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Amphibian and Reptile Biogeographic Regions of Northern Eurasia, Mapped Separately

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Abstract—Distributions of amphibian and reptile faunas were separately delimited on a 1:20 000 000 vegetation map of Northern Eurasia divided into 245 10-degree-longitudinal segments of native subzone within the USSR borders as of 1990. All reptile and amphibian species recorded in every segment were listed, and the Jaccard indices were calculated, and the similarity matrix was studied with cluster analysis. Hierarchic classifications were made: the amphibian one consisting of 3 faunistic regions, divided into 4 subregions, 7 biologic provinces, and 23 districts. The reptile classification includes 4 faunistic regions, 7 subregions, 18 provinces, and 14 districts. The reptile classification has 1.5 times more provincial and district subdivisions than amphibian one. Environmental factors correlating with faunistic nonuniformity were revealed. Our amphibian and reptile schemes are 1.9 and 3.5 times more informative than those proposed earlier and account for 75 and 91% of variance in the faunal similarity coefficient of specific areas, respectively (multiple correlation coefficients 0.87 and 0.95). Environmental factors can explain 84 and 93% of faunistic nonuniformity (correlation coefficients 0.95 and 0.96).

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Key words: zonation, fauna, amphibians, reptiles, Palearctic, Northern Eurasia, cluster analysis, factors, correlation

In biogeography of Northern Eurasia, amphibian and reptile distributions have been usually analyzed jointly [1–5]. Nikol'skii [6] merely extrapolated herptile data to reptiles, yet others studied distributions of the two classes of vertebrates separately [7–10]. Some authors believe that faunistic inhomogeneity of distributions of the two classes of animals should not be analyzed together, but we cannot agree with that as one may make generalizations from an individual level on up to population, subspecies, species, and aggregation levels of any taxonomic unit, and up to the fauna at large. In biogeography, analysis includes vegetation, and in geography one also considers all landscape elements. When analyzing top levels, we lose individual properties of a previous aggregation like in any other classification, but new generalizations appear that were not apparent from previous schemes. Such generalizing approaches have been applied to various systematic groups both in faunistic and animal population analyses. In particular, generalization was used in the analyses of faunas of butterflies, birds, and bats, or populations of amphibians, birds, and small mammals, as well as diversity (information value) of land flora, fauna, and soil humus [11–13]. With the increase of species diversity, spatial inhomogeneity becomes less informative at the levels of species and previous aggregations, but a body of emergent properties (i.e., properties of the system that cannot be reduced to the sum of the system's parts) of a complex under study enlarges.

We have already presented ornithofaunistic [14] and herpetofaunistic [5] zonations of Northern Eurasia. These works set out principles, materials, and methods used in the analyses, so this paper only presents separate results for amphibian and reptile faunas and compares them with previous classifications.

ZONATION RESULTS

Amphibians

The amphibian classification includes 3 faunistic regions: (1) Northern, (2) Northeastern, and (3) Southwestern (Fig. 1). No amphibians were recorded in the first region, in the second and third regions 22 and 24 amphibian species occurred, respectively. The Northeastern and Southwestern regions are divided into 2 subregions each, the subregions of the second region are subdivided into 7 provinces, and provinces of the third region coincide with the subregions. The number of extra separated provinces in both regions totals 7 and that of districts 23.

The amphibian faunistic classification is as follows.

1. Northern region (1.1, Arctic subregion; 1.1.1, Arctic province): No amphibians recorded.

2. Northeastern (Kola–Kamchatka) region: prevailing species, % of average occurrence: *Rana arvalis* 20, *Bufo bufo* 14, *Rana temporaria* 12, *Rana amurensis* 8,

Salamandrella keyserlingii 7; average total occurrence, the number of sites 5/the total number of species 22.[1]

2.1. Northwestern (2.1.1, Kola–Baikal province): *Rana arvalis* 30, *Rana temporaria* 30, *Bufo bufo* 14, *Salamandrella keyserlingii* 11, *Rana amurensis* 5; 3/9.

Districts

2.1.1.1. Kola–Ural: *Rana arvalis* 50, *Rana temporaria* 50; 2/2.

2.1.1.2. Karelia–Pechora: *Bufo bufo* 27, *Rana arvalis* 27, *Rana temporaria* 27, *Triturus vulgaris* 18; 4/4.

2.1.1.3. White Sea–Ob: *Rana arvalis* 33, *Rana temporaria* 33, *Salamandrella keyserlingii* 33; 3/3.

2.1.1.4. Pechora–Irtysh: *Bufo bufo* 21, *Rana arvalis* 21, *Rana temporaria* 21, *Pelobates fuscus* 18, *Salamandrella keyserlingii* 14; 5/6.

2.1.1.5. Ob–Pur: *Rana arvalis* 22, *Rana amurensis* 22, *Rana temporaria* 22, *Salamandrella keyserlingii* 22, *Bufo bufo* 11; 4/5.

2.1.1.6. Tobol–Ob: *Rana arvalis* 33, *Rana temporaria* 33, *Bufo bufo* 27, *Rana amurensis* 7; 3/4.

2.1.1.7. Tobol–Irtysh: *Bufo viridis* 29, *Rana arvalis* 29, *Rana temporaria* 29, *Rana ridibunda* 14; 4/4.

2.1.2. Baltic–Ural province: *Rana arvalis* 11, *Bufo bufo* 10, *Pelobates fuscus* 10, *Rana esculenta* 9, *Rana temporaria* 9; 9/20.

Districts

2.1.2.1. Northern Baltic–Ural: *Bufo viridis* 10, *Rana arvalis* 10, *Pelobates fuscus* 10, *Rana ridibunda* 9, *Bufo bufo* 8; 10/20.

2.1.2.2. Southern Baltic–Ural: *Bufo bufo* 13, *Rana arvalis* 13, *Rana temporaria* 13, *Triturus cristatus* 13, *Triturus vulgaris* 13; 8/10.

2.1.3. Yamal–Baikal province: *Rana arvalis* 24, *Rana amurensis* 24, *Bufo bufo* 23, *Salamandrella keyserlingii* 20, *Bufo raddei* 1; 3/5.

