



Deposited via The University of Sheffield.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/168861/>

Version: Accepted Version

---

**Article:**

Uetz, P., Slavenko, A., Meiri, S. et al. (2020) Gecko diversity : a history of global discovery. Israel Journal of Ecology and Evolution, 66 (3-4). pp. 117-125. ISSN: 1565-9801

<https://doi.org/10.1163/22244662-bja10003>

---

© 2020 Brill. This is an author-produced version of a paper subsequently published in Israel Journal of Ecology and Evolution. Uploaded in accordance with the publisher's self-archiving policy.

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

# Israel Journal of Ecology & Evolution

## Gecko diversity: a history of global discovery

--Manuscript Draft--

<b>Manuscript Number:</b>					
<b>Full Title:</b>	Gecko diversity: a history of global discovery				
<b>Short Title:</b>	Gecko diversity: a history of global discovery				
<b>Corresponding Author:</b>	Peter Uetz Virginia Commonwealth University Richmond, UNITED STATES				
<b>First Author:</b>	Peter Uetz				
<b>Order of Authors:</b>	Peter Uetz Alex Slavenko Shai Meiri Matthew Heinicke				
<b>Abstract:</b>	1921 gecko species were known in Nov 2019 in seven families and 124 genera. These nearly 2000 species were described by ~950 individuals of which 100 described more than 10 gecko species each. Most gecko species were discovered during the past 40 years. The type specimens of all geckos are distributed over 161 collections worldwide, with 20 collections having about two thirds of all types. The type specimens of about 250 gecko taxa have been lost. The phylogeny of geckos is well understood with DNA sequences being available for ~76% of all geckos (compared to ~63% in other reptiles) and morphological characters now being collected in databases. Geographically, geckos occur on five continents and many islands but are most species-rich in Australasia (which also houses the greatest diversity of family-level taxa), Southeast Asia, Africa, Madagascar, and the West Indies. Australia has the highest number of geckos (241 species), with India, Madagascar, and Malaysia being the only other countries with more than 100 described species each.				
<b>Keywords:</b>	Carphodactylidae, Diplodactylidae, Eublepharidae, Gekkonidae, Gekkota, Phyllodactylidae, Pygopodidae, Sphaerodactylidae				
<b>Funding Information:</b>	<table border="1" style="width: 100%;"> <tr> <td>National Science Foundation (US) (DEB-1556585)</td> <td>Dr. Matthew Heinicke</td> </tr> <tr> <td>National Science Foundation (US) (DEB 1657527)</td> <td>Dr. Matthew Heinicke</td> </tr> </table>	National Science Foundation (US) (DEB-1556585)	Dr. Matthew Heinicke	National Science Foundation (US) (DEB 1657527)	Dr. Matthew Heinicke
National Science Foundation (US) (DEB-1556585)	Dr. Matthew Heinicke				
National Science Foundation (US) (DEB 1657527)	Dr. Matthew Heinicke				

# Gecko diversity: a history of global discovery

Peter Uetz<sup>1\*</sup>, Alex Slavenko<sup>2</sup>, Shai Meiri<sup>2,3</sup>, Matthew Heinicke<sup>3</sup>

<sup>1</sup>Center for Biological Data Science, Virginia Commonwealth University, Richmond, VA 23284,  
USA

<sup>2</sup>School of Zoology, Tel Aviv University, Tel- Aviv, Israel, E-mail: [gluttony14@gmail.com](mailto:gluttony14@gmail.com),

<sup>3</sup>[the Steinhardt Museum of Natural History](#), Tel Aviv University, Tel- Aviv, Israel, E-mail:  
[uncshai@tauex.tau.ac.il](mailto:uncshai@tauex.tau.ac.il)

<sup>3</sup>Department of Natural Sciences, University of Michigan-Dearborn, 4901 Evergreen Rd.,  
Dearborn, MI 48128, USA, E-mail: [heinicke@umich.edu](mailto:heinicke@umich.edu)

\*Corresponding authors. E-mail: [uetz@vcu.edu](mailto:uetz@vcu.edu), [heinicke@umich.edu](mailto:heinicke@umich.edu)

**Keywords:** Carphodactylidae, Diplodactylidae, Eublepharidae, Gekkonidae, Gekkota,  
Phyllodactylidae, Pygopodidae, Sphaerodactylidae

## Abstract

1921 gecko species were known in Nov 2019 in seven families and 124 genera. These nearly 2000 species were described by ~950 individuals of which 100 described more than 10 gecko species each. Most gecko species were discovered during the past 40 years. The type specimens of all geckos are distributed over 161 collections worldwide, with 20 collections having about two thirds of all types. The type specimens of about 250 gecko taxa have been lost. The phylogeny of geckos is well understood with DNA sequences being available for ~76% of all geckos (compared to ~63% in other reptiles) and morphological characters now being collected in databases. Geographically, geckos occur on five continents and many islands but are most species-rich in Australasia (which also houses the greatest diversity of family-level taxa), Southeast Asia, Africa, Madagascar, and the West Indies. Australia has the highest number of geckos (241 species), with India, Madagascar, and Malaysia being the only other countries with more than 100 described species each.

*Note: species numbers may be inconsistent across this draft. The final species numbers will be updated in the final revision to match the numbers in the December release of the Reptile Database.*

## Introduction

Geckos (Sauria: Gekkota; 1921 species) are one of three mega-diverse groups of squamate reptiles (lizards, snakes, and amphisbaenians), along with the 1678 species of skinks and 1956

1  
2  
3  
4 species of colubrid snakes (Uetz et al. 2019), that have arisen since the major squamate radiations  
5 began diversifying about 200 million years ago. It is noteworthy that all gecko families are  
6 relatively old compared to either skinks or colubrids (Zheng  
7 & Wiens 2016). Molecular clock estimates place the origins of gecko families deep in the  
8 Mesozoic (Gamble et al. 2008a, 2008b; Gamble et al. 2011; Hedges et al. 2015; Zheng & Wiens  
9 2016), and stem gekkotan fossils dating from the late Jurassic and Cretaceous have been  
10 recovered from multiple distant localities in Eurasia (Daza et al. 2014; Daza et al. 2016; Gauthier  
11 et al. 2012; Simões et al. 2017). Not all gecko lineages have diversified at the same rate. For  
12 example, there are 38 species of Eublepharidae, compared to 1632 species in their sister lineage  
13 (Gekkonidae + Phyllodactylidae + Sphaerodactylidae). Thus, the high species richness of geckos  
14 has been produced largely by diversification of a subset of successful lineages.  
15  
16  
17  
18  
19

20 Here we focus on the history of discovery and description of gecko species. In addition, we review  
21 the diversity of geckos in terms of species numbers, both taxonomically and geographically, but  
22 also in terms of discovery. As mostly small and nocturnal species (Meiri, this volume), many  
23 geckos are easy to overlook, though this is obviously not true for human commensals such as  
24 some *Hemidactylus* or conspicuous day geckos such as *Lygodactylus* or *Phelsuma*. Nevertheless,  
25 many geckos were described early in the history of herpetology. We finally discuss the factors for  
26 species discovery and diversity and how it relates to gecko biology.  
27  
28  
29

