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# 9. THE BIODIVERSITY OF AMPHIBIANS AND REPTILES IN THE BALKAN PENINSULA

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> "The northern Adriatic region, the south-eastern region from the Alps to the Carpathian Mts., Dalmatia and Albania, as well as their neighbouring seas, have a particular biogeographic significance, which I will explain in more detail elsewhere along with the Pendulation theory. Here, we have an ancient corner of Europe and one of the most interesting parts of the whole World." (Simroth, 1907; our translation)

## INTRODUCTION

Biologists have long recognised that the circum-Mediterranean region, and the Balkans in particular, contains an extraordinary variety of life forms in both plant and animal groups (Gaston & David, 1994), which is expressed in terms of biogeographical diversity, including that of amphibians and reptiles. The Mediterranean region of Europe comprises three large southern peninsulas and their archipelagoes. The amphibians and reptiles in this part of Europe exhibit complex biogeographic patterns, with large numbers of endemic taxa, dynamism, and the presence of certain general biological phenomena (see below). Distinguished by a high level of heterogeneity and of mosaicism, and natural fragmentation due to mountain ranges, the Balkan Peninsula is particularly intriguing in this respect.

The biogeographical uniqueness of the peninsula is indisputable. The Balkans are delimited by a strong boundary (which occurs between two regions with significantly different biotas) separating them from the rest of Europe in regard to the distributional pattern of lizards (Ramirez *et al.*, 1992), for example, but are less clearly delimited in terms of the quantitative biogeography of amphibians (Real *et al.*, 1992). It is therefore remarkable that this is the least-studied batrachofauna and herpetofauna of Europe. Publications which deal with particular groups of amphibians and reptiles of the entire Balkan Peninsula are scarce (*e.g.* Radovanović & Martino, 1950), as are general remarks on the Balkan batrachofauna and herpetofauna (Džukić, 1993; Džukić *et al.*, 2001; Borkin, 1998).

The intention of this paper is to assess current evidence for batrachological and herpetological diversity in the Balkans. Because of their limited dispersal ability and temperature dependence, terrestrial and freshwater amphibians and reptiles can be highly sensitive indicators for the study of biogeographic pattern and process. The specific aim of this paper is to provide a holistic treatise on amphibians and reptiles of the Balkan Peninsula, rather than focusing on zoogeographical issues *per se*. Various aspects of diversity are discussed in comparison with statistics for other European faunas of these vertebrates, from the Iberian and Apennine peninsulas in particular. The origins of the present day biodiversity of the Balkan batrachofauna and herpetofauna are also considered. Finally, it is demonstrated that in some general biological phenomena such as hybridisation and hybridogenesis, interspecific and intraspecific heterochronic phenomena, and switching of reproductive modes within a single species, Balkan amphibians and reptiles are distinct in comparison with other European areas.

## PHYSICAL GEOGRAPHY OF THE STUDY REGION

In contrast to the Iberian and Apennine peninsulas, the Balkan Peninsula is not separated physically from the European mainland by mountain barriers. As a result, the northern and, especially, western boundaries of the Balkan Peninsula have never been demarcated precisely. Some suggest that the tributaries of the Black Sea hydrological system which are closest to the Adriatic shore (running in a west-east direction) should be followed. The Kupa-Sava-Danube border is constructed in this way, wherein Rijeka, on the Adriatic coast, is taken to be the westernmost mark. The resultant designated area covers 490,000 km$^2$. Others define a dividing line between the Alps and Dinarides (Dinaric Alps) as a northwestern border. This border follows the Sava River up to the mouth of the Krka and then runs up the Krka to its source. Thereafter, the Vipava and Soča Rivers are followed to their mouths in the Bay of Trieste. The area of the Balkan Peninsula defined in this way comprises 520,000 km$^2$.

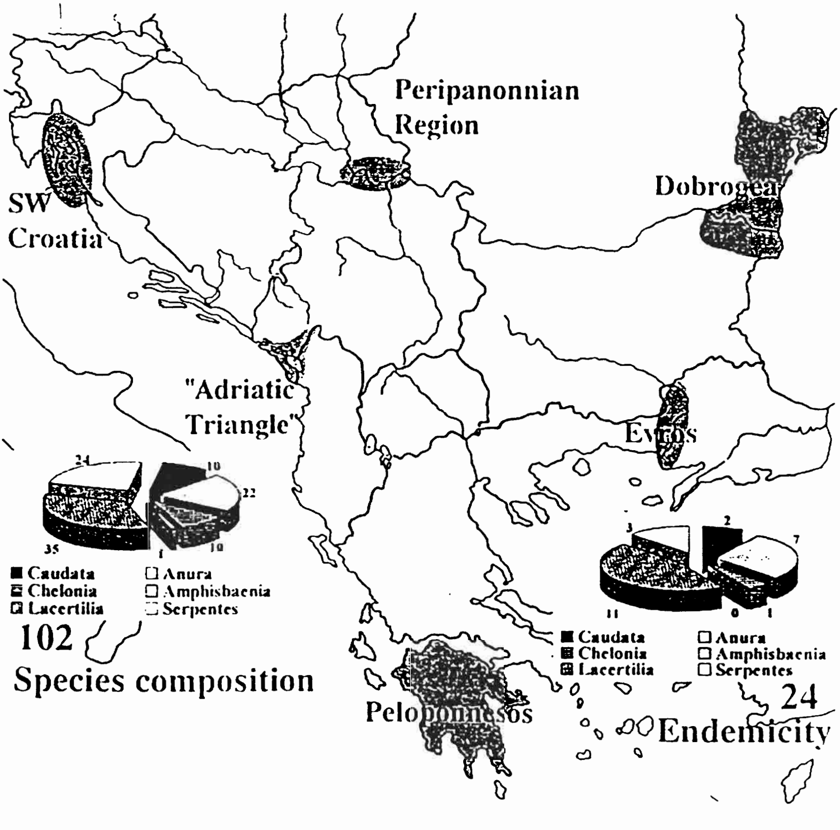

*Figure 1. Map showing the location of the six Balkan study regions, and pie diagrams of the presence of Balkan amphibian and reptile species, and their endemicity.*

In order to assess differences in species richness and levels of endemicity, the following six regions were selected on a rather arbitrary basis: SW Croatia, the Peripannonian region, Dobrugea, the "Adriatic Triangle", the Peloponnisos, and Evros. It was assumed that these regions were large enough to include all relevant attributes of diversity across the Balkans as a whole (Figure 1). The designation of regions was based mainly on their geography, and orography in particular; the altitudinal range of an area was considered to be highly significant. Additional criteria included the variability of habitats and biomes, biogeographical connections with other regions, and previous proposals that some of them be designated hot spots of diversity in this part of Europe and/or set aside as biogenetic reserves (Simroth, 1907; Corbett, 1989). It should be noted that these regions are not zoogeographic entities in any sense. Some of the regions are physiognomically well separated, such as Dobrugea and the Peloponnisos, whilst others (SW Croatia and the Peripannonian, "Adriatic Triangle", and Evros regions) are closely adjacent.

The largest of these six areas is the Peloponnisos region (Peloponnisos and its nearest islands), with an area of 30,200 km$^2$. Dobrugea includes parts of Romania and Bulgaria and has an area of 25,800 km$^2$. With an area of 15,200 km$^2$, SW Croatia consists of the Kvarner area, the eastern part of Istria, and the Velebit and Kapela Mountains. As the northernmost part of the Balkans, the Peripannonian region includes the Central-Balkan edge of the Pannonian Plain, as well as the region's hilly areas and river valleys, all of which cover 10,000 km$^2$. The "Adriatic Triangle" consists of the Prokletije Mountain Massif and the lowland Lake Scutari (= Skadar) area, with an area of 7,500 km$^2$. The Evros is the smallest region (6,700 km$^2$), comprising the lower valley of the Marica River and adjacent areas, including the Evros reservation. With the exception of the Peripannonian region, each of these regions includes a maritime coastal zone.