Districts

2.1.3.1. Yamal–Pyasina: *Rana arvalis* 57, *Salamandrella keyserlingii* 43; 2/2.

2.1.3.2. Pur–Angara: *Rana arvalis* 30, *Rana amurensis* 30, *Salamandrella keyserlingii* 30, *Bufo raddei* 4, *Bufo bufo* 4; 3/5.

2.1.3.3. Ob–Baikal: *Bufo bufo* 32, *Rana arvalis* 29, *Rana amurensis* 25, *Salamandrella keyserlingii* 14; 3/4.

2.1.4. Upper Irtysh province: *Rana arvalis* 50, *Bufo viridis* 33, *Rana amurensis* 17; 2/3.

2.2. Eastern (Pyasina–Kuril) subregion: *Salamandrella keyserlingii* 44, *Rana amurensis* 28, *Rana chensinensis* 9, *Hyla japonica* 5, *Bufo raddei* 4; 2/9.

2.2.1. Pyasina–Okhotsk province: *Salamandrella keyserlingii* 58, *Rana amurensis* 35, *Rana chensinensis* 7; 2/3.

Districts

2.2.1.1. Pyasina–Kamchatka: *Salamandrella keyserlingii*; 1/1.

2.2.1.2. Tunguska–Okhotsk: *Rana amurensis* 51, *Salamandrella keyserlingii* 49; 2/2.

2.2.1.3. Aldan–Amur: *Rana chensinensis* 35, *Salamandrella keyserlingii* 30, *Rana amurensis* 30; 3/3.

2.2.2. Bureya–Vladivostok province: *Rana amurensis* 17, *Salamandrella keyserlingii* 17, *Bufo raddei* 14, *Hyla japonica* 14, *Rana chensinensis* 14; 5/9.

Districts

2.2.2.1. Bureya: *Rana amurensis* 26, *Bufo raddei* 22, *Hyla japonica* 22, *Salamandrella keyserlingii* 22, *Rana chensinensis* 9; 4/5.

2.2.2.2. Primor'e: *Rana chensinensis* 16, *Salamandrella keyserlingii* 16, *Bufo gargarizans* 13, *Rana amurensis* 13, *Bombina orientalis* 11; 5/9.

2.2.3. Sakhalin province: *Bufo gargarizans* 29, *Hyla japonica* 29, *Salamandrella keyserlingii* 29, *Rana chensinensis* 13; 4/4.

3. Southwestern region: *Bufo viridis* 21, *Rana ridibunda* 20, *Bufo danatensis* 7, *Hyla arborea* 6, *Pelobates fuscus* 6; 5/24.

3.1. Carpathian–Central Asian subregion (3.1.1, Carpathian–Central Asian province): *Bufo viridis* 25, *Rana ridibunda* 25, *Bufo danatensis* 10, *Pelobates fuscus* 10, *Rana asiatica* 7; 4/15.

Districts

3.1.1.1. Carpathian: *Bufo viridis* 12, *Bombina variegata* 12, *Bombina bombina* 12, *Hyla arborea* 12, *Rana ridibunda* 12; 8/8.

3.1.1.2. Black Sea–Ural: *Bufo viridis* 21, *Rana ridibunda* 21, *Pelobates fuscus* 21, *Bombina bombina* 16, *Hyla arborea* 13; 5/7.

3.1.1.3. Northern Aral Sea: *Bufo viridis* 42, *Rana ridibunda* 37, *Pelobates fuscus* 16, *Rana temporaria* 5; 2/4.

3.1.1.4. Southern Aral Sea: *Bufo viridis* 25, *Rana ridibunda* 25, *Bufo danatensis* 23, *Rana asiatica* 15, *Rana amurensis* 9; 4/7.

3.2. Priazov'e–Caucasian subregion (3.2.1, Priazov'e–Caucasian province): *Rana ridibunda* 15, *Bufo viridis* 13, *Rana macrocnemis* 13, *Hyla savignyi* 10, *Hyla arborea* 10; 7/13.