### 30 **A history of gecko discovery**

31 Only three geckos were described by Linnaeus (Linnaeus 1758)—the Tokay gecko (*Lacerta*  
32 *Gecko* to Linnaeus, now *Gekko gecko*), Mediterranean House Gecko (as *Lacerta turcica*, now  
33 *Hemidactylus turcicus*), and Moorish gecko (*Lacerta mauritanica*, now *Tarentola mauritanica*). It  
34 then took herpetologists 227 years, from 1758 to 1984, to describe the first 1000 gecko species.  
35 It has taken only 35 to describe the next 921 (not counting subspecies). Early descriptions of  
36 gecko species commonly appeared in regional monographs or travelogues (e.g. Shaw 1790; Spix  
37 1825; Smith 1849) or else more general zoological works (e.g. Daudin 1802, Gray 1831), but also  
38 were appeared as standalone contributions to journals or society proceedings (e.g. Sparrman  
39 1778). Early descriptions peaked in the mid-19<sup>th</sup> century with 19 species described in 1836, 1845,  
40 1870, and 1885 (**Fig. 1**). These numbers were driven by the monumental works of André M.C.  
41 Duméril & Gabriel Bibron (Duméril & Bibron 1836), John E. Gray (Gray 1845), Richard H. Beddome  
42 (Beddome 1870a, 1870b) and George A. Boulenger (Boulenger 1885). They were only exceeded  
43 a century later with 24 species described in 1978. Even though these authors have described  
44 most geckos in single publications, only Gray and Boulenger are among the 10 most prolific gecko  
45 describers (**Table 1**). In the late 20<sup>th</sup> century molecular methods such as karyotyping (e.g. Murphy  
46 1974, King 1982) and allozyme electrophoresis (e.g. Branch et al. 1995) began to be employed to  
47 aid in new species discovery. Discoveries skyrocketed in the 21<sup>st</sup> century (Meiri 2016) with the  
48 advent of new technologies, such as the internet, DNA sequencing, digital photography, and  
49 cheaper travel permitting access to remote areas, as well as the ability for individual researchers  
50 to study collections at distant museums. Nevertheless, even in modern times, gecko discovery  
51 has been driven by relatively few individuals. Thus, the 1921 gekkotans described since 1758  
52 were authored by about 950 individuals (Uetz & Stylianou 2018), of which about 100 described  
53 more than 10 gecko species each. Eight of the ten most prolific describers of new species are  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4 currently active herpetologists, with two (Aaron M. Bauer and L. Lee Grismer) describing more  
5 than 130 species, each (**Table 1**). Unfortunately, it is almost impossible to determine how many  
6 authors were needed to describe some species due to the inclusion of species descriptions in  
7 phylogenetic or other publications that have multiple authorship and may use different citation  
8 or author formats.  
9

10  
11  
12 From the 18<sup>th</sup> through 20<sup>th</sup> centuries, most gecko species were described by one or two authors.  
13 The earliest gecko species description with more than two authors appeared in 1970 (Minton Jr.  
14 et al. 1970). Team taxonomy has become the norm in the 21<sup>st</sup> century, as different scientists are  
15 often needed to carry out distinct tasks in the process of species discovery such as fieldwork,  
16 morphological work, molecular work, specimen comparisons, statistical analysis, and literature  
17 review. In some cases this may result in species descriptions with many authors. For instance,  
18 several gecko species have been described with more than a dozen authors, such as *Cyrtodactylus*  
19 *phuocbinhensis* (Nguyen et al. 2013), *Cyrtodactylus taynguyenensis* Nguyen et al. 2013,  
20 *Cyrtodactylus puhuensis* (Nguyen et al. 2014), and *Cnemaspis bidongensis* (Grismer et al. 2014),  
21 each with 14 authors. None of these approach the reptile species with the highest number of  
22 authors though, which is the leiosaurid *Enyalius capetinga* Breitman et al. 2018, with 27 authors.  
23 Many of the most prolific gecko describers (**Table 1**) have worked together, thus, for example,  
24 almost all the descriptions by Perry Wood and Evan Quah were co-authored by Lee Grismer.  
25  
26  
27  
28  
29

### 30 **Type specimens of geckos**

31 The primary types of the ~2000 species of geckos are kept in 161 collections worldwide, with 20  
32 collections having about two thirds of all types (see Uetz et al. 2019), **Table 2, Fig. 2**). This is  
33 important for researchers who describe new species and need to compare them to the types of  
34 previously described ones. By far the most gecko type specimens are held at the Natural History  
35 Museum, London (BMNH; 279 taxa). Among its collections are most of the types described by  
36 Gray, Boulenger, and Beddome in their major 19<sup>th</sup> century works, along with many types used by  
37 Nicolas Arnold, Albert Günther, Hampton Wildman Parker, Malcolm Smith, and others, and its  
38 type specimens originate from across the globe. The Muséum National d'Histoire Naturelle, Paris  
39 (MNHN) has a similar global scope and many types dating from the 19<sup>th</sup> century work of Duméril  
40 and Bibron with more recent types, e.g. used by Aaron Bauer and Georges Pasteur, among others.  
41 Major collections often have geographic foci that reflect the work of scientists affiliated with  
42 these institutions. The Museum of Comparative Zoology (MCZ), for example, includes many types  
43 of African species from the work of former curator Arthur Loveridge, and a large collection of  
44 West Indian *Spharodactylus* types used by former director Thomas Barbour (plus Albert Schwartz  
45 and Richard Thomas). Interestingly, most of these museums reside in places where no native  
46 gecko species are found (Roll et al. 2017, Meiri, 2020, this volume). Only two of the top ten  
47 collections are held in locations with native geckos: the Western Australian Museum (WAM) and  
48 Ditsong National Museum, Pretoria (DNMNH). All of the types held at these two institutions  
49 originate from their respective continents. Fifty one institutions have only a single (primary)  
50 gecko type specimen and 21 have two.  
51  
52  
53  
54  
55  
56  
57

58 The VertNet database (Constable et al. 2010) is the largest meta-database of vertebrate  
59 collections, and returns 11,888 entries when searched for gekkotans with type status (in Nov  
60  
61  
62  
63  
64  
65

1  
2  
3  
4 2019). However, only 568 of these are primary types (holo-, syn-, lecto-, or neotypes)  
5 corresponding to 430 species in the Reptile Database (possibly up to ~500 when all mismatched  
6 names such as typos and spelling variants are included). That is, ~25% of all Gekkotans have  
7 primary types in Vertnet but the vast majority of all Vertnet “types” represents secondary types,  
8 including 6,542 paratypes, which may be missing from the primary type catalog that Uetz et al.  
9 2019 compiled. VertNet is one of the major North American efforts to consolidate digitized  
10 vertebrate collections, and much more advanced than similar projects in other parts of the world,  
11 so we can conclude that only a fraction of all collections with gecko specimens have been  
12 digitized and submitted to meta-databases, though many collections have in-house databases.  
13  
14  
15

16  
17 A substantial number of gecko type specimens are unknown. Uetz et al. 2019 found the types of  
18 258 valid gekkotan taxa (12%, out of 2117, including subspecies) to be either lost or simply  
19 “unlocated” (i.e. their whereabouts were never made clear, even in the original description; i.e.  
20 for *Tropiocolotes nattereri* Steindachner 1901) -- which means that they are likely lost too. Thus,  
21 geckos are more often lost than reptile types in general, of which “only” 658 (4.9%, out of 13,361  
22 taxa) are lost or unlocated. This may be due to the often small size of geckos, which are not only  
23 hampering their discovery, but also to their maintenance and identification in collections.  
24  
25  
26

