

# Are genetically distinct lizard species able to hybridize? A review

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**Abstract** Animal species are delimited by reproductive isolation mechanisms (RIMs). Postzygotic RIMs are mainly products of genetic differences and thus their strength increases with elapsed divergence time. The relationship between postzygotic reproductive isolation and genetic divergence, however, differs considerably among major clades of vertebrates. We reviewed the available literature providing empirical evidence of natural and/or experimental hybridization between distinct species of lizards (squamates except snakes). We found that hybridization events are widely distributed among nearly all major lizard clades. The majority of research focuses on parthenogenetic species and/or polyploid hybrids in families Lacertidae, Teiidae and Gekkonidae. Homoploid bisexual hybrids are mainly reported within Lacertidae and Iguania groups. As a proxy of genetic divergence of the hybridizing taxa we adopted nucleotide sequence distance (HKY85) of mitochondrial *cyt b* gene. The upper limit of genetic divergence was similar with regard to both parthenogenetic and bisexual hybrids. Maximum values of these distances between hybridizing species of lizards approached 18%–21%, which is comparable to or even exceeds the corresponding values reported for other principal clades of vertebrates. In spite of this, F<sub>1</sub> hybrids are typically at least partially fertile in lizards and thus genetic introgression between highly divergent species is possible. The relationship between the genetic distance and hybrid fertility was not found [*Current Zoology* 61 (1): 155–180, 2015].

**Keywords** Hybridization, Introgression, Fertility, Viability, Genetic divergence, Lizards

Hybridization may be defined as “interbreeding of individuals from what are believed to be genetically distinct populations, regardless of the taxonomic status of such populations” (Rhymer and Simberloff, 1996). Currently, this process has become an important issue in conservation biology (Allendorf et al., 2001). Anthropogenic effects like translocations and habitat modifications facilitate breaking of the natural barriers between genetically distinct populations and/or species. The increased rates of hybridization have some harmful effects sometimes even resulting in extinctions (Rhymer and Simberloff, 1996; Wolf et al., 2001). In contrast to this, the evidence of outbreeding depression is scarce (Edmands, 2007) and, in the past, natural hybridization events may have been really important in the evolution of many plant and animal species, especially during the speciation processes and the emergence of adaptive characters (Mallet, 2007; Genovart, 2009; Abbott et al., 2013). The distinction between species and/or populations that have arisen through natural and anthropogenic hybridization is sometimes difficult. One such example may be represented by the deep divergences in the mitochondrial lineages and their incongruence with nuclear

markers in the endangered South Asian turtles of the genus *Mauremys* (Fong et al., 2007, Somerová et al., in print). Moreover, interbreeding of distinct populations is sometimes the only available way how to avoid inbreeding depression which is becoming an increasingly important cause of decline in endangered species (cf. Miller et al., 2009 for tuatara). Thus, an adequate taxonomic and genetic delimitation of the conservation units is a crucial problem of the conservation policy (Frankham et al., 2009).

Species of sexually reproducing organisms are delimited by prezygotic and/or postzygotic reproductive isolation mechanisms (RIMs). The prezygotic reproduction barriers cause either the premating isolation (e.g., due to different female preferences and different mating behavioral patterns) or the postmating gametic incompatibilities that may be caused by reduced sperm survival in interspecific crosses or through incompatibilities between sperm proteins and egg receptors (examples are reviewed in Servedio, 2001).

The postzygotic RIMs result mainly from the genetic divergence and these consequent incompatibilities cause inviability or sterility of the hybrids (Orr and Presgraves,

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2000; Coyne and Orr, 2004). This makes the avoidance of interbreeding advantageous and further enhances the evolution of the prezygotic, mostly precopulatory, RIMs by reinforcement (Hoskin et al., 2005).

Recently, Matute et al. (2010) demonstrated in two pairs of *Drosophila* species that the number of genes involved in postzygotic isolation increases with the square of the sequence divergence between the hybridizing species. This conforms to the Dobzhansky-Muller model (Dobzhansky, 1936; Muller, 1942) predicting that the incompatibilities are cumulative and the strength of the reproductive isolation increases with elapsed divergence time (Orr and Turelli, 2001). The relationship between postzygotic reproductive isolation and genetic divergence was reported in many studies (e.g., Ayala, 1975; Coyne and Orr, 1989; 1997; 2004; Sasa et al., 1998; Price and Bouvier, 2002; Bolnick and Near, 2005; Sánchez-Guillén et al., 2014). However, the rate of the formation of reproductive isolation barriers differs significantly among major vertebrate clades.

While mammalian species typically lose their ability to form  $F_1$  hybrids after two million years of independent evolution, the cases of successful hybridization of species separated by dozens of million years were reported in teleost fishes, birds and turtles (Wilson et al., 1974; Prager and Wilson, 1975; Karl et al., 1995; Fitzpatrick, 2004; Bolnick and Near, 2005; see Table 1).

When discussing the ability of phylogenetically distant animals to still produce at least viable  $F_1$  hybrids, we can consider the role of the genetic vs. temporal divergence. Many studies show that the mutation rates in various organisms are fundamentally different (Hughes and Mouchiroud, 2001; Edmands, 2002; Ho et al., 2005; Hedges et al., 2006; Jiang et al., 2007; Nabholz et al.,

2009; Eo and DeWoody, 2010; Bromham, 2011; Shaffer et al., 2013). As the elapsed time is a function of both the genetic divergence and the clade specific mutation rate, the period of phylogenetic isolation itself is not suitable for comparative purposes. From this perspective, the divergence of the genome is a better predictor for the estimation of the limits of hybridization and genetic introgression (Galtier et al., 2009).

In recent years, theoretical aspects of evolutionary mechanisms of hybridization have been a focus of many reviews (Seehausen, 2004; Mavárez et al., 2006; Mallet, 2007; Mavárez and Linares, 2008; Barton et al., 2009; Fitzpatrick, 2012; Abbott et al., 2013; Bailey et al., 2013; Barton, 2013; Dittrich-Reed and Fitzpatrick, 2013; Eroukhanoff et al., 2013; Sætre, 2013). Despite of the numerous papers devoted to the theoretical analysis of the proximate mechanisms of hybridization there have been scarce reviews of empirical hybrid studies, especially those concerning reptiles.

Squamates, namely lizards, are the most species-rich clade (5,947 lizard species according to The Reptile Database Uetz and Hošek, 2014) of extant taxa traditionally referred to as reptiles. The phylogenetic position of the squamates as a sister group of the archosaursian clade (including both birds and crocodylians; Pough et al., 2005) and the knowledges concerning their ability to hybridize being crucial for the interpretation of the previously reported sharp differences between mammals and birds in this respect (Fitzpatrick, 2004). The potential ability of genetically divergent species of lizards to hybridize would support the view that such an ability previously reported in birds is not an evolutionary novelty, but rather an ancestral quality of at least the entire Diapsida clade (cf. Li and Lecointre, 2009).

**Table 1** Reported cases of record holders that produce viable hybrids despite their long time of separation in various lineages based on the published articles

Lineage	Family	Time of divergence (million years ago)	References
Fishes	Lepisosteidae	33–100	Hedges et al., 2006; Herrington et al., 2008.
	Centrarchidae	35	Bolnick and Near, 2005.
Frogs	Hylidae	22–80	Karl et al., 1995; Smith et al., 2005.
Lizards	Iguanidae	10–20	Rassmann, 1997.
Snakes	Pythonidae	35	Hoser, 1988; Rawlings et al., 2008.
	Colubridae	30	Hedges et al., 2006; LeClere et al., 2012.
Turtles	Cheloniidae	50–63	Karl et al., 1995; Naro-Maciel et al., 2008.
Crocodiles	<i>Crocodylus</i>	10	Polet et al., 2002; Brochu, 2003.
Birds	Anatidae	28	Gonzalez et al., 2009.
Mammals	Balaenopteridae	5–8	Hedges et al., 2006; Glover et al., 2013.
	Delphinidae	8	Hedges et al., 2006; Zhang et al., 2014.

The empirical evidence about the limits of the hybridization ability and costs associated with outbreeding is also urgently required for the conservation practice. Traditionally, hybridization between distinct populations has been interpreted exclusively as a threat to the genetic assimilation, especially for the population which are smaller and/or competitively inferior. A deliberate introduction of the green iguanas *Iguana iguana* on the Guadeloupean Archipelago resulted in heavy costs for the population of the rare endemic *Iguana delicatissima*. In this particular case, successful hybridization led to introgression and strong reproductive competition (Breuil, 2000). Introduction of the widespread iguanid lizard *Ctenosaura similis* to the Uvilla Island inhabited by the critically endangered *C. bakeri* resulted in only a limited introgression (Pasachnik et al., 2009). Currently, Robbins et al. (2010, 2014) reported that natural hybrids of *Sceloporus woodi* and *S. undulatus* exhibit transgressive phenotypes. This finding highly facilitates a genetic introgression, which has fairly positive effects on the fitness of the interbreeding species. Thus, the role of hybridization for conservation is not exclusively negative.

We felt a review of empirical hybrid studies in lizards would have prudent and informations about the potencial consequences of hybridization ability substantial for conservation. In this paper, we reviewed well-documented empirical cases of natural and/or artificial hybridization between distinct species and/or races of lizards. We did not speculate about the proximate mechanisms of hybridization and speciation, and instead showed the status of empirical knowledge concerning the ability of lizard species to hybridize. We listed pairs of parental species reported to produce hybrids of the first filial generation or higher order hybrids and we explored the limits of between-species hybridization and introgression.

Hybridization success is constrained by proximate mechanisms related to the genetic divergence of the hybridizing parental species. The genetic divergence may be viewed as best surrogate of the evolutionary distance and also the best currency for comparative studies of hybridization (Edmands, 2002). Because the entire genomes and even sequences of multiple nuclear genes are only available in a few model species of reptiles (Organ et al., 2008; Janes et al., 2010), we rely on mitochondrial genes, which are available for the majority of the concerned taxa. Thus, we utilized the sequence divergence of the mitochondrial cytochrome *b* gene and treated these values as a proxy of genetic divergence

between the parental species.