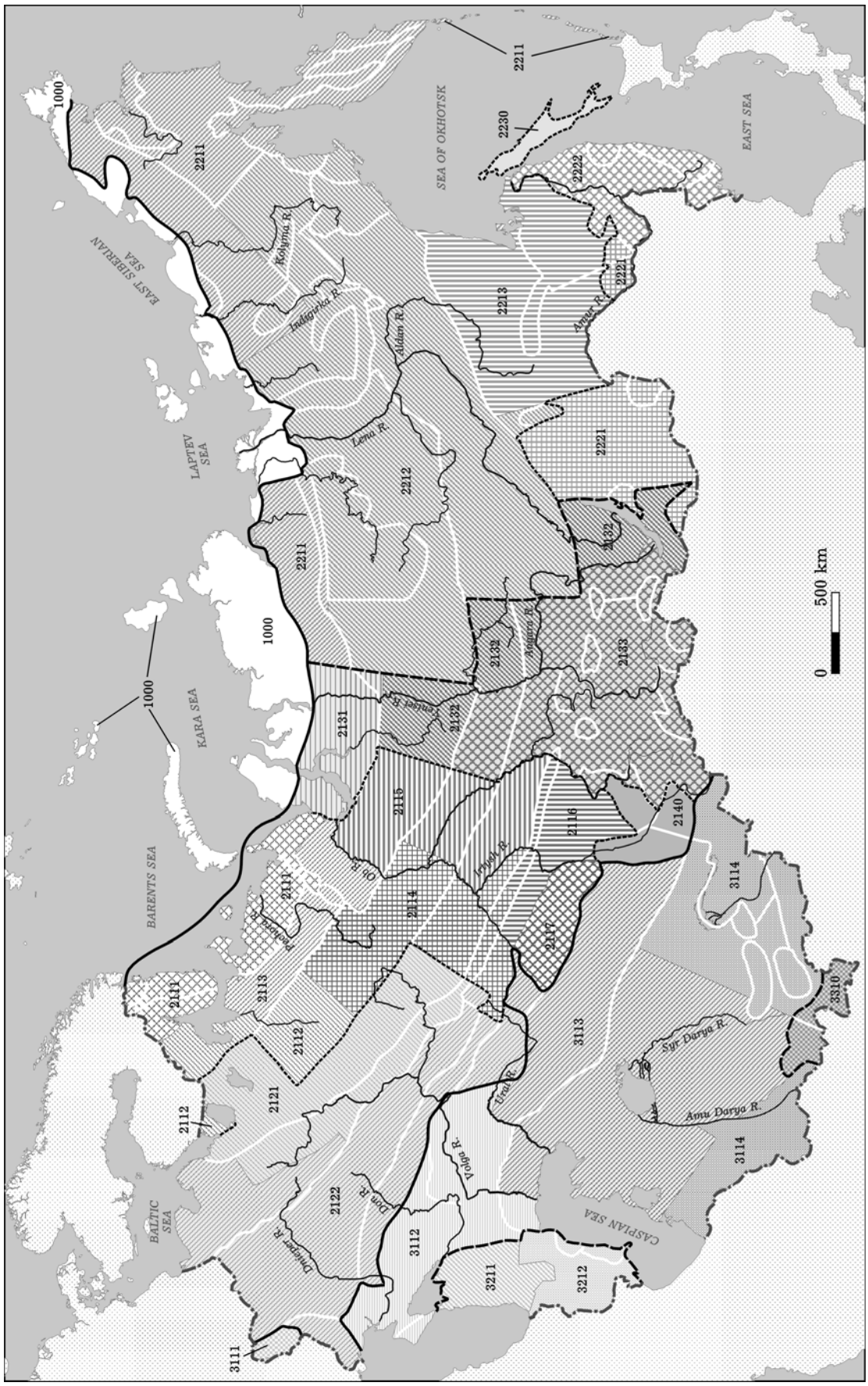
Districts

3.2.1.1. Precaucasian: *Bufo viridis* 12, *Pelodytes caucasicus* 12, *Rana macrocnemis* 12, *Rana ridibunda* 12, *Tritus karelinii* 12; 8/11.

3.2.1.2. Caucasian: *Rana ridibunda* 16, *Bufo viridis* 14, *Hyla savignyi* 14, *Hyla arborea* 14, *Rana macrocnemis* 14; 6/12.

3.3. Pamir subregion (3.3.1, Pamir province): *Bufo viridis* 25, *Bufo danatensis* 25, *Bufo shaartusiensis* 25, *Rana terentievi* 25; 4/4.

[1] Further follow the variables without explanations.


1000
2211
2230
2222
SEA OF OKHOTSK
EAST SEA
EAST SIBERIAN SEA
Kolyma R.
Indigirka R.
2213
Amur R.
2221
Aldan R.
LAPTEV SEA
Lena R.
2212
2132
2211
1000
2133
Ob R.
Yenisei R.
KARA SEA
2131
2116
2140
Irtysh R.
3114
BARENTS SEA
Pechora R.
2114
2111
2113
3310
2112
3113
Syr Darya R.
Ural R.
Amu Darya R.
2121
Volga R.
CASPIAN SEA
2122
Dnepr R.
Don R.
BALTIC SEA
3112
3211
3212
3111
0
500 km