## TAXONOMIC DIVERSITY AND PATTERNS OF SPATIAL DISTRIBUTION

Amphibians and reptiles occur throughout the Balkan Peninsula, regardless of altitude and latitude. Their wide distribution is a function both of the moderate climate (whose characteristics are well within the tolerance limits of the fauna) and the high adaptive ability of amphibians and reptiles which allows them to colonise a variety of biomes. They live either cryptically in secluded places on land or visibly in the open, and some species alternate between these two modes of existence during their life cycle. Several are known to be troglophilous and trogloxenous, including those which are fossorial.

### *Species and Subspecies Diversity*

The Balkans harbour many phylogenetic lineages of reptiles and amphibians, some of which have undergone extensive radiation, which has probably occurred *in situ*. Our current annotated taxonomic list (Appendix) includes 104 species: 33 amphibians and 71 reptiles. Lizards are the most species-rich group, followed by the snakes, tailless amphibians, turtles, and tailed amphibians; amphisbaenians are very rare.

To the best of our knowledge, two species have been introduced to the Balkan Peninsula (a frog *Rana catesbeiana* and a turtle *Trachemys scripta*), probably around 30 years ago or more. It has also been speculated that some taxa in the Mediterranean region, especially on islands and probably including the Balkan Peninsula, are of anthropochorous origin (Corti *et al.*, 1997; 1999). The African chameleon

(*Chamaeleo africanus*), for example, was probably introduced into Greece (the Peloponnisos) during the Mycenaean era between 3200 - 3500 B.C. (Bőhme *et al.*, 1998), being kept as pets by citizens and kings. The Romans might also have had an influence on native herps, by introducing the Aesculapian snake (*Elaphe longissima romana*) and possibly others for religious rituals in temples. This snake was worshipped by followers of the cult of the god Aesculapius during Roman times all over the Balkans, especially in eastern Serbia, where specimens with the characteristics of *E. l. romana* have been found unexpectedly (see Appendix).

As would be expected, species diversity is not distributed evenly across the peninsula. In regard to overall species richness (amphibians + reptiles), the "Adriatic Triangle" appears to be the most species-rich, with 15 amphibians and 39 reptiles (=54 species; Figure 2; Appendix). The southernmost part of the Balkans, the Peloponnisos, has 11 amphibians and 38 reptiles (49 species). Southwestern Croatia has similar species richness, but with more amphibians (16 species) and fewer reptiles (33 species). The Evros area has 12 amphibians and 33 reptiles (45 species). The least species-richness region is the Peripannonian, where amphibians outnumber reptiles (19 and 16 species, respectively), and the most northeastern part of the Balkans (Dobrugea), with 12 amphibians and 23 reptiles (35 species; Figure 2; Appendix).

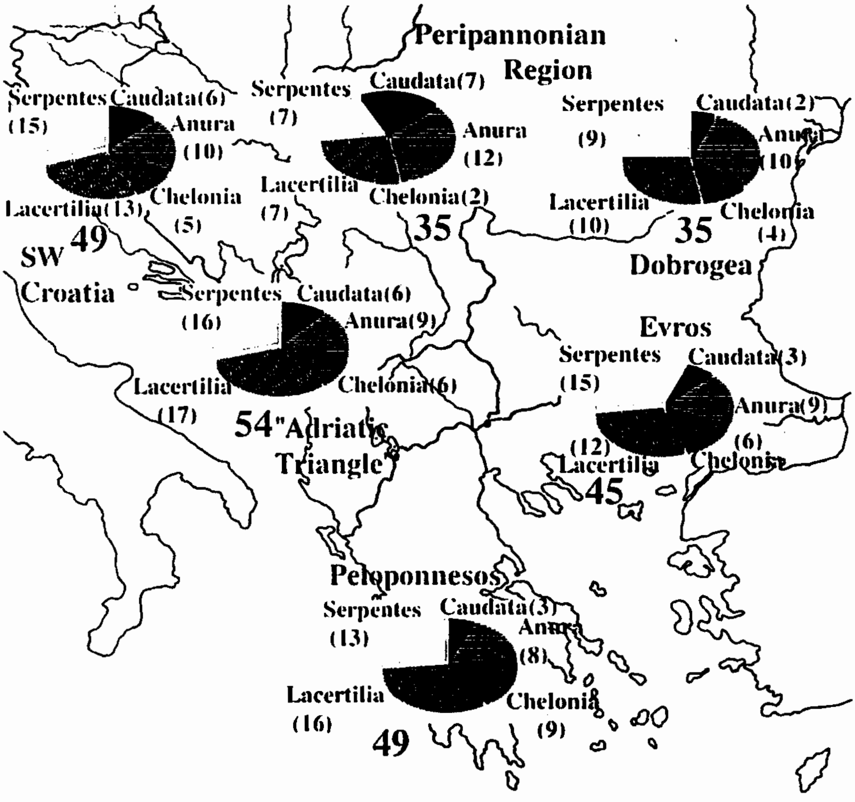

*Figure 2. Spatial pattern of species diversity in the six Balkan study regions.*

There is no correlation between number of species and surface area. The Spearman's nonparametric correlation coefficients between these two variables are negative, but statistically insignificant (rs = -0.36 for amphibians, rs = -0.01 for reptiles, $P > 0.05$). The greatest disproportion between number of species and region size appears in the case of Peloponnisos for the amphibians, where the largest region has the smallest number of species. This relationship is probably due to ecological factors, since the region is climatically unfavorable for amphibians. For reptiles, the greatest disproportion occurs in the case of the "Adriatic Triangle", the fifth region in size but with, as noted, the largest number of reptile species. This is again attributable to environmental factors, with a complex range of habitats varying from low-altitude Mediterranean, to medium-altitude temperate and high-altitude boreal habitats.

The taxonomic richness of the Balkans is especially apparent in a number of sister species (*Triturus cristatus* superspecies, *Rana ridibunda* superspecies, *Podarcis* spp., *Archeolacerta* spp., *Lacerta* spp.). Equally, there is substantial subspecific diversity in the Balkans. As many as 239 autochthonous subspecies of amphibians and reptiles are known, with an average of 1.03 subspecies per amphibian species, and 2.94 subspecies per reptiles species. The most extensive subspecific differentiation occurs among lizards (156 subspecies, Table 1), especially in *Cyrtodactylus kotschyi*, *Podarcis erhardii*, *Podarcis melisellensis* and *Podarcis sicula*. It should be noted that these figures must be taken cautiously, however, since the taxonomic validity of many subspecies has not been established with rigour, and important aspects of their distributions have not yet been resolved. A good example is the alpine newt (*Triturus alpestris*), for which the number of subspecies has been reduced substantially following recent taxonomic revision (Sotiropoulos *et al.*, 2001a). Our list includes all described subspecies that have not been disputed to date.