This approach was previously successfully applied to assess whether genetic divergence predicts reproductive isolation of damselflies (Sánchez-Guillén et al., 2014). Also, recent demonstration of the mutation rates of the mitochondrial genes predicting speciation rates and diversification in sauropsid lineages (Eo and DeWoody, 2010) strongly substantiates the usage of the mitochondrial *cyt b* gene divergence as a proxy of genetic divergence that may constrain hybridization. However, the use of mtDNA is further complicated by the fact that sexual selection operating on males is not properly reflected by maternal genes and the male-based gene flow is not reflected in these data. We excluded snakes from our analyses because their mitochondrial genome includes a duplicated control region, which may confuse the ratio between the substitution rates of the mitochondrial and nuclear genes (Jiang et al., 2007).

## 1 Materials and Methods

We collected as many instances of hybridization in lizards (Squamata without snakes) as we could find. The search of literature was performed in two steps. Since 2005 to 2006 we performed a broad search of literature that included scientific databases Web of Science (<https://apps.webofknowledge.com/>), Biological Abstracts (<http://thomsonreuters.com/zoological-record/>) and Zoological Record (<http://thomsonreuters.com/biological-abstracts/>). Information from other literature sources (coming from amateur herpetologists) was also included. We gathered available information about the distribution of hybridization in lizards, viability and/or fertility of the hybrids and also the occurrence of the parthenogenetic hybrid species. The only criterion was the reliability of the specific information. The second search was performed since January to November 2014 using only the Web of Science. We searched for the keywords: hybrid\* AND reptile; hybrid\* AND the name of the lizard family; hybrid\* AND lizard\*; parthenogen\* AND lizards. Then we selected the records with known parental forms of hybrids and searched for their taxonomic status, geographic localization and genetic identity (including accession numbers of their cytochrome *b* gene sequences when available, see below). These records included both crosses between species and crosses between different subspecies or races. We did not distinguish reciprocal crosses (i.e., with no respect to which of the hybridizing species is maternal and which is paternal; such data are scarce) in further analyses.

To qualify as a hybridizable cross, at least one of the

hybrid offspring must have been hatched alive (if data were available) or this was inferred from the presence of viable later-generation hybrids. For each individual cross, we recorded the fertility of F<sub>1</sub> hybrid. The presence of viable backcrosses, F<sub>2</sub> and later-generation hybrids suggest a potential for the gene flow (Table 2). We distinguished the hybridization records based on the occurrence of bisexual homoploid hybrids from those based on obligatorily parthenogenetic species. We also noted whether the cross originated from the wild or captivity, the mechanisms of sex determination of the species (temperature or genetic), estimation of the divergence time by TimeTree (Hedges et al., 2006) and genetic distance between the parental species. For the purpose of the genetic distance estimation, we downloaded the cytochrome b gene sequences of parental species from NCBI GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>), with the exception of some species, for which cytochrome b gene has not been sequenced yet. In such cases, we used the phylogenetically closest sister species that had their cytochrome b gene sequenced. In the family Lacertidae, *Podarcis raffonei* was substituted for *P. tiliguerta*, *P. wagleriana* was substituted for *P. filfolensis*, *Darevskia alpina* was substituted for *D. saxicola* and in the family Phrynosomatidae, *Phrynosoma goodei* was substituted for *P. platyrhinus*. Nevertheless, there were no equally possible substitutions for some parental species, and thus, we downloaded other available mitochondrial genes: 12 S and 16 S mtDNA for *Aspidoscelis burti*, *A. inornata*, *A. gularis*, *A. sexlineata*, *A. tigris*, *Cnemidophorus lemniscatus*, *C. gramivagus* (Teiidae), *Gymnophthalmus cryptus*, *G. speciosus* (Gymnophthalmidae), *Leiolepis belliana*, *L. guttata*, *L. reevesii* (Agamidae), *Sphaerodactylus nicholsi*, *S. townsendi* (Sphaerodactylidae), *Woodworthia maculata* (Gekkonidae), only 12S mtDNA for *Phrynosoma coronatum*, *P. blainvillii*, *P. cerroense* (Phrynosomatidae) and for three lineages of *Podarcis hispanicus* (Lacertidae), *NADH2* gene for *Heteronotia binoi* SM6, *H. binoi* CA6 (Gekkonidae), *Phrynosoma wigginsi*, *P. cerroense* (Phrynosomatidae), *NADH4* gene for *Iguana iguana*, *I. delicatissima*, *Ctenosaura pectinata*, *C. hemilopha* (Iguanidae), *Lampropholis coggeri* (Scincidae) and *NADH1* gene for *Sceloporus cowlesi* and *S. tristichus* (Phrynosomatidae). For *Sceloporus undulatus*, *S. woodi* and the chromosomal races of *S. grammicus* (Phrynosomatidae), only these parts of mtDNA longer than 2,000 base pairs were available: cytochrome oxidase subunit 3, tRNA-Gly, presumptive protein 3, tRNA-Arg, presumptive protein 4L, presumptive protein 4,

tRNA-His, tRNA-Ser, tRNA-Leu (see Supplementary Materials). The cytochrome b gene was chosen by virtue of having sequences available in GenBank for the largest range of hybridizable lizard species and a faster mutation rate.

The sequences were aligned using BioEdit version 7.0.5.3 (Hall, 1999) and the alignments were manually optimized. For each parental species pair, the alignment had different length from 282 bp to 2,429 bp. Genetic distances between the species (see Table 2) were calculated using uncorrected p distance (that is frequently used in similar studies, e.g., Lijtmaer et al., 2003; Meganathan et al., 2010) and the HKY 85 model, with the transition-transversion ratio estimated from the data in PAUP\* version 4.0b10 (Swofford 2002). We selected HKY 85 model as a reliable compromise between the number of parameters and precision (see Salemi et al., 2009), the model parametrizing nucleotide frequencies and transition transversion ratio has been shown to be appropriate for cyt b data in related species across the vertebrate taxa (e.g., Kotlík et al., 2006; Tang et al., 2006).

We collected data about 93 hybridization events in which the parental species were identified. One additional report of between-generic mating *Ctenosaura* x *Iguana* demonstrates failure of precopulatory RIMs, but only in the combination of these parental species. For four species pairs of geckos, no molecular data were available (see Table 2). Finally, we collected data about 73 bisexual hybrids and 16 unisexual parthenogenetic species. Nevertheless, through inspection of the literature, we found eight records of hybridizations (6 from captivity, 2 from nature) suggesting that the attempts to reproduce the hybrids were not sufficient, e.g., a low number of F<sub>1</sub> hybrids without further breeding attempts. Finally, we statistically analyzed the homogenous set of 65 bisexual species and separately the set of 16 parthenogenetic species.

In the following analyses, we adjusted the genetic distances calculated from 12 S, 16 S, *NADH2* and *NADH4* to cytochrome b genetic distances. With respect to the different mutation rate of the individual genes (Eo and DeWoody, 2010), we estimated the rate coefficients for the above mentioned genes to cytochrome b. We calculated their ratios on the basis of the mean distance calculations for 9 pairs of 12 S and 16 S genes, 12 pairs of 12 S genes independently, 9 pairs of *NADH2* genes and 7 pairs of *NADH4* genes and also the mean of cytochrome b gene distances for the same pairs in separate groups. Using these ratios, we counted the theoretical

**Table 2** Reported cases of hybridization in lizards and selected vertebrate groups

Parental species	Snout-vent length (mm)		Gene flow	Nature/Captivity	Partheno-gensis	Sex determination	Genetic distance of parental species		Sequence length (bp)	Divergence time (my)	References
	1	2					HKY85	uncorrected P			
<b>Agamidae</b>											
<i>Phrynocephalus puijattai</i>	84 <sup>#1</sup>	77	-?	N		ZW	0.051	0.049	288	3.8*	1
<i>Leiolepis belliana</i>	156 <sup>#2</sup>	151 <sup>#3</sup>	+	N		?	0.027 <sup>a</sup>	0.027 <sup>b</sup>	493		2
<i>Leiolepis guttata</i>	184 <sup>#3</sup>	151 <sup>#3</sup>	B	N	P	?	0.169 <sup>a</sup>	0.147 <sup>b</sup>	493		2-4
<b>Iguanidae sensu lato</b>											
<i>Amblyrhynchus cristatus</i>	548 <sup>#4</sup>	480 <sup>#4</sup>	+	N		XY <sup>1</sup>	0.158	0.140	923		5, 6
<i>Ctenosaura pectinata</i> Colima	353	353	+	N		XY <sup>1</sup>	0.039 <sup>s</sup>	0.037 <sup>h</sup>	561		7
<i>Ctenosaura pectinata</i> Colima	353	353	+	N		XY <sup>1</sup>	0.078 <sup>s</sup>	0.072 <sup>h</sup>	561		7
<i>Ctenosaura pectinata</i>	353	400	+	N		XY <sup>1</sup>	0.113 <sup>s</sup>	0.102 <sup>h</sup>	561		8
<i>Ctenosaura bakeri</i>	315	510	+	N		XY <sup>1</sup>	0.135	0.122	1036	5.8***	9-12
<i>Iguana iguana</i>	380	580	+	N		XY <sup>1</sup>	0.155 <sup>s</sup>	0.135 <sup>h</sup>	903		13
<i>Iguana iguana</i>	380	412	M	C		XY <sup>1</sup>					14
<i>Ctenosaura bakeri</i> X <i>C. similis</i>	57 <sup>#5</sup>	59 <sup>#5</sup>	+	N/C		XY <sup>1</sup>	0.027	0.026	306		15
<i>Anolis osa</i>	55	51	+	N		XY	0.150	0.132	957	3 - 6.4 *****	16
<i>Anolis krugi</i>	74	80	+	N		XY	0.183	0.158	988		17
<i>Anolis trinitatis</i>	146	125	+	N		XY <sup>1</sup>	0.025	0.024	416		18-20
<i>Gambelia wislizenii</i>	131	137	+	N		XY	0.037	0.035	423		20, 21
<i>Crotaphytus collaris</i>	131	95 <sup>#6</sup>	+	N		XY	0.115	0.104	423		20, 22, 23
<i>Crotaphytus collaris</i>	55	70	+	N		XY <sup>1</sup>	0.130	0.117	724		24, 25
<i>Liolaemus gracilis</i>	87 <sup>#7</sup>	87 <sup>#7</sup>	+	N		XY <sup>1</sup>	0.045 <sup>i</sup>	0.043 <sup>j</sup>	969		26
<i>Sceloporus tristichus</i> South	91	65	+	N		XY	0.091 <sup>i</sup>	0.084 <sup>j</sup>	2016	1.0*	27
<i>Sceloporus undulatus undulatus</i>	81	81	-	N		XY	0.070 <sup>i</sup>	0.066 <sup>j</sup>	2429		28
<i>Sceloporus grammicus</i> F6	81	81	+	N		XY	0.100 <sup>i</sup>	0.091 <sup>j</sup>	2429		29-32
<i>Sceloporus grammicus</i> F5	81	81	-	N		XY	0.112 <sup>i</sup>	0.102 <sup>j</sup>	2429		33
<i>Sceloporus grammicus</i> FM2	80 <sup>#8</sup>	87 <sup>#7</sup>	+	N		XY <sup>1</sup>	0.116 <sup>i</sup>	0.105 <sup>j</sup>	969		26
<i>Sceloporus grammicus</i> FM2	81	81	+	N		XY	0.122 <sup>i</sup>	0.111 <sup>j</sup>	2429		28, 33
<i>Sceloporus grammicus</i> F6	81	81	-	N		XY	0.143 <sup>i</sup>	0.127 <sup>j</sup>	2429		28
<i>Sceloporus grammicus</i> FM3	81	81	-	N		XY					