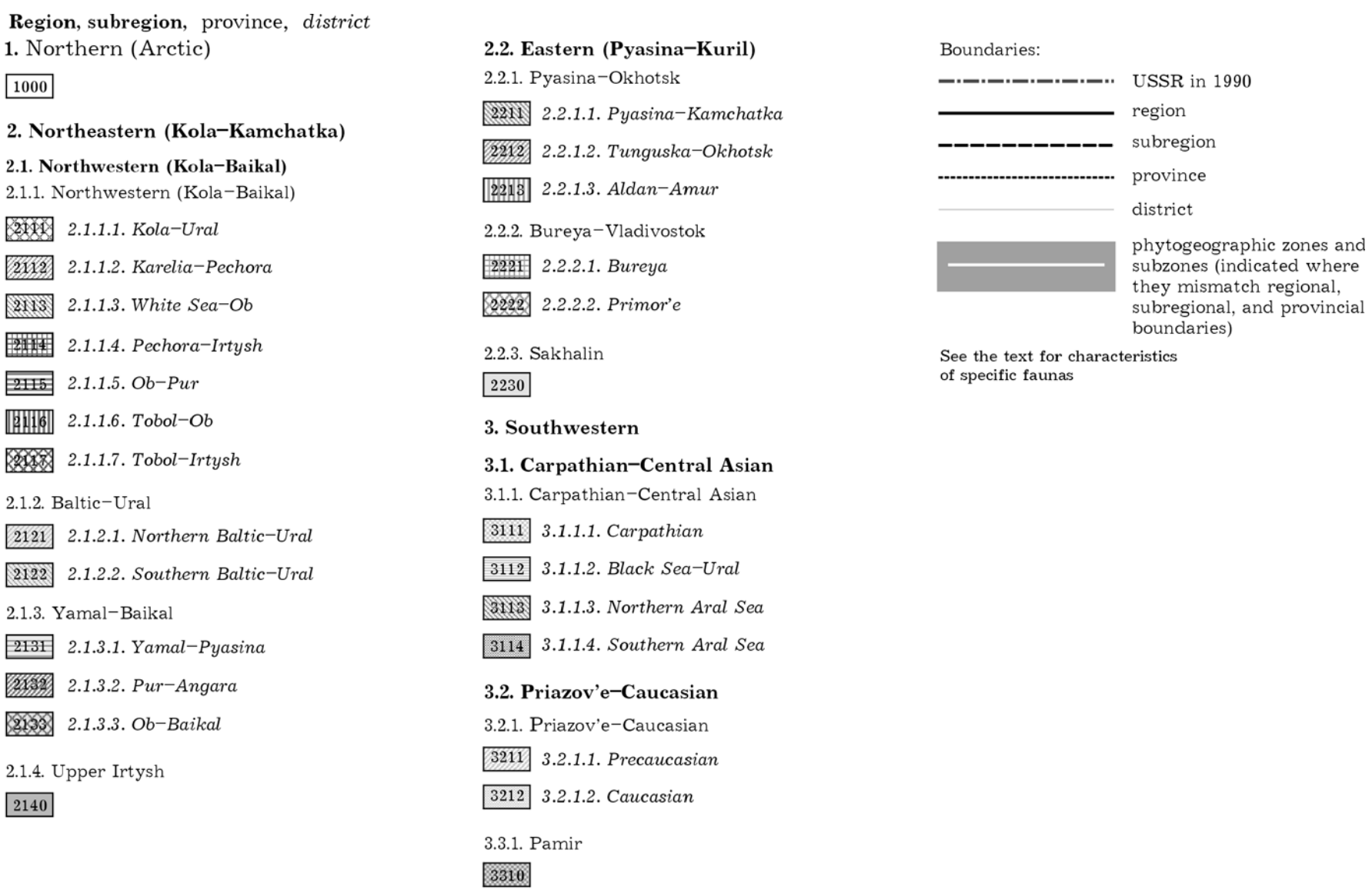
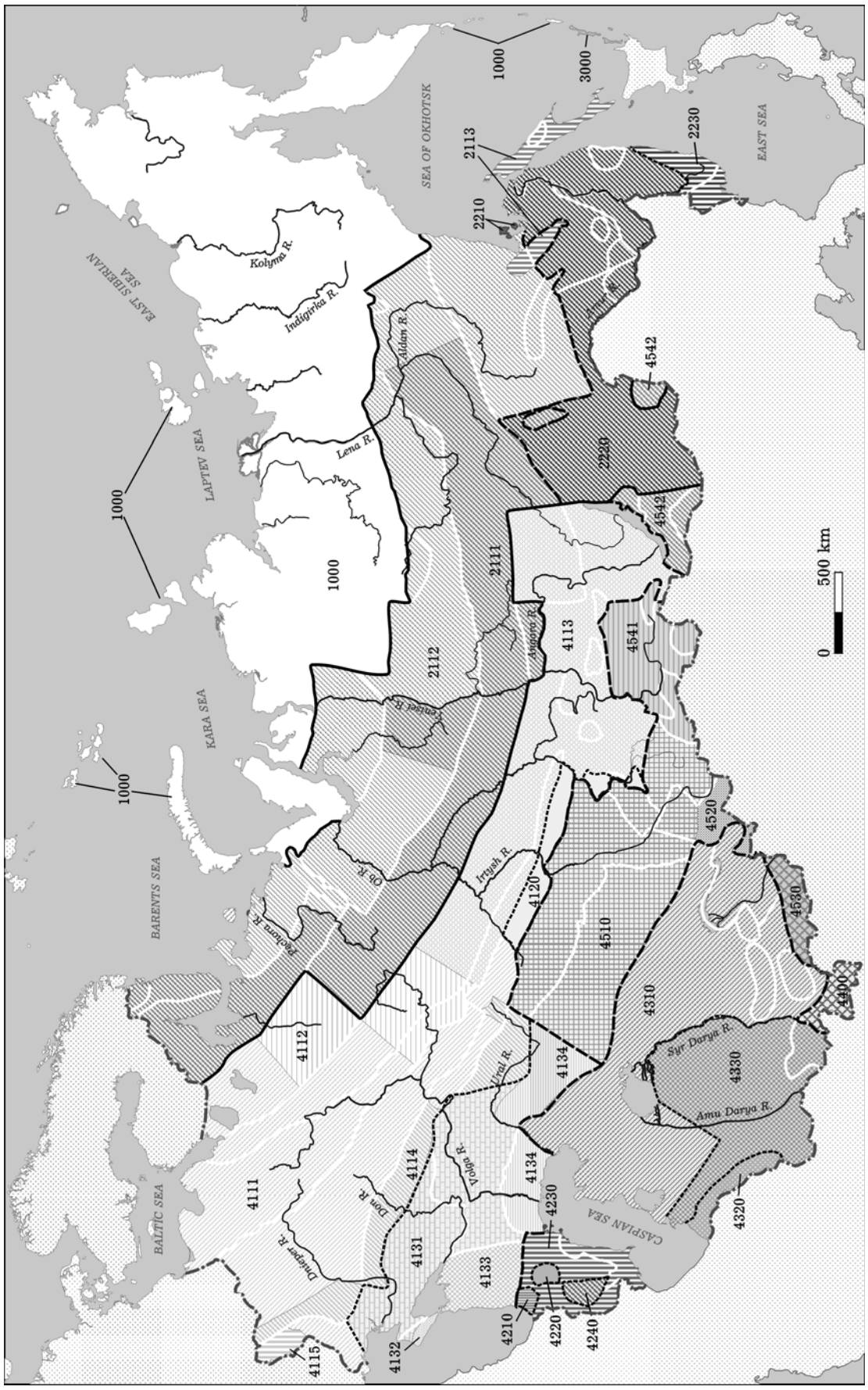


Fig. 1. Amphibian faunistic regions of Northern Eurasia.


EAST SIBERIAN SEA
LAPTEV SEA
KARA SEA
BARENTS SEA
BALTIC SEA
SEA OF OKHOTSK
EAST SEA
CASPIAN SEA
Kolyma R.
Indigirka R.
Lena R.
Aldan R.
Anadyr R.
Yenisei R.
Ob R.
Pechora R.
Irtysh R.
Ural R.
Volga R.
Don R.
Dnepr R.
Syr Darya R.
Amu Darya R.
1000
3000
2230
2113
2210
4542
2220
2111
2112
4113
4541
4520
4120
4630
4510
4310
4400
4330
4134
4112
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4114
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4320
4131
4133
4210
4220
4240
4132
4115
0
500 km