*Table 1. Number of autochthonous Balkan amphibian and reptile taxa, listed according to taxonomic category of the main groups, and the number of species (spp.) which have the marginal zone of their distributional range in the Balkans. (sspp. = subspecies)*

| Order | Families | Spp. | Sspp. | Endemic spp. | Endemic sspp. | Range limits |
|---|---|---|---|---|---|---|
| AMPHIBIA | | | | | | |
| Caudata | 2 | 10 | 21 | 2 | 9 | 8 |
| Anura | 5 | 22 | 12 | 7 | 3 | 11 |
| REPTILIA | | | | | | |
| Testudines | 4 | 10 | 8 | 1 | 2 | 4 |
| Amphisbaenia | 1 | 1 | 1 | 0 | 0 | 1 |
| Lacertilia | 6 | 35 | 156 | 11 | 65 | 19 |
| Serpentes | 4 | 24 | 41 | 3 | 14 | 17 |
| **Total** | **22** | **102** | **239** | **24** | **93** | **60** |

The available evidence suggests that new species emerged during the Tertiary (mostly during the Miocene and Pliocene), while the origin of subspecies was confined to Pleistocene glacial stages (*e.g.* *Triturus* and *Salamandra* taxa: Bolkay, 1928; Wallis & Arntzen, 1989; Oosterbroek & Arntzen, 1992; Crnobrnja-Isailović *et al.*, 1997; Grossenbacher, 1994; Weisrock *et al.*, 2001; Denoël *et al.*, 2001; lacertids: Böhme & Corti, 1993; amphibians and reptiles in general: Paunović, 1990).

Although biogeographical importance does not necessarily correlate directly with the size of a peninsula (as is clear in Scandinavia, where species richness is low), it is generally argued that the potential number of species is proportional to area if geographic locations are similar. This does not hold true in southern Europe, however, wherein the Balkan Peninsula (with 104 amphibian and reptile species) has the highest species richness, and yet is only the second largest peninsula. For purposes of comparison, the Italian Peninsula has 76 amphibians and reptiles within an area of 150,000 km$^2$ (OECD, 1994, cited in European Centre for Nature Conservation, 2001), while the largest European peninsula (the Iberian) has only 78 within an area of 581,000 km$^2$ (World Conservation Monitoring Centre, 1992, cited in European Centre for Nature Conservation, 2001) (for the number of species see also Corbett, 1989; Astudillo & Arano, 1995; World Conservation Monitoring Centre, 1997). As an aside, it is interesting to note that both these peninsulas contain more ancient phylogenetic lineages of some animal groups than in the Balkans (Oosterbroek & Arntzen, 1992).

### *Taxonomic peculiarities*

The list of Balkan amphibian and reptile taxa is sure to increase in the near future. Ongoing detailed morphological research has revealed new evidence for intraspecific differentiation, within species such as the alpine crested newt *Triturus carnifex* (Kalezić *et al.*, 1997), or the eastern spadefoot toad *Pelobates syriacus* (Ugurtas *et al.*, 2002). There is also evidence that a number of morphologically-cryptic taxa may exist, since, in regard to the taxonomy of many amphibians and reptiles (such as the *Archeolacerta* and *Zootoca* lizard groups, or the brown frogs - *'Ranae fuscae'*), the Balkan Peninsula is a highly perplexing region. Future genetically-based taxonomic studies may reveal further species-level diversity amongst existing taxa. Genetic data have already thrown light on old controversies over the origin and evolutionary diversification of some taxa, such as the crested newts (*Triturus cristatus* supespecies; Litvinchuk *et al.*, 1999), viviparous lizards (*Zootoca vivipara*; Mayer *et al.*, 2000), or the fire-bellied toads (*Bombina variegata* group; Radojičić , unpublished data).

Another taxonomic peculiarity of Balkan amphibians and reptiles is the high degree of phenotypic and genotypic variation in their populations, such that there is often a problem in applying diagnostic traits used to differentiate taxa in western and northern Europe, especially near hybrid zones. This is particularly the case where population affinities appear to be highly sensitive to the number of specimens examined from each population, such that many more samples need to be analysed statistically in order to establish firm taxonomical relationships (*e.g.* Arntzen & Wallis, 1999).

In addition, genetic differentiation among congeneric species would appear to be lower on the Balkan Peninsula than in more northern parts of Europe. For example, maximum hybrid index scores between *Bombina bombina* and *B. variegata* in Croatia reach a value of eight, while in Poland this measure of relative genetic distinctness can be as high as 12 (Szymura, 1993). Among *Triturus* species, the smallest genetic difference was found among Balkan congeneric populations (Kalezić & Hedgecock, 1980; Crnobrnja *et al.*, 1989) in comparison with those from western and Central Europe (Rafinski & Arntzen, 1987), and the former USSR (Litvinchuk *et al.*, 1994). Greater genetic differentiation was found in Greek populations of *Triturus* species than in the northern Balkans, Central and Northern Europe (Sotiropoulos *et al.*, 2001b), however.

## ENDEMICITY

The number of endemic taxa present is a very important component of assessing the importance of any fauna. The circum-Mediterranean region, including the Balkans, is already well known as a region of high endemicity (Oosterbroek & Arntzen, 1992; Jong, 1998). Levels of endemicity are especially high for amphibians and reptiles (Sara, 1996).

The Balkan Peninsula has 24 endemic amphibian and reptile species: nine amphibians (28.1% of the total number of autochthonous species) and 15 reptiles (21.4%) (Table 1, Figure 1). Within the most well-represented groups, the highest degree of endemicity occurs in tailless amphibians (31.8%) and the next highest in lizards (31.4%), while snakes have the lowest number of Balkan endemics (12.5%). In general, endemicity at the subspecific level is very high, ranging from 42.9% in Caudata to 25.0% in Testudines, with an average value of 38.9%.

*Figure 3. Incidence of Balkan endemics in the six Balkan study regions.*

In respect to spatial patterns of Balkan endemicity (for regions where diversity has been compared), the "Adriatic Triangle" appears to have the highest concentration of Balkan endemics (ten out of 54 species; 18.5%), followed by the Peloponnisos region (nine out of 49 species; 18.4%) (~~Table 1~~, Figure 3). The "Adriatic Triangle" is part of the Dinaric karst, a unique landscape formation that evolved in the limestone substrate of the Dinarides. However, despite a high number of species, the northern part of the

Dinaric karst (SW Croatia) has a very low proportion of the Balkan endemics (four out of 49 species; 8.2%). The same is true of the Evros region (three endemics out of 45 species; 6.7%). Interestingly enough, the northernmost parts of the Balkans (species-poor areas) lack Balkan endemic species. The Peripannonian region has only one Balkan endemic out of a total of 35 species (2.9%), while the Dobrugèa region is completely without Balkan endemics (Figure 3).

It is well known that centres of species richness tend to coincide with those of endemism (Anderson, 1994; Varga, 1995). This has been demonstrated clearly for Balkan amphibians and reptiles, in regard to six regions of the peninsula. The southern part of the Balkans is also characterised by a few instances of microinsular endemism (some lizards and one snake, *Macrovipera schweizeri*, on the Greek islands). However, in the Balkans most endemic species are not in general restricted to islands, so a higher number of islands does not promote greater probability of high endemism.

The Balkan Peninsula is apparently a core area, of "restricted territories with cumulated presence of stenochorous ("endemic") species" (Varga, 1995, p. 71). It also appears to be the richest centre of European batracho- and herpetofaunal endemism. The Iberian and Apennine peninsulas lag well behind the Balkans in this respect, for example. Although situated outside Europe, the Caucasus region is the area most similar to the Balkan Peninsula in its level of endemicity, but only if Trans-Caucasia is included. The Balkans are characterised by endemism at a taxonomic level as high as that of the genus: the monotypic genus *Proteus*, a troglobiontic tailed amphibian, is restricted in its distribution to the Dinaric karst (Sket, 1997). The general rule that "the level of endemism is highly correlated with the geological age of refuges in which relict-like species could survive and have evolved" (Varga, 1995, p. 85) seems to be confirmed in the case of the Balkan Peninsula.

The relictness of Balkan amphibian and reptile taxa has not been adequately investigated. It is impossible to present even an approximate estimate of the number of relict taxa on the peninsula and their distribution by main groups, since the relevant paleontological and phylogeographical data are lacking. Nevertheless, the data generated to date suggest that numerous relict groups, both glacial and preglacial, can be expected.