Continued Table 2

Parental species	Snout-vent length (mm)		Gene flow	Nature/Captivity	Partheno-genesis	Sex determination	Genetic distance of parental species		Sequence length (bp)	Divergence time (my)	References
	1	2					HKY85	uncorrected P			
<i>Phrynosoma wigginsi</i>	79	85	+	N		XY <sup>1</sup>	0.012 <sup>e</sup>	0.012 <sup>f</sup>	1033		34
<i>Phrynosoma coronatum</i>	100	85	-?	C		XY <sup>1</sup>	0.054 <sup>e</sup>	0.052 <sup>d</sup>	765		35
<i>Phrynosoma blainvillii</i>	100	114	-?	C		XY <sup>1</sup>	0.055 <sup>e</sup>	0.053 <sup>d</sup>	754		35
<i>Phrynosoma mcallii</i>	83 <sup>#9</sup>	88 <sup>#9</sup>	+	N		XY <sup>1</sup>	0.138	0.122	687		36, 37
<i>Phrynosoma coronatum</i>	114	130	+	C		XY <sup>1</sup>	0.185	0.159	1044		35
Gekkonidae sensu lato											
<i>Sphaerodactylus nicholsi</i>	25	28	+	N		?	0.004 <sup>a</sup>	0.004 <sup>b</sup>	883	6.0*	38
<i>Heteronotia binoei</i> SM6	55	55	+	N	P	ZW	0.15 <sup>e</sup>	0.131 <sup>f</sup>	1284		39
<i>Nactus pelagicus</i>	57 <sup>#10</sup>	63 <sup>#4</sup>	-	N	P	?	0.068	0.064	378	> 2.0**	40
<i>Gekko tawaensis</i>	71	74 <sup>#3</sup>	+	N		XY <sup>2</sup>					41
<i>Gekko yakuensis</i>	72	80	+	N		ZW <sup>2</sup>					42
<i>Phyllodactylus guttatus</i>	87 <sup>#11</sup>	78 <sup>#1</sup>	-	N/C		?					43
<i>Phyllodactylus tuberculosus magnus</i>	72 <sup>#12</sup>	81	-	N		ZW <sup>2</sup>					44
<i>Woodworthia maculata</i> Little	57 <sup>#13</sup>	67 <sup>#13</sup>	+	N		?	0.035 <sup>a</sup>	0.032 <sup>b</sup>	600		45
Teiidae											
<i>Aspidoscelis gularis</i>	115 <sup>#14</sup>	64 <sup>#15</sup>	B	N	P	GSD <sup>2</sup>	0.124 <sup>a</sup>	0.110 <sup>b</sup>	771		46, 47
<i>Cnemidophorus lemniscatus</i>	93 <sup>#16</sup>	69 <sup>#17</sup>	B	N	P	GSD <sup>2</sup>	0.127 <sup>a</sup>	0.112 <sup>b</sup>	763		48
<i>Aspidoscelis burri</i>	140	85	no B	N	P	GSD	0.140 <sup>a</sup>	0.123 <sup>b</sup>	787		49
<i>Aspidoscelis tigris</i>	100 <sup>#18</sup>	115 <sup>#14</sup>	B	N	P	XY	0.168 <sup>a</sup>	0.146 <sup>b</sup>	774		50
<i>Aspidoscelis deppoi</i>	87 <sup>#19</sup>	107 <sup>#20</sup>	B	N	P	GSD <sup>2</sup>	0.172	0.151	671		51, 52
<i>Aspidoscelis tigris</i>	100 <sup>#18</sup>	64 <sup>#15</sup>	B	N	P	XY	0.195 <sup>a</sup>	0.167 <sup>b</sup>	791		51, 53, 54
<i>Aspidoscelis tigris</i>	100 <sup>#18</sup>	85	B	N	P	XY	0.213 <sup>a</sup>	0.181 <sup>b</sup>	792		50, 55, 56
<i>Kentropyx striata</i>	127 <sup>#21</sup>	119 <sup>#22</sup>	no B	N	P	GSD <sup>2</sup>	0.153	0.134	819		57
<i>Tupinambis merianae</i>	500	614	+	N		?	0.078	0.073	300		58
Gymnophthalmidae											
<i>Gymnophthalmus cryptus</i>	28	45	no B	N	P	XY	0.141 <sup>a</sup>	0.125 <sup>b</sup>	1764		59

Continued Table 2

Parental species	Snout-vent length (mm)		Gene flow	Nature/ Captivity	Partheno - genesis	Sex determination	Genetic distance of parental species		Sequence length (bp)	Divergence time (my)	References
	1	2					HKY85	uncorrected P			
<b>Lacertidae</b>											
<i>Darevskia caucasica</i>	64 <sup>#23</sup>		+	N		ZW	0.087	0.080	1045		60, 61
<i>Darevskia mixta</i>	63		+	N		ZW	0.103	0.094	1045		60, 61
<i>Darevskia mixta</i>	63		+	N		ZW	0.125	0.112	582		60, 61
<i>Darevskia rudis</i>	85 <sup>#23</sup>		+	N		ZW	0.131	0.116	1045		60, 61
<i>Darevskia alpina</i>	65		+	N		ZW	0.142	0.125	582		60, 61
<i>Darevskia caucasica</i>	64 <sup>#23</sup>		+	N		ZW	0.142	0.125	582		60, 61
<i>Darevskia mixta</i>	63		B	N	P	ZW	0.143	0.125	1045		60-64
<i>Darevskia mixta</i>	63		B	N	P	ZW	0.150	0.131	1045		61, 64
<i>Darevskia derjugini</i>	65		+	N		ZW	0.164	0.143	1045		60, 61
<i>Darevskia narensis</i>	76 <sup>#23</sup>		B	N	P	ZW	0.167	0.144	1044		61-64
<i>Darevskia parvula</i>	57		+	N		ZW	0.170	0.145	1045		60, 61
<i>Darevskia alpina</i>	65		+	N		ZW	0.179	0.153	582		60, 61
<i>Darevskia saxicola</i>	70 <sup>#23</sup>		+	N		ZW	0.179	0.153	582		60, 61
<i>Darevskia raddei</i>	76		B	N	P	ZW	0.182	0.155	1044		61, 64, 65
<i>Iberolacerta monticola</i>	85		+	N		ZW	0.045	0.043	598		66
<i>Lacerta schreiberi</i> EAST	135		+	N		ZW	0.042	0.040	816		67
<i>Lacerta viridis</i>	150		+	C		ZW	0.060	0.057	403		68, 69
<i>Lacerta viridis</i>	150		-?	C		ZW	0.135	0.121	306		70
<i>Lacerta viridis viridis</i>	150		-?	C		ZW	0.148	0.131	388		68
<i>Lacerta schreiberi</i>	135		+	C		ZW	0.159	0.141	306		68, 69
<i>Lacerta strigata</i>	112 <sup>#23</sup>		-?	C		ZW	0.164	0.144	306		68
<i>Lacerta trilineata</i>	153		+	C		ZW	0.166	0.144	403		69, 71
<i>Lacerta viridis</i>	150		+	C		ZW	0.172	0.148	405		72
<i>Lacerta viridis</i>	150		+	C		ZW	0.176	0.151	405		68, 69, 73
<i>Lacerta viridis meridionalis</i>	150		-	C		ZW	0.178	0.153	405		68
<i>Lacerta pamphylica</i>	120		-?	C		ZW	0.179	0.153	405		68
<i>Lacerta schreiberi</i>	135		+	C		ZW	0.191	0.163	663		68, 69, 73
<i>Podarcis muralis</i> Tuscany	80		+	N		ZW	0.031	0.030	887		74, 75