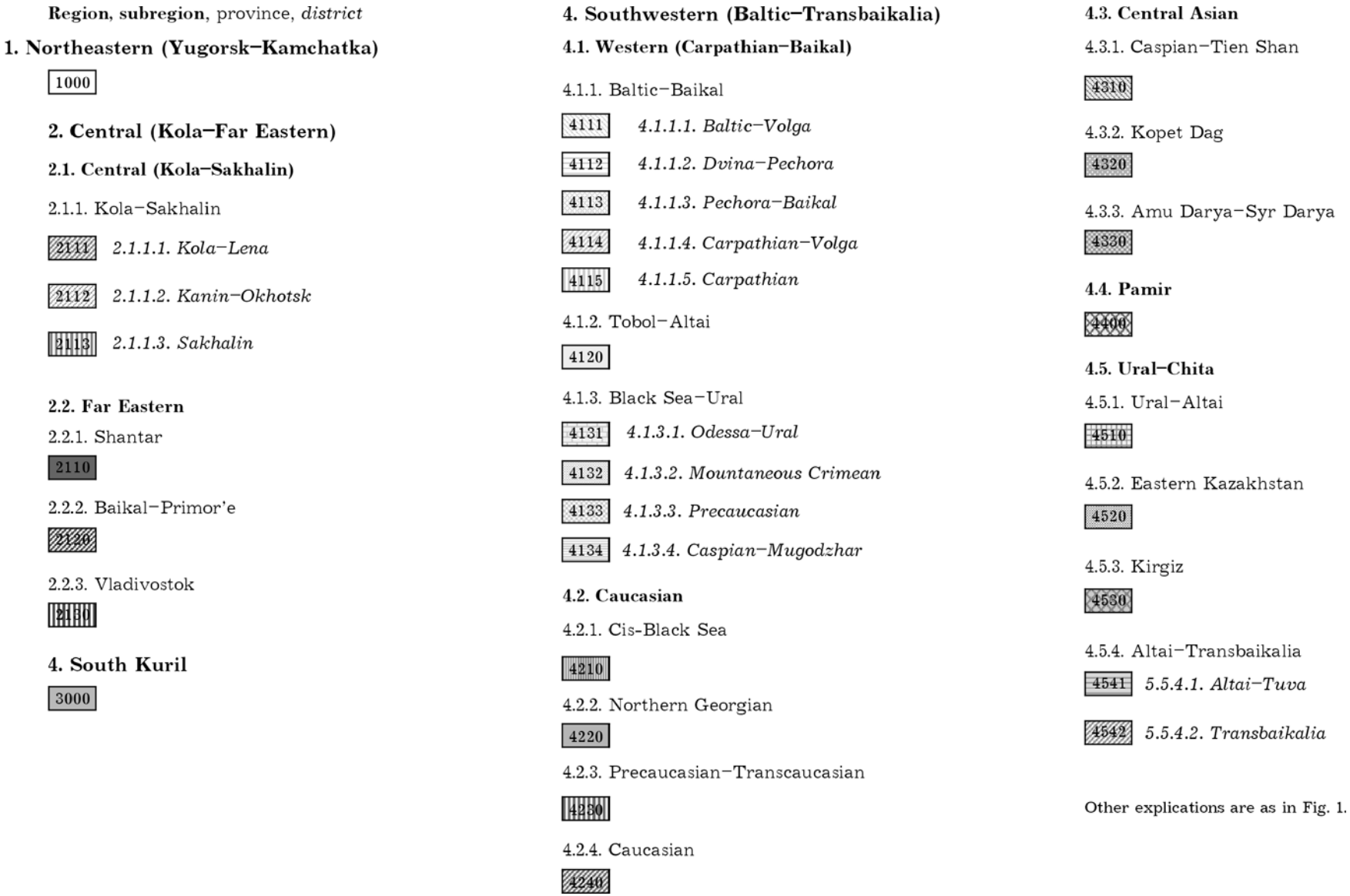

Fig 2. Reptile faunistic regions of Northern Eurasia.

Reptiles

According to reptile distributions, Northern Eurasia is divided into 4 faunistic regions, i.e., the reptile classification has one region more than amphibian one due to a separate taxon—South Kuril region. The region has resulted from, on the one hand, insular impoverishment of fauna that does not result in disappearing of reptiles as this is the case with other northern and remotest eastern islands. On the other hand, thanks to its southern location and proximity to the Japanese islands, the region is inhabited by species exotic to Northern Eurasia. Hence the fauna of the region has been identified as a separate taxon most of which lies to the south (Fig. 2).

Two of the separated regions, Central and Southwestern, are divided into 7 subregions, 18 provinces, and 14 districts. Thus, reptile faunistic classification has more units than amphibian one. This is due to a greater number of species and their greater ecological heterogeneity. In the first region, neither reptiles nor amphibians were recorded, in the second 22 amphibian and 19 reptile species were recorded, and in the third, southernmost, region 24 amphibian and 150 reptile species were recorded, respectively. Therefore, reptile diversity increases southward to a greater extent than that of amphibians that are much less tolerant to both warmth and moisture deficit than reptiles are to moisture deficit. The total number of reptiles recorded in Northern Eurasia is about 4 times higher than that of amphibians (168 and 41, respectively).

Below is the reptile classification of Northern Eurasia.

1. Northeastern (Yugorsk–Kamchatka) region: No reptiles recorded.

2. Central (Kola–Far Eastern) region: *Zootoca vivipara* 37, *Vipera sachalinensis* 13, *Vipera berus* 11, *Elaphe dione* 9, *Gloydius intermedius* 6; 3/19.

2.1. Central (Kola–Sakhalin) subregion (2.1.1, Kola–Sakhalin province): *Zootoca vivipara* 67, *Vipera berus* 25, *Vipera sachalinensis* 6, *Anguis fragilis* 2, *Gloydius halys* 2; 2/5.

Districts

2.1.1.1. Kola–Lena: *Vipera berus* 48, *Zootoca vivipara* 48, *Anguis fragilis* 3; 2/3.

2.1.1.2. Kanin–Okhotsk: *Zootoca vivipara*; 1/1.

2.1.1.3. Sakhalin: *Vipera sachalinensis* 50, *Zootoca vivipara* 50; 2/2.

2.2. Far Eastern subregion: *Vipera sachalinensis* 18, *Elaphe dione* 16, *Zootoca vivipara* 12, *Gloydius ussuriensis* 11, *Gloydius intermedius* 11; 6/17.

