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Gecko diversity: a history of global discovery

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Abstract 1935 gecko species (and 224 subspecies) were known in December 2019 in seven families and 124 genera. These nearly 2000 species were described by ~950 individuals of whom more than 100 described more than 10 gecko species each. Most gecko species were discovered during the past 40 years. The primary type specimens of all currently recognized geckos (including subspecies) are distributed over 161 collections worldwide, with 20 collections having about two thirds of all primary types. The primary type specimens of about 40 gecko taxa have been lost or unknown. The phylogeny of geckos is well studied, 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. Among countries, 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. As expected, when correcting for land area, countries outside the tropics have fewer geckos.

Keywords Carphodactylidae; Diplodactylidae; Eublepharidae; Gekkonidae; Gekkota; Phyllodactylidae; Pygopodidae; Sphaerodactylidae

Introduction

Geckos (Sauria: Gekkota; 1935 species) are one of three mega-diverse lineages of squamate reptiles (lizards, snakes, and amphisbaenians), along with the 1685 species of skinks and 1965 species of colubrid snakes (Uetz et al. 2019), that are known today as result of the major squamate radiations that began diversifying about 200 million years ago. All gecko families are relatively old compared to either skinks or colubrids. Molecular clock estimates place the origins of gecko families deep in the Mesozoic (Gamble et al. 2008a, b, 2011; Hedges et al. 2015; Zheng and 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, 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 2020, 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 (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. Spix 1825) or else more general zoological works (e.g. Daudin 1802). Some also appeared as stand-alone contributions to journals or society proceedings (e.g. Sparrman 1778). Early descriptions peaked in the mid-19th century with 19 species described in each of 1836, 1845, 1870, and 1885 (Fig. 1). These numbers were driven by the monumental works of André M.C. Duméril and Gabriel Bibron (Duméril and Bibron 1836), John E. Gray (Gray 1845), Richard H. Beddome (Beddome

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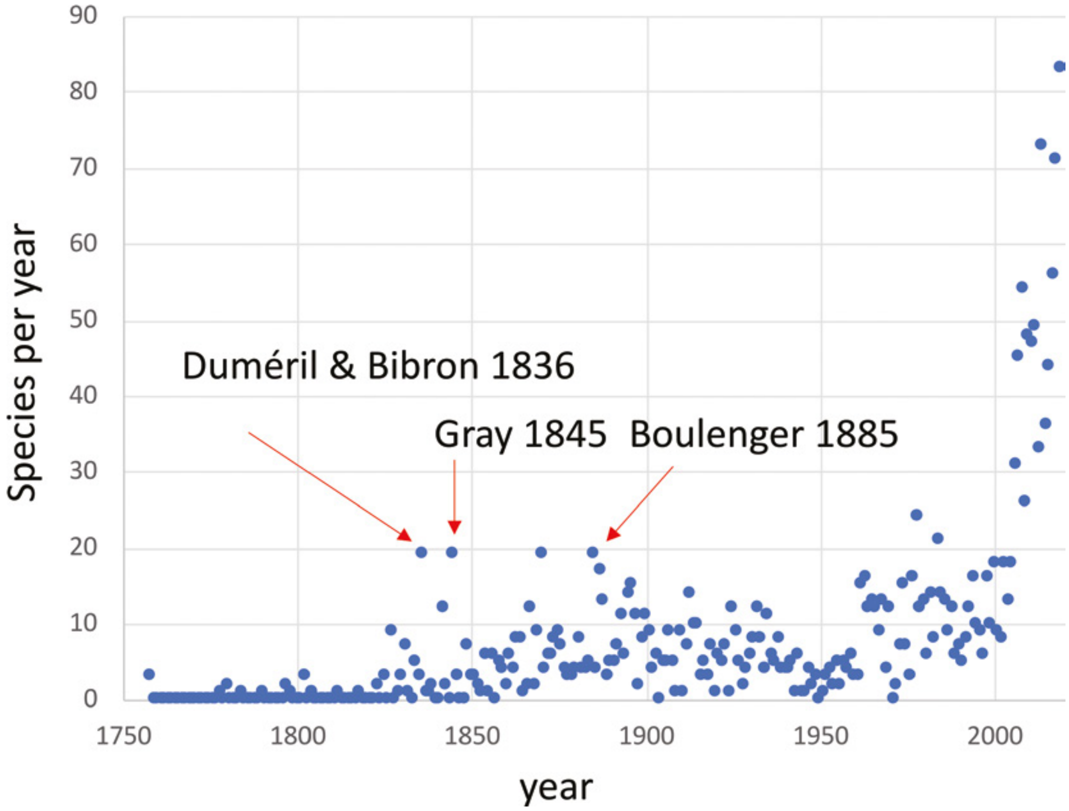