Continued Table 2

Parental species	Snout-vent length (mm)		Gene flow	Nature/Captivity	Parthenogenesis	Sex determination	Genetic distance of parental species		Sequence length (bp)	Divergence time (my)	References
	1	2					HKY85	uncorrected <i>P</i>			
<i>Podarcis muralis</i> East France	80	80	+	N		ZW	0.055	0.052	887		74, 75
<i>Podarcis bocagei</i>	70	74	+	N		ZW	0.098	0.089	282		76
<i>Podarcis hispanicus</i> Valencia	74	74	+	N		ZW	0.117	0.111	379		77
<i>Podarcis hispanicus</i> Valencia	74	74	+	N		ZW	0.137	0.128	379		77
<i>Podarcis bocagei</i>	70	64 <sup>#1</sup>	+	N/C		ZW	0.156	0.135	288		78, 79
<i>Podarcis sicula</i>	90	85	-	N		ZW	0.156	0.137	831		80
<i>Podarcis sicula</i>	90	87	-?	N		ZW	0.161	0.141	674		81
<i>Podarcis sicula</i>	90	76	+	N		ZW	0.171	0.148	859		80
<i>Podarcis sicula</i>	90	74	+	N		ZW	0.182	0.156	887	12.2*	82
<i>Timon lepidus lepidus</i>	260	260	+	N		ZW	0.131	0.116	627		83, 84
<i>Timon lepidus</i>	260	170	-	C		ZW	0.142	0.126	627		85
<i>Zootoca vivipara</i> South France	71 <sup>#23</sup>	71 <sup>#23</sup>	+	N		ZW	0.014	0.014	427		86
<i>Zootoca vivipara vivipara</i>	71 <sup>#23</sup>	71 <sup>#23</sup>	+	C		ZW	0.040	0.039	1143		87
<i>Zootoca vivipara vivipara</i>	71 <sup>#23</sup>	71 <sup>#23</sup>	+	N		ZW	0.058	0.055	1143		88
Scincidae											
<i>Carlia rubrigularis</i> North	60	60	+	N		?	0.154	0.135	399		89
<i>Lampropholis coggeri</i> North	45	45	+	N		XY	0.174 <sup>h</sup>	0.152 <sup>h</sup>	836		90
<i>Oligosoma otagense</i>	133	125	+	N		GSD	0.090	0.083	613		91
<i>Plestiodon laticutatus</i>	80 <sup>#23</sup>	90 <sup>#1</sup>	+	N		GSD	0.126	0.113	910		92
Fishes											
<i>Leptisosteus osseus</i>			-	C		GSD	0.145	0.127	1141	33.1 * - 100 ****	93
<i>Acantharchus pomotis</i>			-	C		GSD	0.202	0.174	1140	33.6*	94
<i>Pomoxis nigromaculatus</i>			-	C		GSD	0.221	0.187	1140	28.9*	94
Frogs											
<i>Pseudacris regilla</i>			-	N		GSD	0.167	0.147	597		95
<i>Pseudacris crucifer</i>			-	N		GSD	0.214	0.181	623	22.1*	95
Snakes											
<i>Pituophis catenifer sayi</i>			+	N		ZW	0.119	0.107	1109	27.9*	96
Turtles											
<i>Chelonia mydas</i>			-	N		TSD <sup>3</sup>	0.109	0.098	429	62.8*	97

Continued Table 2

Parental species	Snout-vent length (mm)		Gene flow	Nature/Captivity	Partheno-genesis	Sex determination	Genetic distance of parental species		Sequence length (bp)	Divergence time (my)	References
	1	2					HKY85	uncorrected P			
<i>Mauremys reevesii</i>			-	C		TSD <sup>3</sup>	0.132	0.118	1140		98
<i>Mauremys sinensis</i>			-	C		TSD <sup>3</sup>	0.142	0.125	1036		99
<i>Cuora flavomarginata</i>			?	N/C		TSD <sup>3</sup>	0.169	0.146	1140		100
Crocodyles											
<i>Crocodylus rhombifer</i>			+	C		TSD <sup>2</sup>	0.127	0.113	1156		101
Birds											
<i>Anas platyrhynchos</i>			-	C		ZW <sup>2</sup>	0.141	0.125	1033		28,9*
Mammals											
<i>Balaenoptera bonaerensis</i>			+	C		XY <sup>2</sup>	0.055	0.052	383		7,6*
<i>Tursiops truncatus</i>			-	C		XY <sup>2</sup>	0.093	0.085	1086		7,0*
<i>Tursiops truncatus</i>			-	C		XY <sup>2</sup>	0.097	0.088	1086		8,9*

“Gene flow” denotes cases with at least partial fertility of hybrids and production of backcrosses by F<sub>1</sub> hybrids or parthenogens of hybrid origin (potential gene flow). Gene flow is coded as present (“+”); it means presence of backcrosses or higher order hybrids; “-”: absence of later hybrids is uncertain, “B”: it means presence of backcrosses in parthenogens, “noB”: it means obligatory parthenogens, “M”: denotes between-species mating without production of hybrids. TSD = temperature sex determination; XY and ZW refers to different modes of GSD. Divergence time was computed by TimeTree (Hedges et al. 2006, <http://www.timetree.net>) or was added from literature.

Snout-vent length: Meiri (2008); #1 Uetz and Hošek (2014); #2 Manthey and Grossmann (1997); #3 Chirio and LeBreton (2007); #4 Zug (2013); #5 Köhler et al. 2010; #6 Axtell (1972); #7 Leache and Cole (2007); #8 Bateman and Chung-MacCoubrey (2012); #9 Young (2010); #10 Wilson and Swan (2010); #11 El Din (2006); #12 Köhler (2000); #13 Fitness et al. (2012); #14 Ramírez-Bautista et al. (2009); #15 Pérez-Ramos et al. (2010); #16 Montgomery et al. (2011); #17 Mesquita and Colli (2003); #18 Walker (1981); #19 Mata-Silva and Ramirez-Bautista (2005); #20 Beargie and McCoy (1964); #21 Gallagher and Dixon (1992); #22 Vitt (1991); #23 Bannikov et al. (1977).

Sex determination: Pokorná and Kratochvíl (2009); <sup>1</sup> Rovatsos et al. (2014); <sup>2</sup> Gamble (2010); <sup>3</sup> Janzen and Phillips (2006).

Genetic distance: <sup>a</sup> estimated from 12S and 16S rRNA gene divergences using rate coefficient 2.0374; <sup>b</sup> estimated from 12S and 16S rRNA gene divergences using rate coefficient 1.9014; <sup>c</sup> estimated from 12S rRNA gene divergences using rate coefficient 2.1104; <sup>d</sup> estimated from 12S rRNA gene divergences using rate coefficient 2.1000; <sup>e</sup> estimated from NADH2 gene divergences using rate coefficient 1.1555; <sup>f</sup> estimated from NADH2 gene divergences using rate coefficient 1.1374; <sup>g</sup> estimated from NADH4 gene divergences using rate coefficient 1.2401; <sup>h</sup> estimated from NADH4 gene divergences using rate coefficient 1.219; <sup>i</sup> substituted by distances computed from composite sequences of mitochondrial genes.

Divergence time: \* Hedges et al. (2006); \*\* Moritz (1987); \*\*\* Gutsche and Köhler (2008); \*\*\*\* Herrington et al. (2008); \*\*\*\*\* Brandley and de Queiroz (2004).

References of hybridization: 1. Jin and Liu (2008); 2. Grismer et al. (2014); 3. Malysheva et al. (2006); 4. Grismer and Köhler (2008); 5. Rassmann et al. (1997); 6. Lückner and Feiler (2002); 7. Zarza et al. (2011); 8. Zarza et al. (2008); 9. Köhler and Blinn (2000); 10. Gutsche and Köhler (2004); 11. Gutsche and Köhler (2008); 12. Pasachnik et al. (2009); 13. Breuil (2000); 14. Dirksen (2004); 15. Köhler et al. (2012); 16. Jezkova et al. (2013); 17. Gorman et al. (1971); 18. Montanucci (1970); 19. Montanucci (1978); 20. McGuire et al. (2007); 21. Montanucci (1974); 22. Axtell (1972); 23. Montanucci (1983); 24. Morando et al. (2007); 25. Olave et al. (2011); 26. Leache and Cole (2007); 27. Jackson (1973); 28. Arévalo et al. (1993); 29. Reed and Sites (1995); 30. Reed et al. (1995a); 31. Reed et al. (1995b); 32. Sites et al. (1995); 33. Hall and Selander (1973); 34. Montanucci (2004); 35. Baur (1984); 36. Leache and McGuire (2006); 37. Mulcahy et al. (2006); 38. Murphy et al. (1984); 39. Moritz (1983); 40. Eckstut et al. (2013); 41. Toda et al. (2006); 42. Toda et al. (2001); 43. Werner and Sivan (1996); 44. Dixon (1996); 45. Fitness et al. (2012); 46. Abuheba (2001); 47. Walker et al. (1989); 48. Cole and Dessauer (1993); 49. Moritz et al. (1989b); 50. Dessauer et al. (1996); 51. Taylor et al. (2001); 52. Hernandez-Gallegos et al. (2003); 53. Parker and Selander (1976); 54. Taylor et al. (2000); 55. Dessauer et al. (2000); 56. Manning et al. (2005); 57. Cole et al. (1995); 58. Cabana et al. (2014); 59. Cole et al. (1993); 60. reviewed by Murphy et al. (2000); 62. Arakelyan (2002); 63. Danielyan et al. (2008); 64. Kupriyanova (2009); 65. MacCulloch et al. (1997); 66. Arribas et al. (2014); 67. Godinho et al. (2008); 68. Rykena (1991); 69. Rykena (2002); 70. Rykena and Henke (1978); 71. Peek (1978); 72. Mayer and Tiedemann (1985); 73. Rykena (1996); 74. Schulte et al. (2013); 75. Schulte et al. (2013); 76. Pinho et al. (2007); 77. Renoult et al. (2009); 78. Galán (2002); 79. Pinho et al. (2009); 80. Capula (1993); 81. Capula (2002); 82. Gorman et al. (1975); 83. Nunes et al. (2011); 84. Miraldo et al. (2013); 85. Bischoff (1981); 86. Mila et al. (2013); 87. Arrayago et al. (1996); 88. Lindtke et al. (2010); 89. Phillips et al. (2004); 90. Singhal and Moritz (2012); 91. Chapple et al. (2012); 92. Okamoto et al. (2013); 93. Herrington et al. (2008); 94. Bolnick and Near (2005); 95. Wilson et al. (1974); 96. LeClere et al. (2012); 97. Karl et al. (1995); 98. Buskirk et al. (2005); 99. Schilde et al. (2004); 100. Otani (1995a, b) ex Buskirk et al. (2005); 101. Polet et al. (2002); 102. Prager and Wilson (1975); 103. Glover et al. (2013); 104. Caballero and Baker (2010); 105. Zhang et al. (2014).

values of cytochrome *b* gene distances for the parental species pairs with unknown sequences of this gene.