Provinces

2.2.1. Shantar: *Vipera sachalinensis* 1/1.

2.2.2. Baikal–Primor'e: *Vipera sachalinensis* 20, *Elaphe dione* 20, *Zootoca vivipara* 19, *Gloydius ussuriensis* 13, *Gloydius intermedius* 9; 5/10.

2.2.3. Vladivostok: *Vipera sachalinensis* 9, *Takydromus amurensis* 9, *Elaphe schrenkii* 9, *Elaphe dione* 9, *Natrix tigrina* 9; 12/15.

3. South Kuril region: *Elaphe quadrivirgata* 20, *Elaphe climacophora* 20, *Elaphe japonica* 20, *Plestiodon latiscutatus* 20, *Dinodon orientale* 20; 5/5.

4. Southwestern (Baltic–Transbaikalia) region: *Lacerta agilis* 7, *Natrix natrix* 6, *Elaphe dione* 4, *Zootoca vivipara* 4, *Vipera renardi* 3; 11/163.

4.1. Western (Carpathian–Baikal) subregion: *Natrix natrix* 16, *Lacerta agilis* 14, *Zootoca vivipara* 11, *Vipera berus* 9, *Coronella austriaca* 7; 6/40.

4.1.1. Baltic–Baikal province: *Natrix natrix* 19, *Zootoca vivipara* 18, *Lacerta agilis* 16, *Vipera berus* 14, *Anguis fragilis* 11; 5/14.

Districts

4.1.1.1. Baltic–Volga: *Natrix natrix* 16, *Anguis fragilis* 16, *Vipera berus* 16, *Lacerta agilis* 16, *Zootoca vivipara* 15; 6/9.

4.1.1.2. Dvina–Pechora: *Anguis fragilis* 25, *Vipera berus* 25, *Natrix natrix* 25, *Zootoca vivipara* 25; 4/4.

4.1.1.3. Pechora–Baikal: *Natrix natrix* 26, *Zootoca vivipara* 26, *Lacerta agilis* 24, *Vipera berus* 19, *Gloydius halys* 3; 4/7.

4.1.1.4. Carpathian–Volga: *Coronella austriaca* 16, *Natrix natrix* 16, *Anguis fragilis* 12, *Zootoca vivipara* 12, *Vipera nikolskii* 9; 6/9.

4.1.1.5. Carpathian: *Anguis fragilis* 12, *Vipera ursinii* 12, *Coronella austriaca* 12, *Natrix natrix* 12, *Emys orbicularis* 12; 8/8.

Provinces

4.1.2. Tobol–Altai: *Natrix natrix* 44, *Lacerta agilis* 33, *Vipera renardi* 22; 2/3.

4.1.3. Black Sea–Ural: *Natrix tessellata* 8, *Natrix natrix* 8, *Emys orbicularis* 8, *Vipera renardi* 7, *Lacerta agilis* 7; 12/37.

Districts

4.1.3.1. Odessa–Ural: *Natrix tessellata* 9, *Natrix natrix* 9, *Emys orbicularis* 9, *Lacerta agilis* 9, *Eremias arguta* 9; 11/15.

4.1.3.2. Mountainous Crimean: *Vipera renardi* 7, *Mediodactylus kotschyi* 7, *Pseudopus apodus* 7, *Coronella austriaca* 7, *Coluber caspius* 7; 14/14.

4.1.3.3. Precaucasian: *Anguis fragilis* 5, *Vipera kaznakovi* 5, *Vipera renardi* 5, *Pseudopus apodus* 5, *Coronella austriaca* 5; 22/22.

4.1.3.4. Caspian–Mugodzhar: *Vipera renardi* 8, *Phrynocephalus guttatus* 8, *Elaphe dione* 8, *Eryx miliaris* 8, *Natrix tessellata* 8; 14/17.

4.2. Caucasian subregion: *Coronella austriaca* 3, *Natrix tessellata* 3, *Natrix natrix* 3, *Lacerta praticola* 3, *Lacerta agilis* 3; 31/78.