Figure 1. Gecko species described per year 1758–2019. Some prolific gecko describers from the 19th century are highlighted. The number of new species descriptions has surged in the past 15 years, supported by widely accessible molecular techniques and other advances.

1870a, b) and George A. Boulenger (Boulenger 1885) that were published in those years. These annual totals were only exceeded a century later with 24 species described in 1978. Even though 19th century 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; Uetz and Stylianou 2018) 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 1935 gekkotans described since 1758 were authored by about 950 individuals (Uetz and Stylianou 2018), of whom 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).

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 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

Table 1. Top-11 authors who described the most gecko species still recognized as valid (i.e. 40 or more).

Author	Species
Aaron M. Bauer	143
L. Lee Grismer	132
Perry L. Wood	98
George A. Boulenger	77
Evan S. H. Quah	63
Olivier S. G. Pauwels	54
John E. Gray	49
Montri Sumontha	45
Thomas Ziegler	44
Paul Doughty	40
Paul M. Oliver	40

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 taynguyenensis* 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 also 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 primary type specimens are held at the Natural History Museum, London (BMNH; types of 285 taxa). Among its collections are most of the types of species described by Gray, Boulenger, and Beddome in their major 19th century works, along with many types designated 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. designated 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 *Sphaerodactylus* types designated 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, 2019, 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 gecko primary 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.

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

Collection	Taxa with types
BMNH (London, UK)	285
MCZ (Cambridge, USA)	130
MNHN-RA (Paris, France)	107
WAM (Perth, Australia)	100
USNM (Washington, DC, USA)	68
CAS (San Francisco, USA)	69
SMF (Frankfurt, Germany)	68
ZMB (Berlin, Germany)	57
ZFMK (Bonn, Germany)	55
DNMNH (Pretoria, South Africa)	52

The VertNet database (Constable et al. 2010) is the largest meta-database of vertebrate collections, and returned 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 species when all mismatched names such as typos and spelling variants are included, ignoring synonyms). That is, ~25% of all Gekkotans have primary types recorded in VertNet but the vast majority of all VertNet-listed types are 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,