## MARGINALITY OF SPECIES RANGES IN THE BALKANS

Besides endemic species, there are a number of otherwise more or less widely-distributed taxa whose range limits are in the Balkans (Table 1). In fact, only four amphibian species and nine reptile species have ranges that extend well into the Balkan region without ending on the Peninsula. Species with the marginal zone of their distributional range in the Balkans comprise more than half of the total number of autochthonous species (19 amphibians and 41 reptiles; see Appendix and Table 1). Among Balkan amphibian species, range borders orientated towards southern Europe appear to be dominant (52.5%), followed by eastern borders (26.5%), in contrast to southeastern and northwestern borders, which are least numerous (10.5% each). Central Europe and, to a lesser extent, western Europe, appear to be the main sources for the Balkan batrachofauna. In contrast to amphibians, the most numerous range borders for reptiles are in the west, north, and northwest (24.4%, 24.4%, and 22.0%, respectively), followed by southern and eastern borders (12.2% each), while southwestern and southeastern range borders are virtually negligible (2.5% each). These facts confirm without doubt that reptiles of the Balkans carry the "seal" of southern and southeastern herpetofaunas.

Marginal zones of distribution ranges are much less frequent in Central and Northern Europe than in the Balkans. This seems to support the Rapoport rescue hypothesis as to the origin of latitudinal gradients in richness, which holds that low-latitude localities have relatively more species near the edge of their range than do high-latitude zones (see Stevens, 1992). In addition, the high level of diversity of amphibians and reptiles in the Balkans is at least partly due to the fact that communities composed of a high percentage of species at the edge of their geographical range are presumed to be more species-rich than communities composed primarily of species at the centre of their distribution. The evolutionary importance of range margins lies in the fact that although most peripheral populations are not going to evolve into distinct entities, there is still an astonishing potential for further diversification of the Balkan batrachofauna and herpetofauna.

## BIOGEOGRAPHICAL DIVERSITY

The Balkan batrachofauna and herpetofauna have varied biogeographical origins and connections with other regions. More specifically, the Balkans appear to have been a centre of speciation within some taxa, such as the crested newts (*Triturus cristatus* superspecies; Crnobrnja-Isailović *et al.*, 1997), the alpine newt (*Triturus alpestris*; Arano & Arntzen, 1987), the "true salamanders" (*Salamandra spp.* and *Mertensiella spp*; Weisrock *et al.* 2001), brown frogs (*"Ranae fuscae"*; Oosterbroek & Arntzen, 1992), the western Palaearctic water frog complex (*Rana* spp.; Plötner & Ohst, 2001); *Anguis* spp. (Grillitsch & Cabela, 1990). In addition, intense migrations of amphibians and reptiles from other zoogeographical areas have occurred over several migration routes. In the first place, there is a large front of contact with steppe in the east and northeast (Pontic area), while the Morava River corridor provides contacts (faunal exchange) in a south-north direction. Finally, the Aegean islands also constituted a connection with the faunas of Africa and Asia. Extensive faunal exchange between Asia Minor and the Balkans might have occurred due to the existence of a Bosphorus land bridge between 20,000 and 10,000 B.C. (Hosey, 1982). Thus, multiple connections followed by vicariant separations have existed between Anatolia and the Balkans (Weisrock *et al.*, 2001). A number of taxon-area cladograms for diverse groups including some amphibians (*Rana* spp. and *Triturus* spp.) revealed that species and subspecies from the Balkans and Western Asia Minor belong to Asia—Transmediterranean phylogenetic lineages (Oosterbroek & Arntzen, 1992).

In contrast to the Iberian and Apennine peninsulas, the Balkan Peninsula is not isolated by any mountain barriers from the European mainland. It is thus broadly connected with Central Europe and the rest of the continent. This has been crucial for the biogeography of the European batrachofauna and herpetofauna. Namely, it has been demonstrated that Central and North Europe were populated by an expansion from Balkan refuges during postglacial warming periods (Hewitt, 1999). Also, certain groups have withdrawn from Northern and Middle European latitudes, some of them being mostly or partially restricted within southern refuge areas (Venczel, 2000).

At the level of demes, changes in the ranges after each Pleistocene glacial episode involved much colonisation, extinction, dispersal, and adaptation. For many groups, it has been assumed that Balkan populations were the main source for the recolonisation of Europe; *e.g. Bombina* spp. (Szymura, 1993), *Triturus* spp. (Oosterbroek & Arntzen, 1992; Crnobrnja-Isailović *et al.*, 1997), *Pelobates* spp. (Eggert, 2000), *Rana temporaria* (Pidancier *et al.*, 2001), *Zootoca* spp. (Guillaume *et al.*, 1997), or *Natrix tessellata* (Guicking *et al.*, 2001). In addition, a considerable number of lineages, subspecies, and species of Balkan amphibians and reptiles are crowded parapatrically into the southern parts of their range, close to where the ice age distribution would presumably have been (*e.g. Triturus* spp., Wallis & Arntzen, 1989; Litvinchuk *et al.*, 1997; Litvinchuk & Borkin, 2000; the western Palaeartic water frog complex, Plötner & Ohst, 2001). If, as it has been argued, northern interglacial expansions were extinguished by subsequent glacial period(s), then it seems likely that the richness of southern taxa has been generated by para-allopatric divergence over several repeated glacial stages.

Serial recolonisation from south to north, west, and east involved a series of bottlenecks for the colonising genome, which led to a loss of alleles and a tendency toward homozygosity (although not in every case; see Carson, 1990). This has been demonstrated for a number of groups (Hewitt, 1996). Also, clear geographical trends in heterozygosity within European amphibians and reptiles have been discovered: northern populations, whose present ranges largely include previously-glaciated terrain and permafrost zones, are less variable than are southern populations. Thus, northern populations of *Bombina bombina* and *B. variegata* show little or no variation at the studied gene loci, while southern populations exhibit numerous polymorphisms (Szymura, 1988). Among European newts, there is a general trend towards greater variation in Balkan populations, in terms of gene locus polymorphism, number of alleles, and levels of heterozygosity, than in conspecific populations from western and Central Europe (Kalezić & Hedgecock, 1980; Rafinski & Arntzen, 1987; Sotiropoulos *et al.*, 2001b; Frelow *et al.*, unpublished data). Also, mtDNA data indicate that southern populations of crested newt (*Triturus cristatus* superspecies), especially *T. carnifex* and *T. karelinii*, exhibit greater variation than more northerly populations (Wallis & Arntzen, 1989). As far as the European pond terrapin (*Emys orbicularis*) is concerned, a number of different mtDNA haplotypes can be recognised in Balkan populations (Lenk *et al.*, 1998; Fritz, personal communication). The same relation appears to exist in the case of the viviparous lizard (*Zootoca vivipara*; Mayer *et al.*, 2000).

Many Balkan amphibians and reptiles show discontinuous patterns of geographical distribution, as this part of Europe is characterised by the presence of many mountain blocks and marine trenches. These geographical barriers contribute to range fragmentation and genetic isolation resulting from long-term extrinsic barriers to gene flow. Low mobility and poor genetic exchange appear to be strong enough to evoke genetic distinctness and prevent gene pools from amalgamating. This has been documented for crested newts in the Balkans (Crnobrnja & Kalezić, 1990).