### 27 **The diversity of geckos**

28 The nearly 2000 species of geckos represent a tremendous variety of adaptations and life styles,  
29 too many to be thoroughly reviewed here (see Meiri 2020, this issue, for more details). However,  
30 the diversity is reflected by their classification into 7 families and 124 genera (**Tables 3, 4, Figs. 3,**  
31 **4**). These were traditionally recognized by morphological characters such as feet (absent in  
32 pygopods), their eyes and eyelids (true eyelids are present only in eublepharids), and their  
33 toepads (carphodactylids and eublepharids both lack adhesive toepads, as do many members of  
34 the toepad-bearing families; Bauer 2013). Of the seven families, Gekkonidae was the first to be  
35 described (Gray 1825), followed by Pygopodidae (as Pygopidae; Gray 1841). Boulenger  
36 (Boulenger 1883) recognized Eublepharidae based on differences in vertebral structure as  
37 compared to all other geckos, and was the first to note morphological similarities between  
38 pygopodids and geckos (Boulenger 1884). Subsequent anatomical studies in the 20<sup>th</sup> century  
39 confirmed the status of pygopodids as gekkotans (e.g. (Underwood 1957)(Kluge 1974)). The  
40 Carphodactylidae (as Carphodactylini), Diplodactylidae (as Diplodactylinae) and  
41 Sphaerodactylidae were described on the basis of anatomical traits (Underwood 1954)(Kluge  
42 1967), though for the remainder of the 20<sup>th</sup> century these groups were often treated as tribes or  
43 subfamilies of Gekkonidae and their content changed as new evidence emerged (reviewed in  
44 (Russell & Bauer 2002)). The contemporary seven family classification stems from molecular  
45 phylogenetic studies that further clarified the content of the major gekkotan clades and identified  
46 the family Phyllodactylidae (Gamble et al. 2008a, 2008b; Han et al. 2004). Within each family  
47 there may be a substantial variation in morphological characters, e.g. most phyllodactylid genera  
48 can be distinguished by variation in the presence and shape of toe pads (**Fig. 5**). The morphology  
49 of the digits (including toepads) and shape of the pupil have historically been the most important  
50 characters used in distinguishing gecko genera. More recent molecular work has shown that  
51 some of these character states have evolved multiple times and generic classification has been  
52 modified accordingly. For example, most leaf-toed geckos were originally placed in the genus  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4 *Phyllodactylus* until it was determined that they actually represented over a dozen distinct  
5 lineages, across four families (Kluge 1983; Bauer et al. 1997; Heinicke et al. 2014). Conversely,  
6 molecular data have also been used to subsume some genera that were previously recognized  
7 on the basis of digital morphology, such as the placement of *Colopus* and *Palmatogecko* in the  
8 synonymy of *Pachydactylus* (Bauer & Lamb 2005)(Heinicke et al. 2017). Although the generic and  
9 familial classification of geckos is now largely stable, there are still a handful of genera, such as  
10 *Cnemaspis* and *Saurodactylus* that molecular data show to be polyphyletic (Gamble et al. 2012,  
11 but also see Javanmardi et al. 2019), implying that some taxonomic revision at the genus level is  
12 still required.  
13  
14  
15

### 16 17 **Gecko traits**

18 There are no comprehensive databases collecting morphological and life history characters  
19 across all geckos or even gecko genera, but some efforts have been made to collect body sizes  
20 (Meiri 2008, Feldman et al. 2015) and other trait data (Meiri 2018) of use for studying gecko  
21 evolution in a phylogenetic context. Some studies have identified morphological synapomorphies  
22 of clades using data sets containing hundreds of characters across multiple species belonging to  
23 multiple gecko lineages (e.g., Daza & Bauer 2012). Evolutionary patterns of many specific traits  
24 of geckos have also been studied. Examples include diurnal activity patterns (Gamble et al. 2015),  
25 gliding adaptations (Heinicke et al. 2012), sex determining mechanisms (Gamble et al. 2015),  
26 habitat-associated diversification and ecomorphology (e.g. (Grismer et al. 2015; Heinicke et al.  
27 2017; Oliver et al. 2019; Vidan et al. 2019), and perhaps most notably, digital morphology (**Fig.  
28 5**) (Bauer 2019; Gamble et al. 2012; Russell & Gamble 2019). These studies often incorporate  
29 data sets comprising a significant fraction of gecko diversity. For example, Gamble et al. (2012)  
30 collected morphological characters of hand and feet of 244 species of geckos representing 107  
31 genera and mapped them to a phylogenetic tree. These authors found that the absence of  
32 adhesive toe pads to be the ancestral state for the extant Gekkota as a whole, and their data are  
33 consistent with independent origins and losses of adhesive toe pads in the Diplodactylidae,  
34 Sphaerodactylidae, Phyllodactylidae, and Gekkonidae, with a strong likelihood of multiple origins  
35 in the latter three families.  
36  
37  
38  
39  
40  
41  
42

### 43 **Geckos and their DNA**

44 With DNA sequences being available for ~76% of all geckos (e.g., Meiri 2018), but only 63% of  
45 non-gekkotan reptiles, they are relatively well-studied phylogenetically. For most of these species  
46 existing sequence data consist only of a few gene fragments (most often, ND2, RAG1 and PDC),  
47 but broader sequence data sets are now becoming more common (e.g. Skipwith et al. 2019;  
48 Wood et al. 2019). More extensive or even complete genome sequences are necessary to address  
49 some biological questions. At present, genomes of only a few geckos have been completely  
50 sequenced though, including *Gekko japonicus* (Liu et al. 2015), *Paroedura picta* (Hara et al. 2018),  
51 and *Eublepharis macularius* (Xiong et al. 2016). Insights into the biology of geckos have begun to  
52 emerge from these genome sequences and other high-throughput sequencing projects. For  
53 instance, Liu et al. 2015 found specific gene families to be related to the formation of adhesive  
54 setae, nocturnal vision and tail regeneration, as well as the diversification of olfactory sensation.  
55 In particular, Liu et al. found that the emergence of setae in geckos is correlated with the  
56 duplication and diversion of  $\beta$ -keratin genes.  
57  
58  
59  
60  
61  
62  
63  
64  
65

## Geckos of the world – a geographic survey

Geckos are not evenly distributed in the world (Fig. 6, Rösler 2017, Meiri 2019, this issue). Most species are found in the tropics, but geckos also occur in many subtropical and warm temperate regions, especially in arid environments, where they penetrate as far north as the Gobi Desert (*Alsophylax*, *Teratoscincus*) and as far south as Patagonia (*Homonota*). There is extensive regional variation in species richness even when comparing regions of similar latitude and climate. Geckos are most species rich in the West Indies, southern and eastern Africa, Madagascar, the Middle East, South and Southeast Asia, and Australasia. At least these are the regions where most species have been discovered. The most gecko-rich countries, with more than 100 species each, are Australia (241 species), India (127), Madagascar (120), and Malaysia (104) (Table 5), although some smaller countries have very high species richness, e.g. New Caledonia with 44 species in a land area of only 18,576 km<sup>2</sup>. When correcting for land area, countries outside the tropics have fewer geckos (Fig. 7). Even though tropical countries have more geckos, there is only a weak correlation of latitudes and species numbers, probably because of variation with area, and because tropical Latin American countries, and desert, North African countries, have relatively few geckos (Meiri this volume, and Fig. 6), but also probably due to an under-count of actual species diversity in the tropics (possibly with the exception of South America which has relatively few geckos). For example, of the ~270 gecko species described in the last 5 years, the vast majority occur in the tropics (and in Australia at tropical, sub-tropical and desert climates), suggesting that as new gecko species are described the proportion of recognized species occurring in the tropics will continue to increase. New descriptions will probably also increase the number of range-restricted species. Currently over 19% of gecko species are known only from their type localities (Meiri et al. 2018). This proportion includes many recently described species which often are discovered in limited habitats such as small islands or areas of exposed karst. The limited ranges of many gecko species also means that local communities are often not nearly as species-rich as country totals indicate. For example, 32 species of *Cyrtodactylus* are known from peninsular Malaysia, Singapore, and adjacent archipelagos, but only one to a few species occurs at any single locality (Grismer & Quah 2019).

