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Frugivory and Seed Dispersal by Lizards: A Global Review

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Birds and mammals are the only vertebrates which receive comprehensive attention in studies of dispersal of fleshy-fruited plant species. However, recently the importance of fleshy fruit in the diet of lizards (order Squamata: suborder Sauria), and their role as seed dispersers have been recognized in a number of studies, especially in studies from arthropod-poor habitats, such as oceanic islands. Here, we revisit the evidence of fruit-eating lizards on a global scale in order to test if fruit consumption is more common on islands than expected by chance. We constructed a database of 470 lizard species (from a global count of 6,515 species), that have been reported to consume fleshy fruits. This set of lizards belong to 27 families with Scincidae ($N = 78$ species), Gekkonidae (69), and Dactyloidae (55) having more frugivorous species than other lizard families. We found that 62.4% of these lizards inhabit islands, whereas only one third (35.3%) of all lizard species inhabit islands. These values support the presence of an “insular phenomenon,” however; we also tested if this biogeographical pattern might be driven by body size and evolutionary history of lizards. Thus, we looked for any phylogenetic signals in the distributions of lizard body size, island-presence, and frugivory and calculated phylogenetically corrected correlations among the three variables on a global subset of 2,417 lizard species for which we had detailed phylogenetic information. Both lizard body size and island-presence were weakly influenced by phylogeny; whereas, frugivory was not. In addition, we found that (1) body size and frugivory were weakly positively correlated; (2) body size and island-presence were uncorrelated; and (3) island-presence and frugivory were strongly positively correlated. Thus, we conclude that the main driver of frugivory on islands is the specific island environment and not lizard body size *per se*. Islands are said to be poor in arthropods and predators, and this may force/allow island lizards to forage for additional food sources, such as fleshy fruits. We also suggest that modern lizards as well as their ancestors may potentially play an important role to many plants as seed dispersers. However, we do not know how tight the correlation is between frugivory and seed dispersal. Thus, lizards repeatedly inspire us to ask new ecological and evolutionary questions.

Keywords: frugivory, lizard, mutualism, plant-animal interaction, saurochory, seed dispersal, island, body size

INTRODUCTION

Birds and mammals are the principal seed dispersers of fleshy-fruited plant species (e.g., van der Pijl, 1982; Jordano, 2013). Fruit pulp is an important resource to these animals, which in return may promote an important ecosystem service, the dispersal of their seeds (e.g., Herrera and Pelmyr, 2002; Forget et al., 2011; Bascompte and Jordano, 2014; Wandrag et al., 2018). By dispersing seeds further away from the mother plants, seed mortality gets

reduced and survival is favored if colonization happens to new microhabitats (e.g., Janzen, 1970; Howe and Smallwood, 1982; Cousens et al., 2008). In addition, seed dispersal promotes gene flow within and among plant populations (e.g., Rousset, 2004; Pérez-Méndez et al., 2018; Wandrag et al., 2018). Until recently, however, few studies have considered the role of other vertebrates as seed dispersers of fleshy-fruited plant species, e.g., fish, chelonians, crocodilians, and lizards (e.g., Olesen and Valido, 2003, 2004; Liu et al., 2004; Correa et al., 2007; Valido and Olesen, 2007; Platt et al., 2013; Falcón et al., 2018).

Here, we focus on lizards (order Squamata: suborder Sauria), because these animals are usually overlooked or dismissed as frugivores and seed dispersers. The main reason is that most are regarded as primarily feeding on small invertebrates (e.g., Greene, 1982; Cooper and Vitt, 2002; Pianka and Vitt, 2003), whereas only a few species bigger in size are herbivorous, i.e., folivorous (**Supplementary Material**: Herbivorous lizards). Thus, since Pough (1973) a relation between lizard body size and herbivory (specifically “folivory”) has been noted. In this respect, larger lizards would present some digestive and physiological modifications which favor an herbivorous diet (e.g., Iverson, 1982; Zimmerman and Tracy, 1989). This idea has also been extended to lizards with frugivorous habits, such as *Anolis*-like species whereas fruit intake has been related to large body size in some species (Herrel et al., 2004a). However, fruit pulp is an easily metabolized plant part, being low in fibers and proteins, and high in soluble carbohydrates (e.g., Valido et al., 2011; Jordano, 2013). Thus, lizards do not require large gape, strong bite or a large digestive system to process these items. In this respect, several studies have shown that small arthropod-eating lizards do consume fruit if their favorite arthropod food is scarce. This is most often observed on islands (e.g., Patterson, 1928; Vinson and Vinson, 1969; Schoener et al., 1982; Cheke, 1984; Whitaker, 1987; Pérez-Mellado and Corti, 1993; Valido and Nogales, 1994; Wotton, 2002; Valido et al., 2003; Hare et al., 2016; Wotton et al., 2016; Melzer et al., 2017; Parejo et al., 2018), where arthropods might be in short supply, but also in arthropod-poor habitats on mainland, such as high mountains and deserts (e.g., Fuentes, 1976; Mautz and Lopez-Forment, 1978; Hódar et al., 1996; Whiting and Greeff, 1997; Kiefer and Sazima, 2002; Espinoza et al., 2004; Valdecantos et al., 2012). By feeding from at least two trophic levels, these lizards become omnivorous. Generally, they do not have any morphological, digestive or physiological modifications related to their frugivorous diet (e.g., Valido and Nogales, 2003; Herrel et al., 2004b; Vidal and Sabat, 2010; but see Sagonas et al., 2015). Alongside their fruit diet choice, they may act as seed dispersers (e.g., Pérez-Mellado and Traveset, 1999; Olesen and Valido, 2003; Godínez-Álvarez, 2004; Valido and Olesen, 2007, 2010).

The full extent of this mutualistic plant-lizard interaction is unknown, because fruit rarely is scored as a separate component in diet studies. In the literature, plant material consumed by lizards is often pooled into one diet component, notwithstanding the wide range in energy content and digestability of various plant parts, e.g., foliage, which is difficult to digest because of the presence of cellulose. In the past, however, mutualistic reptiles were also present in

the past (**Supplementary Material**: Mutualistic reptiles in the past), and the natural history literature is rich in stories about fruit-eating lizards (**Supplementary Material**: Early records of lizard-fruit interactions), but this knowledge is still not integrated into general ecology and evolutionary biology (see Miranda, 2017). Consequently, most reviews about seed dispersal focus on birds and mammals (Traveset et al., 2013; e.g., Jordano, 2013).

Here, our aim is (1) to present a detailed global overview of the extent of fleshy fruit consumption and seed dispersal in lizards, by mapping their geographical and taxonomical distribution, and (2) to test if insularity favors plant-lizard mutualism, if we control for lizard body size and phylogenetic relationships.

MATERIALS AND METHODS

Collection Methods

Variation in collecting efforts and nomenclature changes make the global number of lizard species very dynamic, but on the 29th of August 2018, the number was 6,512 species (Uetz et al., 2018; **Table 1**). The taxonomy of lizards used here follows the *European Molecular Biology Laboratory Reptile Database*, EMBL. Two species were excluded from our analysis because their geographic range were missing in the EMBL, and, additionally, we included four new species from New Zealand and one from the Canary Islands (Hare et al., 2016; **Table S1**). Thus, our database included a total of 6,515 species sorted into 38 families, which further belonged to the infraorders Iguania, Gekkota, Scincomorpha, Diploglossa, Dibamia, and Platynota (Squamata: Sauria). Using this database, we classified lizards according to their geographical distribution, i.e., only island (I), only mainland (M), and both island and mainland (IM). We classified Australia as a mainland together with the other continents, whereas New Zealand, Madagascar, New Guinea, Borneo, Japan, and Taiwan were analyzed as islands. The borderline between island and mainland is obviously subjective. However, in island literature, Australia is most often regarded as a mainland, and here, we prefer to keep it that way. Several IM-species are introductions from their native islands to a mainland, e.g., from the Caribbean Islands to USA (e.g., *Anolis cristatellus*, *Dactyloideae*), from the Balearic Archipelago to the Iberian Peninsula (*Podarcis pityusensis*, *Lacertidae*), or vice versa, from USA to Japanese Ogasawara Islands (*A. carolinensis*), from North Africa to Menorca Island (*Scelarcis perspicillata*). Such species were here categorized as IM. Some lizard species are also island-to-island introductions (e.g., the lacertid *Teira dugesii* from Madeira to the Azores, and *Gallotia stehlini* from Gran Canaria to Fuerteventura). Finally, near-shore islets were regarded as part of their adjacent mainland or island. We also included the continuous variable lizard body size (maximum snout-vent length “max SVL”; Meiri, 2008, 2018), and the binary trait presence of fruits: 0 (absence) and 1 (presence) (see **Supplementary Material**: Quality of the data).

First, we compared species frequencies of fruit-eating lizards on islands and mainland. Our null hypothesis was that the frugivorous lizards had a geographical distribution similar to lizards in general. This was tested with a Chi squared

TABLE 1 | Number of lizard species (Sauria) in the families of the infraorders Iguania, Gekkota, Scincomorpha, Diploglossa, Dibamia, and Platynota, sorted according to their geographic distribution: *I*, island-only species; *M*, mainland-only species; and *IM*, species present on both island and mainland.

Family	Total no. spp.	I-spp (%)	M-spp. (%)	IM-spp (%)
IGUANIA				
Agamidae	489	106 (21.7)	340 (69.5)	43 (8.8)
Chamaeleonidae	210	94 (44.8)	113 (53.8)	3 (1.4)
Corytophanidae	9	0	9 (100)	0
Crotaphytidae	12	0	11 (91.7)	1 (8.3)
Dactyloidae	426	187 (43.9)	230 (54.0)	9 (2.1)
Hoplocercidae	19	0	19 (100)	0
Iguanidae	44	27 (61.4)	9 (20.5)	8 (18.2)
Leiocephalidae	31	31 (100)	0	0
Leiosauridae	33	0	33 (100)	0
Liolemididae	307	0	304 (99.0)	3 (0.98)
Opluridae	8	8 (100)	0	0
Phrynosomatidae	156	12 (7.7)	133 (85.3)	11 (7.1)
Polychrotidae	8	0	6 (75.0)	2 (25.0)
Tropiduridae	137	11 (8.0)	125 (91.2)	1 (0.7)
GEKKOTA				
Gekkonidae	1181	388 (32.9)	720 (61.0)	73 (6.2)
Carphodactylidae	30	0	30 (100)	0
Diplodactylidae	153	58 (37.9)	92 (60.1)	3 (2.0)
Eublepharidae	38	8 (21.1)	25 (65.8)	5 (13.2)
Phyllodactylidae	146	44 (30.1)	96 (65.8)	6 (4.1)
Sphaerodactylidae	218	104 (47.7)	89 (40.8)	25 (11.5)
Pygopodidae	46	1 (2.17)	43 (93.5)	2 (4.4)
SCINCOMORPHA				
Cordylidae	68	0	68 (100)	0
Gerrhosauridae	37	19 (51.4)	17 (45.9)	1 (2.7)
Lacertidae	335	34 (10.2)	273 (81.5)	28 (8.4)
Scincidae	1,656	702 (42.4)	864 (52.2)	90 (5.4)
Xantusiidae	34	1 (2.9)	32 (94.1)	1 (2.9)
Alopoglossidae	23	0	22 (95.6)	1 (4.4)
Gymnophthalmidae	246	2 (0.8)	236 (95.9)	8 (3.3)
Teiidae	160	26 (16.3)	118 (73.8)	16 (10.0)
DIPLOGLOSSA				
Anguidae	78	2 (2.6)	69 (88.5)	7 (9.0)
Diploglossidae	51	26 (50.9)	25 (49.0)	0
Anniellidae	6	0	5 (83.3)	1 (16.7)
Xenosauridae	12	0	12 (100)	0
DIBAMIA				
Dibamidae	24	10 (41.7)	11 (45.8)	3 (12.5)
PLATYNOTA				
Helodermatidae	2	0	2 (100)	0
Lanthanotidae	1	1 (100)	0	0

(Continued)

TABLE 1 | Continued

Family	Total no. spp.	I-spp (%)	M-spp. (%)	IM-spp (%)
Varanidae	80	36 (45.0)	30 (37.5)	14 (17.5)
Shinisauridae	1	0	1 (100)	0
TOTAL	6515	1938	4212	365
(%)		(29.7)	(64.6)	(5.6)

Number of species and their geographic range follow Uetz et al. (2018), update at 29 August 2018.

This table includes 6,515 species. In the analysis, we excluded two species with no information about their geographic range in the Reptile Database: *Diploglossus microlepis* (Diploglossidae) and *Leiolopisma fasciolare* (Scincidae), but we have included four new species from New Zealand, which were not in the Reptile Database: *Oligosoma aff. polychroma* (Scincidae), *Dactylocnemis* "Poor Knights," *Woodworthia aff. brunnea*, and *W. "Southern Alps"* (Diplodactylidae) (Hare et al., 2016). The extinct *Gallotia goliath* (Lacertidae) from Canary Islands was also included, because of available diet information.

test of data from each family separately and for the global count of lizards. Globally, 29.7% of all lizard species are *I*-species, 64.6% only *M*-species, and 5.6% are *IM*-species (Table 1; Figure 1).

We also tested if the variables body size, frugivory, and island-presence in their distribution among lizards had a phylogenetic signal (see below). As backbone lizard phylogeny, we used the one published by Pyron et al. (2013). This phylogeny only included 2,847 lizard species. We pruned the phylogeny for those lizard species without any information about their max SVL or geographic distribution, resulting in 2,417 lizard species, which were included in our phylogenetic analysis.

Phylogenetic Signal

The phylogenetic signal of a trait is a measure of the statistical dependency among values of this trait on the phylogenetic relationships among species in the study sample (e.g., Blomberg and Garland, 2002). If other factors than phylogenetical relatedness influence trait variation, for example convergence due to related ecology, this will reduce the phylogenetic signal.

The phylogenetic signal of a continuous trait (max SVL) can be measured by Blomberg's *K* and Pagel's *λ* (Pagel, 1999; Blomberg et al., 2003). Both measures react slightly different to number of species included in the phylogeny, amount of information about branch length and number of polytomies (Münkemüller et al., 2012). For both measures, the actual observed value is compared to a null model of trait evolution, a Brownian motion (*BM*) evolutionary model (Blomberg et al., 2003), which is based upon either pure genetic drift, randomly varying selection, or varying stabilizing selection, but not on directional selection. According to this *BM* model, trait evolution follows a random walk along the branches of the phylogenetic tree. To test this null hypothesis of no phylogenetic signal, the observed values of the focal trait was compared with values expected under random (1,000 permutations) value distribution by using a likelihood ratio test (Münkemüller et al., 2012).

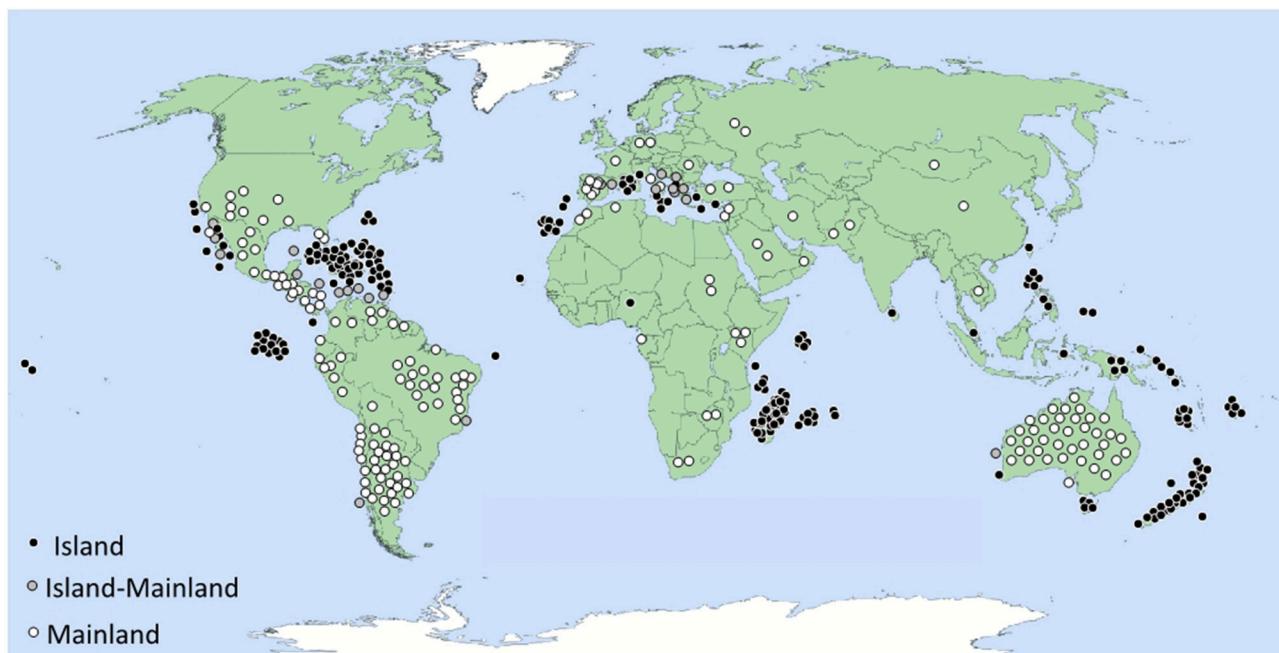


FIGURE 1 | Geographic distribution of 470 fruit-eating lizard species sorted as island-only species (*I*), mainland-only species (*M*) and species present on both island and mainland (*IM*). See also **Table S1** in Supplementary Material for a full list of frugivorous lizard species. The map shows not just the distribution of lizard frugivory, but also the heterogeneous sampling efforts. Note, for example, the absence of dots in Japan and Indonesia, which most likely is caused by insufficient field observation.

Both measures (K , λ) vary from 0 to 1, with values close to zero indicating lack of phylogenetic dependency, i.e., the trait has evolved in response to local selective processes. Whereas, a value close to 1 indicates an evolution according to the *BM*, i.e., a gradual accumulation of changes over time. K may also be larger than one, which indicates a strong phylogenetic signal. At least theoretically, λ might also become slightly larger than one (Münkemüller et al., 2012). The lower and upper bounds of K and λ indicate which of the two scenarios is the most likely.