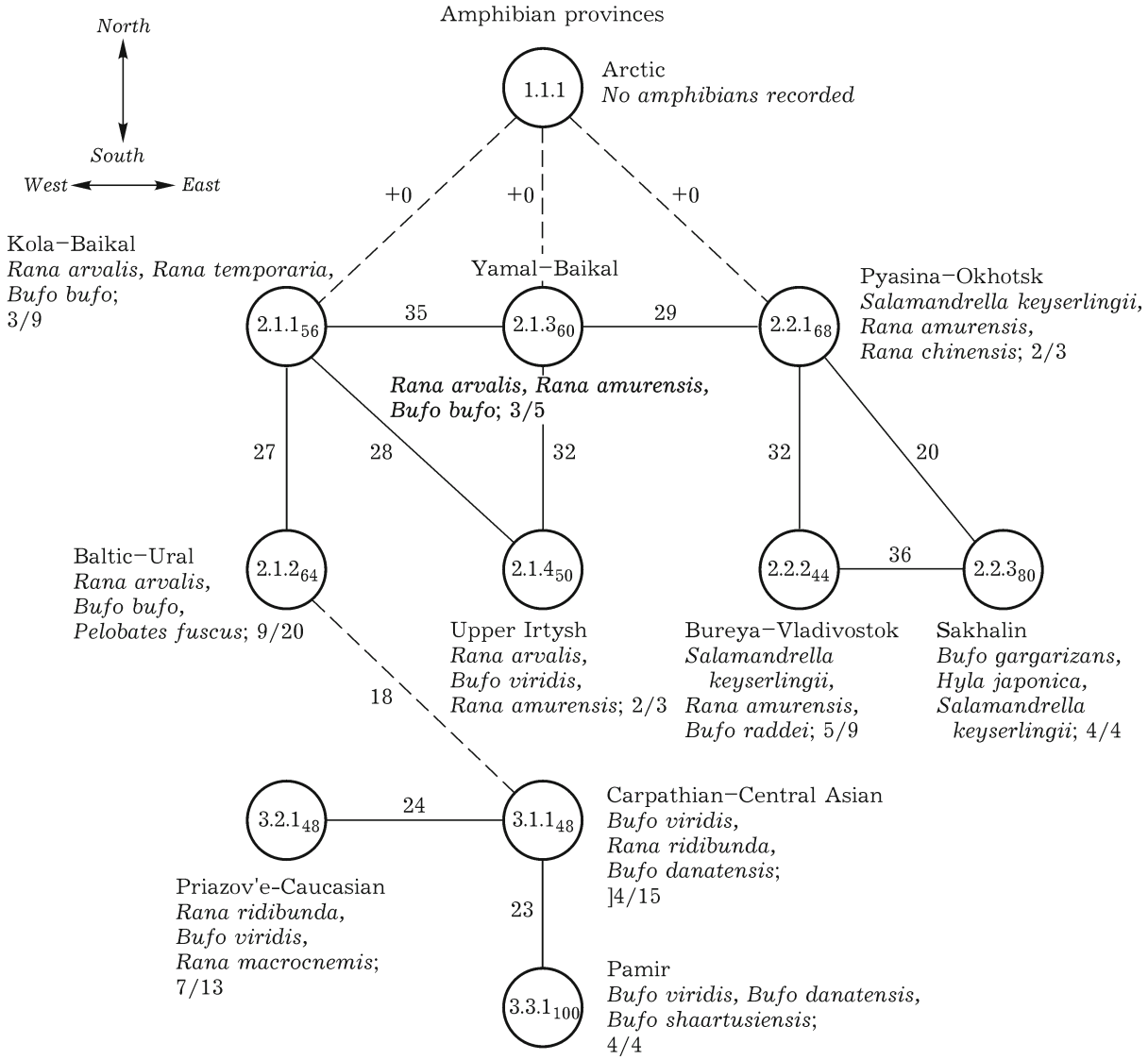

Fig. 3. Spatial-typological structure of the amphibian fauna of Northern Eurasia at provincial level. The figures in the vertices stand for taxon numbers according to the classification, the subscripts, for intragroup similarity. Continuous edges identify significant over-threshold similarity, dash edges identify weak similarity, and dotted edges, assumed similarity. The figures at the edges stand for intergroup similarity; the vertices are accompanied by three most frequent species and total average occurrence in areas/the total number of amphibian or reptile species. The arrows accompanying the main determinant factors indicate direction of the increase and herpetofaunistic trends.

Provinces

4.2.1. Cis-Black Sea: *Vipera kaznakovi* 6, *Coronella austriaca* 6, *Coluber najadum* 6, *Elaphe longissima* 6, *Natrix tessellata* 6; 18/18.

4.2.2. Northern Georgian: *Vipera dinniki* 7, *Vipera lotievi* 7, *Ablepharus pannonicus* 7, *Coronella austriaca* 7, *Elaphe hohenackeri* 7; 14/14.

4.2.3. Precaucasian–Transcaucasian: *Agama caucasica* 3, *Pseudopus apodus* 3, *Telescopus fallax* 3, *Elaphe dione* 3, *Elaphe quatuorlineata* 3; 37/72.

4.2.4. Caucasian: *Agama caucasica* 3, *Agama ruderata* 3, *Anguis fragilis* 3, *Vipera ammodytes* 3, *Vipera renardi* 3; 29/29.

4.3. Central Asian subregion: *Eremias velox* 4, *Trapelus sanguinolentus* 4, *Eryx tataricus* 4, *Natrix tessellata* 4, *Testudo horsfieldii* 4; 26/91.

Provinces

4.3.1. Caspian–Tien Shan: *Elaphe dione* 5, *Eryx tataricus* 5, *Natrix tessellata* 5, *Gloydius halys* 5, *Eremias velox* 5; 21/44.

4.3.2. Kopet Dag: *Agama caucasica* 2, *Trapelus sanguinolentus* 2, *Crossobamon eversmanni* 2, *Cyrtopodion caspius* 2, *Cyrtopodion spinicauda* 2; 44/44.

4.3.3. Amu Darya–Syr Darya: *Trapelus sanguinolentus* 3, *Varanus griseus* 3, *Crossobamon eversmani* 3, *Ablepharus pannonicus* 3, *Macrovipera lebetina* 3; 39/60.