The great age and relatively limited fossil record of geckos obscures some of the biogeographic history of the group. The oldest fossils that are unambiguous geckos are all from Eurasia (Daza et al. 2016). Nonetheless, biogeographic reconstructions indicate that geckos were probably also present on most Southern Hemisphere continents including Australia, Africa, and South America at the time of the breakup of Gondwana during the Mesozoic (Gamble et al. 2008a), (Oliver & Sanders 2009). Subsequently, gecko lineages have colonized or re-colonized additional landmasses including oceanic islands via dispersals, often across wide barriers (e.g. Gamble et al. 2008b, Nielsen et al. 2011, Heinicke et al. 2011, Heinicke et al. 2014, Skipwith et al. 2016, Oliver et al. 2018). As a result, the families Eublepharidae, Gekkonidae, Phyllodactylidae, and Sphaerodactylidae, all occur on multiple continents while the otherwise Australian family Diplodactylidae has also colonized New Caledonia and New Zealand. In contrast, the Carphodactylidae is entirely restricted to Australia – and only two pygopodids (both species of *Lialis*) occur elsewhere – in nearby New Guinea. As a result of this history of dispersals, as many as four families of geckos may occur in sympatry.

1  
2  
3  
4  
5  
6 In summary, discovery of geckos continues unabatedly, despite increasing threat from habitat  
7 destruction and possibly climate change. There is little indication that the rate of species  
8 description will decline soon. Based on past trends, new discoveries are especially likely to  
9 come from regions of warm climate, heterogeneous landscape, and limited previous attention  
10 from systematic herpetologists. Ironically, with the advent of next-generation sequencing, we  
11 will soon have the tools to understand the molecular basis of gecko diversity, both in terms of  
12 populations and traits, but possibly only once many species have gone extinct.  
13  
14

## 15 **Materials and methods**

16 Species and author data were derived from the November 2019 version of the Reptile Database.  
17 Distribution data and species per country were derived from an updated version of (Roll et al.  
18 2017), using ArcGIS. Latitudinal centroids and countries are from the country08 shapefile of  
19 ArcGIS (except South Sudan which was still missing from ArcGIS at the time of writing). Numbers  
20 of species were cross-checked with the Reptile Database and corrected if necessary by manual  
21 inspection.  
22  
23  
24

## 25 **Acknowledgments**

26 MH is supported by the US National Science Foundation (DEB-1556585 and DEB 1657527)  
27  
28  
29

## 30 **References cited**

- 31  
32  
33 Bauer, A. M. (2019) Gecko adhesion in space and time: a phylogenetic perspective on the  
34 scansorial success story. *Integrative and comparative biology*.  
35 Bauer, A. M., Good, D. A. & Branch, W. R. (1997) The taxonomy of the southern African leaf-  
36 toed geckos (Squamata: Gekkonidae), with a review of Old World 'Phyllodactylus'. .  
37 *Proceedings of the California Academy of Sciences*, 49, 447–497.  
38 Bauer, A. M. & Lamb, T. (2005) Phylogenetic relationships of southern African geckos in the  
39 Pachydactylus group (Squamata: Gekkonidae). *African Journal of Herpetology*, 54, 105-  
40 129.  
41  
42  
43 Beddome, R. H. (1870a) Descriptions of new reptiles from the Madras Presidency. *Madras*  
44 *Monthly J. Med. Sci.*, 2, 169-176.  
45 Beddome, R. H. (1870b) Descriptions of some new lizards from the Madras Presidency. *Madras*  
46 *Monthly J. Med. Sci.*, 1.  
47  
48 Boulenger, G. A. (1883) Remarks on the Nyctisaura. *Journal of Natural History*, 12, 308.  
49 Boulenger, G. A. (1884) Synopsis of the families of existing Lacertilia. *Journal of Natural History*,  
50 14, 117-122.  
51  
52 Boulenger, G. A. (1885) *Catalogue of the lizards in the British Museum (Nat. Hist.) I. Geckonidae,*  
53 *Eublepharidae, Uroplatidae, Pygopodidae, Agamidae.* London.  
54 Branch, W. R., Bauer, A. M. & Good, D. A. (1995) Species limits in the Phyllodactylus lineatus  
55 complex (Reptilia: Gekkonidae), with the elevation of two taxa to specific status and the  
56 description of two new species. *Journal of the Herpetological Association of Africa*, 44,  
57 33-54.  
58  
59  
60  
61  
62  
63  
64  
65