The phylogenetic signal for binary traits (frugivory and island-presence) can be measured by D (phylogenetic dispersion) (Fritz and Purvis, 2010). $D = (d_{\text{obs}} - \text{mean } d_b)/(\text{mean } d_r - \text{mean } d_b)$, where d_{obs} is the number of trait state changes needed to get the observed trait state distribution in our phylogeny, d_b is the expected distribution of d under a *BM* model (1,000 permutations) and d_r is the expected distribution of d , if trait states are randomly distributed among species. D typically varies from 0 to 1. $D = 0$ indicates that the trait evolves according to the Brownian model, *BM* (i.e., phylogenetic signal). $D = 1$ indicates that the trait evolves according to a random model (i.e., independent of the phylogeny), $D > 1$, if the trait is phylogenetically overdispersed, and $D < 0$, if the trait is more phylogenetically clustered than expected according to a *BM* model (Nunn, 2011).

The finding of a significant phylogenetic signal in some of these variables requires the use of comparative phylogenetic analysis to test for correlation between traits.

Phylogenetically Corrected Correlations

We tested for correlations between max SVL, island-presence and frugivory, using phylogenetically independent contrasts (PIC), i.e., any influence of statistical dependency among trait values was removed before the correlation analysis. The lizard body size (max SVL) data were log-transformed.

By using the lizard phylogeny (Pyron et al., 2013), and our compiled database including max SVL of lizards (Meiri, 2008, 2018), island-presence and frugivory (**Table S1**), we answered:

1. Is there, globally, any phylogenetic signal in the distribution of frugivory, body size, and island-presence in lizards; and
2. to what extent do island-presence and max SVL influence frugivory after correcting for any phylogenetical influence. For these phylogenetical analyses we used *picante* (Kembel et al., 2018), *geiger* (Harmon et al., 2016), *caper* (Orme et al., 2018), and *ape* (Paradis et al., 2018) R packages (R Core Team, 2014).

RESULTS

Fruit-Eating Lizards

We found reports of 470 lizard species from 27 families and 128 genera consuming fleshy fruits (**Tables 2, S1**). Thus, 7.2% of all lizards use fleshy fruits to some extent in their diet. These species are widely distributed taxonomically, since 71% of all lizard families included some frugivorous members; Scincidae ($N = 78$ species), Gekkonidae (69), and Dactyloidae (55) being most frugivorous. Other lizard families with a high percentage of frugivorous species are Iguanidae (54.5%), Corytophanidae

TABLE 2 | Taxonomic and geographical distribution of fruit-eating lizard families.

Family	Total no. spp.	No. fruit-eating lizards	I (%)	M (%)	IM (%)	P	%
IGUANIA							
Agamidae	489	19	7 (36.8)	12 (63.2)	0	ns	3.9
Chamaeleonidae	210	2	1 (50.0)	1 (50.0)	0	ns	0.9
Corytophanidae	9	4	0	4 (100.0)	0	–	44.4
Crotaphytidae	12	2	0	1 (50.0)	1 (50.0)	–	16.7
Dactyloidae	426	55	47 (85.5)	5 (9.1)	3 (5.5)	***	12.9
Iguanidae	44	24	16 (66.7)	3 (12.5)	5 (20.8)	ns	54.5
Leiocephalidae	31	13	12 (92.3)	0	1 (7.7)	–	41.9
Leiosauridae	33	1	0	1 (100.0)	0	–	3.0
Liolaemidae	307	34	0	34 (100.0)	0	–	11.1
Opluridae	8	2	2 (100.0)	0	0	–	25.0
Phrynosomatidae	156	8	1 (12.5)	6 (75.0)	1 (12.5)	ns	5.1
Polychrotidae	8	4	0	4 (100.0)	0	–	50.0
Tropiduridae	137	24	9 (37.5)	14 (58.3)	1 (4.2)	*	17.5
GEKKOTA							
Gekkonidae	1,181	69	66 (95.7)	3 (4.3)	0	***	5.8
Diplodactylidae	153	17	17 (100.0)	0	0	***	11.1
Phyllodactylidae	146	2	1 (50.0)	1 (50.0)	0	–	1.4
Sphaerodactylidae	218	2	1 (50.0)	1 (50.0)	0	–	0.9
Pygopodidae	46	17	0	17 (100.0)	0	–	37.0
SCINCOMORPHA							
Cordylidae	68	3	0	3 (100.0)	0	–	4.4
Gerrhosauridae	37	7	4 (57.1)	3 (42.9)	0	ns	18.9
Lacertidae	335	38	21 (55.3)	11 (28.9)	6 (15.8)	***	11.3
Scincidae	1,656	78	45 (57.7)	32 (41.0)	1 (1.3)	ns	4.7
Xantusiidae	34	3	2 (66.7)	1 (33.3)	0	ns	8.8
Telidae	160	36	15 (41.7)	19 (52.8)	2 (5.6)	*	22.5
DIPLOGLOSSA							
Anguidae	78	1	0	1 (100.0)	0	–	1.3
Diploglossidae	51	2	2 (100.0)	0	0	ns	3.9
PLATYNOTA							
Varanidae	80	3	3	0	0	ns	3.7
TOTAL (%)	6113	470	272 (57.9)	177 (37.6)	21 (4.5)	***	7.7

I, island-only species; M, mainland-only species; and IM, species present on both island and mainland. P, probability that the geographical distribution of the fruit-eating lizards in a given family differed from a random draw of the same number of species from the world pool of lizards (see Methods). %, percent fruit-eating lizard species out of total count. Number of species and their geographical range follow Uetz et al. (2018), update at the 29 August 2018 (**Table 1**). See also **Table S1** in Supplementary Material for a full list of frugivorous species.
*P < 0.05; ***P < 0.001.

(44.4%), and Leiocephalidae (41.9%) (**Tables 2, S1**, Importance and examples of fleshy fruit to the diet of lizards).

Geographic Distribution of Frugivorous Lizards

64.6%, 29.7% and 5.6% of the 6,515 lizard species in the world inhabit mainlands, islands, and both, respectively (**Table 1**). However, frugivory in lizards were much more frequent among only island species (57.9% of all frugivorous lizards) than among only mainland species (37.6%). Only 4.5% of all frugivorous lizards were found on both island and mainland (**Tables 2, S1**). First, we tested the null-hypothesis H_0 : the frequencies of

fruit-consuming lizard species on islands, mainland and both could be explained by the global geographical distribution of lizards. In this analysis, only the 27 lizard families with reported frugivory were included ($N = 6,113$ species). H_0 was rejected ($P << 0.001$; **Table 2**). Thus, the high frequency of fruit-consuming lizards on islands could not be explained by the general biogeography of the group. This analysis was repeated at family level. Island species were significantly overrepresented as fruit consumers in Dactyloidae, Gekkonidae, Diplodactylidae, and Lacertidae (**Table 2**). In contrast, in the Tropiduridae, frugivory was significantly more frequent on mainland than on islands (**Table 2**). Thus, worldwide fruit-consumption among

lizards is almost twice as common on islands than on mainland, but on the family level there is some variation.

Phylogenetic Correlations

The distribution of max SVL showed a significant, but weak phylogenetical signal ($K = 0.291$; **Table 3**). Pagel's λ was closer to 1 than 0, but it was still significantly different from both values (95% confidence interval = [0.911; 0.941], and both the lower and upper bound were strongly unlikely; **Table 3**). Thus, K and λ showed that phylogeny, but also other factors, were important as drivers of body size variation in lizards. That lizard body size, in general, is influenced by both phylogenetic relationships and other factors (ecology) is certainly also what one would expect.

Our null hypothesis, stating that any presence or absence of lizards on islands is influenced of phylogeny, was not rejected ($P = 0.80$; **Table 3**), and this binary trait was distributed according to a Brownian motion model ($D \approx 0$; **Table 3**). We would also expect evolution to have played a role here, especially because many lizard radiations are endemic to islands.

For the binary trait frugivory, the null model was rejected ($P = 0.003$). Thus, the trait was not distributed according to a Brownian motion model of evolution ($D \approx 1$). However, $D \approx 1$ (no influence of phylogeny) was also rejected ($P < 0.001$). Thus, both phylogeny and other factors (ecological) play a role in the distribution of frugivory among lizards.

After correcting for any influence of phylogeny (PIC, phylogenetically independent contrasts; **Table 4**), we found (1) that body size (max SVL) and frugivory were positively, but weakly correlated; (2) that body size and island-presence were uncorrelated; and (3) that island-presence and frugivory were strongly positively correlated. Thus, in our database, frugivory was significantly associated with insular species after correcting for any influence of evolutionary relationships.

DISCUSSION

In this review, we reported that 470 lizard species consume fleshy fruit, many more than previously thought (Cooper and Vitt, 2002; Olesen and Valido, 2003; Godínez-Álvarez, 2004; Valido and Olesen, 2007; Meiri, 2018). However, it is still low compared to equivalent estimates for birds (around 4,000 bird species consume fleshy fruit, Wenny et al., 2016), but similar to

mammals (460 species are primarily frugivorous, Fleming and Sosa, 1994). In addition, 182 Neotropical freshwater fish are fruit eaters (Correa et al., 2007), and recently Falcón et al. (2018) reported that up to 72 species of turtles include fleshy fruits in their diet.

However, for several reasons our number of frugivorous lizards is clearly an under-estimate: For example: (1) modern researchers have just recently begun to pay more attention to lizards as frugivores/plant mutualists; (2) many omnivorous (i.e., with 10–90% volume (V) plant matter in their diet) and herbivorous (>90%V) lizard examples reported in e.g., Cooper and Vitt (2002) were not incorporated in our database since the original reports did not specify which vegetative parts were consumed, and these species may use fleshy fruit as well; (3) lizard diet sampling conducted outside the fruiting period will not detect frugivory, and (4) for most lizards we did not find any data about their diet, particularly for endemics inhabiting remote islands, although some of their congeners are in our database. Thus, we believe that many more fruit-eating and seed-dispersing lizards are waiting to be discovered.

Evolution of Frugivorous Lizards

Irrespectively of recent finding of an herbivorous lizard from early Cretaceous (Evans and Manabe, 2008), carnivory is the ancestral feeding mode in modern lizard species and most species are still exclusively or mainly carnivorous (e.g., Cooper and Vitt, 2002). However, trends toward true herbivory are seen repeatedly (Iverson, 1982; King, 1996; Cooper and Vitt, 2002), e.g., ~18 herbivory origins within the South American

TABLE 4 | Phylogenetic independent contrasts (PIC) correlations between "max SVL," "frugivory," and "island-presence" of 2,417 lizard species, based on the phylogeny of Pyron et al. (2013).

Correlation	F _{phy} 1,2414	P _{phy}
Max SVL × island-presence	0.029	0.86
Max SVL × frugivory	8.793	0.004
Island-presence × frugivory	52.31	0.001

"Island-presence" and "frugivory" were categorized as binary variables (0, 1) (see Methods for details). P_{phy} is the probability that there is no correlation between two variables.

TABLE 3 | Size of phylogenetic signal in the distribution of the continuous trait "max SVL" (K , λ), and the binary traits "island presence" and "frugivory" (D) of 2,417 lizard species, according to the phylogeny of Pyron et al. (2013).

Trait	K	P(K)	λ	Confidence interval of λ	P(λ) (lower bound)	P(λ) (upper bound)
Max SVL	0.291	<0.001	0.927	[0.911; 0.941]	0.001	0.001
D					P ($D \approx 0$)	P ($D \approx 1$)
Island presence	-0.080				0.80	0.001
Frugivory	0.314				0.003	0.001

P of null model of Brownian motion (BM) (see Methods for details).

K ≈ 0 no influence of phylogeny; K ≈ 1 trait evolution according to BM model; K > 1 trait is phylogenetically clustered; λ ≈ 0 no influence of phylogeny; λ ≈ 1 trait evolution according to BM model; D < 0 trait values are phylogenetically clustered; D ≈ 0 trait evolution according to BM model; D ≈ 1 no influence of phylogeny.

Liolaemus (Espinoza et al., 2004). These lizards are smaller (max. SVL <100 mm) than other herbivorous species, and also inhabit mainland cold areas. Thus, small montane lizards may keep a higher body temperature (Vitt, 2004), being necessary for microbial hindgut endosymbionts, by digesting plant fibers. Cooler habitats have fewer insects and selection may favor a switch to herbivory (Pearson, 1954; Fuentes and Di Castri, 1975; Jaksic, 1978). However, the rarity of plant-eating lizards also suggests that herbivory in lizards is constrained (Szarski, 1962; Ostrom, 1963; Sokol, 1967; Pough, 1973; Espinoza et al., 2004). Here, we demonstrate that the use of easily digestible plant matter (i.e., fleshy pulp) is relatively frequent, occurring in several lizard lineages. However, the extent of this shift to frugivory in lizards is affected by insularity and body size.

Insularity

One third of all lizard species live on islands, but two thirds of all the fruit-consuming lizards are reported from islands. This geographical pattern is not caused by a higher number of scientists working both on seed dispersal (e.g., Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey et al., 2002; Dennis et al., 2007; and references therein) or diet of lizards on islands compared to mainland habitats (Meiri, 2018). In addition, the pattern is not caused by a presence of more fleshy-fruited plant species on islands compared to mainland habitats; on the contrary, islands have fewer fleshy-fruited plant species than comparable mainland habitats (e.g., Heleno and Vargas, 2015). Herrel et al. (2004a) compared the geographic distribution of frugivory among 45 island and 16 mainland *Anolis* species and also demonstrated that fruit in the diet of lizards is more common on islands (90% of all cases) than on mainland (10%). Analyzing many lizard species, but pooling all dietary plant parts, earlier studies also found this relationship (e.g., van Damme, 1999; Cooper and Vitt, 2002). However, island lizards include fleshy fruit, but also other vegetable food items, into their diet because they may be food limited (Janzen, 1973; Andrews, 1979; Schlüter, 1984; Pérez-Mellado and Corti, 1993; van Damme, 1999; Cooper and Vitt, 2002; Polis et al., 2002; Olesen and Valido, 2003; Barret et al., 2005). This recurrent island phenomenon is an example of “niche expansion” or interaction release (*sensu* Traveset et al., 2015) and was first demonstrated for island birds (Grant, 1966; MacArthur et al., 1972). This pattern is possibly caused by a three-step process: 1) Compared to mainland, islands usually support fewer insect taxa (Gulick, 1932; MacArthur and Wilson, 1967) of a lower overall abundance (Allan et al., 1973; Janzen, 1973); 2) island lizards are less exposed to interspecific competition and predation because of a general low species density (MacArthur et al., 1972; Case, 1975; Andrews, 1979), and 3) some island lizard species respond to 2) by density compensation (MacArthur et al., 1972; Case, 1975; Rodda et al., 2001), resulting in intense intraspecific competition and consequently an expansion of their feeding niche toward the use of alternative resources, such as fleshy fruits (Olesen and Valido, 2003). However, only scant information is available on island arthropod abundance (Allan et al., 1973; Janzen, 1973; Andrews, 1979; Case, 1982; Faeth, 1984), but the impression from the general island biology literature is that arthropods are less

abundant on islands and that they do not density compensate. On tiny islets, however, where coastline habitats dominate, flies functioning as decomposers of algae may be so abundant (Polis et al., 2002), that, at least theoretically, arthropod-eating lizards may be less inclined to shift to fruit.

On many islands, lizards have higher densities than related groups from adjacent mainland (Rodda and Dean-Bradley, 2002; Buckley and Jetz, 2007). Exceptionally high densities of lizards on islands have attracted considerable attention (Case, 1975; Case and Bolger, 1991; Rodda et al., 2001; Buckley and Jetz, 2007). The world record seems to be >5 *Sphaerodactylus macrolepis* individuals/m² in the Virgin Islands (Rodda et al., 2001). Insular founders may reach such high densities in just 3 years (Schoener, 1989). Density compensation in island lizards is a ubiquitous and global phenomenon, and total island lizard density is an order of magnitude higher than on mainland (128 vs. 1,920 individuals/ha) (Rodda et al., 2001; Buckley and Jetz, 2007). Many of these density-compensating island lizards are also present in our database (genera *Anolis*, *Gallotia*, *Gehyra*, *Hemidactylus*, *Lepidodactylus*, *Oligosoma*, *Phelsuma*, *Podarcis*, *Xantusia*, etc.). Reduction in species richness of predators (e.g., birds of prey) and number of competitors (insectivorous birds) may be the dominant drivers of lizard abundance on islands (Schoener and Schoener, 1978; Andrews, 1979; Wright, 1979; Buckley and Jetz, 2007). Density compensation in fruit-consuming lizards may thus be of high importance to seed dispersal in many plant species, influencing their chance of colonization and establishment on small islands, and their general population structure. Besides, the poor ability of mammals to reach remote islands will leave part of the diet niche dimension empty for other animal groups to explore (Whittaker and Fernández-Palacios, 2007).

Fruit -eating lizards are also observed in mainland habitats poor in arthropods. Frugivory in lizards inhabiting desert-like habitats (e.g., Clark and Comanor, 1976; Vitt et al., 1981; Hódar et al., 1996; Whiting and Greeff, 1997; Belver and Avila, 2002), high mountains (e.g., Hurtubia and Di Castri, 1973; Fuentes, 1976), cerrado habitats (e.g., Vitt, 1993; Mesquita and Colli, 2003) and caves (Mautz and Lopez-Forment, 1978) make up most of the mainland observations. Seasonal scarcity of arthropods and frugivory in lizards are also reported (e.g., Schleich et al., 1996; Duffield and Bull, 1998; Fialho et al., 2000). Thus, the arthropod-scarcity hypothesis can also explain mainland observations of lizards as fruit eaters.

Lizard Body Size

Since the review by Pough (1973) about lizard body size and herbivory diet, the generalization that only lizards >300 g (>217 mm SVL) are truly herbivorous and that medium-sized lizards, 100–300 g (150–217 mm SVL) are omnivorous have become a dogma in lizard ecology. It has been used to explain the paucity of modern, truly herbivorous lizards. However, a debate about this has also been running for more than 50 years (Szarski, 1962; Ostrom, 1963; Sokol, 1967; Pough, 1973; Iverson, 1982; van Devender, 1982; Auffenberg, 1988; King, 1996; van Damme, 1999; Cooper and Vitt, 2002; Cooper, 2003; Espinoza et al., 2004; Herrel et al., 2004a,b, 2008), including issues about predation

risk, insularity, lizard body size, and digestive and physiological adaptative modifications. However, Espinoza et al. (2004), and more recently Vervust et al. (2010) demonstrated true herbivory in smaller species (max. SVL <100 mm) than in other known herbivorous species. These species were inhabiting insular (-like) habitats and true islands.