In terms of zoogeography, the Balkan Peninsula is characterised by numerous discontinuities. The zoogeographical map is very complex with elaborate subdivisions, and a wealth of preglacial faunal elements (Hadži, 1935; Matvejev, 1961; Haxhiu, 1994).The biogeographical diversity of the so-called "Adriatic Triangle" aroused great interest among biologists in the first half of the 20th century (Simroth, 1907), and comprises nearly the entire richness of the Balkan Peninsula. It is interesting to note that a popular and long-standing hypothesis of Simroth (1907) linked the biogeographical "wealth" of the Balkans with the general theory of pendulation, which has been proposed to explain climatic change the origin of

Quaternary glaciation. This view has been accepted by many authors, including the famous Russian ichthyologist Berg, the Serbian ecologist Stanković, the Czech hydrobiologist Komarek and the Austrian botanist Hanausek.

As shown above, the "Adriatic Triangle" is an area within the Balkans with highly specious amphibian and reptile groups and a high degree of endemism. As such, it is acknowledged to be one of the main European biogenetic reserves containing rare and endemic taxa. Many of these rare and endemic taxa are under threat (Džukić, 1995; Crnobrnja-Isailović & Džukić, 1995; Haxhiu, 1998).

In general, the genesis of diversity among Balkan amphibians and reptiles has (as elsewhere) been dictated by many proximate factors, such as habitat heterogeneity, topographic diversity (mostly influenced by Pleistocene glaciation), great climatic variation, differences of immigration rates, etc. However, it can also be assumed that historical events had a fundamental role to play in the generation of this versatility (Humphries & Parenti, 1986). This could be especially true in the case of the Balkan Peninsula, as its geological history and palaeogeography have undergone complex perturbations, especially during the Tertiary.The Mesozoic and Caenozoic geological development of the Mediterranean in general can be regarded tectonically as the evolution of a continental collision zone that originally separated Eurasia (the ancient Laurasian continental landmass) from Africa (Gondwanaland). During its unique and dynamic geological history, small terrestrial regions made up the margin of the growing area termed the Balkans, which became a part of Eurasia much later than western parts of the circum-Mediterranean region (Hadzi *et al.*, 1974; Hsu & Bernoulli, 1978; Oosterbroek & Arntzen, 1992; Steininger & Rogl, 1996; Rage, 1997). Thus, the southern margins of the Balkan Peninsula represent a collision zone between ancient Gondwanan tectonic fragments and are geologically active. This may have been crucial to the development Balkan faunistic diversity, as tectonic plates introduced new faunal elements (Macey *et al.*, 2000), while mountain building in the suture zone is important in causing high levels of genetic diversity among faunal elements.

Two models of speciation apparently occurred on the Balkan Peninsula: speciation due to climatic-ecological fluctuations during the Tertiary and Quaternary, and speciation due to tectonic-palaeogeographical change. The latter is demonstrated indirectly by the correspondence of zoogeographical boundaries with that of deep lithospheric fractures, or crustal megablocks (Sikošek, 1986) which has been noted on several occasions (*e.g.* Hadži, 1935; Szyndlar, 1984). Geological events might have profoundly affected the evolutionary history of at least some Balkan amphibians. This has been suggested for the origin of the crested newts (*Triturus cristatus* superspecies, Crnobrnja-Isailović *et al.*, 1997).

## HYBRIDISATION AND HYBRIDOGENESIS

Hybrid zones are predominantly narrow regions in which genetically-distinct populations meet, mate, and produce hybrids. Because the hybridising populations exchange genes and yet remain distinct, and because of striking patterns of variation along the contact zone, hybrid zones have constantly attracted the attention of taxonomists and evolutionary biologists (*e.g.* Barton & Hewitt, 1989; Harrison, 1993). This is especially true in the Balkans, where (as in other southern regions) hybrid zones appear to be more numerous than in the rest of Europe, a situation that can be attributed to both population genetics and geographic factors (Hewitt, 1999), since populations that are at present close to each other in space may have quite distant geographical origins and divergent genomes.

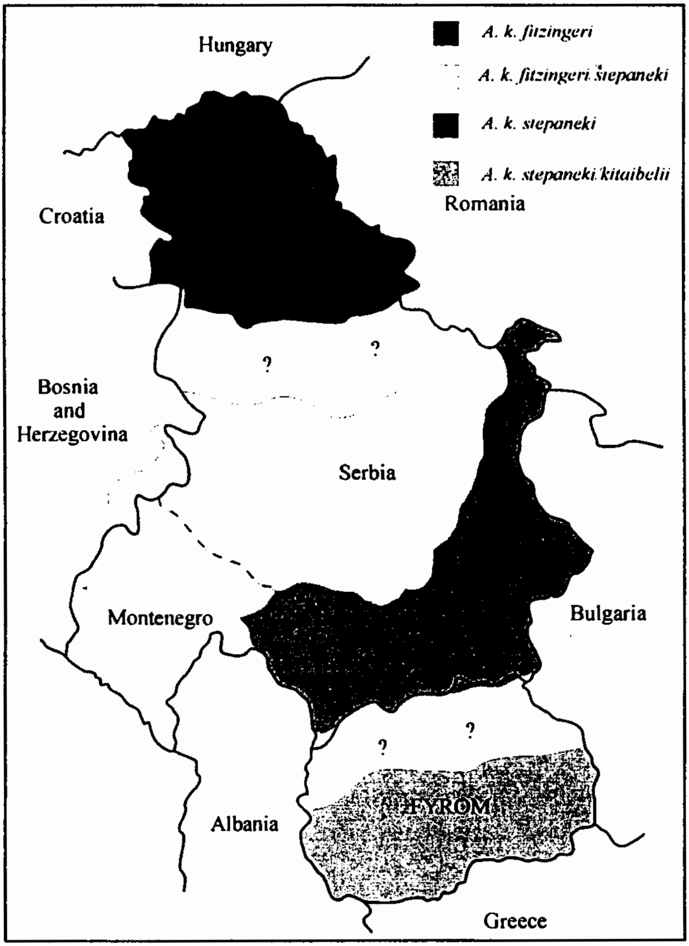

*Figure 4. Spatial pattern of the intergradation zones between subspecies of the snake-eyed skink (*Ablepharus kitaibelii*) in the central Balkans (modified from Ljubisavljević* et al.*, 2002, with permission of the Managing Editor of Herpetozoa).*

Several species show western and eastern forms in Europe, with hybrid zones running roughly north-to-south from Scandinavia down to the Alps, marking the southwestern and southeastern glacial refugia from which they have expanded. On the Balkan Peninsula, hybridisation and intergradation zones are differently orientated in space, including N-S, NW-SE, and W-E distributions. Thus, rather broad intergradations of subspecies zones occur in bands running mainly in a W-E direction, between populations of the snake-eyed skink (*Ablepharus kitaibelii*; Ljubisavljević *et al.*, 2002; Figure 4). Similar W-E clines of morphological characters and allozymes are found among *Triturus cristatus* superspecies in Greece (Sotiropoulos *et al.*, 1999). Multivariate analysis of morphological characters indicates that the transitional zone between two subspecies of sand viper (*Vipera ammdytes*) in Kosovo and Metohija is orientated in a NW-SE direction (Tomović & Džukić, *in press*).

Individuals of some taxa that usually form distinct taxonomic clusters reproduce without recombination. Hybridogenetic hybrids in the western Palaearctic water frog complex are of general biological interest because this complex appears to be a suitable model for studying genetic diversity as an integral part of biodiversity (Plötner & Schmeller, 2001), as well as because of the unique population genetics of the *Rana* synklepton *esculenta*. Studies of hybridogenesis, particularly those which deal with different hybridogenetic population systems on the Balkan Peninsula (which is characterised by the strong evolutionary divergence of water frog taxa; Plötner & Ohst, 2001), can be of special importance due to several peculiarities. In addition to the fact that those individuals of *R. ridibunda* (the common parent of all lineages of hybridogenetic taxa) which are of Balkan origin are known to be resistant to hybridogenesis (Guerrini *et al.*, 1997), it is also noteworthy that the genomes of two Balkan water frogs (*R. epeirotica* and *R. shqiperica*), and most likely *Rana balcanica*, are at least partially resistant to germ line exclusion in hybrids. The overall pattern of reproductive relationships of water frogs in the Balkans is therefore very complex. Unfortunately, studies on such relationships in this part of Europe have only been anecdotal to date (Gavrilović, 1997; Spasić-Bošković *et al.*, 1999).