- 1  
2  
3  
4 Constable, H., Guralnick, R., Wieczorek, J., Spencer, C., Peterson, A. T. & VertNet Steering, C.  
5 (2010) VertNet: a new model for biodiversity data sharing. *PLoS Biol*, 8, e1000309.  
6  
7 Daza, J. D. & Bauer, A. M. (2012) A new amber-embedded sphaerodactyl gecko from Hispaniola,  
8 with comments on morphological synapomorphies of the Sphaerodactylidae. *Breviora*,  
9 529, 1-28.  
10  
11 Daza, J. D., Bauer, A. M. & Snively, E. D. (2014) On the fossil record of the Gekkota. *The*  
12 *Anatomical Record*, 297, 433-462.  
13  
14 Daza, J. D., Stanley, E. L., Wagner, P., Bauer, A. M. & Grimaldi, D. A. (2016) Mid-Cretaceous  
15 amber fossils illuminate the past diversity of tropical lizards. *Science Advances*, 2,  
16 e1501080.  
17  
18 Duméril, A. M. C. & Bibron, G. (1836) *Erpetologie Générale ou Histoire Naturelle Complete des*  
19 *Reptiles*. Vol. 3. PARIS: Libr. Encyclopédique Roret.  
20  
21 Feldman, A., Pyron, R. A., Sabath, N., Mayrose, I. & Meiri, S. (2015) Body-sizes and  
22 diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology*  
23 *and Biogeography*, 25, 187–197.  
24  
25 Gamble, T., Bauer, A. M., Greenbaum, E. & Jackman, T. R. (2008a) Evidence for Gondwanan  
26 vicariance in an ancient clade of gecko lizards. *Journal of Biogeography*, 35, 88-104.  
27  
28 Gamble, T., Bauer, A. M., Greenbaum, E. & Jackman, T. R. (2008b) Out of the blue: a novel,  
29 trans?Atlantic clade of geckos (Gekkota, Squamata). *Zoologica Scripta*, 37, 355-366.  
30  
31 Gamble, T., Colli, G., Rodrigues, M. T., Werneck, F. P. & Simons, A. M. (2011) Phylogeny and  
32 cryptic diversity in geckos (Phyllopezus; Phyllodactylidae; Gekkota) from South  
33 America's open biomes. *Molecular Phylogenetics and Evolution*, 62, 943-953.  
34  
35 Gamble, T., Coryell, J., Ezaz, T., Lynch, J., Scantlebury, D. P. & Zarkower, D. (2015) Restriction  
36 site-associated DNA sequencing (RAD-seq) reveals an extraordinary number of  
37 transitions among gecko sex-determining systems. *Molecular Biology and Evolution*, 32,  
38 1296-1309.  
39  
40 Gamble, T., Greenbaum, E., Jackman, T. R. & Bauer, A. M. (2015) Into the light: diurnality has  
41 evolved multiple times in geckos. *Biological Journal of the Linnean Society*, 115, 896-910.  
42  
43 Gamble, T., Greenbaum, E., Jackman, T. R., Russell, A. P. & Bauer, A. M. (2012) Repeated origin  
44 and loss of adhesive toepads in geckos. *PLoS One*, 7, e39429.  
45  
46 Gauthier, J. A., Kearney, M., Maisano, J. A., Rieppel, O. & Behlke, A. D. (2012) Assembling the  
47 squamate tree of life: perspectives from the phenotype and the fossil record. *Bulletin of*  
48 *the Peabody Museum of Natural History*, 53, 3-309.  
49  
50 Gray, J. E. (1825) A synopsis of the genera of reptiles and Amphibia, with a description of some  
51 new species. *Annals of Philosophy*, 10, 193-217.  
52  
53 Gray, J. E. (1841) A catalogue of the species of reptiles and Amphibia hitherto described as  
54 inhabiting Australia, with a description of some new species from Western Australia. In:  
55 G. Grey (Ed), *Journals of Two Expeditions of Discovery in Northwestern and Western*  
56 *Australia, during the years 1837, 38, and 39, under the authority of Her Majesty's*  
57 *Government*. T. and W. Boone, London, pp. 422-449.  
58  
59 Gray, J. E. (1845) *Catalogue of the specimens of lizards in the collection of the British Museum*.  
60 London: Trustees of die British Museum/Edward Newman.  
61  
62  
63  
64  
65

- 1  
2  
3  
4 Grismer, L. L. & Quah, E. S. (2019) An updated and annotated checklist of the lizards of  
5 Peninsular Malaysia, Singapore, and their adjacent archipelagos. *Zootaxa*, 4545, 230-  
6 248.  
7  
8 Grismer, L. L., Wood, P. L., Jr., Ahmad, A. B., Sumarli, A. S., Vazquez, J. J., Ismail, L. H., et al.  
9 (2014) A new species of insular Rock Gecko (Genus *Cnemaspis* Strauch, 1887) from the  
10 Bidong Archipelago, Terengganu, Peninsular Malaysia. *Zootaxa*, 3755, 447-456.  
11 Grismer, L. L., Wood, P. L., Ngo, V. T. & Murdoch, M. L. (2015) The systematics and independent  
12 evolution of cave ecomorphology in distantly related clades of Bent-toed Geckos (Genus  
13 *Cyrtodactylus* Gray, 1827) from the Mekong Delta and islands in the Gulf of Thailand.  
14 *Zootaxa*, 3980, 106-126.  
15  
16 Han, D., Zhou, K. & Bauer, A. M. (2004) Phylogenetic relationships among gekkotan lizards  
17 inferred from C-mos nuclear DNA sequences and a new classification of the Gekkota. .  
18 *Biological Journal of the Linnean Society*, 83, 353-368.  
19  
20 Hara, Y., Takeuchi, M., Kageyama, Y., Tatsumi, K., Hibi, M., Kiyonari, H., et al. (2018) Madagascar  
21 ground gecko genome analysis characterizes asymmetric fates of duplicated genes. *BMC*  
22 *Biol*, 16, 40.  
23  
24 Hedges, S. B., Marin, J., Suleski, M., Paymer, M. & Kumar, S. (2015) Tree of life reveals clock-like  
25 speciation and diversification. . *Molecular Biology and Evolution*, 32, 835-845.  
26  
27 Heinicke, M. P., Daza, J. D., Greenbaum, E., Jackman, T. R. & Bauer, A. M. (2014) Phylogeny,  
28 taxonomy and biogeography of a circum-Indian Ocean clade of leaf-toed geckos  
29 (Reptilia: Gekkota), with a description of two new genera. *Systematics and Biodiversity*,  
30 12, 23-42.  
31  
32 Heinicke, M. P., Greenbaum, E., Jackman, T. R. & Bauer, A. M. (2011) Phylogeny of a  
33 trans?Wallacean radiation (Squamata, Gekkonidae, Gehyra) supports a single early  
34 colonization of Australia. . *Zoologica Scripta*, 40(6), 584-602.  
35  
36 Heinicke, M. P., Greenbaum, E., Jackman, T. R., Bauer, A. M., Heinicke, M. P., Daza, J. D., et al.  
37 (2012) Evolution of gliding in Southeast Asian geckos and other vertebrates is  
38 temporally congruent with dipterocarp forest development  
39  
40 Phylogeny, taxonomy and biogeography of a circum-Indian Ocean clade of leaf-toed geckos  
41 (Reptilia: Gekkota), with a description of two new genera. *Biology Letters*, 8, 994-997.  
42  
43 Heinicke, M. P., Jackman, T. R. & Bauer, A. M. (2017) The measure of success: geographic  
44 isolation promotes diversification in *Pachydactylus* geckos. *BMC evolutionary biology*,  
45 17, 9.  
46  
47 Javanmardi, S., Vogler, S. & Joger, U. (2019) Phylogenetic differentiation and taxonomic  
48 consequences in the *Saurodactylus brosetti* species complex (Squamata:  
49 *Sphaerodactylidae*), with description of four new species. *Zootaxa*, 4674, 401-425.  
50  
51 King, M. (1982) Karyotypic Evolution in *Gehyra* (Gekkonidae: Reptilia) II.\* A New Species from  
52 the Alligator Rivers Region in Northern Australia. *Australian Journal of Zoology*, 30, 93-  
53 101.  
54  
55 Kluge, A. G. (1967) Higher taxonomic categories of gekkonid lizards and their evolution. *Bulletin*  
56 *of the American Museum of Natural History*, 135, 1-60., 147, 1-221.  
57  
58 Kluge, A. G. (1974) A taxonomic revision of the lizard family Pygopodidae. *Miscellaneous*  
59 *Publications, Museum of Zoology, University of Michigan*, 1-221.  
60  
61 Kluge, A. G. (1983) Cladistic relationships among gekkonid lizards. *Copeia*, 1983, 465-475.  
62  
63  
64  
65