Many small (<150 mm SVL) lizards are being classified as frugivorous, e.g., species of *Gallotia*, *Podarcis* (Lacertidae), *Anolis* (Dactyloidae), *Carinascincus*, *Trachylepis* (Scincidae), *Gehyra*, *Phelsuma* (Gekkonidae), *Platysaurus* (Cordylidae), *Ameiva*, *Cnemidophorus* (Teiidae), *Leiocephalus* (Leiocephalidae), *Microlophus* (Tropiduridae), and *Lepidophyma smithii* (Xantusiidae). Large lizards have large gapes and a strong bite (e.g., Herrel et al., 1999, 2004a,b), and this may be advantageous if the diet is vegetarian, because it allows the lizards to crush the material efficiently (Szarski, 1962; Sokol, 1967). Fleshy fruits, on the other hand, do not require this.

Frugivorous Lizards as Legitimate Seed Dispersers

Lizards do not fully chew their food and seeds passing through their gut may remain intact. Reviewing experimental studies of 40 plant species and 17 lizard species, Traveset (1998) and A. Valido (*unpublished*) concluded that seeds dispersed by lizards germinated just as well as seeds dispersed by frugivorous birds and mammals. The proportions of experiments in which germination of seeds was enhanced (25%), unaffected (57%) and inhibited (18%) after lizard gut passage were similar to figures for seed-dispersing birds (36, 48, and 16%, respectively), non-flying mammals (39%, 42%, 19%), and bats (25%, 67%, 8%). Here, we summarize some of these results.

Iverson (1985) detected a 6% increase in seed germination of *Coccoloba uvifera* (Polygonaceae) after passage through the gut of *Cyclura* compared to controls. Studies of other rock iguanas gave similar results. Within Lacertidae, a significant increase in germination in *Gallotia*-consumed seeds of *Withania aristata* (Solanaceae) has been reported (Valido and Nogales, 1994). Other reports from the Canaries and Balearics show similar results (Nogales et al., 1998; Castilla, 2000; Pérez-Mellado and Riera, 2004; Pérez-Mellado et al., 2005; Rodríguez-Pérez et al., 2005). Thus, many of these island lizards may contribute to plant fitness. However, for *Cnemidophorus murinus* from Bonaire Island, Lesser Antilles, Schall (1996) did not find any germination response for *Erihalis fruticosa* (Rubiaceae).

In Brazilean *Melocactus violaceus* (Cactaceae), 36% of the seeds passing through *Tropidurus torquatus* germinated compared to no germination at all for controls (Cortes-Figueira et al., 1994). Fruits of *Melocactus* species appear to be consumed by lizards only (Dearing and Schall, 1992). On Chiloé Island, Chile, Rubiaceae seeds defecated by *Liolaemus pictus* germinated better or to the same extent as controls (Willson et al., 1996). Seeds of *Genipa americana* (Rubiaceae) and *Cereus peruvianus* (Cactaceae) consumed by *Salvator merianae* germinated significantly better and/or to the same extent as controls, respectively (De Castro and Galetti, 2004). Vasconcellos-Neto et al. (2009) showed that seeds of *Solanum*

thomasiifolium (Solanaceae) were dispersed less frequently by lizards (4%) than by birds (77%) and foxes (19%), but with higher germination rate (80%) compared to birds (64%) and foxes (53%).

The digestive treatment of seeds seems to be quite similar among different frugivore groups (Valido and Olesen, 2007). Although examples are still scarce, lizards seem to be in the same seed disperser league as the classical and better studied frugivorous birds and mammals. However, the series of seed germination studies mentioned above suggests that frugivory may not just lead to dispersal of seeds, but also to dispersal of viable seeds, which may germinate and increase plant fitness. However, we do not know how strong frugivory is as a proxy for plant fitness, and we also lack an experimental comparison of seed germination after passage through sympatric native lizards, birds and mammals, with the control treatment of intact fruits (Samuels and Levey, 2005).

CONCLUSIONS

Many lizard species are potential seed dispersers, and fruit feeding among lizards is taxonomically and geographically widespread, including 7.2% of all lizard species. It is especially important in species and populations inhabiting islands (62.4% of all reported cases). Finally, compared to other, more classical vertebrate mutualists (birds, mammals) seed dispersal by lizards is relatively poorly documented, but may be just as effective in terms of the quantitative and qualitative component of the seed dispersal effectiveness (*sensu* Schupp et al., 2010).

We believe that the results presented here are only the tip of the “lizard-plant seed dispersal iceberg.” Thus, we find that fruit is an important supplementary diet component for island lizards. Other easily digestable plant material, like nectar and pollen, may show the same difference between islands and mainland, whereas we expect consumption of fiber-rich plant parts to show a deviating pattern. In general, much about lizard diet and its ecological and evolutionary consequences remain unknown. Our review may encourage ecologists, herpetologists, island biologists and natural historians in general to pay more attention to this type of plant-animal interaction, which may expand our general understanding of the ecology and evolution of mutualisms. For several decades, lizards have offered us outstanding opportunities for many kinds of ecological and evolutionary study (e.g., Pianka and Vitt, 2003; Losos, 2009), and here a new research line about lizard-plant mutualisms is suggested.

DATA AVAILABILITY

The datasets analyzed for this study are available in Supporting Information (Table S1) and the lizard phylogeny in Pyron et al. (2013).

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00049/full#supplementary-material>

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Supplementary Material

Frugivory and Seed Dispersal by Lizards: A Global Review

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1 Supplementary Data

1.1 Herbivorous Lizards

Classical herbivorous lizards include all Iguanidae (44 species), *Uromastyx* (15) and *Hydrosaurus* (3) (Agamidae), all *Phymaturus* (44), some *Liolaemus* (Tropiduridae), desert skinks (*Egernia* spp., *Tiliqua* spp.; Scincidae), and the arboreal Prehensile-Tailed Skink from the Solomon Islands (*Corucia zebrata*), among others. These are strict herbivores (i.e. folivores) and almost all possess some digestive traits efficient in processing fiber-rich leaves.

Fibers are less energy and nutrient rich than animal tissues (e.g. Pough, 1973; Iverson, 1982; O'Grady et al., 2005). Thus, ~3% of all lizards are considered strict vegetarians while ~12% are omnivorous (Iverson, 1982; Cooper and Vitt, 2002; Espinoza et al., 2004), and this has raised a debate, which is still running, about evolution of herbivory in lizards: from the classics of Szarski (1962), Ostrom (1963), Sokol (1967) and Pough (1973) to the more recent of van Damme (1999), Cooper and Vitt (2002), Cooper (2003), Espinoza et al. (2004), Herrel, Vanhooydonck and Joachim (2004a), Herrel et al., (2004b), Herrel et al. (2008), and Vervust et al. (2010).

Digestion of foliage requires hydrolysis of the β-1, 4 linked residues forming the framework of the fibers (e.g. Nagy, 1977; Mautz & Nagy, 1987; Bjorndal, 1991). Consequently, compared to carnivores, herbivores have specializations in acquiring, digesting, and subsisting on foliage, e.g. larger body size (Szarski, 1962; Pough, 1973; Iverson, 1982; Schluter, 1984; Chapple, 2003; O'Grady et al., 2005; Herrel et al., 2008), greater bite force (Herrel et al., 1999), larger gut/SVL (snout-vent-length) ratio (Skoczyłas, 1978; van Devender, 1982; Dearing, 1993; Herrel et al., 2004b; O'Grady et al., 2005; Vervust et al., 2010), presence of intestinal caeca and colonic valves (Iverson, 1982; Zug, 1993; Herrel et al., 2004b), and microbial-nematodes hindgut endosymbionts (Troyer, 1991; O'Grady et al., 2005; Roca et al., 2005). These adaptations improve, for example, fermentation of energy-rich fatty acids, and their absence in most lizards explains the paucity of a vegetarian diet.

A surprising outcome of our data compilation of plant-mutualistic lizards is that not only the classical true herbivorous lizards mentioned above, but also the omnivorous, insectivorous and mainly carnivorous species extensively consume fleshy fruits and thus may service as plant mutualists. For example, within the anoles (Dactyloidae), which are classical arthropod feeders (Schwartz and Henderson, 1991), 55 species have been reported eating fruits. Some varanids, considered truly carnivores, feed extensively (*V. olivaceus*; Auffenberg, 1988; Bennett, 2005), mostly (*V. mabitang*; Struck et al., 2002), or sporadically (*Varanus* spp.; Yasuda et al., 2005) on fleshy fruits. Two chamaeleonid (considered as a strictly insectivorous group) is also included in our database as fruit feeders (Takahashi, 2008; Meiri, 2018).

1.2 Mutualistic Reptiles in the Past

The deep evolutionary history and ecology of reptiles and fruit include the most fascinating and astonishing natural histories. Mutualistic reptiles were indeed present in the past, especially among frugivores (Labandeira, 2002; Tiffney, 2004). Herbivorous and omnivorous reptiles were assumed to interact mutualistically with ancient gymnosperms and early angiosperms prior to the radiations of birds and mammals (van der Pijl, 1982; Tiffney, 1984; Weishampel, 1984; Howe and Westley, 1988; Fleming and Lips, 1991; Wing and Tiffney, 1992; King, 1996; Barrett and Willis, 2001). However, it is uncertain whether the origin of a

juicy sarcotesta or fleshy layers enveloping seeds mainly functioned as a seed disperser attractant (Herrera, 1982; Cipollini and Levey, 1997; Tiffney, 2004), because there is an extensive time gap between the appearance of these structures in Paleozoic Pteridosperms and Gymnosperms and in early Mesozoic Angiosperms and the later arrival of frugivorous birds and mammals. During this time gap, sauropod dinosaurs dominated as vertebrate herbivores. Thus these animals, and also early lizards (see below), might have functioned as plant mutualists (e.g. van der Pijl, 1982; Tiffney, 1984, 2004; Weishampel, 1984). Omnivory and low-fiber herbivory were probably a common feeding mode among these reptiles. For example, from the Carboniferous-Permian boundary, i.e. when seed ferns were already present, we have the earliest reports of herbivory by <3 m mammal-like reptiles (e.g. *Edaphosaurus*, *Bolosaurus*). Ferns provide a potential energy source to animals, especially if food is scarce (Ramos 1994, 1995; Arosa et al., 2009). By feeding on fern sporangia, animals may then function as potential dispersers of spores (Boch et al., 2016). Today, this kind of dispersal has been very rarely reported, e.g. for woodmouse in Spain (Arosa et al., 2010), reindeer in Norway (Bråthen et al., 2007), and mallard in Hungary (Lovas-Kiss et al., 2018). However, although not documented, we can assume that it took place from the very early origin of ferns and other old plant groups.

From Late Permian, fossils of arillated seeds of *Podocarpus* (Conifers) in preserved gut content (cololites) and fossil faecal pellets (coprolites) from *Protorosaurus* (lizard-like reptiles) have repeatedly been found (Weigelt, 1930; Munk and Sues, 1993). Thus, since the Paleozoic, reptilian herbivores could have been dispersers of seeds of these plants. Frugivorous pterosaurs have been also suggested as “the missing seed dispersers of Cretaceous angiosperms” (Fleming and Lips, 1991).

Although direct evidence, such as coprolites, is lacking, lizards have occurred together with dinosaurs since Jurassic. For example, a primitive lizard, an acrodont Iguanian (*Bharatagama*), was found in India and dated to the early-mid Jurassic (Evans, 2003). Besides, remains of a more primitive and true lizard family found in Japan, an herbivorous teiid-like scincomorpha (*Kuwajimalla kagaensis*; SVL= 150 mm), were already present since early Cretaceous (Evans and Manabe, 2008). Plants with pulp-covered diaspores dominated pre-Cretaceous vegetation, e.g. seed ferns, cycads and ginkgos (Janzen and Martin, 1982; van der Pijl, 1982; Weishampel, 1984; Eriksson et al., 2000; Tiffney, 2004), e.g. seeds of *Allicospermum retemirum* have been found in coprolites from small herbivorous vertebrates (lizards? Harris, 1945, 1956). Thus during the long span of the Mesozoic, both early lizards and herbivorous dinosaurs may have been plant mutualists.

1.3 Early records of lizard-fruit interactions

The first “report” of fruit-eating lizards is painted motives on pottery from the desert coast of N Peru, showing *Dicrodon* sp. (Teiidae) eating fruits of *Prosopis juliflora* (Fabaceae). The ceramics date back to the Mochica culture (200-100 BC to 700 AD; Larco, 2001). These herbivorous lizards were hunted for food, which they still may be today (Holmberg, 1957). The lizards climb the small, spiny tree and eat ripe and unripe fruits. Some fruits are also brought back to their burrows and stored for the winter.

The first written evidence, known to us, may refer to a Canarian lizard species. Fructuoso (1590) writes about extensive consumption of grapes by *Gallotia galloti* (Lacertidae) on La Palma. Viera y Clavijo (1866) also documented this interaction for other Canarian lizards and today, lizards are still regarded as a pest in vineyards. On Gran Canaria, Steindachner (1891)

observed *G. stehlini* (Lacertidae) eating berries of the Canarian endemic shrub *Plocama pendula* (Rubiaceae).

From the Mascarene Islands, Leguat (1708) writes that palm trees and plantanes are always loaden with lizards and suggests that palm fruits are a common food source to the giant *Phelsuma edwardnewtoni* (Gekkonidae), a now extinct species. On the Mascarene Rodrígues, Liénard (1842) observed fruit consumption by the other extinct giant gecko from the archipelago, *P. gigas*. On Galápagos, Darwin (1839) also noticed the use of fruits by lizards. He writes that the land iguana (*Conolophus subcristatus*, Iguanidae) eats “the acid and astringent berries of the guayavita” (*Psidium galapageium*, Myrtaceae). In the Caribbean, the now presumably extinct Jamaican Giant Galliwasp (*Celestus occiduus*, Diploglossidae; max SVL = 305 mm) was reported as a fruit-eater by Gosse (1851 in Schwartz and Henderson, 1991).

From New Zealand, White (1887 in Whitaker, 1987) cited from Maori legends the frugivorous habits of a giant, now extinct arboreal lizard, inhabiting the forest of the North Island, which ate the large fruits of *Beilschmiedia tawa* (Lauraceae). It may be the same as the recently described *Hoplodactylus delcourtii*, Diplodactylidae (Bauer and Russell, 1986). It may be the largest (SVL = 370 mm) known gecko. To date, 11 gecko (*Hoplodactylus*, *Woodworthia*, *Dactylocnemis*, *Toropuku* and *Naultinus*) and 20 skink species (*Oligosoma*) have been reported eating fruits (Table S1).

In 1911, the Italian botanist Borzí reviewed seed dispersal in Sauria (saurochory). He mentioned several lizards as frugivores and seed dispersers: *Hydrosaurus amboinensis* (Agamidae) in the Mollucas, *Conolophus subcristatus* (Iguanidae) from Galápagos (maybe cited from Darwin), *Tupinambis teguixin* and *Ameiva ameiva* (Teiidae) from Brazil and Guyana, and also *Anolis carolinensis* (Dactyloidae), *Iguana iguana* (Iguanidae), *Egernia kingii* (Scincidae), and *Uromastix aegyptia* (Agamidae). The information in this 100 y-old review was based on Borzí’s own observations and on his reading of naturalists, such as Brehm’s *La vita degli animali* (1869), and Beccari’s *Della disseminazione delle Palmae* (1877). The latter also found “great amount” of Pandanaceae fruits in the stomach of *Hydrosaurus amboinensis* (Agamidae). Borzí also suggested that fruits on trunks and branches (caulifruity) might be an adaptation to frugivorous reptiles and proposed various types of saurochorous fruits.

Early in the last century, two monographs about dispersal were published: *Observations of a Naturalist in the Pacific between 1896 and 1899. Vol. II. Plant Dispersal* (Guppy, 1906) and *The Dispersal of Plants Throughout the World* (Ridley, 1930), but only the latter mentioned (p. 515) some examples of seed dispersal by herbivorous lizards, e.g. *Cyclura carinata* (Iguanidae) eating fruits of *Genipa clusiifolia* (Rubiaceae) on Turks and Caicos Islands (citation from Guppy, 1917), *Conolophus subcristatus* (Iguanidae) swallowing cactus fruits on Galápagos (from Beebe, 1924), and cf. *Iguana iguana* (Iguanidae) eating fruits of *Celtis iguanea* (Ulmaceae) in Mexico (from Standley, 1922).

These references tell us that frugivory and seed dispersal by lizards were widely suggested by early naturalists.

1.4 Importance and examples of fleshy fruit to the diet of lizards

Many fruit-eating lizards are also seed dispersers. To estimate their seed dispersal effectiveness, we need to know the importance of the fruit component in their diet, the treatment of seeds in the digestive tract, the spatial post-seed dispersal distribution, and the establishment probability of plants in their microhabitats (Schupp et al., 2010). Thus, lizard seed dispersal effectiveness can be analyzed quantitatively as number of dispersed seeds and qualitatively as the chance that a seed recruits a new adult (Jordano and Schupp, 2000). We only know three studies, which have done this, viz. Valido (1999) studying the Canarian *Gallotia galloti* (Lacertidae)-*Plocama pendula* (Rubiaceae) interactions, Wotton (2002) studying the New Zealand *Woodworthia maculata* (Diplodactylidae) and their interactions with *Croprosma propinqua* (Rubiaceae), and more recently González-Castro et al., (2015) to compare lizard and bird species on 11 plant species from Canary Islands. These examples show that frugivorous lizards were effective seed dispersers because: *i*) they consumed a considerable amount of fruit; *ii*) their ingestion of fruit did not harm later seed germination; and *iii*) lizards often dropped seeds in microhabitats suitable for germination and seedling establishment. Thus, lizards may be effective seed dispersers, but more comparisons of seed dispersal effectiveness among lizards, birds and mammals are needed.

Data about the contribution of fruit to the diet in various lizard species and families tell us that many lizards may be effective seed dispersers. Here, we summarize examples, where a considerable consumption of fleshy fruit was reported (>25% frequency of occurrence or volume), and also examples where classical seed germination experiments were made with both mainland and island lizard species.

Research of the quantitative contribution of fleshy fruit to the diet of lizards suffers from two shortcomings. First, information from different sources is generally pooled, especially data about the content of digestive tracts (e.g. Sadek, 1981; Vitt and de Carvalho, 1995) and fecal pellets (e.g. Arena and Wooller, 2003; Valido et al., 2003), and such data cannot always be compared. For example, larger prey items may be over-represented in the stomach content (e.g. Floyd and Jenssen, 1984) or food plants vary in their digestibility. However, in Angelici et al., (1997) and Valido and Nogales (2003) amounts of invertebrates and fruits were represented equally in the analyses of droppings and stomach content. Secondly, quantitative diet data are not always presented in a comparable way in different studies. The applied quantitative diet descriptors are frequency of occurrence (%FO), i.e. percentage of individuals or pellets containing fruit remains (e.g. Nogales et al., 1998), percentage of a food item of the total number of items (e.g. Pérez-Mellado and Corti, 1993), percent volume (%V) (e.g. Schoener et al., 1982), and percent weight (e.g. Allison, 1982). However, here we mainly use %FO, although it does not tell anything about numerical abundance of fruit in the individual diet. Our reason is that %FO is, by far, the most frequently used in lizard diet studies and it is made in a similar way in analyses of digestive tracts and droppings.