## HETEROCHRONY

Heterochrony, *i.e.* a shift in the timing and/or rates of processes underlying development in a descending ontogeny, has long been recognised as constituting a major class of developmental dissociation during evolution (*e.g.* Raff & Kaufman, 1983). Some heterochronic changes lead to paedomorphosis. Paedomorphic descendants pass through fewer stages of ontogenetic development than do their ancestors, so descendant adults resemble larvae or juveniles of their ancestors. Paedomorphosis can be recognised at both interspecific and intraspecific levels (Reilly *et al.*, 1997). The term paedogenesis was suggested for the general process that produces an intraspecifically truncated pattern. Both paedomorphosis and paedogenesis occur in tailed amphibians of the Balkans: paedomorphosis in the olm (*Proteus anquinus*) and paedogenesis in the newts (*Triturus* spp.) (Kalezić, 2002).

Paedogenesis appears to be rather common in the genus *Triturus*, especially in the smooth newt and alpine newt, and is particularly limited to the southern margin of the distribution area, *i.e.* to meridional subspecies on the Italian and Balkan peninsulas (Džukić *et al.*, 1990; Denoël *et al.*, 2001). The current distribution of paedogenetic populations is linked to Holocene colonisation. It is in fact restricted to the Italian and Balkan peninsulas, which are thought to have acted as refuges during Quaternary glacial events. Whether paedogenesis first appeared during the harsh conditions of the Pleistocene or earlier remains unknown. In the alpine newt, intraspecific differentiation occurred between the Upper Miocene and the Pleistocene (Arano, 1988). Thus, paedogenesis might have appeared as early as the Miocene in one or several of the subspecies. The Balkan and Italian peninsulas were connected during the Würm (Furon, 1950), during which time exchange of genes would have been possible, and might explain the occurrence of paedogenesis on the two peninsulas.

The simultaneous occurrence of paedogenesis in syntopic populations of two *Triturus* species (*T. carnifex* and *T. vulgaris*) has only been recorded in one pond of the Submediterranean part of Montenegro (Džukić *et al.*, 1990), although the ranges of these newts overlap significantly.

## INTRASPECIFIC VARIATION IN REPRODUCTIVE MODES (OVIPARITY *VS.* VIVIPARITY)

Reproductive bimodality within a single species is a very rare phenomenon among amphibians and reptiles and is of general interest for the study of the evolution of viviparity. Among reptiles, it has been reliably reported for a few lizards and snakes (Shine, 1985). These include the viviparous lizard (*Zootoca vivipara*), which has allopatric oviparous and viviparous populations. Viviparity here appears to be the much more common reproductive mode, occurring over the greatest part of this lizard's range, whereas oviparity is restricted to northern Spain, the Pyrenees, southern France, and a small area in the northwestern Balkans.

Oviparous and viviparous strains differ in many respects, including the presence of genetic markers (*i.e.* diagnostic gene loci and different mtDNA haplotypes). It has been suggested that viviparity as a derived reproductive mode (oviparity is ancestral for the vertebrates in general) evolved recently in *Z. vivipara*, probably during ecological changes of the last Pleistocene glaciations (60,000-20,000 years ago) (Heulin *et al.*, 1993; Arrayago *et al.*, 1996). According to this scenario, viviparity first appeared and was subsequently propagated as an adaptation to cold climatic conditions in eastern populations (somewhere between the Balkan Peninsula and the Altai Mountains), while oviparity remained unchanged in isolated southern refuges (Heulin *et al.*, 1993; Guillaume *et al.*, 1997). Oviparity has thus far been confirmed in samples of five Slovenian populations and one population from Croatia (Böhme *et al.*, 1999; Heulin *et al.*, 2000; Mayer *et al.*, 2000). There is not yet any firm evidence indicating that oviparous populations might be more common on the Balkan Peninsula, which marks the southernmost extent of this lizard's range and where it is considered to be a glacial relict. The only viviparous populations to have been found thus far are in Bulgaria and Serbia (Guillaume *et al.*, 1997; Heulin, personal communication, respectively). It should be noted that the oviparous populations from Slovenia and Austria differ substantially from other conspecific populations. It follows that a new subspecies of viviparous lizard has been described, whose range extends to the northwestern part of the Balkan Peninsula (Mayer *et al.*, 2000).

Among European amphibians, reproductive bimodality has been reported for the fire salamandar (*Salamandra salamandra*), viviparous specimens of which have been found on the Iberian Peninsula (in the Pyrenees and Cantabrian Mountains) and whose evolution can be linked with glaciation events in the region (Alcobendas *et al.*, 1996). The presence of viviparity has also been reported in Balkan populations (in Greece; Sotiropoulos, personal communication).

## OUTLOOK FOR FUTURE RESEARCH

It is not yet possible to reconstruct the evolutionary history of the Balkan batrachofauna and herpetofauna or even to decide which model best fits the present data. All sets of data, both modern and historical, show many gaps and are frequently subject to conflicting interpretations. However, some points may help to guide future discussions.

There is a need for a great deal of research to be done in order to understand of history of the Balkan Peninsula and the origins of its high biodiversity. In the first place, we need to know more about taxonomy (even at the level of basic taxonomical questions) and require more detailed faunal surveys. There is still a paucity of data on long-standing taxonomical problems, the population structure of many species, and the distributional characteristics of taxa - including size, shape, boundaries, overlaps, and the definition of geographic ranges. The latter applies in particular to those taxa which can be considered as "zoogeographic paradoxes", *i.e.* where they occur as isolated populations far from the the known limits of their geographical ranges; examples include exotic species such as *Blanus strauchi*, *Laudakia stellio*, *Chamaeleo* spp., and *Macrovipera* sp. Secondly, the biogeographical patterns of many taxa remain virtually unexplored to date, and matters such as phylogenetic relationships and taxon-area cladograms have escaped analysis. Finally, studies of the age of present taxa based mainly on DNA techniques are needed in order to estimate a time span that can be correlated with possible causes of cladogenetic events. Our aim in the future is essentially to reconstruct the biogeographic history of differentiation of populations (*i.e.* centres of origin, patterns of relictness, refuge areas during glacial phases, postglacial recolonisation routes, *etc.*). In summary, we are confident that surprises, wonders, and even a few dangers await discovery in the study of the batrachofauna and herpetofauna of the Balkans.

## CONCLUSIONS

Balkan amphibians and reptiles are diverse in many respects. Species richness is very high, with a total of 104 species (33 amphibians and 71 reptiles), two of which are introduced. It is likely that a number of morphologically cryptic taxa also exist. The highest level of species diversity is recorded in the region of the "Adriatic Triangle" (the Prokletije Mountain Massif and adjacent areas), while the Peripannonian area and Dobrugea are the most species-poor regions.

The Balkans are the centre of endemicity in Europe, with *ca.* 28% of amphibians and 21% of reptiles being endemic. In addition, more than half of the rest of the autochthonous species have the marginal zone of their distributional range in the Balkans, with marked differences between amphibians and reptiles in regard to the orientation of dominant range borders.