In order to determine which factors, if any, predict the fertility of  $F_1$  hybrids and thus the possibility for a gene flow, we used marginal models (GEE - Generalized Estimating Equation approach; it is GLM class model enabling correction for intra-class correlations among observations). The fertility of the  $F_1$  hybrids and thus the potential for a gene flow was given as a dependent variable with binomial distribution. The genetic distance of hybridizable pairs was given as a continuous predictor. Bisexual/pathenogenetic reproduction mode of the hybrids and natural versus artificial origin of the crossing were both introduced as categorical explanatory variables. The identity of the principal clades present in our data set (i.e., Gekkota, Iguania, Lacertidae, Teiidae/Gymnophthalmidae and Scincidae) was included in the model to account for phylogenetic dependence of the species data. The calculations were performed using `geeglm` function of `geepack` package in the R environment (R Core Team, 2013).

For each successfully hybridizing species pair, we calculated a ratio between the snout-vent length of the smaller parental species and that of the larger one (Fig. 3). These ratios, expressed in percents, were further referred to as a similarity in body sizes of the parental species. The ratio was set to 100% for within-species hybridizations in which the relevant body sizes were not available for both parental subspecies.

Visualisation of the hybridization events on a tree depicting phylogenetic relationships among families was done using `Mesquite` package (Maddison and Maddison, 2009). For a reconstruction of ancestral states of the hybridization presence/absence, we chose the maximum parsimony method. The topology of the tree was adopted from Pyron et al. (2013).

## 2 Results

### 2.1 List of hybridization events among genetically distinct lizard species/subspecies

We gathered literature records describing the hybridization in 94 pairs of genetically distinct lizard species/subspecies; 78 of which produced bisexual hybrids (61 and 17 from wild and captivity, respectively) while the remaining 16 pairs were parental forms that gave rise to parthenogenetic species. The families represented the most often were the Lacertidae (42 pairs), Phrynosomatidae (13 pairs), Teiidae (9 pairs), Iguanidae (7 pairs), Gekkonidae (5 pairs), Scincidae (4 pairs), Crotophytidae (3 pairs), Dactyloidae (3 pairs), Agamidae (3

pairs), and Phyllodactylidae (2 pairs); Sphaerodactylidae, Liolaemidae and Gymnophthalmidae were each represented by a single species pair. Altogether, 13 of 42 families of extant lizards (Squamata without snakes) were represented in this list and their distribution on the phylogenetic tree (cf. Pyron et al., 2013) suggests that the hybridization events can be found in multiple clades across the tree topology (see Fig. 1). The distribution of the hybridizing species pairs among the principal clades of the lizards is, however, highly biased in favour of the most studied clades; the hybridizing species belong to the Lacertoidea (52 pairs), Iguania (30 pairs), Gekkota (8 pairs) and Scincoidea (4 pairs), (see Table 2).

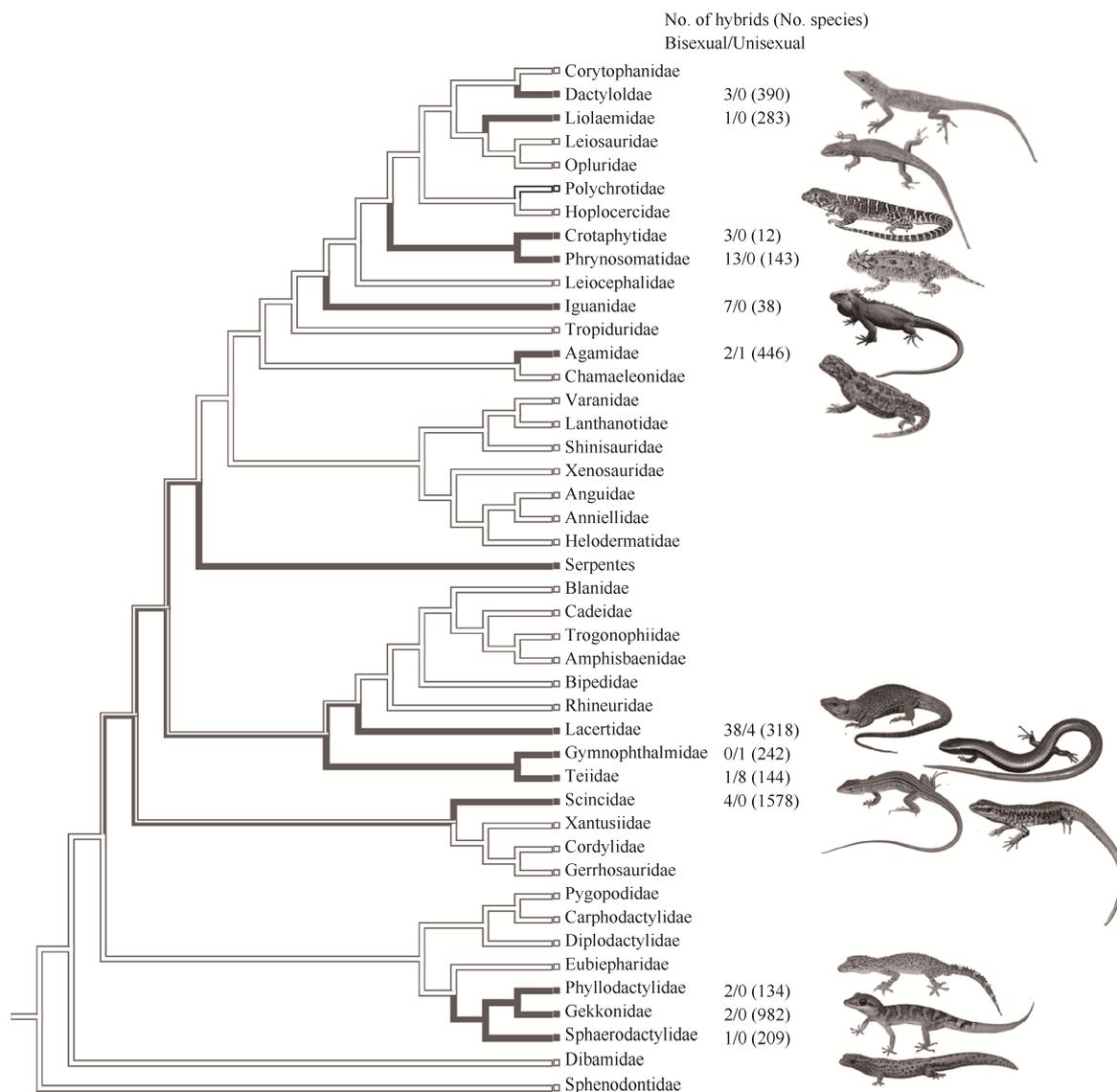
In almost all cases, the hybridizing pair belongs to the same genus. The only exception is the hybridization between the two morphologically and ecologically distinct, but phylogenetically closely related species of the Galapagos iguanas *Amblyrhynchus cristatus* and *Conolophus subcristatus*. However, their hybrids are viable and at least partially fertile (Rassmann et al., 1997; Lückner and Feiler, 2002).

### 2.2 Genetic divergence between parental forms of viable bisexual hybrids and parthenogenetic hybrid species

In our dataset (Table 2), the mean genetic distances within pairs of parental species computed from the mitochondrial DNA sequences (cyt *b* gene, HKY85 model) were higher in the parthenogenetic hybrid species (0.154,  $n = 16$ ) than in the viable bisexual hybrids (0.113,  $n = 73$ ). Non-parametric Mann-Whitney test revealed that this difference is statistically significant ( $Z = 2.69$ ,  $P = 0.0071$ ). The lowest genetic distance between the parental forms of the parthenogenetic hybrid species was 0.068 in *Nactus pelagicus* and *N. multicarinatus* (Gekkonidae, Eckstut et al., 2013), while 21 of the 73 distances computed for the parental pairs of bisexual hybrids were smaller to this value (the lowest value was 0.004 for *Sphaerodactylus nicholsi* and *S. townsendi*; Sphaerodactylidae, Murphy et al., 1984). In contrast to this, the maximum value (0.213) for the parental species pair of the parthenogenetic hybrid species (*Aspidoscelis tigris* and *A. inornata*; Teiidae, Dessauer et al., 1996) was close to that found in the parents of the bisexual hybrids (0.191, *Lacerta agilis* and *L. schreiberi*, Lacertidae, Rykena, 2002; see Figure 2).