- 1  
2  
3  
4 Linnaeus, C. (1758) *Systema naturae, Vol. 1, No. part 1*. Stockholm: Laurentii Salvii.
- 5 Liu, Y., Zhou, Q., Wang, Y., Luo, L., Yang, J., Yang, L., et al. (2015) Gekko japonicus genome  
6 reveals evolution of adhesive toe pads and tail regeneration. *Nat Commun*, 6, 10033.
- 7 Meiri, S. (2008) Evolution and ecology of lizard body sizes. *Global Ecology and Biogeography*.
- 8 Meiri, S. (2016) Small, rare and trendy: traits and biogeography of lizards described in the 21st  
9 century. *Journal of Zoology*.
- 10  
11 Meiri, S. (2018) Traits of lizards of the world: Variation around a successful evolutionary design.  
12 *Global Ecol Biogeogr*, 27, 1168– 1172.
- 13  
14 Minton Jr., S. A., Anderson, S. C. & Anderson, J. A. (1970) Remarks on some geckos from  
15 southwest Asia, with descriptions of three new forms and a key to the genus  
16 *Tropicolotes*. *Proc. Cal. Acad. Sci.*, 37, 333–362.
- 17  
18 Murphy, R. W. (1974) A New Genus and Species of Eublepharine Gecko (Sauria, Gekkonidae)  
19 from Baja California, Mexico. *California Academy of Sciences*, 40, 87-92.
- 20  
21 Nguyen, S. N., Le, T. N., Tran, T. A., Orlov, N. L., Lathrop, A., Macculloch, R. D., et al. (2013)  
22 Phylogeny of the *Cyrtodactylus irregularis* species complex (Squamata: Gekkonidae)  
23 from Vietnam with the description of two new species. *Zootaxa*, 3737, 399-414.
- 24  
25 Nguyen, S. N., Yang, J. X., Le, T. N., Nguyen, L. T., Orlov, N. L., Hoang, C. V., et al. (2014) DNA  
26 barcoding of Vietnamese bent-toed geckos (Squamata: Gekkonidae: *Cyrtodactylus*) and  
27 the description of a new species. *Zootaxa*, 3784, 48-66.
- 28  
29 Nielsen, S. V., Bauer, A. M., Jackman, T. R., Hitchmough, R. A. & Daugherty, C. H. (2011) New  
30 Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with  
31 trans-Tasman affinities. *Molecular Phylogenetics and Evolution*, 59, 1-22.
- 32  
33 Oliver, P. M., Ashman, L. G., Bank, S., Laver, R. J., Pratt, R. C., Tedeschi, L. G., et al. (2019) On  
34 and off the rocks: persistence and ecological diversification in a tropical Australian lizard  
35 radiation. *BMC evolutionary biology*, 19, 81.
- 36  
37 Oliver, P. M., Brown, R. M., Kraus, F., Rittmeyer, E., Travers, S. L. & Siler, C. D. (2018) Lizards of  
38 the lost arcs: mid-Cenozoic diversification, persistence and ecological marginalization in  
39 the West Pacific. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20171760.
- 40  
41 Oliver, P. M. S., K. L (2009) Molecular evidence for Gondwanan origins of multiple lineages  
42 within a diverse Australasian gecko radiation. *Journal of Biogeography*, 36, 2044-2055.
- 43  
44 Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., et al. (2017) The  
45 global distribution of tetrapods reveals a need for targeted reptile conservation. *Nat  
46 Ecol Evol*, 1, 1677-1682.
- 47  
48 Rösler, H. (2017) Gecko-Chorologie (Squamata: Gekkota). *Gekkota, Supplement*, 4, 1-160.
- 49  
50 Russell, A. P. & Bauer, A. M. (2002) Underwood's Classification of the Geckos: A 21st Century  
51 Appreciation. *Bull. Nat. Hist. Mus. London (Zool.)*, 68, 113-121.
- 52  
53 Russell, A. P. & Gamble, T. (2019) Evolution of the Gekkotan Adhesive System: Does Digit  
54 Anatomy Point to One or More Origins? *Integr Comp Biol*, 59, 131-147.
- 55  
56 Simões, T. R., Apesteguía, S., Hsiou, A. S., Daza, J. D., Introduction, L. f. G. A., 297, J. o. H., et al.  
57 (2017) Lepidosaurs from Gondwana: An Introduction. *Journal of Herpetology*, 51, 297-  
58 299.
- 59  
60 Skipwith, P. L., Bauer, A. M., Jackman, T. R. & Sadlier, R. A. (2016) Old but not ancient:  
61 coalescent species tree of New Caledonian geckos reveals recent post?inundation  
62 diversification. *Journal of Biogeography*, 43, 1266-1276.
- 63  
64  
65

- 1  
2  
3  
4 Skipwith, P. L., Bi, K. & Oliver, P. M. (2019) Relicts and radiations: Phylogenomics of an  
5 Australasian lizard clade with east Gondwanan origins (Gekkota: Diplodactyloidea).  
6 *Molecular Phylogenetics and Evolution*, 140, 106589.  
7  
8 Uetz, P., Cherikh, S., Shea, G., Ineich, I., Campbell, P. D., Doronin, I. V., et al. (2019) A global  
9 catalog of primary reptile type specimens. *Zootaxa*, 4695, 438–450.  
10  
11 Uetz, P., Freed, P. & Hošek, J. (2019) Reptile Database. *In*.  
12  
13 Uetz, P. & Stylianou, A. (2018) The original descriptions of reptiles and their subspecies.  
14 *Zootaxa*, 4375, 257-264.  
15  
16 Underwood, G. (1954) On the classification and evolution of geckos. *Proceedings of the*  
17 *Zoological Society of London*, 124, 469-492..  
18  
19 Underwood, G. (1957) On lizards of the family Pygopodidae. A contribution to the morphology  
20 and phylogeny of the Squamata. *Journal of Morphology*, 100, 207-268.  
21  
22 Vidan, E., Bauer, A. M., Herrera, F.-C., Chirio, L., Nogueira, C. C., Doan, T. M., et al. (2019) The  
23 global biogeography of lizard functional groups. *Journal of Biogeography*, 46, 2147-  
24 2158.  
25  
26 Wood, P. L., Guo, X., Travers, S. L., Su, Y. C., Olson, K. V., Bauer, A. M., et al. (2019) Parachute  
27 geckos free fall into synonymy: Gekko phylogeny, and a new subgeneric classification,  
28 inferred from thousands of ultraconserved elements. *bioRxiv*, 717520.  
29  
30 Xiong, Z., Li, F., Li, Q., Zhou, L., Gamble, T., Zheng, J., et al. (2016) Draft genome of the leopard  
31 gecko, *Eublepharis macularius*. *Gigascience*, 5, 47.  
32  
33 Zheng, Y. & Wiens, J. J. (2016) Combining phylogenomic and supermatrix approaches, and a  
34 time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes  
35 and 4162 species. *Mol Phylogenet Evol*, 94, 537-547.  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1  
2  
3  
4 **Tables**  
5  
6

7 **Table 1. Top-10 authors who described the most gecko species (i.e. 40 or more).**  
8

9

<b>Author</b>	<b>species</b>
Aaron M. Bauer	144
Lee L. Grismer	132
Perry Wood	98
George Alfred Boulenger	77
Evan Quah	63
Olivier Pauwels	54
John Edward Gray	49
Montri Sumontha	45
Thomas Ziegler	43
Paul Doughty	40

10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24

25 **Table 2. The top-10 collections that hold the most gekkotan primary types.** For additional type  
26 information see Uetz et al. 2019.  
27

28

<b>Collection</b>	<b>Taxa with types</b>
BMNH (London, UK)	279
MCZ (Cambridge, USA)	129
MNHN-RA (Paris, France)	106
WAM (Perth, Australia)	100
USNM (Washington, DC, USA)	66
CAS (San Francisco, USA)	65
SMF (Frankfurt, Germany)	64
ZMB (Berlin, Germany)	57
ZFMK (Bonn, Germany)	54
DNMNH (Pretoria, South Africa)	53