(a) *Scincidae*

Frugivory is known for 78 skink species, and a FO of <46% is recorded (Arena and Wooller, 2003). Since the first observation of frugivory in *Trachylepis atlantica* from the Brazilian Fernando de Noronha islands (Travassos, 1946), frugivory by skinks has repetitively been reported. Unfortunately, only a few quantitative examples are known. For example, in Australia, *Ctenotus grandis* and *Egernia kingii* (pooled data from analyses of stomachs and scats) had <46%FO of seeds and remains of fruit pulp (Twigg et al., 1996; Arena and

Wooller, 2003). Dubas and Bull (1991) found that 15% of total wet weight of ten stomach contents of the *Tiliqua rugosa* (max. SVL = 341 mm) were remains of berries from especially *Enchylaena tomentosa* (Chenopodiaceae) with 40%FO.

For some island skinks, high levels of fruit consumption are also reported. For example, the nocturnal *Oligosoma alani* (max. SVL = 125 mm) from the Mercury Islands, New Zealand, fruit constituted up to 32%FO of the diet in parts of the year (Southey, 1985 in Whitaker, 1987). On the same islands, other different endemic *Oligosoma* species also used fruit frequently, although in lower amounts (Whitaker, 1987; Wotton et al., 2016). In the Krakatau Islands, 35% of *Eutropis multifasciata* individuals had fruit remains (Iwamoto, 1986). On Round Island, Mauritius, the Telfair's Skink *Leiolopisma telfairii* (max. SVL = 165 mm) had repeatedly been shown to be frugivorous (e.g. Vinson, 1975; Bullock, 1986). Pernetta et al., (2005) showed that <25%FO of its fecal droppings included fruit, e.g. the introduced *Passiflora suberosa* (Passifloraceae) accounted for <15%FO in 59 droppings. This lizard also climbed the *Pandanus* trees and swallowed its <5 cm long fruits. Other consumed fruits were from the introduced *Solanum americanum* (Solanaceae), and the natives *Latania loddigesii* (Palmae) and *Pandanus vandermeerschii* (Pandanaceae). Today, this lizard is confined to Round Island but has earlier occurred on “mainland” Mauritius and adjacent islets, and it must have used many fleshy-fruited species. The same must have been the case for *Leiolopisma mauritiana* (Mauritius) and *Chioninia coctei* (Cape Verde), two larger and presumably extinct skinks, which according to their tooth morphology and historical reports might have been important insular frugivores (Vinson and Vinson, 1969; Greer, 1976).

(b) *Gekkonidae, Diplodactylidae, Phyllodactylidae*

Frugivory is known for 88 species of “classical” geckos, and a FO of <80% is recorded (Wotton et al. 2016). However, quantitative data are only available for several species from New Zealand. For example, on The Brothers Islands, *Hoplodactylus duvaucelii* (Diplodactylidae) (max. SVL = 160 mm) had <25%FO of fruits (Barwick, 1982 in Whitaker, 1987) and Whitaker (1987) reported <65%FO of fruits in gut content from *Woodworthia maculata* (Diplodactylidae). For the latter, D. Wotton reported 39%FO in Mana Island (Wotton, 2002), and up to 80%FO of fruit remains in Stephen Island (Wotton et al., 2016); most fruits came from the divaricate shrub *Coprosma propinqua* (Rubiaceae) (95% of all seeds in droppings), the vine *Muehlenbeckia complexa* (Polygonaceae), and the introduced *Phytolacca octandra* (Phytolaccaceae). Other New Zealand geckos, e.g. the diurnal *Naultinus grayii*, may also seasonally eat much fruit (Whitaker, 1987). This author listed ten other plant species frequently being used by geckos as fruit food, e.g. *Hymenanthera alpina* (Violaceae). Only lizards were presumably consuming the white berries of the latter species. These fruits are found on the underside of the stems and are thus protected from above by divaricating twigs. This type of fruits hidden to birds is also found in other New Zealand species, and today, seeds of divaricated species may only be dispersed by lizards (Whitaker, 1987; Lord and Marshall, 2001; Lord et al., 2002; Wotton et al., 2016).

Large, but now extinct Mauritian geckos were also frugivores, viz. *Phelsuma edwardnewtonii* and *P. gigas* (Gekkonidae) (Leguat, 1708; Liénard, 1842).

(c) Dactyloidae, Polychrotidae

Frugivory is known for 55 species of *Anolis*, and a FO of <40% is recorded (Brach, 1976; Dalrymple, 1980). In 1928, Patterson discovered that *Anolis cuvieri* from Puerto Rico was frugivorous. From the same species, Rand and Andrews (1975) estimated fruit to have a 7%FO, and Losos et al., (1990) collected 11 unidentified seeds from three individuals. In another Puerto Rican species, *A. cristatellus*, 15 out of 100 individuals had considerable amounts of fruit remain in their stomach (Wolcott, 1924).

Since its introduction to Miami, Florida, in 1952, the giant Cuban *A. equestris* (max. SVL = 188 mm) has now become abundant (Brach, 1976; Dalrymple, 1980). Here, FO of fruits of *Ficus religiosa* (Moraceae) and an unidentified ornamental palm reached 40% (Brach, 1976). Qualitative reports of frugivory of this anole from its natural habitat in Cuba are also available (e.g. Buide, 1985; Rodríguez-Schettino, 1999), but no published quantitative dietary data exist. From Jamaica, Herrel et al., (2004a) published diet data for *Anolis garmani*, *A. grahami*, *A. lineatopus*, and *A. valencienni*. All were frugivorous, but high values of FO of fruit were only obtained from the stomach contents of *A. garmani* (39%FO) and *A. valencienni* (29%FO). *Anolis roosevelti* (max. SVL = 160 mm) from Culebra Island, Puerto Rico, has not been observed since 1932. It inhabited the *Bursera-Ficus* forests and in 1931 a collector reported it to eat figs (Campbell and Dodd, 1982).

Fruit consumption is also reported from the mainland anoles, e.g. remains of fruit were in the stomach of two out of six individuals of *A. marmoratus* (Polychrotidae) from S Venezuela (Beebe, 1944).

(d) Agamidae

Agamids are well known herbivores (Taylor, 1922), consuming leaves and flowers, but 19 species have been reported eating fruits (e.g. Fenner, 2000). The large, omnivorous *Stellagama stellio* has <78%FO of fruits of *Pistacia terebinthus* (Anacardiaceae) on the Greek Island of Nisyros (Lo Cascio et al., 2001) and in a sample of 25 stomachs, *Hypsilurus papuensis* from New Guinea had <30% dry weight vegetative matter (mostly fruits) in its diet (Allison, 1982).

(e) Tropiduridae

Frugivory is known for 24 species and a FO of <80% is known (Côrtes-Figueira et al., 1994). This high value was observed for *Tropidurus torquatus* eating fruits of especially *Melocactus violaceus* (Cactaceae) in Brazil. In Venezuela, 60%FO of fruit was observed in 44 stomachs from *T. torquatus* (León et al., 1969-1970). *Melocactus caesius* was here the main fruit item. In sand dunes in Brazil, Fialho et al. (2000) found 35-39%FO of fruit in stomachs of *T. torquatus*. In the dry Chaco forest in Argentina, the larger *T. spinulosus* (max. SVL = 140 mm) had <24%FO of fruit from especially *Celtis tala* (Ulmaceae) and *Ziziphus mistol* (Rhamnaceae) in stomachs (Cruz, 1998). Here, species with fleshy fruits are relatively abundant, and lizards take ripe fruits from the ground.

(f) Liolaemidae

In *Liolaemus* (~260 spp.), herbivory has evolved more frequently and faster than in all other squamate lizards (Espinoza et al., 2004). About 60 species are herbivorous/omnivorous,

however, frugivory has only been quantified in 34 species. For example, in an annual diet study of *L. nigromaculatus* from Chile, 77 fruit items (<55%FO during the summer) were identified in 29 stomachs (Ortiz and Riveros, 1976).

(g) *Lacertidae*

Frugivory is known for 38 species (11% of family) and a FO of <95% is reported (Valido et al., 2003). In the E Pyrenees, fruit remains of *Bryonia dioica* (Cucurbitaceae) were found in the stomach of one individual out of ten *Timon lepidus* (Peters, 1962), and 24 *Juniperus phoenicea* (Cupressaceae) fruit remains were found in eight individuals in Almería (Valverde, 1967). Frugivory in *T. lepidus* is well supported from most of its range (e.g. Hódar et al., 1996; Thirion et al., 2009). Hódar et al., (1996) got an FO of 53% fruit remains, mainly from *Capparis spinosa* (Capparidaceae) in droppings from Spanish Granada. The highest FO-values came from late-summer samples, when insects were low in abundance (Hódar et al., 1996). Thirion et al., (2009) reported seasonal variation in the diet on the isolated French Oléron Island. Here, fruit of *Ephedra distachya* (Ephedraceae) had a 20%FO in 102 fecal pellets. High values of frugivory are also known for other species, e.g. *Podarcis bocagei* (Calviño-Cancela, 2005) and *Darevskia rufa* (Franzen, 1991).

All Canarian, Madeiran and Balearic lacertids are mainly omnivores, and amount of fruit in their diet varies with habitat and time of year (e.g. Sadek, 1981; Valido, 1999). On Rey Islet, near Menorca, Pérez-Mellado et al., (2005) got a FO of 73% (*Phillyrea media*, Oleaceae) from droppings of *P. lilfordi*, and from the nearby Aire Islet, Pérez-Mellado et al., (2000a) got up to 70%FO of fruit remains from *Dracunculus muscivorus* (Araceae) from 99 droppings. On Tenerife, Barquín and Wildpret (1975) counted up to 495 seeds of *Plocama pendula* (Rubiaceae) from 10 droppings of the medium-sized *G. galloti* (max. SVL = 145 mm) (90%FO). The highest FO-value, 95%, also came from a population of this species in the xerophytic vegetation on Tenerife (Valido et al., 2003). During one year, 1120 droppings were analyzed with a total of 4,710 seeds from mainly *Rubia fruticosa* and *P. pendula* (Rubiaceae), *Withania aristata* and *Lycium intricatum* (Solanaceae), *Neochamaelea pulverulenta* (Rutaceae), and the invasive *Opuntia dillenii* (Cactaceae). For the larger *G. stehlini* (max. SVL = 248 mm), Naranjo et al., (1991) reported an FO-value of 49% in droppings from an introduced population on Fuerteventura. Consumed fruits were mainly *Phoenix canariensis* (Palmae). The smaller *G. atlantica* (max. SVL = 96 mm) may be slightly less dependent upon fruit on Alegranza Islet and Fuerteventura with a <32%FO (Nogales et al., 1998; Valido and Nogales, 2003). In total, Canarian lizards feed on fleshy fruit from <43 species (Valido, 1999). Based on the intensive frugivory of the seven extant *Gallotia* species (Valido, 1999) and paleo-diet evidence (Bocherens et al., 2003), the extinct Canarian giant *Gallotia goliath* (SVL < 546 mm) and *G. auaritae* (SVL < 444 mm) might have been an important frugivore and seed disperser, as well.

In Madeira, the endemic *Teira dugesii* has 46%FO of fruit based on 289 analyzed stomachs from lizards caught in cultivated land (Sadek, 1981).

(h) *Teiidae*

Teiids are regarded as the Nearctic ecological equivalent to lacertids. Although most are carnivorous, frugivory is reported for 36 species and a FO of <83% is known (Janzen, 1973). For example, on Puerto Rico and Mona Island, Patterson (1928) found “chiefly large number of red-coated seeds” in the stomachs of twenty individuals of the common lizard

Pholidoscelis exsul (47%FO). From savannas in the Brazilian Amazonas, 30-57%FO of fruit in stomachs from *Cnemidophorus lemniscatus* is reported (Vitt and de Carvalho, 1995; Vitt et al., 1997).

Islands show extremely high values, e.g. 83%FO of fruit in *A. ameiva* and *C. lemniscatus* from Providence Island (Janzen, 1973). Samples of the endemic insular *C. murinus*, from Bonaire Island and *C. arubensis* from Aruba Island also contain much fruit, viz. 23-34%V (Schall and Ressel, 1991; Dearing and Schall, 1992).

(i) *Varanidae*

Monitor lizards are truly carnivorous, but in Malaysia and the Philippines some are frugivorous as well, e.g. *Varanus olivaceus* (Auffenberg, 1988; Bennett, 2005), *V. mabitang* (Struck et al., 2002), and the recently discovered species, *V. bitatawa* (Welton et al., 2010). In addition, using camera-traps, some unidentified monitor lizards were discovered to consume fruits from the ground in the lowland tropical rainforest in Peninsular Malaysia (Yasuda et al., 2005). However, quantitative data are only available for *V. olivaceus* (max. SVL = 690 mm). It was discovered in 1845, believed extinct, and then rediscovered in the lowland dipterocarp forest on Luzon, Philippines (Auffenberg, 1979). It had 11%FO of fruit remains in a sample of 218 stomachs and droppings (Auffenberg, 1988). Recently, analysis of 735 droppings from Polillo Island, gave 98%FO (Benett, 2005; D. Benet, *pers. com.*). The lizard is the main seed disperser of *Pandanus* spp. (Pandanaceae) and *Canarium* spp. (Burseraceae).

(j) *Iguanidae*

Iguanas and Spinytail Iguanas are unique, because all 44 species are entirely herbivorous as adults. However, data about fruit consumption are scarce, but a FO of fruit of <97% is known (Beovides-Casas and Mancina, 2006). Frugivory is mainly reported from islands, but mainland data exist as well. In Costa Rica, large individuals (SVL = 235 mm) of *Ctenosaura similis* take as much fruit as 73%V, but the average is 24%V (van Devender, 1982). A shift with age from insectivory to herbivory has been shown for *C. pectinata* (Durtsche, 2000).

The fruit diet of island iguanas is more extensively studied. Galápagos land iguanas (*Conolophus* spp.) feed on many species depending on season and habitat, but especially *Opuntia* (Cactaceae) (Traveset et al., 2016). Up to 95%FO and 25%FO of cactus remains (mostly fruits) in scats from *C. pallidus* ($N = 10$) and *C. subcristatus* ($N = 50$), respectively (Carpenter, 1969). Hendrix and Smith (1986) found 800 seeds of *Solanum erianthum* (Solanaceae) in nine scats from the latter species.

The 1-kg *Sauromalus hispidus* (chuckwalla) and 200-g *S. varius*, inhabiting islands in the Gulf of California, are primarily consuming annual plants. On four islands, fruit remains constituted the largest FO proportion of their diet. Adult *S. hispidus* consumed fruits of *Ferocactus peninsulae* and *Opuntia echinocarpa* (Cactaceae), and *Agave deserti* (Agavaceae) (Case, 1982).

Today, on the Antilles islands, rock iguanas (*Cyclura*) are the largest, native herbivores. They include eight recognized species and <16 subspecies (Malone et al., 2000). In scats of the native Cuban *C. nubila*, fruits had an 80-100%FO (Perera, 1985). The order of preference is foliage first, then fruits and flowers to the same extent, and lastly stems (González-Rossell et al., 2001). In the same species, <97%FO of fleshy fruits was found in 30 droppings collected

in the fruiting season on the islet Cayos San Felipe, Cuba (Beovides-Casas and Mancina, 2006). Finally, the introduced population of *C. nubila* on Isla Mayagüez, Puerto Rico, feeds on the fleshy red sarcotesta of seeds from cones of the cycad *Zamia portoricensis* (Zamiaceae) (Lewis et al., 1993). On Caicos, 14%FO of the items in the diet of *C. carinata* was fruit (Auffenberg, 1982). Fruit was consumed independently of its density in the habitat, showing active fruit preference. Much ripe fruit was sampled from the ground. However, *C. carinata* may climb up to 7 m into a fruiting canopy. Frugivory is well known in *C. cornuta* on Mona Island, Puerto Rico. Navarro and Ayensa (2002) reported 49%FO of fruit remains in 101 droppings. Seeds from nine fleshy-fruited plants were found in the scats (L. Navarro, *pers. com.*).

Rock iguanas are probably the only vertebrates capable of consuming the large fruits of *Hippomane mancinella* (Euphorbiaceae), *Reynosia uncinata* (Rhamnaceae) and *Chrysobalanum icaco* (Chrysobalanaceae), and also the fruits of some toxic plants, e.g. *Metopium toxiferum* (Anacardiaceae). However, Heleno et al., (2013) reported giant tortoise eating *H. mancinella*. Thus, these iguanas may be key seed dispersers in the Caribbean (e.g. Beovides-Casas and Mancina, 2006; A. Valido, *unpublished data*).

Iguana iguana is mainly arboreal, eating foliage, but fruit is also reported from its diet (Lara-López and González-Romero, 2002; Morales-Mávil et al., 2002).

(k) *Corytophanidae and other families*

Although *Basiliscus* (Corytophanidae) is omnivorous, frugivory is only documented for a few species. In Nicaragua, *Basilicus plumifrons* had up to 28%V of fruit (Vitt and Zani, 1998). *Basiliscus vittatus* feeds mostly on insects but also on berries from the ground (Campbell, 1998). In other lizard families, known as classical insect eaters, high levels of frugivory are observed for desert species, e.g. in *Gambelia wislizenii* (Crotaphytidae) from Nevada (Tanner and Krogh, 1974).

Thus many lizards are quantitatively important fruit-eaters and potential seed dispersers and maybe more so on islands. Thus, lizards might have a significant influence on the fitness of their food plants.

