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Gecko diversity: a history of global discovery

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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.
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Gecko diversity: a history of global discovery

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

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

A history of gecko discovery

Only three geckos were described by Linnaeus (Linnaeus 1758)—the Tokay gecko (*Lacerta Gecko* to Linnaeus, now *Gekko gecko*), Mediterranean House Gecko (as *Lacerta turcica*, now *Hemidactylus turcicus*), and Moorish gecko (*Lacerta mauritanica*, now *Tarentola mauritanica*). It then took herpetologists 227 years, from 1758 to 1984, to describe the first 1000 gecko species. It has taken only 35 to describe the next 921 (not counting subspecies). Early descriptions of gecko species commonly appeared in regional monographs or travelogues (e.g. Shaw 1790; Spix 1825; Smith 1849) or else more general zoological works (e.g. Daudin 1802, Gray 1831), but also were appeared as standalone contributions to journals or society proceedings (e.g. Sparrman 1778). Early descriptions peaked in the mid-19th century with 19 species described in 1836, 1845, 1870, and 1885 (**Fig. 1**). These numbers were driven by the monumental works of André M.C. Duméril & Gabriel Bibron (Duméril & Bibron 1836), John E. Gray (Gray 1845), Richard H. Beddome (Beddome 1870a, 1870b) and George A. Boulenger (Boulenger 1885). They were only exceeded a century later with 24 species described in 1978. Even though these authors have described most geckos in single publications, only Gray and Boulenger are among the 10 most prolific gecko describers (**Table 1**). In the late 20th century molecular methods such as karyotyping (e.g. Murphy 1974, King 1982) and allozyme electrophoresis (e.g. Branch et al. 1995) began to be employed to aid in new species discovery. Discoveries skyrocketed in the 21st century (Meiri 2016) with the advent of new technologies, such as the internet, DNA sequencing, digital photography, and cheaper travel permitting access to remote areas, as well as the ability for individual researchers to study collections at distant museums. Nevertheless, even in modern times, gecko discovery has been driven by relatively few individuals. Thus, the 1921 gekkotans described since 1758 were authored by about 950 individuals (Uetz & Stylianou 2018), of which about 100 described more than 10 gecko species each. Eight of the ten most prolific describers of new species are currently active herpetologists, with two (Aaron M. Bauer and L. Lee Grismer) describing more than 130 species, each (**Table 1**). Unfortunately, it is almost impossible to determine how many authors were needed to describe some species due to the inclusion of species descriptions in phylogenetic or other publications that have multiple authorship and may use different citation or author formats.

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

Type specimens of geckos

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

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

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

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

The diversity of geckos

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

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

Gecko traits

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

Geckos and their DNA

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

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^2. 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.

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

Materials and methods

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

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Tables

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

Author	species
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

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

Collection	Taxa with types
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

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

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

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.

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

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

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

Figures

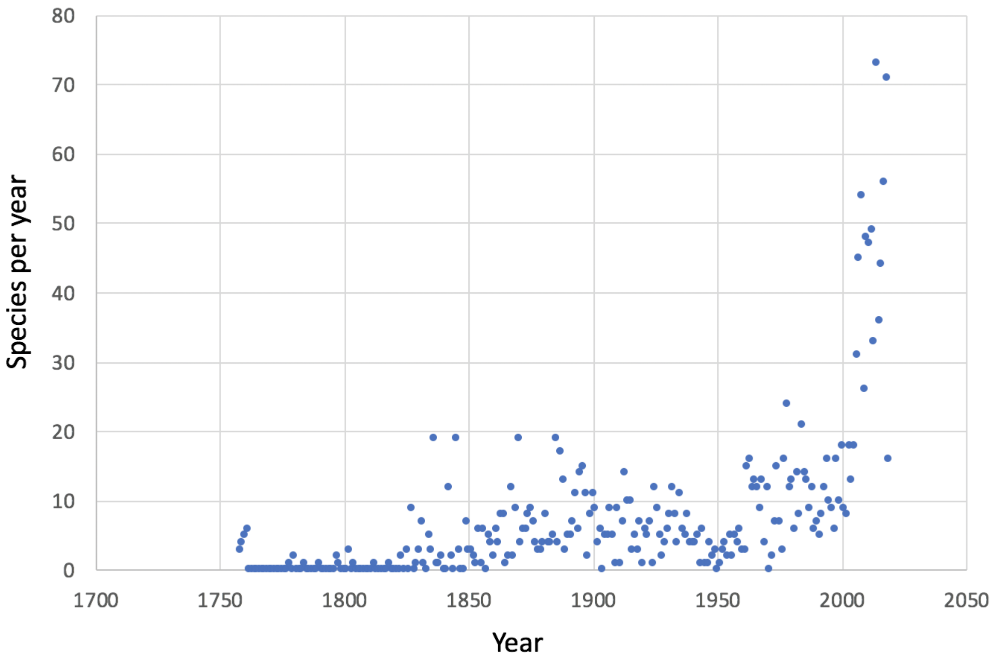

Fig. 1. Gecko species described per year. The number of new species descriptions has surged in the past 15 years, supported by widely accessible molecular techniques.