### 2.3 Genetic distance of parental species and a potential for gene flow

Most of the parthenogenetic hybrid species (12 of 16) were reported to produce viable hybrids with at least one of their parental species. Even the *Aspidoscelis neo-*



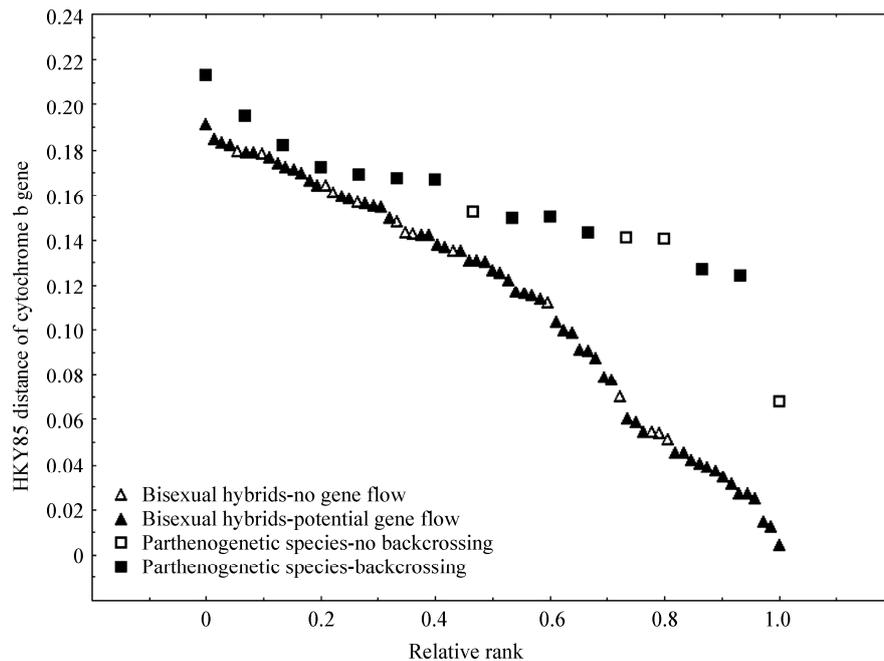
**Fig. 1 Families of extant lizards which are represented in this list and their distribution on the phylogenetic tree (cf. Pyron et al., 2013) suggests that hybridization events can be found in multiple clades across tree topology**

The distribution of hybridizing species pairs among the principal clades of lizards is, however, highly biased; the hybridizing species belong to Lacertoidea (52), Iguania (30), Gekkota (8 pairs) and Scincoidea (4 pair), see Table 2.

*mexicana*, a unisexual parthenogenetic hybrid of the bisexual species *A. tigris* and *A. inornata*, is still able to backcross with both of the parental taxa (Teiidae, Des-sauer et al., 1996; 2000; Manning et al., 2005, for details see Table 2). Fertility of such hybrids is often prevented by the parthenogenetic mode of the reproduction itself and/or polyploidy (Dowling and Secor, 1997). These specific mechanisms have been repeatedly reviewed (Fujita and Moritz, 2009) and thus, we further focused only on the bisexual diploid hybrids.

In 59 of 73 parental pairs of bisexual hybrids, a potential gene flow (for definition see under the Materials and Methods) has been reported. Thus, the potential for

a gene flow was not proved in only 14 pairs of the parental species! Moreover, clear evidence against such a gene flow was available in just six of these pairs. The marginal geeglm of our dataset (Table 2) accounting for the phylogenetic clade revealed that the genetic distance between the parental species has no effect on the presence/absence of the potential gene flow ( $\chi^2 = 0.60, P = 0.4369$ ). This result has remained unchanged ( $\chi^2 = 0.59, P = 0.4424$ ) when eight uncertain cases (six of which coming from breeding experiments in captivity) were excluded. No effects of captivity/wild origin of the data as well as relative difference between the parental species in their body sizes were found.



**Fig. 2** Plot of genetic divergences between hybridizing parental species, given as HKY85 distance in nucleotide sequence of mitochondrial *cyt b* gene, against relative rank order of this value

Ranks of bisexual homoploid hybrids (triangles) and parthenogens of hybrid origin (squares) were treated separately. Cases with at least partial fertility of hybrids and production of backcrosses were documented close to upper limits of divergence in both  $F_1$  hybrids and hybrid parthenogens. These cases are denoted by filled marks (triangles and squares).

The most genetically distant parental species of the bisexual hybrids have documented a potential for a gene flow. The viable and fertile  $F_1$  hybrids were experimentally proved in *Lacerta agilis* and *L. schreiberi* exhibiting genetic distance of 19% (Lacertidae, Rykena, 2002), *Phrynosoma coronatum* and *P. cornutum* (18%; Phrynosomatidae, Baur, 1984). Natural hybridization between parents with greater divergence was also reported. Hybridization between *Anolis trinitatis* and *A. aeneus* (18%; Dactyloidae) showed that the reproductive function was affected and thus the backcross hybrids were rare in nature (Gorman et al., 1971). Nevertheless, the fertile hybrids of the species pairs exhibiting comparable genetic distances were also repeatedly detected in nature: e.g., *Podarcis sicula* and *P. melisellensis* (18%), *P. sicula* and *P. wagleriana* (17%; Gorman et al., 1975; Capula, 1993), *Darevikia saxicola* and *D. brauneri* (18%; Lacertidae; MacCulloch et al., 1997; for review see Fu, 1999; Murphy et al., 2000).

#### 2.4 Body size differences within pairs of hybridizing species

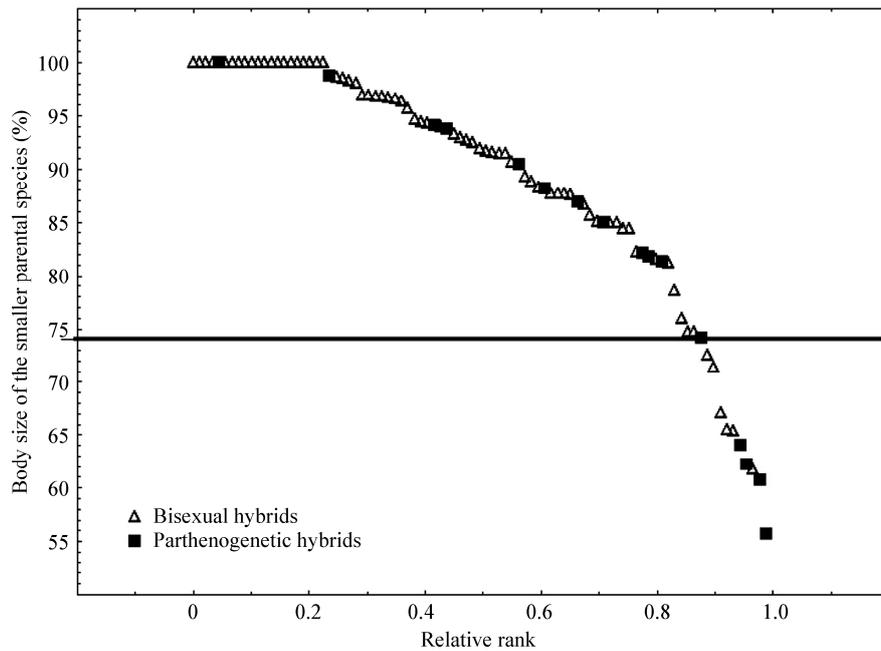
The minimum value of the similarity in body sizes of the parental species was 56% in the case of a parthenogenetic hybrid of the *Aspidoscelis gularis* and *A. sexlineata* (Teiidae). The median value was 92% and only 10 percent of the values were smaller than 72% (Fig. 3).

The similarity in body sizes of the parental species was higher in the bisexual hybrids (median = 93%, percentile 10 = 75%, minimum = 62%) than in the parthenogenetic hybrid species (median = 84%, percentile 10 = 61%; Mann-Whitney test:  $Z = -2.80$ ,  $P = 0.0050$ ) and this difference has remained significant even when the hybrids of the genetically related species ( $HKY85 < 0.068$ , i.e., that between *Nactus pelagicus* and *N. multicarinatus*) were excluded ( $n_{\text{bisexual}} = 53$ ,  $n_{\text{parthenogenetic}} = 16$ ,  $Z = -2.28$ ,  $P = 0.0225$ ).

### 3 Discussion

#### 3.1 List of hybridizing species/subspecies

The number of reliable literature records of hybridization between distinct species of lizards is surprisingly small, especially when compared with the huge number of such records available in other vertebrates, in particular birds, mammals, turtles, and fishes (Grant and Grant, 1992; Galgon and Fritz, 2002; Fitzpatrick, 2004; Bolnick and Near, 2005; Buskirk et al., 2005; McCarthy, 2006). The hybridization records are heavily biased towards taxa occurring in Europe (lacertids) and North America (iguonids, phrynosomatids and teiids), where lizard faunas are relatively poor, but herpetological research has the longest tradition. Thus, it is likely that some hybrids of lizard species may have been over-



**Fig. 3** Body size differences within pairs of hybridizing species, i.e., the ratio between snout-vent length of the smaller and larger-bodied species (in percents), plotted against the relative rank of this value in our sample (data are ordered from the smallest value to the maximum and scaled to the total number of the examined parental pairs)

The line shows the value 0.74, which was previously reported for Squamata by Shine and Charnov (1992) as mean relative ratio between the body size at sexual maturity and the maximum adult body size.

looked by scientists rather than entirely absent. This view is further supported by putative hybrid records between lizard and (especially) snake species, which are occasionally reported by hobbyists (Hoser, 1988; 1991; Lásková, 2006). However, these reports were usually too poorly documented to be included in our analyses.

It is surprising that our list is missing hybridization examples of species with temperature-determined sex. It is known that many phylogenetically divergent species of turtles and crocodiles with temperature-determined sex often hybridize (Conceicao et al., 1990; Karl et al., 1995; Harding and Davis, 1999; Parham et al., 2001; Fritz and Mendau, 2002; Galgon and Fritz, 2002; Ray et al., 2004; Schilde et al., 2004; Buskirk et al., 2005; Rodriguez et al., 2008; Weaver et al., 2008). One could assume that species without differentiated sex chromosomes would hybridize more successfully than species with genetically determined sex, in which a higher degree of sterility frequently occurs in the heterogametic sex with XY or ZW chromosomes (Haldane, 1922; Presgraves, 2010). Unfortunately, we were unable to verify this hypothesis in our study.