1.5 Quality of the Data

In order to cover a geographical and taxonomical range as wide as possible, we made an extensive literature search on lizard diet studies in journals compiled in *HerpLit Database*, but also in *Web of Science*, *Zoological Record*, herpetofaunal regional books and journals, and personal communications with seed dispersal biologists, and herpetologists (see Acknowledgments). However, the data varied much in accessibility and quality and most information about lizards feeding on fleshy fruit is only scant; qualitative observations and information about the mutualistic role of lizards are even more meagre. In general, the prey and plant components of the diet of lizards are resolved to a different degree. Prey is often sorted into order, or less frequently to genus or even species, whereas plant food, generally, is reported as “plant material”. Only reports, which explicitly classified plant food as fruit (or seeds from fleshy fruits), were included in our dataset. However, in some cases, we got additional information directly from authors, when we asked them to clarify the type of “plant material” listed in their diet study (e.g. *Anolis homolechis*, Sampedro-Marín et al., 1982; *Tropidurus itambere*, van Sluys, 1993), or in their field observations of interactions between

lizards and fruits (e.g. *Matobosaurus validus*, Broadley, 1962). All reports about lizards in captivity were excluded if the report did not include additional field observations. For example, in captivity, many lizards readily feed on fleshy fruit (e.g. Kopstein, 1924; Rensch and Eisentraut, 1927; Roux, 1936; Broadley, 1962; Schwartz and Henderson, 1991; Schleich et al., 1996; Rogner, 1997; Bauer and Sadlier, 2000; Greer, 2005). Generally, unclear and ambiguous reports about ingestion of fruit were also excluded. Partial frugivory has been reported for the tuatara (*Sphenodon punctatus*, Sphenodontidae) from Stephens and Middle Islands, New Zealand (Walls, 1981; Southey in Whitaker, 1987; Ussher, 1999), and recently confirmed by Bredeweg and Nelson (2010). However, we did not include this lizard species in our study, because it now is included in a different order, the Rynchocephalia. We also excluded reports about seeds (or fruit remains) in the stomach or droppings of lizards from non-fleshy fruits.



Photo - In order to test for frugivory in the Komodo Dragon (*Varanus komodoensis*, Varanidae), an adult male was offered a ripe and open Jackfruit (*Artocarpus heterophyllus*, Moraceae). It smelled to the fruit, but without tasting it, the varan immediately left the trail, heading for the nearby shrub (Photo: 9th December 2006, The Island of Komodo, Dennis M. Hansen and Jens M. Olesen).

Table S1.- Lizard species (Squamata, Sauria: Iguania, Gekkota, Scincomorpha, Diploglossa, and Platynota) reported as fruit eaters and/or seed dispersers. Geographic range, native and introduced (*i*) of species: *I*, island; *M*, mainland; *I-M*; island+mainland; †, presumably recent extinct species. The geographic range and nomenclature of lizard species follow Uetz et al. (2018), update at 29 August 2018.

Species; Geographic Range	Observation Sites	References
IGUANIA		
Agamidae		
<i>Acanthosaura nataliae</i> Orlov, Trung & Sang, 2006; M	Vietnam, Laos	Orlov et al. (2006)
<i>Agama agama</i> (Linnaeus, 1758); I-M	Gabon	Meiri (2018)
<i>Agama lionotus</i> Boulenger, 1896; M	Kenya	Meiri (2018)
<i>Agama mwanzae</i> Loveridge, 1923; M	Kenya	Meiri (2018)
<i>Hydrosaurus amboinensis</i> (Schlosser, 1768); I	Mollucas Islands	Beccari (1877); Kopstein (1924); Brehm (1932); Bellairs (1975)
<i>Hydrosaurus pustulatus</i> (Eschscholtz, 1829); I	Panay Island (Philippines)	Gaulke & Curio (2001); Struck et al. (2002); M. Gaulke <i>pers. com.</i>
<i>Hypsilurus godeffroyi</i> (Peters, 1867); I	Bougainville Island (Solomon Islands; Papua New Guinea)	Parker (1983); McCoy (2000)
<i>Hypsilurus macrolepis</i> Peters, 1872; I	Solomon Islands	McCoy (2015) <i>in</i> Meiri (2018)
<i>Hypsilurus papuensis</i> (Macleay, 1877); I	Papua New Guinea	Allison (1982)

<i>Intellagama lesueurii</i> (Gray, 1831); I-M	Australia	Rose (1974); Clifford & Hamley (1982); Cogger (1992)
<i>Laudakia melanura</i> Blyth, 1854; M	Pakistan	Minton (1966)
<i>Laudakia nupta</i> (De Filippi, 1843); M	Iran	Anderson (1999)
<i>Lophosaurus boydii</i> (Macleay, 1884); M	Australia	Torr (1997)
<i>Lyriocephalus scutatus</i> (Linnaeus, 1758); I	Sri Lanka	Somaweera & Somaweera (2009) <i>in</i> Meiri (2018)
<i>Paralaudakia caucasia</i> (Eichwald, 1831); M	Russia	Orlowa (1981)
<i>Phrynocephalus maculatus</i> Anderson, 1872; M	Pakistan	Minton (1966)
<i>Stellagama stellio</i> (Linnaeus, 1758); I-; M	Nisyros Island (Greece)	Lo Cascio et al. (2001)
<i>Uromastyx aegyptia</i> (Forskal, 1775); M	Arabian Peninsula	Al-Hazmi (2001); Cunningham (2001); Wilms et al. (2009)
<i>Uromastyx ornata</i> Heyden, 1827; M	Israel	Bronstein et al. (2007)
Chamaeleonidae		
<i>Chamaeleo chamaeleon</i> (Linnaeus, 1758); I-M	Italy	Corti & Cascio (2002) <i>in</i> Meiri (2018)
<i>Furcifer oustaleti</i> (Mocquard, 1894); I-Mi	Madagascar	Takahashi (2008)
Corytophanidae		
<i>Basiliscus basiliscus</i> (Linnaeus, 1758); M	Costa Rica; Barro Colorado (Panamá)	Barden (1943); Fleet & Fitch (1974); van Devender (1978, 1991); Glander (1979); Savage (2002)

<i>Basiliscus galeritus</i> Duméril, 1851; M	Colombia	Arteaga et al. 2013) <i>in Meiri</i> (2018)
<i>Basiliscus plumifrons</i> Cope, 1876; M	Nicaragua	Vitt & Zani (1998); Savage (2002); L.J. Vitt <i>pers. com.</i>
<i>Basiliscus vittatus</i> Wiegmann, 1828; M	Panama; Costa Rica; Guatemala	Hallinan (1920); Hirth (1963); Campbell (1998); Savage (2002)
Crotaphytidae		
<i>Crotaphytus collaris</i> (Say, 1823); M	Kansas	Banta (1960)
<i>Gambelia wislizenii</i> (Baird & Girard, 1852); I-M	Nevada; Cedros and Santa Margarita islands (Baja California)	Stebbins (1966); Tanner & Krogh (1974); Skydancer (1998)
Dactyloidae		
<i>Anolis aeneus</i> Gray, 1840; I	Grenada (Lesser Antilles)	Lazell (1972); Schwartz & Henderson (1991); Simmons et al. (2005)
<i>Anolis agassizi</i> Stejneger, 1900; I-M	Malpelo Island (Colombia)	Rand et al. (1975)
<i>Anolis allisoni</i> Barbour, 1928; I-M	Cuba	Rodríguez-Schettino (1999)
<i>Anolis barahonae</i> Williams, 1962; I	Hispaniola	Bowersox et al. (1994)
<i>Anolis barbatus</i> (Garrido, 1982); I	Cuba	Martínez-Reyes (1998); Rodríguez-Schettino (1999)

<i>Anolis bartschi</i> (Cochran, 1928); I	Cuba	Rodríguez-Schettino & Martínez (1992)
<i>Anolis beckeri</i> Boulenger, 1881; M	Mexico	Pérez-Higareda et al. (1997)
<i>Anolis bimaculatus</i> (Sparrman, 1784); I	Lesser Antilles	Schwartz & Henderson (1991); Powell et al. (2005); J.D. Lazell <i>pers. com.</i>
<i>Anolis biporcatus</i> (Wiegmann, 1834); M	Central America	Meiri (2018)
<i>Anolis blanquillanus</i> Hummelinck, 1940; I	Los Hermanos Islands (Venezuela)	Rivas & Barros (2010)
<i>Anolis carolinensis</i> Voigt, 1832; M-Ii	Anguilla (Lesser Antilles)	Hodge et al. (2003)
<i>Anolis chamaeleonides</i> Duméril & Bibron, 1837; I	Cuba	L.V. Moreno <i>pers. com.</i>
<i>Anolis coelestinus</i> Cope, 1862; I	Dominican Republic	Sifers et al. (2001)
<i>Anolis conspersus</i> Garman, 1887; I	Grand Cayman (Cayman Islands)	Schoener (1967)
<i>Anolis cristatellus</i> Duméril & Bibron, 1837; I-Mi	Puerto Rico; Guana Island (British Virgin Islands); Dominica (Lesser Antillas); Florida	Wolcott (1924); Patterson (1928); Behler & King (1979); Schwartz & Henderson (1991); Lazell & Perry (1997); Daniells et al. (2008); Vega-Castillo (2014); J.D. Lazell, S. Vega-Castillo & T.A. Carlo <i>pers. com.</i>

<i>Anolis cuvieri</i> Merrem, 1820; I	Puerto Rico	Patterson (1928); Rand & Andrews (1975); Pérez-Rivera (1985); Losos et al. (1990); Schwartz & Henderson (1991); Vega-Castillo & Puente-Rolón (2011); S.I. Vega-Castillo <i>pers. com.</i>
<i>Anolis cybotes</i> Cope, 1862; I-Mi	Dominican Republic	Sifers et al. (2001)
<i>Anolis distichus</i> Cope, 1861; I-Mi	Dominican Republic	Cast et al. (2000)
<i>Anolis equestris</i> Merrem, 1820; I-Mi	Cuba; Florida	Ruibal (1964); Brach (1976); Buide (1985); Dalrymple (1980); Schwartz & Henderson (1991); Rodríguez-Schettino (1999); Giery et al. (2013, 2017)
<i>Anolis evermanni</i> Stejneger, 1904; I	Puerto Rico	Lister (1981); Reagan (1996)
<i>Anolis extremus</i> Garman, 1887; I	Lesser Antilles	Henderson & Powell (2009)
<i>Anolis garmani</i> Stejneger, 1899; I-Mi	Jamaica	Herrel et al. (2004a)
<i>Anolis gingivinus</i> Cope, 1864; I	Anguilla; St. Maarten (Lesser Antilles)	Eaton et al. (2002); Powell et al. (2005)
<i>Anolis grahami</i> Gray, 1845; I	Bermuda; Jamaica	Simmonds (1958); Herrel et al. (2004a)

<i>Anolis griseus</i> Garman, 1887; I	St. Vincent (Lesser Antilles)	Lazell (1972); Schwartz & Henderson (1991)
<i>Anolis guamuhaya</i> (Garrido, Pérez & Moreno, 1991); I	Cuba	L.V. Moreno <i>pers. com.</i>
<i>Anolis gundlachi</i> Peters, 1877; I	Puerto Rico	Lister (1981); Schwartz & Henderson (1991); Vega-Catillo & Puente-Rolón (2011)
<i>Anolis homolechis</i> (Cope, 1864); I	Cuba	Sampedro-Marín et al. (1982); L. Rodríguez-Schettino <i>pers. com.</i>
<i>Anolis jubar</i> Schwartz, 1968; I	Cuba	A. Fong-Grillo <i>pers. com.</i>
<i>Anolis krugi</i> Peters, 1877; I	Puerto Rico	Vega-Castillo & Puente-Rolón (2011); Vega-Castillo (2014); T.A. Carlo & S. Vega-Castillo <i>pers. com.</i>
<i>Anolis leachii</i> Duméril & Bibron, 1837; I	Antigua (Lesser Antilles); Bermuda	Simmonds (1958); Lazell (1972)
<i>Anolis lineatopus</i> Gray, 1840; I	Jamaica	Schwartz & Henderson (1991); Herrel et al. (2004a)
<i>Anolis lucius</i> Duméril & Bibron, 1837; I	Cuba	Rodríguez-Schettino & Martínez (1994); Rodríguez-Schettino (1999)
<i>Anolis luteogularis</i> Noble & Hassler, 1935; I	Cuba	Martínez-Reyes (1998); Rodríguez-Schettino (1999)

<i>Anolis monensis</i> Stejneger, 1904; I	Mona Island (Puerto Rico)	Gorman & Stamm (1975); Schwartz & Henderson (1991)
<i>Anolis noblei</i> Barbour & Shreve, 1935; I	Cuba	L.V. Moreno <i>pers. com.</i>
<i>Anolis oculatus</i> (Cope, 1879); I	Dominica (Lesser Antilles)	Daniells et al. (2008)
<i>Anolis pentaprion</i> Cope, 1863; M	Costa Rica	Savage (2002)
<i>Anolis petersii</i> Bocourt, 1873; M	Mexico	Villareal (1997) <i>in</i> McCranie & Kohler 2015
<i>Anolis pigmaequestris</i> Garrido, 1975; I	Cayo Frances (Cuba)	Fernández & Manso (1998)
<i>Anolis pogus</i> Lazell, 1972; I	St. Maarten (Lesser Antilles)	Powell et al. (2005)
<i>Anolis porcatus</i> Gray, 1840; I-Mi	Cuba; Florida	Meshaka et al. (1997); Rodríguez-Schettino (1999); A. Fong-Grillo <i>pers. com.</i>
<i>Anolis porcus</i> (Cope, 1864); I	Cuba	L.V. Moreno <i>pers. com.</i>
<i>Anolis proboscis</i> Peters & Orces, 1956; M	Ecuador	Losos et al. (2012)
<i>Anolis pulchellus</i> Duméril & Bibron, 1837; I	Caribbean Islands	Wolcot (1923); Schwartz & Henderson (1991); Rivero (1998)
<i>Anolis richardii</i> Duméril & Bibron, 1837; I-Mi	Grenada (Lesser Antilles)	Lazel (1972); Simmons et al. (2005); R. Powell <i>pers. com.</i>
<i>Anolis roosevelti</i> Grant, 1931; I	Culebra Island (Puerto Rico)	Campbell & Dodd (1982)

<i>Anolis sabanus</i> Garman, 1887; I	Saba Island (Lesser Antilles)	Powell et al. (2005)
<i>Anolis sagrei</i> Duméril & Bibron, 1837; I-Mi	Bimini Islands (Bahamas); Cuba; Florida	Schoener (1968); Sampedro-Marín et al. (1982); Steinberg (2010); Hollbrook (2012); L. Rodríguez-Schettino <i>pers. com.</i>
<i>Anolis schwartzi</i> Lazell, 1972; I	St. Eustatius (Lesser Antilles)	Powell et al. (2005)
<i>Anolis smallwoodi</i> Schwartz, 1964; I	Cuba	L.V. Moreno <i>pers. com.</i>
<i>Anolis stratulus</i> Cope, 1861; I	Puerto Rico	Wolcott (1924); Lister (1981); Rivero (1998); Vega-Catillo & Puente-Rolón (2011)
<i>Anolis valencienni</i> Duméril & Bibron, 1837; I	Jamaica	Herrel et al. (2004a)
<i>Anolis vermiculatus</i> Cocteau, 1837; I	Cuba	Rodríguez-Schettino & Novo-Rodríguez (1985); Schwartz & Henderson (1991); Rodríguez-Schettino et al. (2010)
<i>Anolis wattsii</i> Boulenger, 1894; I	Lesser Antilles	Meiri (2018)
Iguanidae		
<i>Brachylophus bulabula</i> Fisher, Harlow, Edwards & Keogh, 2008; I	Fiji Islands	Harlow et al. (2004)
<i>Brachylophus fasciatus</i> (Brongniart, 1800); I	Fiji Islands	Zug (1991); Harlow et al. (2004)

<i>Brachylophus vitiensis</i> Gibbons, 1981; I	Fiji Islands	Gibbons & Watkins (1982); Laurie et al. (1987); Harlow et al. (2004, 2007); Morrison et al. (2007)
<i>Conolophus pallidus</i> Heller, 1903; I	Santa Fe (Galapagos Islands)	Carpenter (1969); Racine & Downhower (1974); Christian et al. (1984)
<i>Conolophus subcristatus</i> (Gray, 1831); I	Santa Cruz, Fernandina (Galapagos Islands)	Darwin (1845); Loveridge (1946); Carpenter (1969); Racine & Downhower (1974); Eibl-Eibesfeldt (1984); Hendrix & Smith (1986); Traveset et al. (2016)
<i>Ctenosaura bakeri</i> Stejneger, 1901; I	Utila Island (Honduras)	Meiri (2018)
<i>Ctenosaura hemilopha</i> (Cope, 1863); I-M	Baja California	Case (1982); Blázquez & Rodríguez-Estrella (2001)
<i>Ctenosaura palearis</i> Stejneger, 1899; M	Guatemala	Cotí & Ariano-Sánchez (2008); Vásquez-Contreras & Ariano-Sánchez (2016)
<i>Ctenosaura pectinata</i> (Wiegmann, 1834); I-M	Mexico, Isla Isabel (Mexico)	Evans (1951); Mandujano et al. (1994); Rodríguez-Juarez & Osorno (1998); Durtsche (2000)

<i>Ctenosaura quinquecarinata</i> (Gray, 1842); M	Nicaragua	Villa & Scott (1967)
<i>Ctenosaura similis</i> (Gray, 1831); I-M	Costa Rica; Guatemala; Gasparilla Island (Florida); Caribbean Islands	Klein (1977); Janzen (1982, 1985); van Devender (1982, 1985); Roberts & Heithaus (1986); Traveset (1990); Fitch & Hackforth-Jones (1991); Schwartz & Henderson (1991); Campbell (1998); Savage (2002); Jackson & Jackson (2007)
<i>Cyclura carinata</i> Harlan, 1824; I	Bahamas, Turks and Caicos Islands	Auffenberg (1982); Iverson (1979, 1985); Schwartz & Henderson (1991); Gerber & Iverson (1999)
<i>Cyclura collei</i> Gray, 1845; I	Jamaica	Vogel (1999)
<i>Cyclura cornuta</i> (Bonnaterre, 1789); I	Caribbean Islands	Wilcox et al. (1973); Carey (1975); Wiewandt (1977); Iverson (1979); Schwartz & Henderson (1991); Rivero (1998); Hartley et al. (2000); Navarro & Ayensa (2002); Pasachnik & Martin-Velez (2017); L. Navarro <i>pers. com.</i>

<i>Cyclura cychlura</i> (Cuvier, 1829); I	Bahamas	Wilcox et al. (1973); Schwartz & Henderson (1991); Knapp (1999)
<i>Cyclura nubila</i> (Gray, 1831); I	Cuba; Cayman Islands; Puerto Rico	Sutcliffe (1952); Iverson (1979); Perera (1985); Schwartz & Henderson (1991); Lewis et al. (1993); Brunt & Davies (1994); Alberts (1999); Beovides-Casas & Mancina (2006); Marichal (2016)
<i>Cyclura pinguis</i> Barbour, 1917; I	Anegada (Lesser Antilles)	Grant (1937); Carey (1975); Iverson (1979); Mitchell (1999)
<i>Cyclura ricordi</i> (Duméril & Bibron, 1837); I	Hispaniola	Carey (1975); Hartley et al. (2000); Pasachnik & Martin-Velez (2017)
<i>Cyclura rileyi</i> Stejneger, 1903; I	Bahamas	Iverson (1985)
<i>Iguana delicatissima</i> Laurenti, 1768; I	Lesser Antilles	Schwartz & Henderson (1991); Breuil (2002); Powell et al. (2005); Lorvelec et al. (2007); Daniells et al. (2008)
<i>Iguana iguana</i> (Linnaeus, 1758); I-M	Panama; Mexico; Dutch islands in the Lesser Antilles; Puerto Rico;	Swanson (1950); Lazell (1973); van Devender (1982); Rand et al. (1990); Campbell (1998); Lara-