29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43

44 **Table 3. Diversity of geckos in terms of families and species numbers.**  
45

46

<b>Family</b>	<b>species</b>	<b>genera</b>
Carphodactylidae	31	7
Diplodactylidae	154	25
Eublepharidae	38	6
Gekkonidae	1281	57
Phyllodactylidae	148	10
Pygopodidae	45	7
Sphaerodactylidae	224	12
<b>All Gekkota</b>	<b>1921</b>	<b>124</b>
<b>% of all reptiles</b>	<b>17%</b>	<b>10%</b>

47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

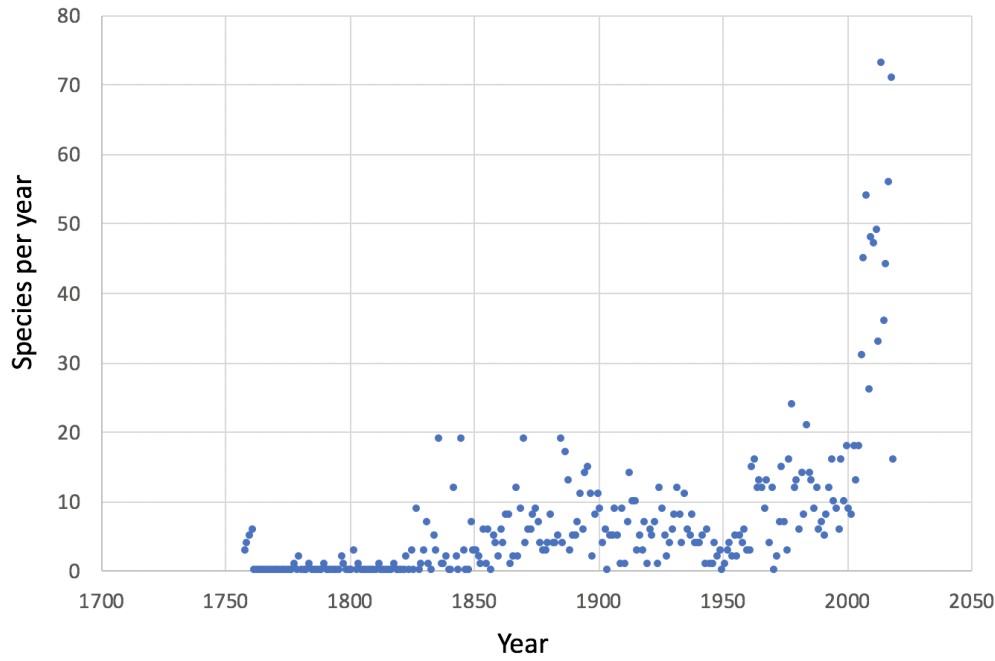
**Table 4. The top-10 most speciose genera of geckos.** The largest 10 genera have more than 50 species each and together include more than 50% of all gekkotan species. Compare to Fig. 4 for the remainder of gekkotan genera.

<b>Genus</b>	<b>Species</b>
<i>Cyrtodactylus</i>	287
<i>Hemidactylus</i>	158
<i>Cnemaspis</i>	157
<i>Sphaerodactylus</i>	105
<i>Lygodactylus</i>	65
<i>Gekko</i>	60
<i>Gehyra</i>	59
<i>Pachydactylus</i>	57
<i>Phyllodactylus</i>	55
<i>Phelsuma</i>	52

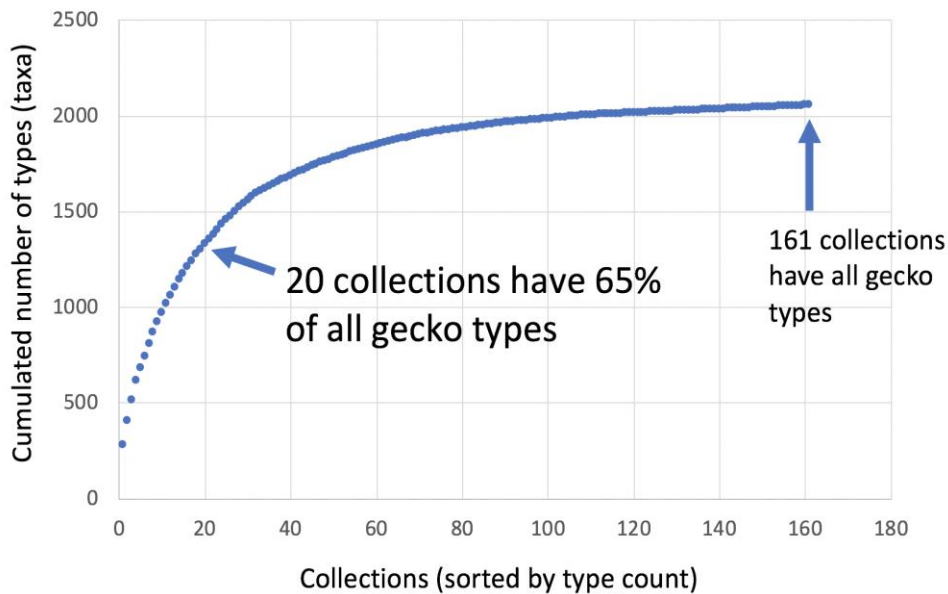
**Table 5. The Top-10 most gecko-rich countries of the world, each with more than 65 species.** Compare to Fig. 6.

<b>Country</b>	<b>species number</b>
Australia	241
India	127
Madagascar	120
Malaysia	104
Indonesia	96
Vietnam	90
South Africa	89
Thailand	83
Namibia	70
Iran	69