### 3.2 Genetic divergence between parental forms of viable bisexual hybrids and parthenogenetic hybrid species

Moritz et al. (1989a) predict that there should be a

threshold of divergence between bisexual species below which hybrids do not reproduce parthenogenetically. In agreement to this, the parental species of parthenogens in our sample are typically genetically well-differentiated species ( $> 0.123$  sequence divergence, except the case of *Nactus* 0.068). Our review also revealed that the upper limit of the genetic distances between parental species is approximately the same in both parthenogenetic (0.213 for *Aspidoscelis tigris* x *A. inornata*) and bisexual (0.191 for *Lacerta schreiberi* x *L. agilis*) hybrids (see Table 2). In contrast to the parthenogens, the divergence between the parental forms of bisexual hybrids covers a full range, including the zone of close similarity (e.g., Toda et al., 2001; 2006).

### 3.3 Genetic divergence between parental species/subspecies and potential for gene flow

The absence of a significant relationship between the genetic distance of the parental species and the potential for a gene flow (the presence of fertility in  $F_1$  hybrids and viable later hybrids) was surprising as this relationship was previously demonstrated in various animal taxa (cf. Edmands, 2002; Sánchez-Guillén et al., 2014; but see Lessios and Cunningham, 1990). In lizards, the most complex hybridization experiments were carried out in a series of species belonging to the genus *Lacerta* sensu stricto (Rykena and Henke, 1978; Rykena, 1991;

1996; 2002). These studies reported that an increasing phylogenetic distance of the hybridizing species was positively associated with an increasing proportion of sterile hybrids, especially in females. Genetic introgression was enabled by crossing fertile males with the parental species (Rykeno, 2002). In our dataset, we did not find a significant relationship between the genetic distance of the parental species and the potential for a gene flow, probably due to the statistical distribution of the data. The vast majority of  $F_1$  hybrids usually appeared fertile in lizards, allowing the existence of backcrosses with at least one parental species. These results may be affected due to lack of variance in presence/absence coded data. Moreover, reliable records of hybridization among lizard species are scarce and possibly affected by a publication bias against negative results. Thus, we cannot exclude the existence of more genetically divergent species pairs, which are able to produce infertile hybrids but still have remained unexplored. Alternatively, the hybridization of genetically more divergent species of lizards is constrained by the divergence of sexual and/or species recognition signals and consequent emergence and completion of precopulatory isolation mechanisms prior to the appearance of entirely infertile hybrids (cf. Price, 1998; Servedio, 2001; Coyne and Orr, 2004 but see Gage et al., 2002).

One would expect that in a laboratory, where are no ecological differences keeping the lizards apart, a greater success in hybridization could be achieved. However, we did not find any evidence of distantly related species in captivity hybridizing at a more successful rate than those in nature. It may be argued, however, that in the wild, infertile  $F_1$  hybrids may be easily recognized, but due to their infrequent origin, they may be easily overlooked.

### 3.4 Hybridization, taxonomy and conservation

A high occurrence of hybrid fertility and thus at least a theoretical chance for an introgression of some genes from species to species has serious potential consequences for understanding of lizard diversity. Despite the increasing genetic divergence in lizards, the potential for hybridization may further complicate the application of the biological species concept, which postulates interbreeding of natural populations that are reproductively isolated from other such groups (Mayr, 1942). Moreover, taxonomic recommendation regarding the status of reptilian subspecies are biased towards splitting; when the genetic analyses (genetic distance values) are used, then subspecies are more likely elevated to the status of a species without regard to any

species concept (Torstrom et al., 2014).

These findings suggest that artificial hybridization occurring in nature (mainly in secondary contact zone) is common. We must be cautious and do not underestimate the situation, especially when it concerns small populations of endangered species of lizards. Relatively good fertility of hybrids leading to gene introgression could result in the merging of species and the extinction of the endangered species (Allendorf et al., 2001; Rhymer and Simberloff, 1996). Where possible, it is good to control and limit the introduction of non-native species, while establishing a genetically pure population in captivity, which would be able to reproduce and, in the future, allow for the reintroduction to the areas where the species has already gone extinct (e.g., in *Iguana Breuil*, 2000). However, where populations are very small and vulnerable to other factors (such as domestic animal introduction, destruction of natural habitats, etc.), then it is not effective to discriminate lizards to small taxonomic units on the basis of only genetic differences and thus protect too small population of lizards. Moreover on the basis of empirical studies, the inbreeding depression threat of small population is more urgent than the potential disadvantages of outbreeding (Edmands, 2007). When protecting a species, we need to approach the problem of its survival individually, building a plan tailored to the particular species. It is because hybridization can have quite different consequences in individual cases (Allendorf et al., 2001). When a protection management plan of an endangered species is discussed, not only the genetic distance between both hybridizing species needs to be considered, but also the context of the environment and selection pressures.

### 3.5 Body size differences within pairs of hybridizing species

Differences in body size may contribute not only to pre-mating isolation mechanisms, but also to postzygotic RIMs (Bolnick et al., 2006). We found that body size differences within pairs of parental species reported to hybridize are typically small. In 90% of bisexual hybrids, the body size of smaller parental species represented more than 75% of the body size of the larger one. This value is close to the 74% reported for a typical relation of the body size at maturity to the maximum body size reported within lizard species (around 70% for other reptiles; Shine and Charnov, 1992; Shine and Iverson, 1995). Thus, the body size differences between the hybridizing lizard species are comparable to those among conspecifics participating in reproduction.

Although the statistical distribution of lizard body sizes was carefully examined (Meiri, 2008), reliable estimates of this distribution in species pairs having opportunities to hybridize in nature have remained unexplored. It is due to non-trivial interactions between phylogenies, character displacement and biogeography. Thus, it is still impossible to directly test the deviations of the observed body size differences between the hybridizing species pairs from the expected distribution of this variable.

### 3.6 Comparison of lizards with other principal clades of vertebrates

It seems that lizards are similar to fishes and frogs in the ability to produce hybrids when genetic distances measured as the sequence divergence of *cyt b* gene between the parental species approach 21%, but this genetic distance is higher than that found in hybrids of snakes, turtles, crocodylians, birds, and mammals, which belong to the record holders in hybridization between a lot of phylogenetically distant species (Table 2).

The rates of sequence divergence in mitochondrial genes reported between parental species of lizards are considerably higher than those reported in other clades of vertebrates (e.g., mammals, turtles, crocodiles, birds, but not snakes see Nabholz, 2009; Eo and DeWoody, 2010 and references herein). Also, the nuclear genes of squamates exhibit a faster evolutionary rate than birds, turtles and crocodiles (Hughes and Mouchiroud, 2001). Thus, high values of the genetic divergence between parental species of lizard hybrids do not mean longer elapsed time from the last common ancestor of the hybridizing species. Nevertheless, a supposed constant ratio between evolutionary rates of mitochondrial and nuclear genes (but see Grechko, 2013 for criticism of widespread misuse of the mitochondrial genes) would still suggest that lizards are able to hybridize with less similar genomes than other vertebrates. The data presented here support the idea that a gene flow may exist between congeneric lizard species, and are consistent with the general idea of the semipermeable nature of species boundaries given by Flegr (2013) and Harrison and Larson (2014). The idea of continuity between varieties and species has been proposed by Charles Darwin (Darwin, 1859). Recently, this issue was addressed again by Mallet (2008a, b). The divergence of hybridizing species can be maintained despite the gene flow, due to varying permeability of particular genome region, therefore the hybridizing taxa often remain distinct for only a part of the genome (Harrison and Larson, 2014).

An important question, which our review could not

address, is whether particular divergences between the parental species are associated with either beneficial (hybrid vigour) or detrimental effects (outbreeding depression, genetic incompatibility, etc.) on fitness in lizards. Most of the available records reporting between-species hybrids come either from field studies relying on molecular evidence but lacking fitness parameters, or from casual observations made by private breeders. Properly documented experimental hybridizations are surprisingly rare. The absence of such evidence calls for further experimental studies.

In conclusion, we found that lizards are exceptional among vertebrates in their ability to hybridize despite being highly genetically divergent. Reliable records of hybridization are scarce, however, probably due to an insufficient effort devoted to this topic. We also found that despite high genetic divergence (roughly up to 20% of mitochondrial *cyt b* gene sequences), the hybridizing species are usually morphologically similar enough to be formally classified as congeners by current taxonomists. Lastly, our review revealed that more data on the occurrence of hybridization in lizards are necessary, both for better understanding of the role of hybridization in evolution and for better planning in conservation efforts, an aspect that has remained unexplored. Our review has revealed much with regard to the limits of successful lizard hybridization. To further explore these limits, we must gather more experimental evidence of hybridization between distant lizard species, including pairs of species more divergent than those known to produce fertile hybrids.