	Costa Rica; Brazil; Colombia	López & González-Romero (2002) ; Morales-Mávil et al. (2002); Savage (2002); Powell et al. (2005); Govender et al. (2012); Lasso & Barrientos (2015); Moura et al. (2015); Burgos-Rodríguez et al. (2016); V. Parra-Tabla <i>pers. com.</i>
<i>Sauromalus ater</i> Duméril, 1856; I-M	Baja California and adjacent islands	Nagy (1973); Behler & King (1979)
<i>Sauromalus hispidus</i> Stejneger, 1891; I	San Lorenzo, Angel de la Guarda and Mejia islands (Baja California)	Case (1982); Smits (1985 a, b); Sylber (1988)
<i>Sauromalus varius</i> Dickerson, 1919; I	San Esteban Island (Baja California)	Sylber (1988)
Leiocephalidae		
<i>Leiocephalus barahonensis</i> Schmidt, 1921; I	Hispaniola	Micco et al. (1997)
<i>Leiocephalus carinatus</i> Gray, 1827; I-Mi	Cuba; Bahamas; Florida	Schoener et al. (1982); de Armas (1987); Schwartz & Henderson (1991); Silva (1997); Rodriguez- Barbosa et al. (2017)

<i>Leiocephalus cubensis</i> (Gray, 1840); I	Cuba	Martínez & Fernández (1994); Silva (1997); Y. Rodríguez <i>pers. com.</i>
<i>Leiocephalus inaguae</i> Cochran, 1931; I	Bahamas	Schoener et al. (1982); Schwartz & Henderson (1991)
<i>Leiocephalus loxogrammus</i> (Cope, 1887); I	Bahamas	Schoener et al. (1982); Schwartz & Henderson (1991)
<i>Leiocephalus macropus</i> (Cope, 1863); I	Cuba	Silva (1997); Y. Alfonso <i>pers. com.</i>
<i>Leiocephalus onaneyi</i> Garrido, 1973; I	Cuba	Silva (1997)
<i>Leiocephalus psammodromus</i> Barbour, 1920; I	Turks and Caico Islands (Lesser Antilles)	Henderson & Powell (2009)
<i>Leiocephalus punctatus</i> Cochran, 1931; I	Bahamas	Schoener et al. (1982); Schwartz & Henderson (1991)
<i>Leiocephalus raviceps</i> Cope, 1863; I	Cuba	Silva (1997); Y. Alfonso <i>pers. com.</i>
<i>Leiocephalus schreibersii</i> (Gravenhorst, 1838); I-Mi	Dominican Republic	Nelson et al. (2001)
<i>Leiocephalus semilineatus</i> Dunn, 1920; I	Dominican Republic	Nelson et al. (2001)
<i>Leiocephalus stictigaster</i> Schwartz, 1959; I	Cuba	Martínez et al. (1990); Rodríguez-Schettino (1999); A. Fong <i>pers. com.</i>

Leiosauridae

Pristidactylus scapulatus (Burmeister, 1861); M

Argentina

Acosta et al. (2004)

Liolaemidae

Liolaemus baguali Cei & Scolaro, 1983; M

Argentina

Vanhoooydonck et al. (2010)

Liolaemus bellii Gray, 1845; M

Chile

Celedón-Neghme et al. (2008)

Liolaemus bibronii (Bell, 1843); M

Argentina

Belver & Avila (2002)

Liolaemus boulengeri Koslowsky, 1898; M

Argentina

L.J. Avila *pers. com.*

Liolaemus canqueli Cei, 1975; M

Argentina

Vanhoooydonck et al. (2010)

Liolaemus chehuachekenk Avila, Morando & Sites, 2008; M

Argentina

Avila et al. (2008)

Liolaemus crepuscularis Abdala & Díaz-Gomez, 2006; M

Argentina

Semhan et al. (2013)

Liolaemus cuyanus Cei & Scolaro, 1980; M

Argentina

Moreno-Azócar & Acosta (2011)

Liolaemus darwinii (Bell, 1843); M

Argentina

Videla (1983)

Liolaemus eleodori Cei, Etheridge & Videla, 1985; M

Argentina

Astudillo et al. (2013, 2015)

Liolaemus elongatus Koslowsky, 1896; M

Argentina

Quatrini et al. (2001)

Liolaemus escarchadosi Scolaro, 1997; M

Argentina

Vanhoooydonck et al. (2010)

Liolaemus fitzingerii (Duméril & Bibron, 1837); M

Argentina

Videla (1983), Vanhooydonck et al. (2010)

Liolaemus fuscus Boulenger, 1885; M

Chile

Fuentes (1976)

Liolaemus hatcheri Stejneger, 1909; M

Argentina

Vanhoooydonck et al. (2010)

Liolaemus juanortizi Young-Downey & Moreno, 1992; M

Chile

Meiri (2018)

Liolaemus kingii (Bell, 1843); M

Argentina

Vanhoooydonck et al. (2010)

Liolaemus kolengh Abdala & Lobo, 2006; M

Argentina

Vanhoooydonck et al. (2010)

<i>Liolaemus laurenti</i> Etheridge, 1992; M	Argentina	Galdeano et al. (2013)
<i>Liolaemus morenoi</i> Etheridge & Christie, 2003; M	Argentina	Vanhoooydonck et al. (2010)
<i>Liolaemus multicolor</i> Koslowsky, 1898; M	Argentina	S. Valdecantos <i>pers. com.</i>
<i>Liolaemus nigromaculatus</i> (Wiegmann, 1834); M	Chile	Ortiz & Riveros (1976)
<i>Liolaemus nigroviridis</i> Müller & Hellmich, 1932; M	Chile	Fuentes (1976)
<i>Liolaemus pictus</i> (Duméril & Bibron, 1837); I-M	Chiloé Archipelago (Chile); Chile	Willson et al. (1996); Aizen et al. (2002); Vidal & Sabat (2010)
<i>Liolaemus poecilochromus</i> Laurent, 1986; M	Argentina	Valdecantos et al. (2012)
<i>Liolaemus ruibali</i> Donoso-Barros, 1961; M	Argentina	Villavicencio et al. (2005); Nieva et al. (2011); R.A. Nieva & S. Castro <i>pers. com.</i>
<i>Liolaemus vallecurensis</i> Pereyra, 1992; M	Argentina	Meiri (2018)
<i>Liolaemus xanthoviridis</i> Cei & Scolaro, 1980; M	Argentina	Vanhoooydonck et al. (2010)
<i>Phymaturus aguanegra</i> Lobo, Laspiur & Acosta, 2013; M	Argentina	Lobo et al. (2013)
<i>Phymaturus antofagastensis</i> Pereyra, 1985; M	Chile, Argentina	Celedón-Neghme et al. (2005); Acosta et al. (2008)
<i>Phymaturus palluma</i> (Molina, 1782); M	Argentina	Videla (1983)
<i>Phymaturus punae</i> Cei, Etheridge & Videla, 1985; M	Argentina	Córdoba et al. (2015)
<i>Phymaturus spurcus</i> Barbour, 1921; M	Argentina	Scolaro et al. (2008)
<i>Phymaturus williamsi</i> Lobo, Laspiur & Acosta, 2013; M	Argentina	Lobo et al. (2013); Castro et al. (2013); S.A. Castro <i>com. pers.</i>

Opluridae

<i>Chalarodon madagascariensis</i> (Peters, 1854); I	Madagascar	Blanc (1969)
<i>Oplurus cuvieri</i> (Gray, 1831); I	Madagascar	Henkel & Schmidt (2000); Hasegawa et al. (2009); Randriamahazo & Mori (2012); Razafindratsima (2014)

Phrynosomatidae

<i>Phrynosoma platyrhinos</i> Girard, 1852; M	Nevada	Banta (1961)
<i>Sceloporus clarkii</i> Baird & Girard, 1852; I-M	Coastal islands of Baja California	Meiri (2018)
<i>Sceloporus magister</i> Hallowell, 1854; I-M	Utah, Arizona; Magdalena and Santa Margarita islands (Baja California)	Knowlton (1934); Vitt et al. (1981); Skydancer (1998)
<i>Sceloporus orcutti</i> Stejneger, 1893; M	California	Stebbins (1966)
<i>Sceloporus poinsettii</i> Baird & Girard, 1852; M	Texas	Smith & Milstead (1971)
<i>Sceloporus torquatus</i> Wiegmann, 1828; M	Mexico	Ortiz et al. (2001)
<i>Urosaurus graciosus</i> Hallowell, 1854; M	Arizona	Vitt et al. (1981)
<i>Urosaurus ornatus</i> (Baird & Girard, 1852); M	Arizona	Vitt et al. (1981)

Polychrotidae

<i>Polychrus acutirostris</i> Spix, 1825; M	Brazil	Vitt & Lacher (1981)
<i>Polychrus gutturosus</i> Berthold, 1846; M	Costa Rica	Savage (2002)
<i>Polychrus liogaster</i> Boulenger, 1908; M	Bolivia	Greene (1986)

Polychrus marmoratus (Linnaeus, 1758); M

Venezuela; Guyana

Beebe (1944)

Tropiduridae

Microlophus albemarlensis (Baur, 1890); I

Santa Cruz, Fernandina,
Isabela (Galapagos
Islands)

Stebbins et al. (1967); Heleno et
al. (2013); Parejo et al. (2018)

Microlophus bivittatus (Peters, 1871); I

San Cristobal (Galapagos
Islands)

Heleno et al. (2013); Moore et al.
(2017); Nogales et al. (2017);
Parejo et al. (2018)

Microlophus delanonis (Baur, 1890); I

España (Galapagos
Islands)

Werner (1978); Parejo et al.
(2018)

Microlophus duncanensis (Baur, 1890); I

Pinzón (Galapagos
Islands)

Parejo et al. (2018)

Microlophus grayii (Bell, 1843); I

Floreana (Galapagos
Islands)

Parejo et al. (2018)

Microlophus habelii (Steindachner, 1876); I

Marchena (Galapagos
Islands)

Loveridge (1946); Parejo et al.
(2018)

<i>Microlophus indefatigabilis</i> (Baur, 1890); I	Santa Cruz, Santa Fe (Galapagos Islands)	Lewbart et al. (2017); Nogales et al. (2017); Parejo et al. (2018)
<i>Microlophus jacobii</i> (Baur, 1892); I	Santiago (Galapagos Islands)	Parejo et al. (2018)
<i>Microlophus koepckeorum</i> (Mertens, 1956); M	Peru	Alcántara (1971) in Pollack et al. (2007)
<i>Microlophus pacificus</i> (Steindachner, 1876); I	Pinta (Galapagos Islands)	Schluter (1984); Parejo et al. (2018)
<i>Microlophus peruvianus</i> (Lesson, 1830); M	Chile	Donoso-Barroso (1948); A. Catenazzi <i>pers. com.</i>
<i>Microlophus thoracicus</i> (Tschudi, 1845); M	Peru	Alcántara (1971) in Pollack et al. (2007); Dixon & Writght (1975)
<i>Tropidurus cocorobensis</i> Rodrigues, 1987; M	Bahia (Brazil)	Fonseca (2004); Fonseca et al. (2008, 2012)
<i>Tropidurus erythrocephalus</i> Rodrigues, 1987; M	Bahia (Brazil)	Figueira-Fontes et al. (2003)
<i>Tropidurus etheridgei</i> Cei, 1982; M	Argentina	Cruz et al. (1998)
<i>Tropidurus hispidus</i> (Spix, 1825); I-M	Brazil; Margarita Island (Venezuela)	Vitt & de Carvalho (1995); Vitt et al. (1996); van Sluys et al. (2004); Guerrero et al. (2012); Maia-Carneiro et al. (2017); L.J. Vitt & V. Sanz <i>pers. com.</i>
<i>Tropidurus hygomi</i> Reinhardt & Lütken, 1861; M	Bahia (Brazil)	Xavier & Dias (2015 a)

<i>Tropidurus itambere</i> Rodrigues, 1987; M	Brazil	van Sluys (1993); M. van Sluys <i>pers. com.</i>
<i>Tropidurus montanus</i> Rodrigues, 1987; M	Minas Gerais (Brazil)	van Sluys et al. (2004)
<i>Tropidurus oreadicus</i> Rodrigues, 1987; M	Brazil	Colli et al. (1992); Vitt (1993); Rocha & Siqueira (2008)
<i>Tropidurus pinima</i> (Rodriguez, 1984); M	Bahia (Brazil)	Xavier & Dias (2017 a, b)
<i>Tropidurus semitaeniatus</i> (Spix, 1825); M	Bahia, Catinga (Brazil)	Fonseca (2004); Ribeiro et al. (2008); Fonseca et al. (2012); Gomes et al. (2014, 2016); Maia- Carneiro et al. (2017)
<i>Tropidurus spinulosus</i> (Cope, 1862); M	Argentina; Brazil	Colli et al. (1992); Cruz (1998); G.R. Colli <i>pers. com.</i>
<i>Tropidurus torquatus</i> (Wied-Neuwied, 1820); M	Brazil; Venezuela; Argentina	León et al. (1969-1970); Álvarez et al. (1985); Fialho (1990); Côrtes-Figueira et al. (1994); Teixeira & Giovanelli (1999); Fialho et al. (2000); Vasconcellos-Neto et al. (2000); Carvalho et al. (2007); Vasconcellos-Neto et al. (2009); da Costa et al. (2011); Dutra et al.

(2011); Pietczak et al. (2013);
Koski et al. (2018)

GEKKOTA

Gekkonidae

Ailuronyx tachyscopaeus Gerlach & Canning, 1996; I

Christinus guentheri Boulenger, 1885; M

Geckolepis maculata Peters, 1880; I

Gehyra australis (Gray, 1845); M

Gehyra brevipalmata (Peters, 1874); I

Gehyra dubia (Macleay, 1877); I-M

Gehyra oceanica (Lesson, 1830); I

Gehyra vorax Girard, 1858; I

Gekko remotus Rösler, Ineich, Wilms & Böhme, 2012; I

Lepidodactylus lugubris (Duméril & Bibron, 1836); I-M

Lepidodactylus pumilus (Boulenger, 1885); I-M

Lygodactylus arnoulti Pasteur, 1965; I

Lygodactylus blancae Pasteur, 1965; I

Seychelles	Schönecker (2008)
Phillip Island (Australia)	Cogger et al. (1993)
Madagascar, Comoro Islands	Schönecker (2008)
Australia	King & Horner (1993)
Palau Islands	Crombie & Pregill (1999)
Australia	Burnett & Nolen (1996)
Cook Islands; Solomon Islands	Crombie & Steadman (1986); Beckon (1992); McCoy (2000); Staddon et al. (2010)
New Caledonia; Fiji Islands	Gibbons & Clunie (1984); Zug (1991); Bauer & Sadlier (2000 a)
Palau Islands	Rösler et al. (2012)
New Caledonia	Bauer & Sadlier (2000 a)
Australia	Henkel (2010)
Madagascar	Schönecker (2008)
Madagascar	Schönecker (2008)

<i>Lygodactylus decaryi</i> Angel, 1930; I	Madagascar	Schönecker (2008)
<i>Lygodactylus expectatus</i> Pasteur & Blanc, 1967; I	Madagascar	Schönecker (2008)
<i>Lygodactylus guibei</i> Pasteur, 1965; I	Madagascar	Schönecker (2008)
<i>Lygodactylus heterurus</i> Boettger, 1913; I	Madagascar	Schönecker (2008)
<i>Lygodactylus intermedius</i> Pasteur, 1965; I	Madagascar	Schönecker (2008)
<i>Lygodactylus klemmeri</i> Pasteur, 1965; I	Madagascar	Schönecker (2008)
<i>Lygodactylus madagascariensis</i> (Boettger, 1881); I	Madagascar	Schönecker (2008)
<i>Lygodactylus miops</i> Günther, 1891; I	Madagascar	Schönecker (2008)
<i>Lygodactylus mirabilis</i> (Pasteur, 1962); I	Madagascar	Schönecker (2008)
<i>Lygodactylus montanus</i> Pasteur, 1965; I	Madagascar	Schönecker (2008)
<i>Lygodactylus pictus</i> (Peters, 1883); I	Madagascar	Schönecker (2008)
<i>Lygodactylus rarus</i> Pasteur & Blanc, 1973; I	Madagascar	Schönecker (2008)
<i>Lygodactylus tolampyae</i> (Grandidier, 1872); I	Madagascar	Schönecker (2008)
<i>Lygodactylus tuberosus</i> Mertens, 1965; I	Madagascar	Schönecker (2008)
<i>Lygodactylus verticillatus</i> Mocquard, 1895; I	Madagascar	Schönecker (2008)
<i>Nactus serpensinsula</i> (Loveridge, 1951); I	Mauritius (Mascarene Islands)	Schönecker (2008)
<i>Phelsuma antanasy</i> Raxworthy & Nussbaum, 1993; I	Madagascar	Schönecker (2008)
<i>Phelsuma barbouri</i> Loveridge, 1942; I	Madagascar	Schönecker (2008)
<i>Phelsuma berghofi</i> Krüger, 1996; I	Madagascar	Schönecker (2008)
<i>Phelsuma borbonica</i> Mertens, 1966; I	Reunion (Mascarene Islands)	Schönecker (2008)