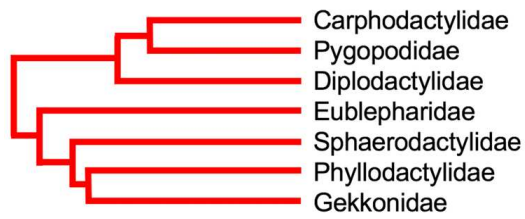
1  
2  
3  
4 **Figures**  
5  
6  
7



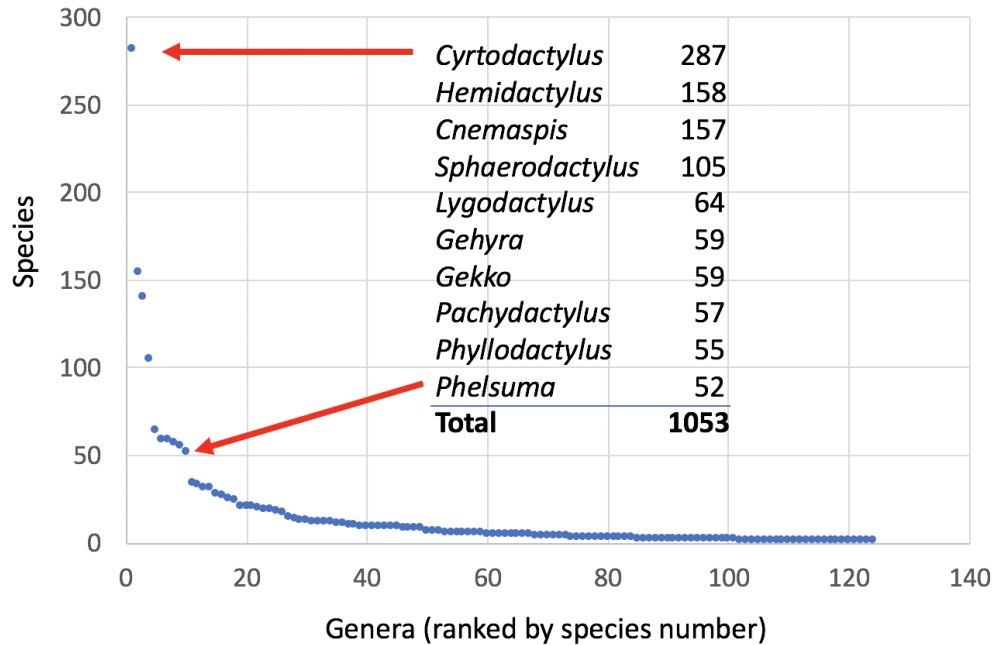
31 **Fig. 1. Gecko species described per year.** The number of new species descriptions has surged in  
32 the past 15 years, supported by widely accessible molecular techniques.  
33  
34



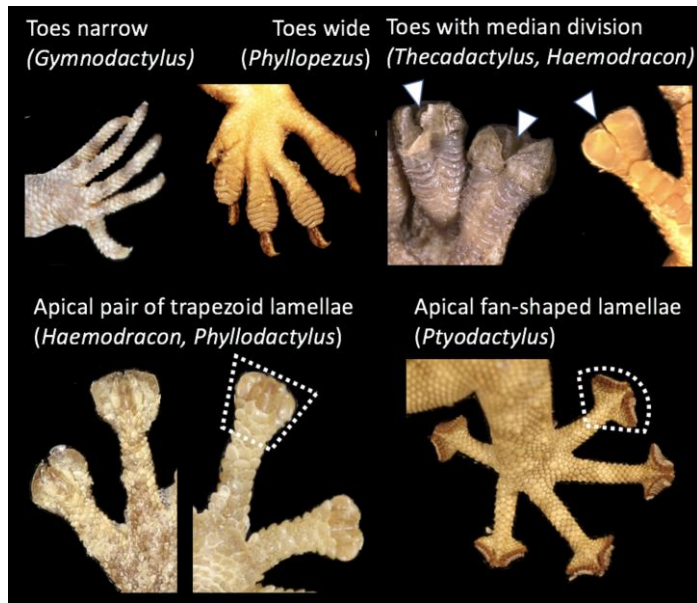
57 **Fig. 2. All primary types of the world's geckos are in 161 collections** with 20 collections having  
58 about two thirds of all types.  
59  
60  
61  
62  
63  
64  
65



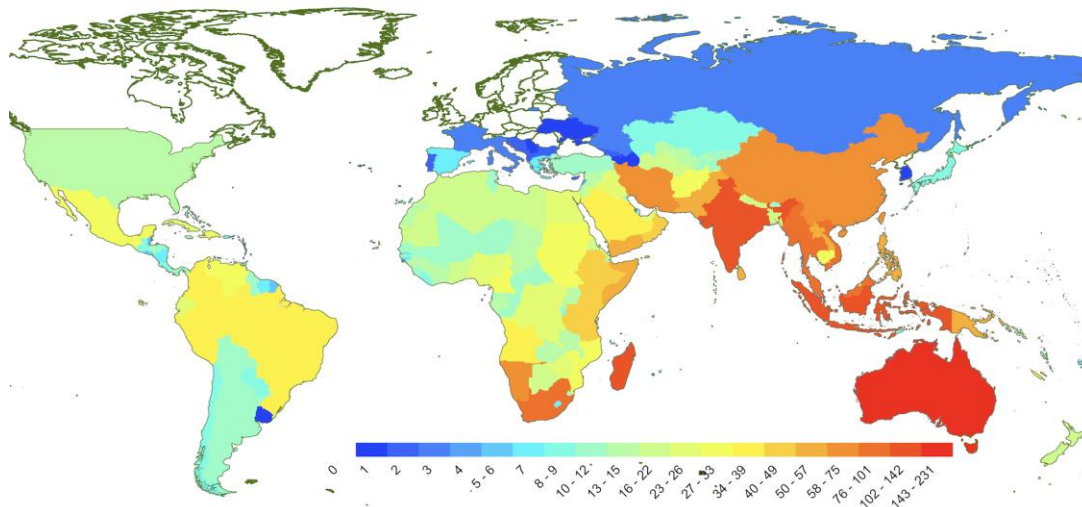
**Fig. 3. Phylogenetic relationship of gecko families.** Relationships are based on recent comprehensive molecular phylogenetic studies (Han et al. 2004; Gamble et al. 2008a, b; 2012; Zheng & Wiens 2016)



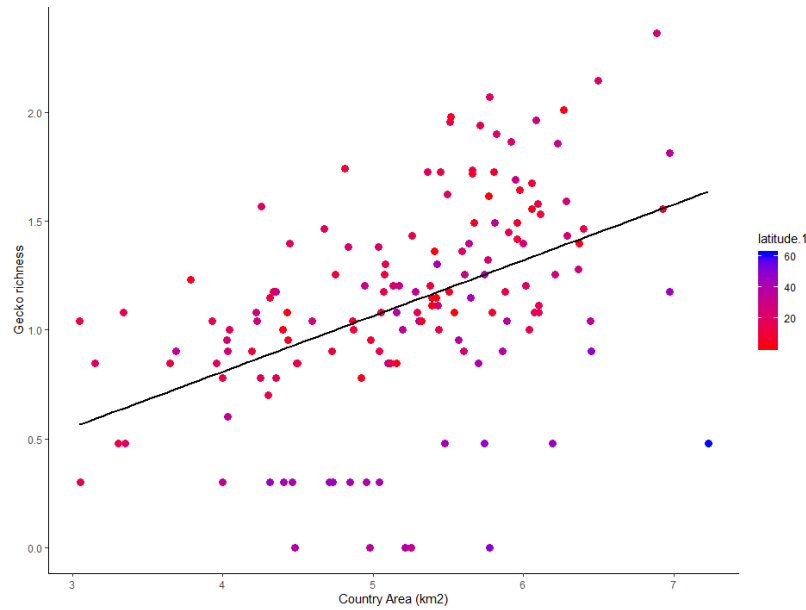
**Fig. 4. The most speciose gecko genera.** The 10 most speciose genera currently contain more than 1,000 species, or about 50% of all geckos, and about 10% of all reptiles. *Cyrtodactylus* is the most speciose genus of geckos, and the most species-rich reptilian genus after *Anolis*.



**Fig. 5. Key features of gecko feet diagnostic for genera of the family Phyllodactylidae.** Only 6 of the 10 genera are shown as they represent the character diversity within the family. Photos by Peter Uetz.



**Fig. 6. Number of gecko species per country.** Geckos are concentrated in the areas surrounding the Indian Ocean. Compare to species richness map in Meiri 2020 (this issue).



**Fig. 7. The larger a country is, the more geckos it has.** As expected, countries outside the tropics (purple-blue) have fewer species (latitude of the geographical centroids of each country encoded by color), but the effect of area is stronger. Country sizes and species numbers are given on a log-scale. Bottom right: Russia (3 species).