The Balkan batrachofauna and herpetofauna have varied biogeographical origins and connections with other regions. The Balkans appear to have been a centre of intense speciation within some taxonomic groups. Also, there has been a significant number of migrations of amphibians and reptiles from other zoogeographical areas. Central and Northern Europe appear to have been populated repeatedly by an expansion from Balkan refugia during Pleistocene interglacials. Certain groups have withdrawn from northern and mid-European latitudes, some of them being restricted to southern refuge areas. The zoogeographical map of the Balkan Peninsula is very complex, with elaborate subdivisions and numerous discontinuities, as well as a wealth of preglacial faunal elements.

In terms of general biological phenomena such as hybridisation and hybridogenesis, interspecific and intraspecific heterochronic phenomena (paedomorphosis *vs.* paedogenesis), and switching of reproductive modes (oviparity *vs.* viviparity) within a single species, amphibians and reptiles on the Balkan

Peninsula show numerous distinctive features in comparison with other European areas.

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## APPENDIX

Annotated checklist of Balkan amphibians and reptiles with taxonomic inferences. Amphibian and reptile species affiliations to the six regions defined for the Balkans regions are given in parentheses (see text for explanation). Regions are abbreviated as follows: AT - "Adriatic Triangle", P - Peloponnisos, SWC - South-west Croatia, E - Evros, PP - Peripannonian region, D - Dobrogea. Other abbreviations and symbols: * - endemic taxon, Rb - range border (taxon with marginal populations in the Balkans), E - eastern range border (marginal part of the species range on the Balkans is orientated towards Eastern Europe), N - northern range border, NW - northwestern range border, S - southern range border, SE - southeastern range border. A question mark (?) denotes that the presence of a taxon in the Balkans is probable, but not confirmed.

### CAUDATA

1. *Proteus anguinus** (AT, SWC)
   Subspecies: *anguinus, parkelj*
2. *Salamandra atra* Rb.S. (AT, SWC)
   Subspecies: *atra, prenjensis**
3. *Salamandra salamandra* Rb.E. (AT, P, SWC, E, PP)
   Subspecies: *beshkovi*, salamandra, werneri**
4. *Mertensiella luschani**
   Subspecies: *helverseni*
5. *Triturus alpestris* Rb.SE. (AT, P, SWC, PP)
   Subspecies: *alpestris, serdarus*, veluchiensis**
6. *Triturus cristatus* Rb.S. (PP)
7. *Triturus dobrogicus* Rb.S. (PP, D)
   Subspecies: *dobrogicus, macrosomus*
8. *Triturus carnifex* Rb.E. (AT, SWC, PP)
   Subspecies: *carnifex, macedonicus**
9. *Triturus karelinii* Rb.NW. (E, PP)
   Subspecies: *arntzeni*, ?karelinii*
10. *Triturus vulgaris* Rb.S. (AT, P, SWC, E, PP, D)
    Subspecies: *graecus*, meridionalis, tomasinii*, vulgaris*
    Comment: To judge from male qualitative characteristics of many populations, the separate subspecific status of tomasinii appears to be confirmed (Križmanić *et al*., 1997), but for different opinion see Raxworthy (1990).

### ANURA

11. *Bombina bombina* Rb.S. (E, PP, D)
    Subspecies: *bombina*
12. *Bombina variegata* Rb.SE. (SWC, PP)
    Subspecies: *variegata*
13. *Bombina scabra** (AT, E)
    Comment: Taxonomic status uncertain. To judge from allozyme analysis, the distinctiveness of *scabra* at the specific level appears to be proved conclusively

proved (Radojičić *et al.*, unpublished data). Szymura *et al.* (2000) would disagree, however.

14. *Pelobates fuscus* Rb.S. (SWC, PP, D)
    Subspecies: *fuscus*
15. *Pelobates syriacus* Rb.NW. (P, E, PP, D)
    Subspecies: *balcanicus**, unnamed subspecies*
    Comment: Our morphological analysis shows that populations from Serbia are distinct from the Macedonian, Bulgarian, and Turkish Thrace (Edirne) ones, which belong to the subspecies *P. s. balcanicus* (Ugurtas *et al.*, 2002).
16. *Bufo bufo* (AT, P, SWC, E, PP, D)
    Subspecies: *bufo*, cfr. *spinosus*
17. *Bufo viridis* (AT, P, SWC, E, PP, D)
    Subspecies: *viridis*
18. *Hyla arborea* (AT, P, SWC, E, PP, D)
    Subspecies: *arborea, kretensis**
19. *Hyla intermedia* Rb.E.
20. *Rana* kl. *esculenta* Rb.S. (SWC, PP, D)
21. *Rana lessonae* Rb.S. (PP, D)
22. *Rana ridibunda* (AT, P, SWC, E, PP, D)
23. *Rana shqiperica** (AT)
24. *Rana balcanica* (=kurtmuelleri)*
    Comment: The specific status of this taxon has been refuted recently (Plötner & Schmeller, 2001). However, bioacoustic data and electrophoretic investigations (Sofianidou *et al.*, 1994), as well as morphological study (Gavrilović *et al.*, 1999) clearly distinguished it from nearby populations of *R. ridibunda*.
25. *Rana epeirotica** (P)
26. *Rana cerigensis**
27. *Rana cretensis**
28. *Rana latastei* Rb.E.
29. *Rana dalmatina* Rb.E. (AT, P, SWC, E, PP, D)
30. *Rana temporaria* Rb.S. (AT, SWC)
    Subspecies: *temporaria*
31. *Rana graeca** (AT, P, E, PP)
32. *Rana arvalis* Rb.S. (SWC)
    Subspecies: *wolterstorffi*

? 33. *Rana catesbeiana* Introduced

## CHELONIA

1. *Caretta caretta* (AT, P, SWC, E, D)
   Subspecies: *caretta*
2. *Chelonia mydas* (AT, P, SWC, E, D)
   Subspecies: *mydas*
3. *Eretmochelys imbricata*
4. *Dermochelys coriacea* (AT, P, SWC)
5. *Emys orbicularis* (AT, P, SWC, E, PP, D)
   Subspecies: *orbicularis, hellenica**
6. *Mauremys caspica* Rb.NW.(AT, P, E)
   Subspecies: *rivulata*

7. *Trachemys scripta* Introduced
   Subspecies: *elegans*
8. *Testudo graeca* Rb. NW. (P, E, D)
   Subspecies: *ibera*
9. *Testudo hermanni* Rb.N. (AT, P, SWC, E, PP)
   Subspecies: *hermanni, boettgeri**
   Comment: Subspecies distinctness and its distribution seem to be much more complex than was previously thought (Bour, 1997). The presence of ssp. *hermanni* in the northwestern part of the Balkans is suggested (*e.g.* Lapini *et al*., 1999).
10. *Testudo marginata* Rb.N. (P)
11. *Testudo weissingeri** (P)

## AMPHISBAENIA

12. *Blanus strauchi* Rb.W.
    Subspecies: *strauchi*
    Comment: Distribution is restricted to one Adriatic island (see Karaman, 1921). It was previously considered an introduced species, but paleontological and palaeogeographic data (Delfino, 1995, 1997) suggest it is autochthonous.

