of the group.

Distribution. Inhabit the sand dunes of the desert of Central Asia (beginning from southern Kazakhstan and including Uzbekistan, Turkmenistan, and Tajikistan) and Middle East (northern and eastern Iran, Afghanistan, and Pakistan).

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