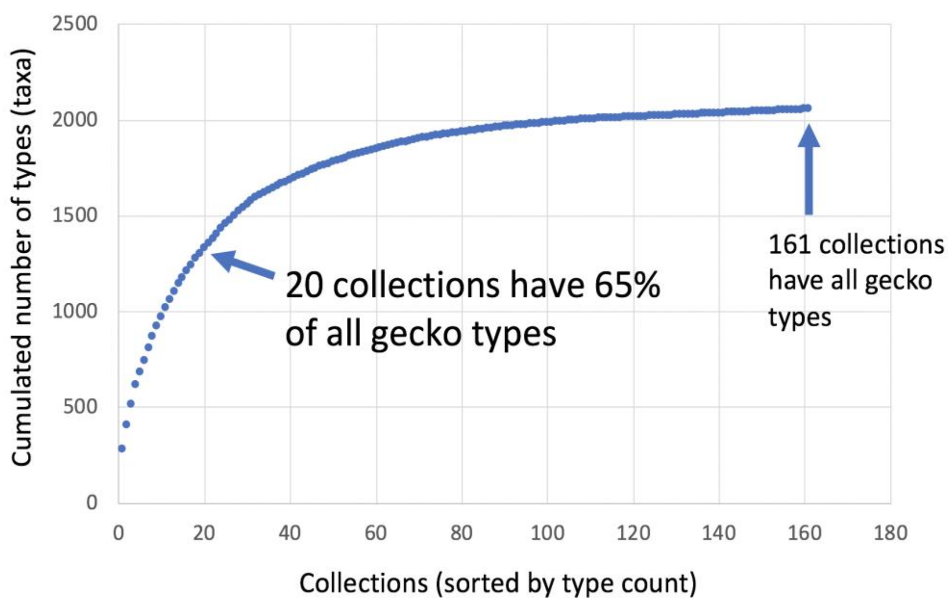

Fig. 2. All primary types of the world's geckos are in 161 collections with 20 collections having about two thirds of all types.

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)

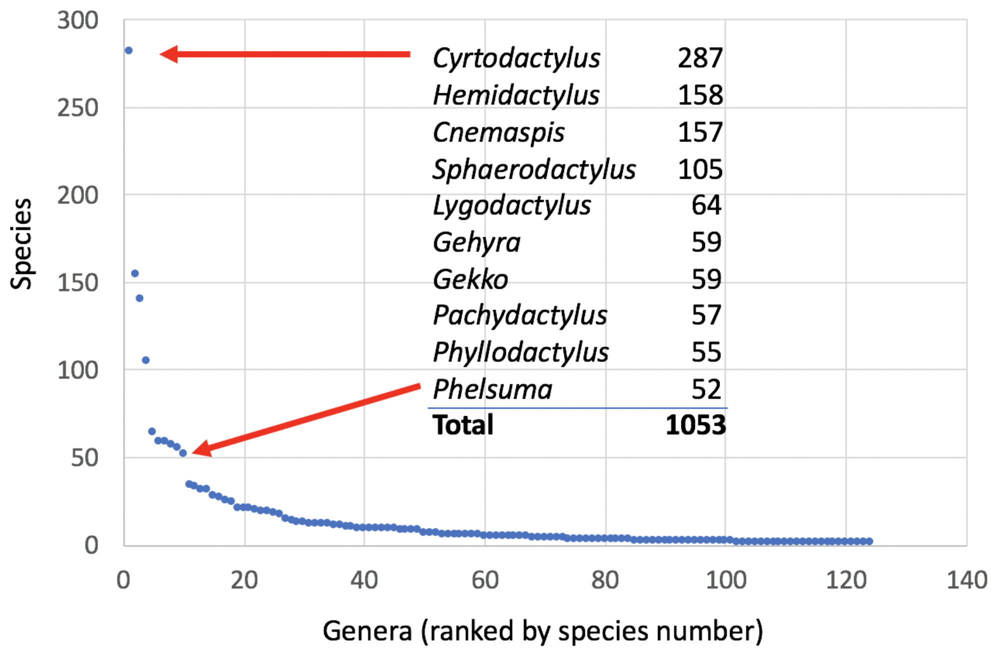

Fig. 4. The most speciose gecko genera. The 10 most speciose genera currently contain more than 1,000 species, or about 50% of all geckos, and about 10% of all reptiles. *Cyrtodactylus* is the most speciose genus of geckos, and the most species-rich reptilian genus after *Anolis*.