## LACERTILIA

13. *Laudakia stellio* Rb.W.
    Subspecies: *daani, stellio*
14. *Anguis cephallonicus** (P)
15. *Anguis fragilis* Rb.S. (AT, SWC, E, PP, D)
    Subspecies: *colchicus, fragilis*
16. *Pseudopus apodus* Rb.NW. (AT, P, SWC, E, D)
    Subspecies: *thracius*
17. *Chamaeleo africanus* Rb.N. (P)
18. *Chamaeleo chamaeleo* Rb.N
19. *Cyrtodactylus kotschyi* (AT, P, E)
    Subspecies: *adelphiensis**, *bartoni**, *beutleri**, *bibroni, bileki**, *buchholzi**, *danilewskii**, *fuchsi**, *kalypsae**, *kotschyi**, *oertzeni**, *rarus**, *rumelicus**, *saronicus**, *schultzewestrumi**, *skopjensis**, *solerii**, *stepaneki**, *stubbei, tinensis**, *unicolor**, *weltsteini**
20. *Hemidactylus turcicus* Rb.N. (AT, P, SWC, E)
    Subspecies: *H. t. turcicus*
21. *Tarentola mauritanica* Rb.N. (AT, P, SWC)
    Subspecies: *mauritanica, fascicularis**
22. *Algyroides moreoticus** (P)
23. *Algyroides nigropunctatus** (AT, SWC)
    Subspecies: *nigropunctatus, kephallithacius*
24. *Eremias arguta* Rb. SW. (D)
    Subspecies: *deserti*
25. *Lacerta agilis* Rb.S. (AT, SWC, PP, D)
    Subspecies: *agilis, argus, bosnica**, *chersonensis*
26. *Lacerta bilineata* Rb.E. (SWC)

27. *Lacerta trilineata* Rb.NW. (AT, P, SWC, E, D)
    Subspecies: *cariensis*, citrovittata*, diplochondrodes, dobrogica*, hansschweizeri*, major*, polylepidota*, subcellata*, trilineata*
28. *Lacerta viridis* (AT, E, PP, D)
    Subspecies: *citrovittata*, meridionalis*, viridis*
29 *Iberolacerta horvathi* (SWC)
30. *Darevskia praticola* (E, PP, D)
    Subspecies: *?hungarica, pontica, praticola*
31. *Archaeolacerta graeca** (P)
32. *Archaeolacerta mosorensis** (AT)
33. *Archaeolacerta oxycephala** (AT)
    Subspecies: *oxycephala, tomasinii*
34. *Zootoca vivipara* Rb.SE. (AT, SWC)
    Subspecies: *pannonica, vivipara, carniolica*
35. *Ophisops elegans* Rb.W. (E)
    Subspecies: *ehrenbergii*, macrodactylus*
36. *Podarcis erhardii** (P, E)
    Subspecies: *amorgensis, biinsulacola, buchholzi, cretensis, elaphonisi, erhardii, kinarensis, levithensis, leukaorii, livadiaca, makariaisinii, megalophthenae, mykonensis, naxensis, ophidusae, pachiae, phytiusae, punctigularis, rechingeri, riveti, ruthveni, schiebeli, subobscura, syrinae, thermiensis, thessalica, werneriana, zafranae*
37. *Podarcis melisellensis** (AT, SWC)
    Subspecies: *aeoli, bokicae, caprina, curzolensis, digenea, fiumana, galvagnii, gigantea, gigas, jidulae, kammereri, kornatica, lissana, lupa, melisellensis, mikavicae, plutonis, pomoensis, thetidis, traguriana*
38. *Podarcis milensis**
    Subspecies: *adolfjordansi, gaigeae, gerakuniae, milensis, schweizeri, weigandi*
39. *Podarcis muralis* Rb.E. (AT, P, SWC, E, PP, D)
    Subspecies: *albanica*, maculiventris, muralis*
40. *Podarcis peloponnesiaca** (P)
    Subspecies: *lais, peloponnesiaca, thais*
41. *Podarcis sicula* Rb.E. (AT, SWC)
    Subspecies: *adriatica*, astorgae*, bagnolensis*, bolei*, campestris*, dupenici*, fiumanoidae*, flavigula*, hadzii*, hieroglyphica*, insularum*, kattaroi*, kolombatovici*, kurtklari*, laganjensis*, nikolici*, pelagosae*, pirosoensis*, polenci*, pohlibensis*, premudensis*, premudana*, pretneri*, radovanovici*, ragusae*, samogradi*, veseljuhi*, zeii**
42. *Podarcis taurica* Rb.NW. (AT, P, E, PP, D)
    Subspecies: *ionica*, taurica, thasopulae**
43. *Ablepharus kitaibelii* Rb.W. (AT, P, E, PP, D)
    Subspecies: *fabichi*, fitzingeri, kitaibelii, stepaneki*
44. *Chalcides moseri**
    Comment: dubious taxon (Mertens & Wermuth, 1960; Bringsoe, 1988)
45. *Chalcides ocellatus* Rb.N. (P)
    Subspecies: *ocellatus**
46. *Mabuya aurata* Rb.W.
    Subspecies: *fellowsii**
47. *Ophiomorus punctatissimus* (P)

## SERPENTES

48. *Typhlops vermicularis* Rb.NW. (AT, P, SWC, E)

49. *Eryx jaculus* Rb.N. (P, E, D)
    Subspecies: *turcicus*

50. *Coluber caspius* Rb.W. (AT, E, PP, D)

51. *Coluber gemonensis** (AT, P, SWC)

52. *Coluber najadum* Rb.NW. (AT, P, SWC, E)
    Subspecies: *dahlii*

53. *Coluber nummifer (=revergieri*) Rb.W.
    Subspecies: *nummifer*

54. *Coluber rubriceps* Rb.W.
    Subspecies: *thracius**

55. *Coluber viridiflavus* Rb.E. (SWC)
    Subspecies: *carbonarius, cfr. viridiflavus*
    Comment: see Mršić (1978) for the presence of two morphotypes in the Velebit Mountains

56. *Coronella austriaca* Rb.S. (AT, P, SWC, E, PP, D)
    Subspecies: *austriaca*

57. *Eirenis modestus* Rb.W.
    Subspecies: *modestus*

58. *Elaphe longissima* (AT, P, SWC, E, PP, D)
    Subspecies: *longissima, rechingeri*, romana*
    Comment: Džukić (1975) pointed out the morphological characteristics of *E. longissima* from Serbia, which according to Schulz & Entzeroth (1996), should be assigned to *E. l. romana*. See text for possible introduction of *E. l. romana* in the Balkans.

59. *Elaphe quatuorlineata* Rb.N. (AT, P, SWC, E, D)
    Subspecies: *quatuorlineata, muenteri*, sauromates*

60. *Elaphe situla* Rb.NW. (AT, P, SWC, E)

61. *Malpolon monspessulanus* Rb.N. (AT, P, SWC, E)
    Subspecies: *fuscus, insignitus*

62. *Natrix natrix* (AT, P, SWC, E, PP, D)
    Subspecies: *helvetica, ?dalmatina, natrix, ?persa, schweizeri**

63. *Natrix tessellata* (AT, P, SWC, E, PP, D)
    Subspecies: *tessellata, heinroth**

64. *Telescopus fallax* Rb.NW. (AT, P, SWC, E)
    Subspecies: *fallax, intermedius*, multisquamatus*, pallidus*, rhodicus**

65. *Vipera ammodytes* (AT, P, SWC, E, PP, D)
    Subspecies: *ammodytes*, gregorwallneri, illyrica*, meridionalis, montandoni*

66. *Vipera aspis* Rb.E.
    Subspecies: ?*atra, francisciredii*

67. *Vipera berus* Rb.S. (AT, SWC, E, PP)
    Subspecies: *berus, bosniensis**

? 68. *Macrovipera* sp.* (AT)
    Comment: There has long been controversy about the existence of a unusual viper species in Boka Kotorska (Hirtz, 1937). Kincel (1962, 1969) assigned this viper to *lebetina* species. In the absence of recently-captured specimens (this viper might be

extinct now), we still do not know to which species of the genus *Macrovipera* this snake should be assigned.

69. *Macrovipera schweizeri**
70. *Vipera ursinii* Rb.S. (AT, SWC, D)
    Subspecies: *macrops**, *rakosiensis, graeca**
71. *Vipera xanthina* Rb.W. (E)
    Subspecies: *xanthina*