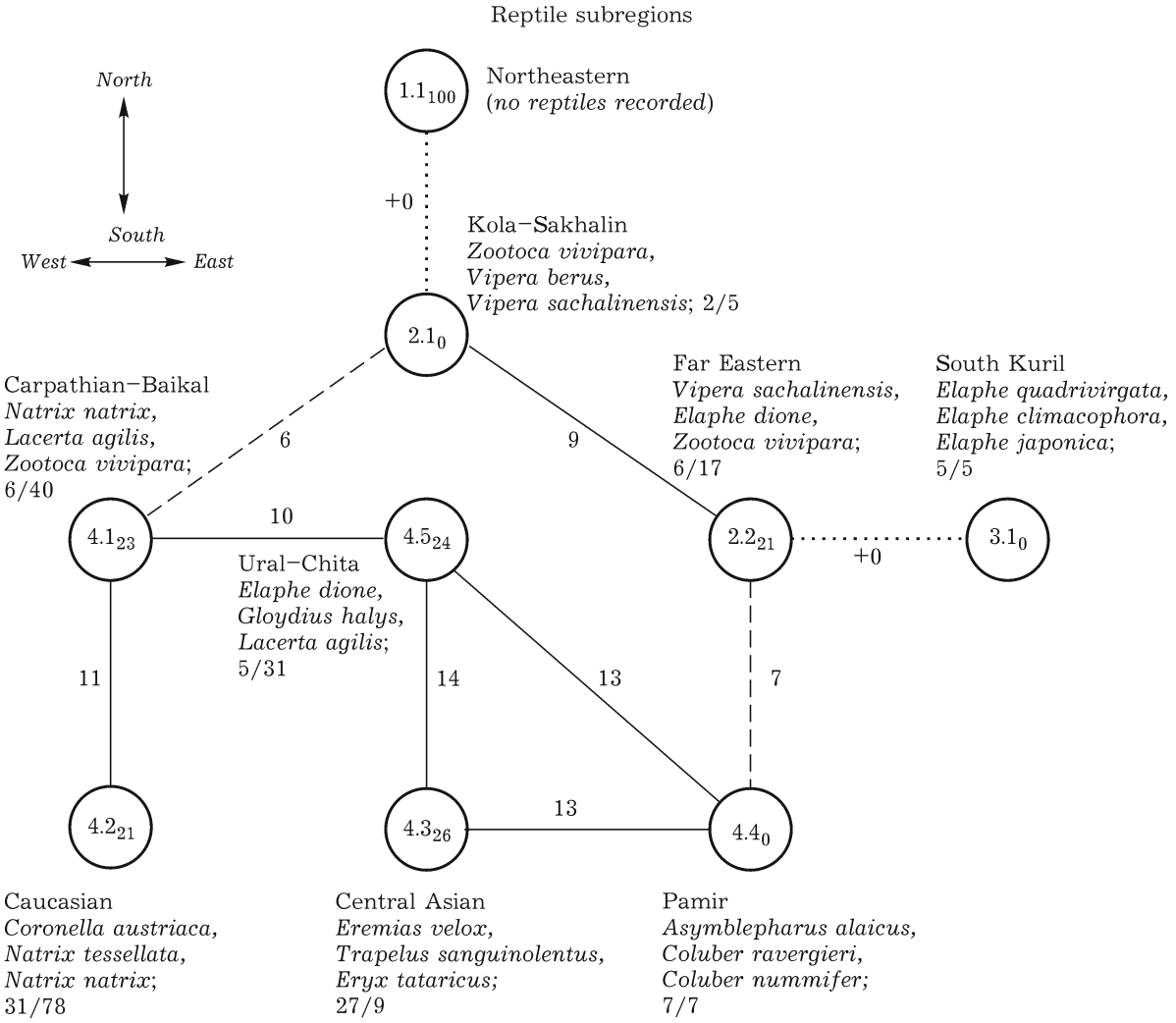

Fig. 4. Spatial-typological structure of the reptile fauna of Northern Eurasia at subregional level. Explications are as in Fig. 3.

4.4. Pamir subregion: *Asymblepharus alaicus* 14, *Ablepharus darvazi* 14, *Coluber ravergieri* 14, *Coluber nummifer* 14, *Elaphe dione* 14; 7/7.

4.5. Ural–Chita subregion: *Elaphe dione* 18, *Gloydius halys* 16, *Lacerta agilis* 14, *Vipera renardi* 10, *Eremias arguta* 7; 5/31.

Provinces

4.5.1. Ural–Altai: *Elaphe dione* 20, *Lacerta agilis* 20, *Vipera renardi* 16, *Gloydius halys* 16, *Eremias arguta* 11; 5/12.

4.5.2. Eastern Kazakhstan: *Trapelus sanguinolentus* 8, *Vipera renardi* 8, *Phrynocephalus guttatus* 8, *Phrynocephalus melanurus* 8, *Phrynocephalus versicolor* 8; 12/12.

4.5.3. Kirgiz: *Asymblepharus alaicus* 6, *Ablepharus deserti* 6, *Vipera renardi* 6, *Alsophylax tokobajevi* 6, *Elaphe dione* 6; 17/17.

4.5.4. Altai–Transbaikalia: *Gloydius halys* 26, *Elaphe dione* 26, *Zootoca vivipara* 16, *Lacerta agilis* 10, *Eremias argus* 10; 3/9.

Districts

4.5.4.1. Altai–Tuva: *Gloydius halys* 29, *Zootoca vivipara* 29, *Elaphe dione* 14, *Natrix natrix* 14, *Lacerta agilis* 14; 4/5.

4.5.4.2. Transbaikalia: *Elaphe dione* 29, *Gloydius halys* 24, *Zootoca vivipara* 14, *Eremias argus* 14, *Vipera berus* 5; 4/8.

Spatial-typological structure of the Northern Eurasian fauna. Similarity graphs for the two animal classes are essentially similar and have nearly the same number of taxa (Figs. 3 and 4). Although the schemes differ in the taxon boundaries, sizes, and rank, they clearly illustrate that faunistic inhomogeneities are related to hydrothermal regime, i.e., warmth deficit for both groups and moisture deficit for reptiles. The diagonal shift of taxon boundaries that had been found in

the herptile classification and causal factors are even more obvious in the separate graphs and maps.

Informativeness of classifications. The reptile and amphibian classifications outlined herein approximate 75 and 91% of variance in the similarity matrix, correlation coefficients being approximately 0.87 and 0.95, respectively. The classifications by Bobrov and Aleshchenko [7–9] explain 66 and 28% of variance (0.81 and 0.53). Therefore, these classifications are by 14% and 3.5 times less informative compared to our classification with the smallest taxonomic units as we delimit them. Extrapolation of herptile results to each of the classes, as was done by Nikol'skii [6], does not significantly improve explained variance (23% before and 25% after extrapolation). The amphibian classification by Borkin [10] accounts for as much variance (25%, correlation coefficient 0.5). The zoo- and biogeographic, as well as landscape, classifications [15–18] approximate from 15 to 25% of variance (correlation coefficient 0.39–0.5). Limitations and legitimacy of such comparisons have been discussed earlier in Blinova and Ravkin [19].

Spatial-typological organization of the amphibian and reptile faunas in Northern Eurasia. The most important factors affecting the homogeneity of the faunas are warmth supply (30% for each class) and zonal–subzonal climatic changes correlated with it (19% for amphibians and 21% for reptiles). Provincial differences approximate 22% and 12% of variance for amphibians and reptiles, respectively, whereas postglacial dispersal 12 and 5%. Zonality does not appear to have any significant effect on the faunistic inhomogeneities (3 and 2%). All the mentioned environmental factors can explain 43 and 35% of variance in the similarity coefficients for amphibians and reptiles, respectively (correlation coefficients 0.66 and 0.59).

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