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**Supplementary Materials:** Accession numbers of the mitochondrial gene sequences of the parental species downloaded from the Genebank

Species	Cyt <i>b</i>	12S	16S	NADH2	NADH4	mtDNA
<b>Agamidae</b>						
<i>Leiolepis belliana</i>			AF378379			
<i>Leiolepis guttata</i>			AF378377			
<i>Leiolepis reevesii</i>			AF378376			
<i>Phrynocephalus putjatia</i>	KF691634					
<i>Phrynocephalus vlangalli</i>	KF691642					
<b>Iguanidae sensu lato</b>						
<i>Amblyrhynchus cristatus</i>	AY948118				U66234	
<i>Conolophus subcristatus</i>	AY948122				U66235	
<i>Ctenosaura bakeri</i>	GU331976				EU407507	
<i>Ctenosaura hemilopha</i>					U66227	
<i>Ctenosaura pectinata</i> Colima					EU246700	
<i>Ctenosaura pectinata</i> Balsas					EU246769	
<i>Ctenosaura pectinata</i> North					EU246713	
<i>Ctenosaura pectinata</i>					EU246730	
<i>Ctenosaura similis</i>	GU331975				EU407509	
<i>Iguana delicatissima</i>					AF217783	
<i>Iguana iguana</i>					AF217786	
<i>Anolis aeneus</i>	EU557103			AF055950		
<i>Anolis krugi</i>	GU057654					
<i>Anolis osa</i>	HQ641730					
<i>Anolis polylepis</i>	HQ641741					
<i>Anolis pulchellus</i>	GU057619					
<i>Anolis trinitatis</i>	AF493592			AY909781		
<i>Gambelia sila</i>	EU037370			EU038401		
<i>Gambelia wislizenii</i>	EU037415			EU038446		
<i>Crotaphytus bicinctores</i>	EU037682			EU038711		
<i>Crotaphytus collaris</i>	EU037482			EU038513		
<i>Crotaphytus reticulatus</i>	EU037745			EU038774		
<i>Liolaemus bibroni</i>	JN410531					
<i>Liolaemus gracilis</i>	JN410538					
<i>Sceloporus cowlesi</i>						EF031648
<i>Sceloporus grammicus</i> F5						L32581
<i>Sceloporus grammicus</i> F6						L32580
<i>Sceloporus grammicus</i> FM2						L32585
<i>Sceloporus grammicus</i> FM3						L32583
<i>Sceloporus grammicus</i> HS						L32579
<i>Sceloporus grammicus</i> LS						L32578
<i>Sceloporus tristichus</i> North						EF031668
<i>Sceloporus tristichus</i> South						EF031890
<i>Sceloporus tristichus</i> West						EF031657
<i>Sceloporus undulatus undulatus</i>						AF440075

Continued Table

<i>Species</i>	<i>Cyt b</i>	12S	16S	NADH2	NADH4	mtDNA
<i>Sceloporus woodi</i>						AF440089
<i>Phrynosoma blainvillii</i>		GQ279564				
<i>Phrynosoma cerroense</i>		GQ279507		DQ385347		
<i>Phrynosoma cornutum</i>	AY141087	DQ385390		DQ385344		
<i>Phrynosoma coronatum</i>	AY141097	DQ385396		DQ385349		
<i>Phrynosoma goodei (platyrhinos)</i>	(EU543746)	DQ385391		DQ385345		
<i>Phrynosoma mcallii</i>	AY141098	DQ385402		DQ385355		
<i>Phrynosoma wigginsi</i>				DQ385348		
Gekkonidae <i>sensu lato</i>						
<i>Sphaerodactylus nicholsi</i>		KC840509	KC840603			
<i>Sphaerodactylus townsendi</i>		KC840513	KC840607			
<i>Heteronotia binoi</i> CA6				DQ000967		
<i>Heteronotia binoi</i> SM6				DQ000789		
<i>Nactus multicaeratus</i>	KC581486			JQ627854		
<i>Nactus pelagicus</i>	KC581545			JQ627855		
<i>Woodworthia maculata</i> Large			HM542435			
<i>Woodworthia maculata</i> Little			HQ343302			
Teiidae						
<i>Aspidoscelis angusticeps</i>	KF555516				KF555554	
<i>Aspidoscelis burti</i>		AY046428	AY046470			
<i>Aspidoscelis deppiei</i>	AF006303	AY046431			KF555559	
<i>Aspidoscelis gularis</i>		AY046443	AY046485			
<i>Aspidoscelis inornata</i>		AY046436	AY046478			
<i>Aspidoscelis sexlineata</i>		AY046445	AY046487			
<i>Aspidoscelis tigris</i>		AY046452	AY046494			
<i>Cnemidophorus gramivagus</i>		AY046432	AY046474			
<i>Cnemidophorus lemniscatus</i>		AY046438	AY046480			
<i>Kentropyx calcarata</i>	JQ639739	AY046458	AY046500			
<i>Kentropyx striata</i>	JQ639672	AY046460	AY046502			
<i>Tupinambis merianae</i>	KF034084					
<i>Tupinambis rufescens</i>	KF034091					
Gymnophthalmidae						
<i>Gymnophthalmus cryptus</i>			AF101362			
<i>Gymnophthalmus speciosus</i>			AF101368			
Lacertidae						
<i>Darevskia alpina (saxicola)</i>	(U88617)					
<i>Darevskia brauneri</i>	AF206181					
<i>Darevskia caucasica</i>	U88616					
<i>Darevskia clarkorum</i>	U88605					
<i>Darevskia daghestanica</i>	AF206171					
<i>Darevskia derjugini</i>	AF206172					
<i>Darevskia mixta</i>	AF147796					
<i>Darevskia nairensis</i>	AF164081					

Continued Table

<i>Species</i>	<i>Cyt b</i>	12S	16S	NADH2	NADH4	mtDNA
<i>Darevskia parvula</i>	U88609					
<i>Darevskia portschinskii</i>	U88615					
<i>Darevskia raddei</i>	AF164076					
<i>Darevskia rudis</i>	U88614					
<i>Darevskia saxicola</i>	U88617					
<i>Darevskia valentini</i>	U88611					
<i>Iberolacerta galani</i>	HQ234901					
<i>Iberolacerta monticola</i>	HQ234897					
<i>Lacerta agilis</i>	AF373032	AF149947	DQ494823		NC021766	
<i>Lacerta bilineata</i>	AF233415	AF149957	AY714979			
<i>Lacerta media israelica</i>	KC896975	KC896891	KC896947			
<i>Lacerta pamphylica</i>	DQ097089					
<i>Lacerta schreiberi</i>	AF372103	EF422436	DQ097097			
<i>Lacerta schreiberi</i> EAST	AF386785					
<i>Lacerta schreiberi</i> WEST	AF386784					
<i>Lacerta strigata</i>	DQ097091	DQ097095	DQ097099			
<i>Lacerta trilineata</i>	AF233427	AF149953	AF149969			
<i>Lacerta viridis</i>	AF233425	AF149962	KC621334		KC621628	
<i>Lacerta viridis meridionalis</i>	AM087228					
<i>Podarcis bocagei</i>	AF372087	AF469421			EF081132	
<i>Podarcis carbonelli</i>	AF372079	AF469418			EF081152	
<i>Podarcis hispanicus</i>	AF372084	AF469443			DQ081163	
<i>Podarcis hispanicus</i> Valencia		HQ898210				
<i>Podarcis hispanicus hispanicus</i>		HQ898179				
<i>Podarcis hispanicus liolepis</i>		HQ898166				
<i>Podarcis melisellensis</i>	AY185036	AY185004				
<i>Podarcis muralis</i> East France	DQ001029					
<i>Podarcis muralis</i> Tuscany	DQ001028					
<i>Podarcis muralis</i> Venetian	HQ652905					
<i>Podarcis raffonei</i> (tiliguerta)	(JX852113)	AJ250157			KJ027980	
<i>Podarcis sicula</i>	AY770890	AY770907		EU006727	KF372035	
<i>Podarcis tiliguerta</i>	JX852113	DQ017658		JX852139		
<i>Podarcis wagleriana</i> (filfolensis)	(KF022066)	DQ017659		(KF022078)	KJ027979	
<i>Timon lepidus lepidus</i>	JX626302			DQ902256	DQ902324	
<i>Timon lepidus nevadensis</i>	JX626247					
<i>Timon pater</i>	AF378964			DQ902258	DQ902326	
<i>Zootoca vivipara carniolica</i>	AY714929	AF247375	AF247050			
<i>Zootoca vivipara louislantzii</i>	AY714919	AF247372	AF247047			
<i>Zootoca vivipara vivipara</i>	AY714913	AF247370	AF247045			
<i>Zootoca vivipara</i> North Spain	AF247998					
<i>Zootoca vivipara</i> South France	AF248003					
Scincidae						
<i>Carlia rubrigularis</i> North	AF181042					

## Continued Table

<i>Species</i>	<i>Cyt b</i>	12S	16S	NADH2	NADH4	mtDNA
<i>Carlia rubrigularis</i> South	AF181056					
<i>Lampropholis coggeri</i> North					HM029922	
<i>Lampropholis coggeri</i> South					HM029999	
<i>Oligosoma otagense</i>	JN999970			JN999934		
<i>Oligosoma waimatense</i>	JN999978			JN999942		
<i>Plestiodon japonicus</i>	EU203134					
<i>Plestiodon latiscutatus</i>	EU203035					
Fishes						
<i>Atractosteus spatula</i>	JF912043					
<i>Lepisosteus osseus</i>	JF912059					
<i>Acantharchus pomotis</i>	AY115994					
<i>Micropterus salmoides</i>	AY115999					
<i>Pomoxis nigromaculatus</i>	AY115992					
Frogs						
<i>Pseudacris crucifer</i>	AY210883					
<i>Pseudacris nigrita</i>	KJ536229					
<i>Pseudacris regilla</i>	KJ536196					
<i>Pseudacris triseriata</i>	KJ536224					
Snakes						
<i>Pantherophis vulpinus</i>	FJ267681					
<i>Pituophis catenifer sayi</i>	AF337112					
Turtles						
<i>Caretta caretta</i>	AY678314					
<i>Chelonia mydas</i>	EU918368					
<i>Cuora flavomarginata</i>	AY434606					
<i>Cyclemys shanensis</i>	AJ604513					
<i>Geoemyda japonica</i>	AY434602					
<i>Mauremys reevesii</i>	AY434567					
<i>Maremys sinensis</i>	AY434615					
<i>Sacalia quadriocellata</i>	AY434618					
Crocodiles						
<i>Crocodylus rhombifer</i>	HQ595019					
<i>Crocodylus siamensis</i>	GU331906					
Birds						
<i>Anas platyrhynchos</i>	EU585609					
<i>Anser anser</i>	EU585613					
Mammals						
<i>Balaneoptera acutorostrata</i>	HM034299					
<i>Balaenoptera bonaerensis</i>	HM034297					
<i>Grampus griseus</i>	AF084059					
<i>Sotalia guianensis</i>	DQ086827					
<i>Tursiops truncatus</i>	JN571480					