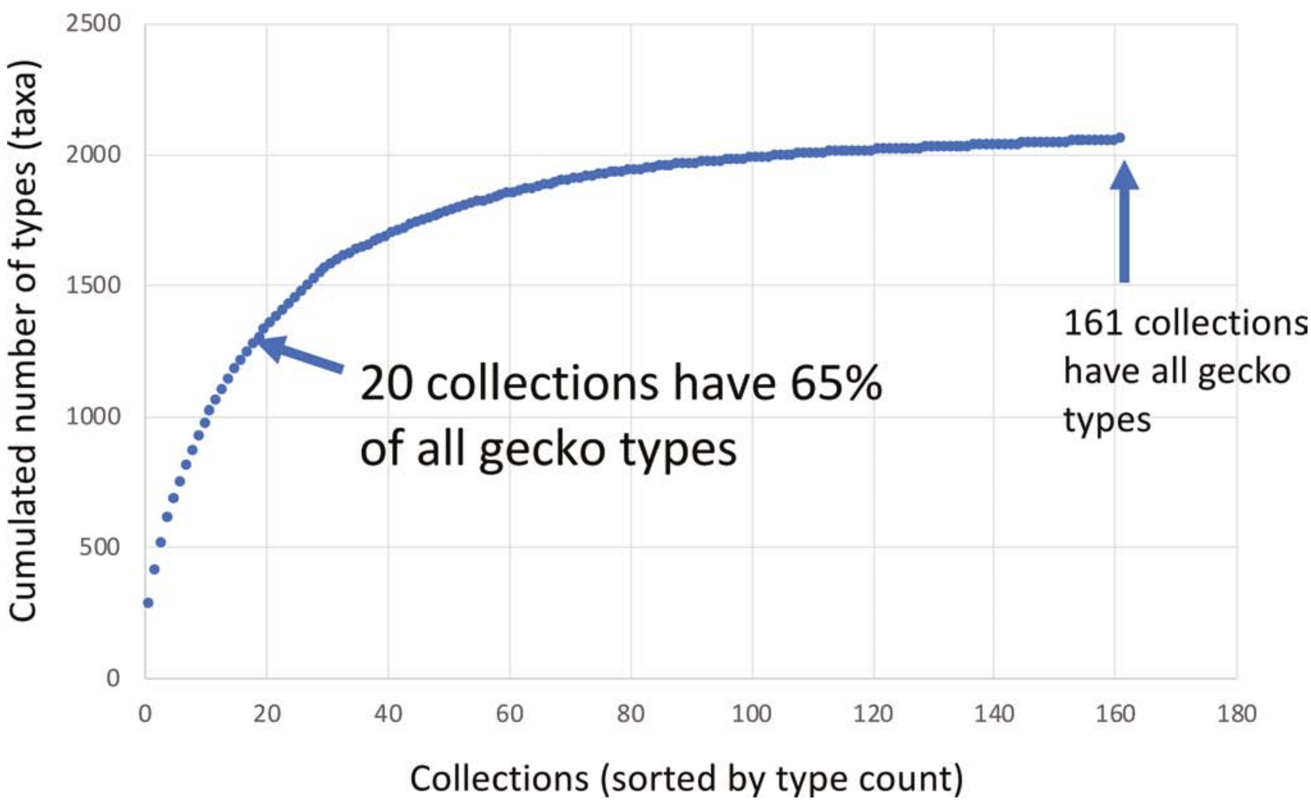

Figure 2. All primary types of the world's geckos are in 161 collections with 20 collections having about two thirds of all types. Type count (X axis) is the number of currently valid taxa (species and subspecies) with primary types.

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	1295	57
Phyllodactylidae	148	10
Pygopodidae	45	7
Sphaerodactylidae	224	12
All Gekkota	**1935**	**124**
% of all reptiles	17%	10%

Figure 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 and Wiens 2016).

and much more advanced than similar projects in other parts of the world. Thus potentially only a small fraction of all collections with gecko specimens have submitted their collection data to meta-databases, though many collections have in-house databases.

A relatively small number of primary gecko type specimens are unknown. We found the types of 40 valid gekkotan taxa (~2%, out of 2159, including subspecies) to be either lost or simply "unlocated" (i.e. their whereabouts were never made clear, even in the original description; e.g. for *Tropiocolotes nattereri* Steindachner 1901) — which means that they are likely lost too. Thus, surprisingly, geckos are less often lost than non-gekkotan types, of which more than 5% are lost or unlocated (Uetz et al. 2019). This is despite the often small size of geckos, but likely due to the fact that most geckos were described only recently and thus had less time to get lost.

The diversity of geckos

The nearly 2000 species of geckos represent a tremendous variety of adaptations and lifestyles, 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 (Table 3, 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 currently recognized families, Gekkonidae was the first to be described (Gray 1825), followed by Pygopodidae (as Pygopidae in Gray 1841). Boulenger (1883) recognized Eublepharidae based on differences in vertebral structure as compared to all other geckos, and was the first to note morphological