<i>Phelsuma breviceps</i> Boettger, 1894; I	Madagascar	Schönecker (2008)
<i>Phelsuma cepediana</i> (Milbert, 1812); I	Mauritius (Mascarene Islands)	Hansen & Müller (2009 a, b)
<i>Phelsuma comorensis</i> Boettger, 1913; I	Comoro Islands	Schönecker (2008)
<i>Phelsuma dubia</i> (Boettger, 1881); I-M	Madagascar, Comores Islands	Schönecker (2008)
<i>Phelsuma edwardnewtoni</i> (†) Vinson & Vinson, 1969; I	Rodrigues Island (Mascarene Islands)	Leguat (1708; reprinted in 1981)
<i>Phelsuma flavigularis</i> Mertens, 1962; I	Madagascar	Schönecker (2008)
<i>Phelsuma gigas</i> (†) Liénard, 1842; I	Rodrigues Island (Mascarene Islands)	Liénard (1842) <i>in</i> Vinson & Vinson (1969)
<i>Phelsuma grandis</i> Gray, 1870; I	Reunion Island (Mascarene Islands)	Dervin et al. (2013); S. Dervin <i>pers. com.</i>
<i>Phelsuma guentheri</i> Boulenger, 1885; I	Round Island (Mascarene Islands)	Vinson & Vinson (1969); Bullock (1986); D.M. Hansen <i>pers. com.</i>
<i>Phelsuma guimbeaui</i> Mertens, 1963; I	Mascarene Islands	Schönecker (2008)
<i>Phelsuma guttata</i> Kaudern, 1922; I	Madagascar	Schönecker (2008)
<i>Phelsuma hielscheri</i> Rösler, 2001; I	Madagascar	Schönecker (2008)
<i>Phelsuma inexpectata</i> Mertens, 1966; I	Mascarene Islands	Schönecker (2008)
<i>Phelsuma kely</i> Schönecker, Bach & Glaw, 2004; I	Madagascar	Schönecker (2008)
<i>Phelsuma klemmeri</i> Seipp, 1991; I	Madagascar	Schönecker (2008)

<i>Phelsuma laticauda</i> (Boettger, 1880); I	Madagascar, Comores Islands	Schönecker (2008)
<i>Phelsuma lineata</i> Gray, 1842; I	Madagascar	Schönecker (2008)
<i>Phelsuma madagascariensis</i> Gray, 1831; I-M	Madagascar	G. García <i>pers. com.</i>
<i>Phelsuma malamakibo</i> Nussbaum et al., 2000; I	Madagascar	Schönecker (2008)
<i>Phelsuma masohoala</i> Raxworthy & Nussbaum, 1994; I	Madagascar	Schönecker (2008)
<i>Phelsuma modesta</i> Mertens, 1970; I	Madagascar	Schönecker (2008)
<i>Phelsuma mutabilis</i> (Grandidier, 1869); I	Madagascar	Schönecker (2008)
<i>Phelsuma nigristriata</i> Meier, 1984; I	Comoro Islands	Schönecker (2008)
<i>Phelsuma ornata</i> Gray, 1825; I	Mauritius (Mascarene Islands)	Bullock (1986); D.M. Hansen <i>pers. com.</i>
<i>Phelsuma parkeri</i> Loveridge, 1941; I-M	Pemba Island (Tanzania)	Schönecker (2008)
<i>Phelsuma pronki</i> Seipp, 1994; I	Madagascar	Schönecker (2008)
<i>Phelsuma pusilla</i> Mertens, 1964; I	Madagascar	Schönecker (2008)
<i>Phelsuma quadriocellata</i> Peters, 1883; I	Madagascar	Schönecker (2008)
<i>Phelsuma ravenala</i> Raxworthy et al., 2007; I	Madagascar	Schönecker (2008)
<i>Phelsuma robertmertensi</i> Meier, 1980; I	Comoro Islands	Schönecker (2008)
<i>Phelsuma rosangularis</i> Vinson & Vinson, 1969; I	Mauritius (Mascarene Islands)	Schönecker (2008)
<i>Phelsuma seippi</i> Meier, 1987; I	Madagascar	Schönecker (2008)
<i>Phelsuma serraticauda</i> Mertens, 1963; I	Madagascar	Schönecker (2008)
<i>Phelsuma standingi</i> Methuen & Hewitt, 1913; I	Madagascar	Schönecker (2008)

<i>Phelsuma vanheygeni</i> Lerner, 2004; I	Madagascar	Schönecker (2008)
<i>Phelsuma v-nigra</i> Boettger, 1913; I	Comoro Islands	Schönecker (2008)
Diplodactylidae		
<i>Correlophus ciliatus</i> Guichenot, 1866; I	New Caledonia	Kullmann (1995); Bauer & Sadlier (2000 b)
<i>Dactylocnemis pacificus</i> (Gray, 1842); I	Poor Knights Islands (North Island, New Zealand)	Hare et al. (2016)
<i>Dactylocnemis</i> ‘Poor Knights’; I	Poor Knights Islands (North Island, New Zealand)	Whitaker (1968); Hare et al. (2016); Wotton et al. (2016)
<i>Eurydactylodes vieillardi</i> (Bavay, 1869); I	New Caledonia	Bauer & Sadlier (2000 a)
<i>Hoplodactylus delcourtii</i> (†) Bauer & Russell, 1986; I	North Island (New Zealand)	Whitaker (1987); Russell & Bauer (1991)
<i>Hoplodactylus duvaucelii</i> (Duméril & Bibron, 1836); I	Poor Knights Islands (North Island, New Zealand)	Whitaker (1968); Southey (1985) and Barwick (1982) <i>in</i> Whitaker (1987); Hare et al. (2016); Wotton et al. (2016)
<i>Mniarogekko chahoua</i> (Bavay, 1869); I	New Caledonia	Bauer (1985); Bauer & Sadlier (2000 b); A.M. Bauer <i>pers. com.</i>
<i>Mniarogekko jalu</i> Bauer, Whitaker, Sadlie & Jackman, 2012; I	New Caledonia	Bauer et al. (2012)

<i>Naultinus gemmeus</i> McCann, 1955; I	South Island (New Zealand)	Burrows (1994)
<i>Naultinus grayii</i> Bell, 1843; I	North Island (New Zealand)	Bellingham, M. <i>in</i> Whitaker (1987); Hare et al. (2016); Wotton et al. (2016)
<i>Naultinus stellatus</i> Hutton, 1872; I	New Zealand	Hare et al. (2016)
<i>Rhacodactylus leachianus</i> (Cuvier, 1829); I	New Caledonia	Bauer & Sadlier (2000 b)
<i>Rhacodactylus trachyrhynchus</i> Bocage, 1873; I	New Caledonia	Bauer & Sadlier (2000 b)
<i>Toropuku stephensi</i> (Robb, 1980); I	Stephens Island (New Zealand)	Hare et al. (2016); Wotton et al. (2016)
<i>Woodworthia cf. brunnea</i> ; I	South Island (New Zealand)	Freeman (1994); Hare et al. (2016); Wotton et al. (2016)
<i>Woodworthia maculata</i> (Gray, 1845); I	Mana Island (New Zealand)	Whitaker (1987); Burrows (1994); de Lange & Jones (2000); Wotton (2002); Hare et al. (2016); Wotton et al. (2016)
<i>Woodworthia</i> ‘Southern Alps’; I	South Island (New Zealand)	Hare et al. (2016); Wotton et al. (2016)
Phyllodactylidae		
<i>Homonota andicola</i> Cei, 1978; M	Argentina	Blanco et al. (2009); J.C. Acosta <i>pers. com.</i>

<i>Tarentola mauritanica</i> (Linnaeus, 1758); I-M	Cabrera Island (Balearic Islands)	Salvador (1978)
Sphaerodactylidae		
<i>Aristelliger lar</i> Cope, 1861; I	Hispaniola	Schwartz & Henderson (1991); DeBoer et al. (2018)
<i>Teratoscincus roborowskii</i> Bedriaga, 1906; M	China	Shi & Wang (2015)
Pygopodidae		
<i>Delma australis</i> Kluge, 1974; M	Australia	Henkel (2010)
<i>Delma borea</i> Kluge, 1974; M	Australia	Henkel (2010)
<i>Delma butleri</i> Storr, 1987; M	Australia	Henkel (2010)
<i>Delma desmosa</i> Maryan, Aplin & Adams, 2007; M	Australia	Henkel (2010)
<i>Delma elegans</i> Kluge, 1974; M	Australia	Henkel (2010)
<i>Delma grayii</i> Smith, 1849; M	Australia	Henkel (2010)
<i>Delma impar</i> (Fischer, 1882); M	Australia	Henkel (2010)
<i>Delma labialis</i> Shea, 1987; M	Australia	Henkel (2010)
<i>Delma mitella</i> Shea, 1987; M	Australia	Henkel (2010)
<i>Delma molleri</i> Lütken, 1863; M	Australia	Henkel (2010)
<i>Delma pax</i> Kluge, 1974; M	Australia	Henkel (2010)
<i>Delma plebeia</i> De Vis, 1888; M	Australia	Henkel (2010)
<i>Delma tealei</i> Maryan, Aplin & Adams, 2007; M	Australia	Henkel (2010)
<i>Delma tincta</i> De Vis, 1888; M	Australia	Henkel (2010)
<i>Delma torquata</i> Kluge, 1974; M	Australia	Henkel (2010)

<i>Pletholax gracilis</i> (Cope, 1864); M	Australia	Henkel (2010)
<i>Pygopus steelescoti</i> James, Donnellan & Hutchinson, 2001; M	Australia	Henkel (2010)
SCINCOMORPHA		
Cordylidae		
<i>Platysaurus broadleyi</i> Branch & Whiting, 1997; M	South Africa	Whiting & Greeff (1997); Greeff & Whiting (1999, 2000)
<i>Platysaurus capensis</i> Smith, 1884; M	South Africa	Pianka & Vitt (2003)
<i>Platysaurus intermedius</i> Matschie, 1891; M	Zimbabwe	D.G. Broadley <i>pers. com.</i>
Gerrhosauridae		
<i>Broadleysaurus major</i> (Duméril, 1851); M	Kenya to Ghana	Meiri (2018)
<i>Gerrhosaurus flavigularis</i> Wiegmann, 1828; M	Africa	Rogner (1997)
<i>Matobosaurus validus</i> (Smith, 1849); M	Zimbabwe	Broadley (1962); D.G. Broadley <i>pers. com.</i>
<i>Zonosaurus laticaudatus</i> (Grandidier, 1869); I	Madagascar	Meier (1988); Raselimanana (2003); Hasegawa et al. (2009); Razafindratsima (2014); G. García <i>pers. com.</i>
<i>Zonosaurus madagascariensis</i> (Gray, 1831); I	Madagascar	Meier (1988); Henkel & Schmidt (2000)
<i>Zonosaurus quadrilineatus</i> (Grandidier, 1867); I	Madagascar	Meier (1988); Henkel & Schmidt (2000)

Zonosaurus trilineatus Angel, 1939; I

Madagascar

Henkel & Schmidt (2000)

Lacertidae

Algyroides nigropunctatus (Duméril & Bibron, 1839); I-M

Bisage Island
(Montenegro)

Polovic et al. (2013)

Archaeolacerta bedriagae (Camerano, 1885); I

Corsica (France)

Schneider (1984)

Atlantolacerta andreanskyi (Werner, 1929); M

Morocco

Schleich et al. (1996)

Darevskia brauneri (Méhely, 1909); M

Russia

Darevsky (1967) *in* Golynsky & Doronin (2014)

Darevskia clarkorum (Darevsky & Vedmederja, 1977); M

Turkey

Franzen (1991)

Darevskia rudis (Bedriaga, 1886); M

Turkey

Franzen (1991)

Eremias multiocellata Günther, 1972; M

Central-East Asia

Szczerbak (2003) *in* Meiri (2018)

Gallotia atlantica (Peters & Doria, 1882); I

Lanzarote, Fuerteventura
(Canary Islands)

Bischoff (1998); Nogales et al.
(1998); Valido (1999); Valido &
Nogales (2003); Nogales et al.
(2005)

Gallotia avaritae (†) Mateo et al., 2001; I

La Palma (Canary
Islands)

Mateo (2009)

Gallotia bravoana Hutterer, 1985; I

La Gomera (Canary
Islands)

Mateo (2006); A. Valido *pers.
obs.*

Gallotia caesaris (Lehrs, 1914); I

La Gomera, El Hierro
(Canary Islands)

Machado (1985); Bischoff
(1998); Valido (1999); Pérez-
Méndez et al. (2016)

<i>Gallotia galloti</i> (Oudart, 1839); I	Tenerife, La Palma (Canary Islands)	Fructuoso (1590; reprinted in 1964); Barquín & Wildpret (1975); Valido & Nogales (1994); Valido (1999); Valido et al. (2003); Rodríguez et al. (2008); Padrón et al. (2011); Rumeu et al. (2011); Pérez- Méndez et al. (2016)
<i>Gallotia goliath</i> † (Mertens, 1942); I	Tenerife (Canary Islands)	Bocherens et al. (2003)
<i>Gallotia intermedia</i> Hernández, Nogales & Martín, 2000; I	Tenerife (Canary Islands)	Fariña & Martín (2013); A. Valido <i>pers. obs.</i>
<i>Gallotia simonyi</i> (Steindachner, 1889); I	El Hierro (Canary Islands)	Machado (1985); Pérez-Mellado et al. (1999)
<i>Gallotia stehlini</i> (Schenkel, 1901); I	Gran Canaria (Canary Islands)	Steindachner (1891); Barquín et al. (1986); Naranjo et al. (1991); Valido (1999); Carretero et al. (2006); Pérez-Méndez et al. (2016)
<i>Lacerta bilineata</i> Daudin, 1802; I-M	Italy; Iberian Peninsula	Bruno & Maugeri (1977) <i>in</i> Angelici et al. (1997); Barbadillo et al. (1999)
<i>Lacerta schreiberi</i> Bedriaga, 1878; M	Iberian Peninsula	Braña (1984)

<i>Lacerta trilineata</i> Bedriaga, 1886; I-M	Corfu Island (Greece)	Valakos et al. (2008) <i>in Meiri</i> (2018)
<i>Lacerta viridis</i> (Laurenti, 1768); I-M	Germany; Iberian Peninsula	Braña (1984); Nettmann & Rykena (1984)
<i>Omanosaura jayakari</i> (Boulenger, 1887); M	Oman	Arnold (1972); Bischoff (1981)
<i>Phoenicolacerta troodica</i> (Werner, 1936); I	Cyprus	Baier et al. (2009) <i>in Meiri</i> (2018)
<i>Podarcis bocagei</i> (Lopez-Seoane, 1885); I-M	Iberian Peninsula	Calviño-Cancela (2005)
<i>Podarcis erhardii</i> (Bedriaga, 1882); I-M	Naxos Island, Andros Island (Greece)	Brock et al. (2014); K. Brock <i>pers. com.</i>
<i>Podarcis filfolensis</i> (Bedriaga, 1876); I	Sicily; Malta; Pelagie Islands (Italy)	Sorci (1990); Fici & Lo Valvo (2004); Bombi et al. (2005); Carretero et al. (2010); G. Sorci & A. Sciberras <i>pers. com.</i>
<i>Podarcis gaigeae</i> (Werner, 1930); I	Skyros Archipelago (Greece)	Brock et al. (2014); K. Brock <i>pers. com.</i>
<i>Podarcis hispanicus</i> (Steindachner, 1870); I-M	Columbretes Islands (Spain)	Castilla & Bauwens (1991); Barbadillo et al. (1999)
<i>Podarcis lilfordi</i> (Günther, 1874); I	Cabrera (Balearic Islands)	Salvador (1986 a); Pérez-Mellado & Corti (1993); Sáez & Traveset (1995); Traveset (1997); Pérez-Mellado et al. (2000, 2005),

<i>Podarcis melisellensis</i> (Braun, 1877); I-M	Adriatic Islands	2006); Traveset & Riera (2005); Schulte (2008); Rodríguez-Pérez & Traveset (2010); Rodríguez-Pérez et al. (2012)
<i>Podarcis milensis</i> (Bedriaga, 1882); I	Milos Island (Greece)	Gelineo & Gelineo (1963); Tiedeman & Henle (1986)
<i>Podarcis muralis</i> (Laurenti, 1768); I-M	Bulgaria; Iberian Peninsula; Germany; Tuscan Archipelago (Italy)	Adamopoulou & Legakis (2002) Braña (1984); Gruschwitz & Böhme (1986)
<i>Podarcis pityusensis</i> (Boscá, 1883); I-M	Ibiza, Formentera (Balearic Islands); Iberian Peninsula	Salvador (1986 b); Pérez-Mellado & Corti (1993); Riera (2000); Carretero et al. (2001); Rodríguez-Pérez et al. (2005); Sanz-Azkue et al. (2005); Schulte (2008)
<i>Podarcis siculus</i> (Rafinesque-Schmaltz, 1810); I-M	Tuscan Archipelago, Sicily, Capri Island (Italy); Dubrounik, Veruda Island (Croatia)	Bolkay (1923); Butz & Kuenzer (1956); Henle (1984); Henle & Klaver (1986); Sorci (1990); Macat et al. (2015); G. Sorci <i>pers. com.</i>

<i>Podarcis waglerianus</i> Gistel, 1868; I	Sicily	Sorci (1990); Lo Cascio & Pasta (2006); G. Sorci <i>pers. com.</i>
<i>Psammodromus algirus</i> (Linnaeus, 1758); I-M	Isola dei Conigli (Pelagie Islands, Italy); Sicily; Iberian Peninsula	di Palma (1984); Sorci (1990); Barbadillo et al. (1999); G. Sorci <i>pers. com.</i>
<i>Scelarcis perspicillata</i> (Duméril & Bibron, 1839); Ii-M	North Africa; Menorca (Balearic Islands)	Doumergue (1901) <i>in</i> Schleich et al. (1996); Richter (1986); Perera et al. (2006)
<i>Teira dugesii</i> (Milne-Edwards, 1829); I-Mi	Madeira and Salvage Islands (Portugal)	Sadek (1981)
<i>Timon lepidus</i> (Daudin, 1802); M	Iberian Peninsula; France	Peters (1962); Valverde (1967); Mellado et al. (1975); Bischoff et al. (1984); Braña (1984); Mateo (1988); Castilla et al. (1991); Hódar et al. (1996); Thirion et al. (2009); Tatin et al. (2012)
Scincidae		
<i>Bellatorias frerei</i> (Günther, 1897); I-M	Australia	Swan (1995)
<i>Bellatorias major</i> (Gray, 1845); M	Australia	Conran (1983); Shea (1999); Chapple (2003); Greer (2005)
<i>Brasiliscincus agilis</i> (Raddi, 1823); I-M	Abrolhos Archipelago (Brazil)	Vrcibradic & Rocha (1996); Rocha et al. (2002)