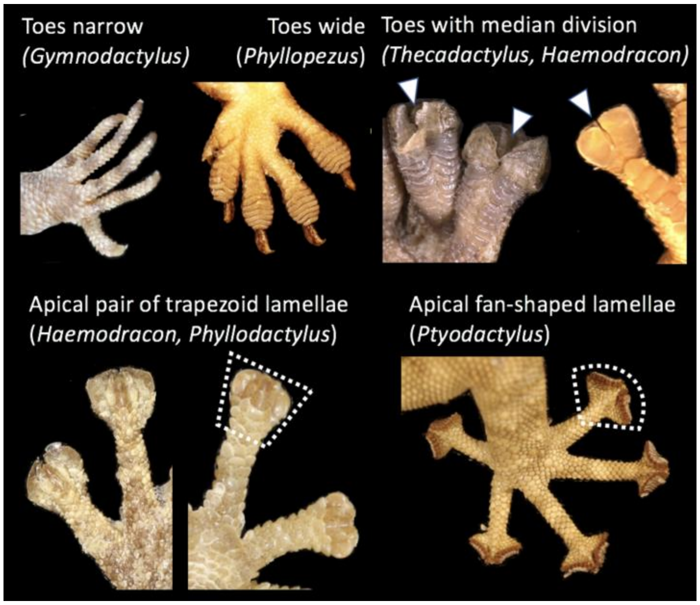

Fig. 5. Key features of gecko feet diagnostic for genera of the family Phyllodactylidae. Only 6 of the 10 genera are shown as they represent the character diversity within the family. Photos by Peter Uetz.

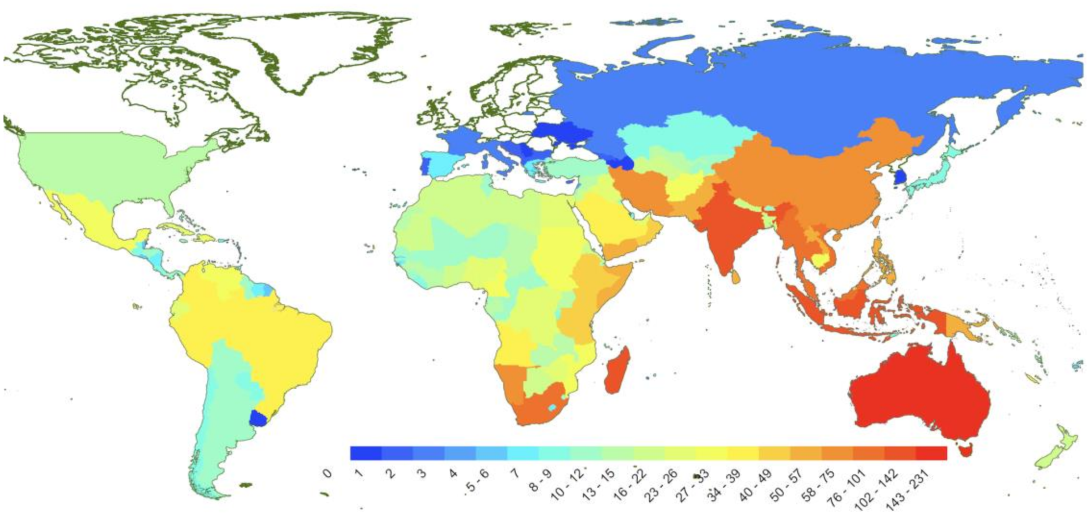

Fig. 6. Number of gecko species per country. Geckos are concentrated in the areas surrounding the Indian Ocean. Compare to species richness map in Meiri 2020 (this issue).

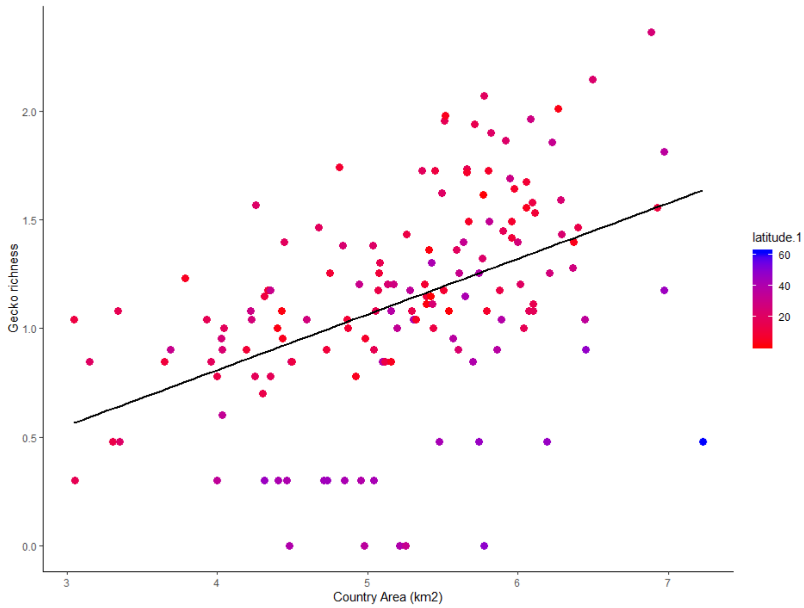

Fig. 7. The larger a country is, the more geckos it has. As expected, countries outside the tropics (purple-blue) have fewer species (latitude of the geographical centroids of each country encoded by color), but the effect of area is stronger. Country sizes and species numbers are given on a log-scale.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