<i>Caledoniscincus austrocaledonicus</i> (Bavay, 1869); I	Baie de Goro Island (New Caledonia)	Sherred et al. (2004)
<i>Carinascincus greeni</i> (Rawlinson, 1975); I	Tasmania	Hutchinson et al. (2001); R. Swain <i>pers. com.</i>
<i>Carinascincus microlepidotus</i> (O'Shaughnessy, 1874); I	Tasmania	R. Swain <i>pers. com.</i>
<i>Carinascincus ocellatus</i> (Gray, 1845); I	Tasmania	Wapstra & Swain (1996); Hutchinson et al. (2001)
<i>Chalcides ocellatus</i> (Forskal, 1775); I-M	Pelagie Islands (Italy)	Lo Cascio et al. (2008); Carretero et al. (2010); P. Lo Cascio, <i>pers. com.</i>
<i>Chalcides polylepis</i> Boulenger, 1890; I-M	Fuerteventura (Canary Islands)	Barbadillo et al. (1999)
<i>Chalcides sexlineatus</i> Steindachner, 1891; I	Gran Canaria (Canary Islands)	Barbadillo et al. (1999)
<i>Chalcides viridanus</i> (Gravenhorst, 1851); I	Canary Islands	Barbadillo et al. (1999)
<i>Chioninia coctei</i> (†) (Duméril & Bibron, 1839); I	Cape Verde Islands	Greer (1976)
<i>Corucia zebrata</i> Gray, 1855; I	Papua New Guinea; Solomon Islands	Parker (1983); Harmon (2002)
<i>Ctenotus grandis</i> Storr, 1969; M	Australia	Twigg et al. (1996); Greer (2005)
<i>Ctenotus robustus</i> Storr, 1970; M	Australia	Wathanow (1998) <i>in</i> Greer (2005)
<i>Ctenotus uber</i> Storr, 1969; M	Australia	Bedford (1992) <i>in</i> Greer (2005)
<i>Dasia grisea</i> (Gray, 1845); I-M	Luzon (Philippines)	Auffenberg & Auffenberg (1988)

<i>Dasia vittata</i> (Edeling, 1865); I	Luzon (Philippines)	Auffenberg & Auffenberg (1988)
<i>Egernia cunninghami</i> (Gray, 1832); M	Australia	Brown (1991); Carr (1993)
<i>Egernia hosmeri</i> Kinghorn, 1955; M	Australia	Shea (1995); Chapple (2003)
<i>Egernia kingii</i> (Gray, 1838); I-M	Penguin Island (Australia)	Arena & Woodler (2003)
<i>Egernia saxatilis</i> Cogger, 1960; M	Australia	Brown (1991)
<i>Egernia stokesii</i> (Gray, 1845); M	Australia	Symon (1979); Duffield & Bull (1998)
<i>Emoia concolor</i> (Duméril, 1851); I	Fiji Islands	Brown (1991)
<i>Eulamprus leuraensis</i> Wells & Wellington, 1983; M	Australia	Lebreton (1992) <i>in</i> Greer (2005)
<i>Eulamprus tympanum</i> (Lönnberg & Andersson, 1915); I-M	Australia	Webb & Simpson (1985) <i>in</i> Greer (2005); Robertson (1998); G. Petterson <i>pers. com.</i>
<i>Eumece algeriensis</i> Peters, 1864; M	North Africa	Schleich et al. (1996)
<i>Eumece schneideri</i> (Daudin, 1802); I-M	Russia	Darewskij (1981)
<i>Eutropis longicaudata</i> (Hallowell, 1857); I-M	Orchid Island (Taiwan)	Huang (2006)
<i>Eutropis multifasciata</i> (Kuhl, 1820); I-M	Krakatoa Islands (Indonesia); Luzon (Philippines)	Iwamoto (1986); Auffenberg & Auffenberg (1988)
<i>Lamprolepis smaragdina</i> (Lesson, 1826); I	Cook Islands; Luzon (Philippines); Palau Islands; Solomon Islands	Auffenberg & Auffenberg (1988); Crombie & Pregill (1999); Perry & Buden (1999); McCoy (2000)

<i>Leiolopisma telfairii</i> (Desjardin, 1831); I	Round Island (Mascarene Islands)	Vinson (1975); Bullock (1986); Pernetta et al. (2005); D.M. Hansen <i>pers. com.</i>
<i>Liburnascincus scirtetis</i> (Ingram & Covacevich, 1980); M	Australia	Goodman (2004)
<i>Liopholis guthega</i> (Donnellan et al., 2002); M	Australia	Atkins et al. (2018)
<i>Liopholis kintorei</i> (Stirling & Zietz, 1893); M	Australia	McAlpin (2001) <i>in Chapple</i> (2003)
<i>Liopholis slateri</i> (Storr, 1968); M	Australia	Pavey et al. (2010); C.R. Pavey <i>pers. com.</i>
<i>Liopholis whitii</i> (Lacépède, 1804); I-M	Australia	Brown (1991)
<i>Lipinia pulchella</i> (Gray, 1845); I	Luzon (Philippines)	Auffenberg & Auffenberg (1988)
<i>Lissolepis coventryi</i> (Storr, 1978); M	Australia	Douch (1994) <i>in Chapple</i> (2003); Clemann et al. (2004)
<i>Oligosoma aeneum</i> (Girard, 1858); I	North Island (New Zealand)	McCann (1955); Hare et al. (2016)
<i>Oligosoma alani</i> (Robb, 1970); I	Mercury Islands (New Zealand)	Southey (1985) <i>in Whitaker</i> (1987); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma fallai</i> (McCann, 1955); I	Three Kings Islands (New Zealand)	McCann (1955); Whitaker (1987); Parrish & Gill (2003); Hare et al. (2016); Wotton et al. (2016)

<i>Oligosoma grande</i> (Gray, 1845); I	South Island (New Zealand)	Whitaker (1987); Whitaker & Loh (1995); Tocher (2003); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma inconspicuum</i> (Patterson & Daugherty, 1990); I	South Island (New Zealand)	Patterson (1990, 1992); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma infrapunctatum</i> (Boulenger, 1887); I	New Zealand	Hare et al. (2016)
<i>Oligosoma kokowai</i> Melzer, Bell & Patterson, 2017; I	New Zealand	Spencer et al. (1998); Melzer et al. (2017)
<i>Oligosoma lineoocellatum</i> (Duméril, 1851); I	New Zealand	Spencer et al. (1998); Marshall (2005); Hare et al. (2016); Wotton et al. (2016); Melzer et al. (2017)
<i>Oligosoma maccanni</i> (Hardy, 1977); I	New Zealand	Patterson (1990, 1992); Hare et al. (2016); Wotton et al. (2016); A.H. Whitaker <i>pers. com.</i>
<i>Oligosoma moco</i> (Duméril & Bibron, 1839); I	North Island (New Zealand)	Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma nigriplantare</i> (Peters, 1874); I	Chatham Islands (New Zealand)	Barwick (1959) <i>in</i> Whitaker (1987); Patterson (1990, 1992); Freeman (1997); Udy (2004)

<i>Oligosoma oliveri</i> (McCann, 1955); I	Poor Knights Islands (New Zealand)	Southey (1985) <i>in</i> Whitaker (1987); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma otagense</i> (McCann, 1955); I	South Island (New Zealand)	Whitaker (1987); Whitaker & Loch (1995); Patterson (1997); Tocher (2003); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma polychroma</i> (Patterson & Daugherty, 1990); I	New Zealand	Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma</i> aff. <i>polychroma</i> ; I	South Island (New Zealand)	Patterson (1992); Freeman (1994); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma smithi</i> (Gray, 1845); I	North Island (New Zealand)	Whitaker (1968); Sladden & Falla (1928) and Southey (1985) <i>in</i> Whitaker (1987); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma striatum</i> (Buller, 1871); I	North Island (New Zealand)	Whitaker (1998); A.H. Whitaker <i>pers. com.</i>
<i>Oligosoma waimatense</i> (McCann, 1955); I	South Island (New Zealand)	Whitaker (1987); Whitaker & Loh (1990); Patterson (1997); Hare et al. (2016); Wotton et al. (2016)

<i>Oligosoma whitakeri</i> (Hardy, 1977); I	Mercury Islands (New Zealand)	Southey (1985) <i>in</i> Whitaker (1987); Hare et al. (2016); Wotton et al. (2016)
<i>Oligosoma zelandicum</i> (Gray, 1843); I	North Island (New Zealand)	Barwick (1959) <i>in</i> Whitaker (1987)
<i>Pinoyscincus jagori</i> (Peters, 1864); I	Luzon (Philippines)	Auffenberg & Auffenberg (1988)
<i>Plestiodon laticeps</i> (Schneider, 1801); M	Louisiana (USA)	Cooper, W.E. <i>in</i> Patton & Messinger (2002); Cooper & Vitt (2002)
<i>Plestiodon longirostris</i> Cope, 1861; I	Bermuda Island	Edgar et al. (2010), J. Davenport <i>pers. com.</i>
<i>Pseudemoia entrecasteauxii</i> Duméril & Bibron, 1839; I-M	Australia	Webb, G.A. <i>in</i> Greer (2005)
<i>Pseudemoia spenceri</i> (Lucas & Frost, 1894); M	Australia	Webb & Simpson (1985) <i>in</i> Greer (2005)
<i>Psychosaura macrorhyncha</i> (Hoge, 1946); M	Barra de Marica (Brazil)	Vrcibradic & Rocha (1996, 2005)
<i>Scincus mitranus</i> Anderson, 1871; M	Arabian Peninsula	Al-Johany, A.M. <i>in</i> Cooper et al. (2000)
<i>Spondylurus sloanii</i> (Daudin, 1803); I	Virgin Islands (Lesser Antilles)	Henderson & Powell (2009)
<i>Tiliqua gigas</i> (Schneider, 1801); I	Papua New Guinea	Allison (1982)
<i>Tiliqua multifasciata</i> Sternfeld, 1919; M	Australia	Shea (2006)

<i>Tiliqua nigrolutea</i> (Quoy & Gaimard, 1824); I-M	Australia; Tasmania	Webb & Simpson (1985) <i>in</i> Greer (2005); Hutchinson et al. (2001)
<i>Tiliqua occipitalis</i> (Peters, 1863); M	Australia	Roberts (1984) <i>in</i> Greer (2005); Hoser (1989); Shea (2006);
<i>Tiliqua rugosa</i> (Gray, 1825); I-M	Rottnest Island (Australia)	Symon (1979); Shea (1989); Dubas & Bull (1991); Cogger (1992)
<i>Tiliqua scincoides</i> (White, 1790); M	Australia	Rose (1974); Symon (1979); Cogger (1992)
<i>Trachylepis atlantica</i> (Schmidt, 1945); I	Fernando de Noronha Archipelago (Brazil)	Travassos (1946); A. Klier-Péres <i>pers. com.</i>
<i>Trachylepis quinquetaeniata</i> (Lichtenstein, 1823); M	East Africa	Broadley & Bauer (1999)
<i>Trachylepis sechellensis</i> (Duméril & Bibron, 1839); I	Seychelles	Cheke (1984); Le Maitre (1998) <i>in</i> Fieldsend & Burnham (2018)
<i>Trachylepis wrightii</i> (Boulenger, 1887); I	Seychelles	Cheke (1984)
<i>Tropidophorus grayi</i> Günther, 1861; I	Luzon (Philippines)	Auffenberg & Auffenberg (1988)
Xantusiidae		
<i>Cricosaura typica</i> Gundlach, 1863; I	Cuba	A. Fong-Grillo <i>pers. com.</i>
<i>Lepidophyma smithii</i> Bocourt, 1876; M	Mexico	Mautz & Lopez-Forment (1978)
<i>Xantusia riversiana</i> Cope, 1883; I	Santa Barbara Island (Baja California)	Knowlton (1949); Fellers & Drost (1991)

Teiidae

<i>Ameiva ameiva</i> (Linnaeus, 1758); I-M	Argentina; Brazil; Costa Rica; Providencia Island (Colombia); Trinidad (Venezuela)	Janzen (1973); Magnusson & Sanaiotti (1987); Vega et al. (1988); Magnusson & Da Silva (1993); Vitt & de Carvalho (1995); Murphy (1997); Zaluar & Rocha (2000)
<i>Ameiva bifrontata</i> Cope, 1862; I-M	Margarita Island (Venezuela)	Guerrero et al. (2012); V. Sanz <i>pers. com.</i>
<i>Ameiva provitae</i> García-Pérez, 1995; M	Venezuela	Casado & Soriano (2010)
<i>Ameivula ocellifera</i> (Spix, 1825); M	Bahia, Ceará (Brazil); Monte Quemado (Argentina)	Tedesco et al. (1995); Fonseca (2004); Dias & Rocha (2007); Fonseca et al. (2008, 2012); Menezes et al. (2011); Passos et al. (2013)
<i>Aspidoscelis deppii</i> (Wiegmann, 1834); M	Nicaragua	Vitt et al. (1993)
<i>Aspidoscelis marmoratus</i> (Baird & Girard, 1852); M	Chihuahuan Desert (Mexico)	Ballesteros-Barrera et al. (2009)
<i>Callopistes flavipunctatus</i> (Duméril & Bibron, 1839); M	Perú	Crespo & Koch (2015)
<i>Callopistes maculatus</i> Gravenhorst, 1838; M	Chile	Fuentes (1976)
<i>Cnemidophorus arenivagus</i> Markezich, Cole & Dessauer, 1997; M	Venezuela	Markezich et al. (1997)

<i>Cnemidophorus arubensis</i> Lidth de Jeude, 1887; I	Aruba Island (Dutch Antilles)	Schall (1973); Schall & Ressel (1991)
<i>Cnemidophorus lemniscatus</i> (Linnaeus, 1758); I-M	Brazil; Venezuela; Providencia Island (Colombia)	Janzen (1973); Magnusson & Sanaiotti (1987); Magnusson & da Silva (1993); Vitt & de Carvalho (1995); Vitt et al. (1997); Casado & Soriano (2010)
<i>Cnemidophorus murinus</i> (Laurenti, 1768); I	Bonaire Island (Dutch Antilles)	Dearing & Schall (1992); Schall (1996)
<i>Cnemidophorus senectus</i> Ugueto, Harvey & Rivas, 2010; I	Margarita Island (Venezuela)	Guerrero et al. (2012); V. Sanz <i>pers. com.</i>
<i>Cnemidophorus vanzoi</i> (Baskin & Williams, 1966); I	Maria Island (St. Lucia, Lesser Antilles)	Corke (1987); Schwartz & Henderson (1991); Dickinson et al. (2001)
<i>Dicrodon guttulatum</i> Duméril & Bibron, 1839; M	Peru	Pollack et al. (2007); van Leeuwen et al. (2011)
<i>Dicrodon heterolepis</i> (Tschudi, 1845); M	Peru	Luján (1981) <i>in</i> Pollack et al. (2007)
<i>Dicrodon holmbergi</i> Schmidt, 1957; M	Peru	Holmberg (1957); Huey (1969)
<i>Glaucomastix abaetensis</i> (Reis Dias, Rocha & Vrcibradic, 2002); M	Brazil	Dias & Rocha (2007); Gomes et al. (2012); Xavier & Dias (2015 b)

<i>Glaucomastix littoralis</i> (Rocha, et al., 2000); M	Barra de Maricá (Brazil)	Teixeira-Filho et al. (2003)
<i>Kentropyx striata</i> (Daudin, 1802); I-M	Brazil	Magnusson & da Silva (1993); Vitt & de Carvalho (1995)
<i>Pholidoscelis astratus</i> (Garman, 1887); I	Redonda Island (Lesser Antilles)	Meiri (2018)
<i>Pholidoscelis auberi</i> Cocteau, 1838; I	Cuba	A. Fong-Grillo <i>pers. com.</i>
<i>Pholidoscelis chrysolaemus</i> (Cope, 1868); I	Dominican Republic	Schell et al. (1993)
<i>Pholidoscelis corax</i> (Censky & Paulson, 1992); I	Anguilla (Lesser Antilles)	E.J. Censky <i>pers. com.</i>
<i>Pholidoscelis erythrocephalus</i> (Shaw, 1802); I	St. Eustatius (Lesser Antilles)	Powell et al. (2005)
<i>Pholidoscelis exsul</i> Cope, 1862; I	Caribbean Islands	Patterson (1928); Lewis & Saliva (1987); Schwartz & Henderson (1991)
<i>Pholidoscelis fuscatus</i> (Garman, 1887); I	Dominica (Lesser Antilles)	Bullock & Jury (1990); Powell et al. (2005); Daniells et al. (2008); Rudman et al. (2009)
<i>Pholidoscelis griswoldi</i> (Barbour, 1916); I	Antigua (Lesser Antilles)	Pregill (1984) <i>in</i> Meiri (2018)
<i>Pholidoscelis plei</i> (Duméril & Bibron, 1839); I	St. Martin (Lesser Antilles)	Breuil (2002); Powell et al. (2005)
<i>Pholidoscelis pluvianotatus</i> (Garman, 1887); I	Montserrat (Lesser Antilles)	Pregill (1984) <i>in</i> Meiri (2018)
<i>Salvator duseni</i> (Lönnberg, 1910); M	Brazil	G. Gottsberger <i>pers. com.</i>

<i>Salvator merianae</i> (Duméril & Bibron, 1839); M	Sao Paulo, Carajas, Paraná (Brazil)	Mercolli & Yanosky (1994); Avila-Pires (1995); Kiefer & Sazima (2002); Pérez (2003); de Castro & Galetti (2004); Machado (2007)
<i>Salvator rufescens</i> (Günther, 1871); M	Argentina	Donadío & Gallardo (1984); Bolkovic et al. (1989); Cei (1993); Williams et al. (1993)
<i>Teius oculatus</i> (D'Orbigny & Bibron, 1837); M	Argentina	Álvarez et al. (1992)
<i>Teius teyou</i> (Daudin, 1802); M	Argentina	Álvarez et al. (1992); Varela & Bucher (2002); Blanco et al. (2013)
<i>Tupinambis teguixin</i> (Linnaeus, 1758); I-M	Brazil; Argentina	Milstead (1961); Donadío & Gallardo (1984); Mercolli & Yanosky (1994); Dessem (1985); Cei (1986); Griz & Machado (2001)

DIPLOGLOSSA

Anguidae

<i>Pseudopus apodus</i> (Pallas, 1775); I-M	Jordan	Disi et al. (2014)
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Diploglossidae

Celestus costatus Cope, 1861

Hispaniola

Henderson & Powell (2009)

Celestus occiduus (†) (Shaw, 1802); I

Jamaica

Gosse (1851) *in* Schwartz &
Henderson (1991); Lynn & Grant
(1940)

PLATYNOTA

Varanidae

Varanus bitatawa Welton et al., 2010; I

Luzon (Philippines)

Welton et al. (2010)

Varanus mabitang Gaulke & Curio, 2001; I

Panay (Philippines)

Gaulke & Curio (2001); Struck et
al. (2002)

Varanus olivaceus Hallowell, 1857; I

Luzon, Polillo
(Philippines)

Auffenberg (1979); Auffenberg
& Auffenberg (1988); Bennett
(2005, 2014)

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