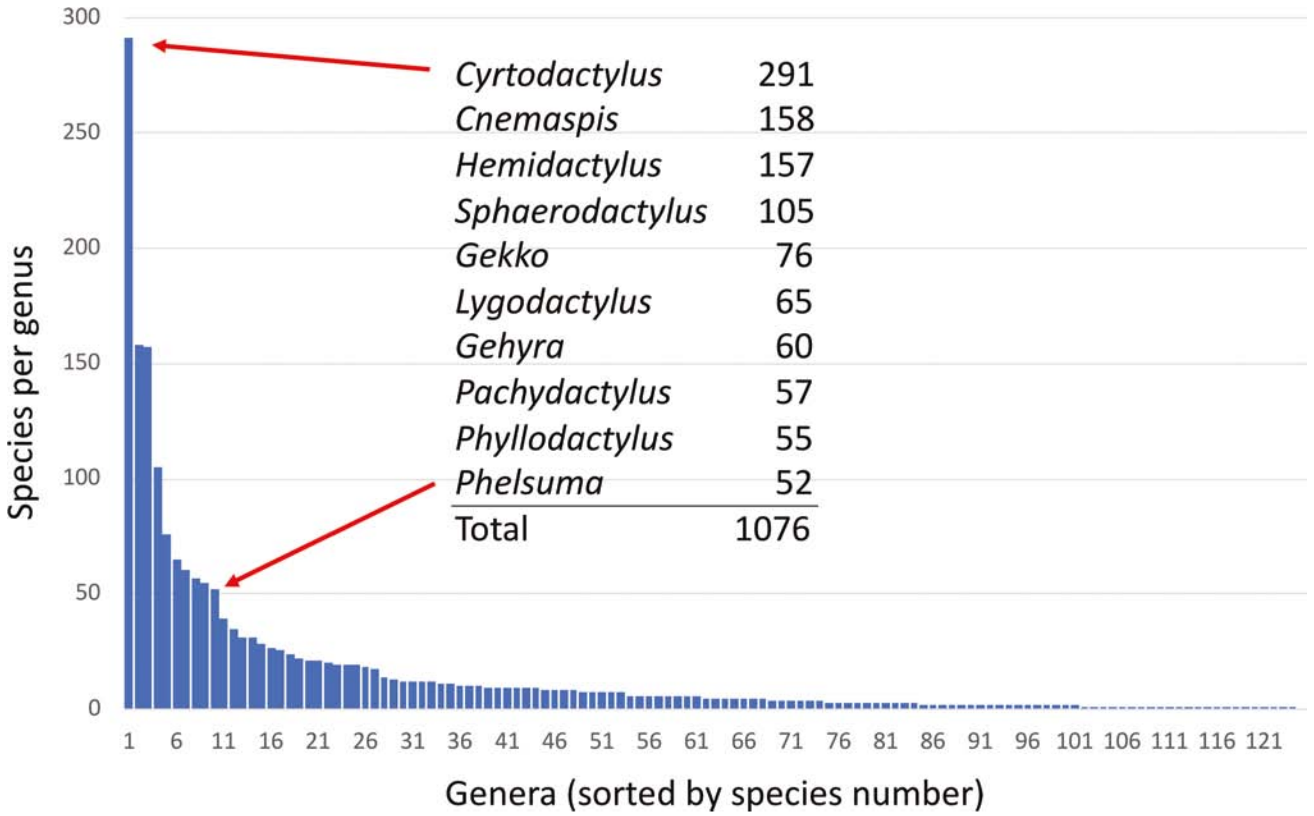

Figure 4. Species numbers among gecko genera. The 10 most speciose genera (listed) currently contain more than 1,000 species, or about 50% of all geckos, and about 10% of all reptiles. *Cyrtodactylus* is the most speciose genus of geckos, and the most species-rich reptilian genus after *Anolis*. For detailed numbers of smaller genera see the latest release of the Reptile Database and its regularly updated spreadsheet.

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 by Russell and 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 Phyllodactylidae (Gamble et al. 2008a, b; 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. 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* (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, 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 and Bauer 2012). Evolutionary patterns of many specific traits of geckos have also been studied. Examples include diurnal activity patterns (Gamble et al. 2015b), gliding adaptations (Heinicke et al. 2012), sex determining mechanisms (Gamble et al. 2015a), 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 (Bauer 2019; Gamble et al. 2012; Russell and 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 genes or fragments thereof (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, they found that the emergence of setae in geckos is correlated with the duplication and diversification of β-keratin genes.

Geckos of the world – a geographic survey

Geckos are not evenly distributed in the world (Fig. 5, 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 4), 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. 6). 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

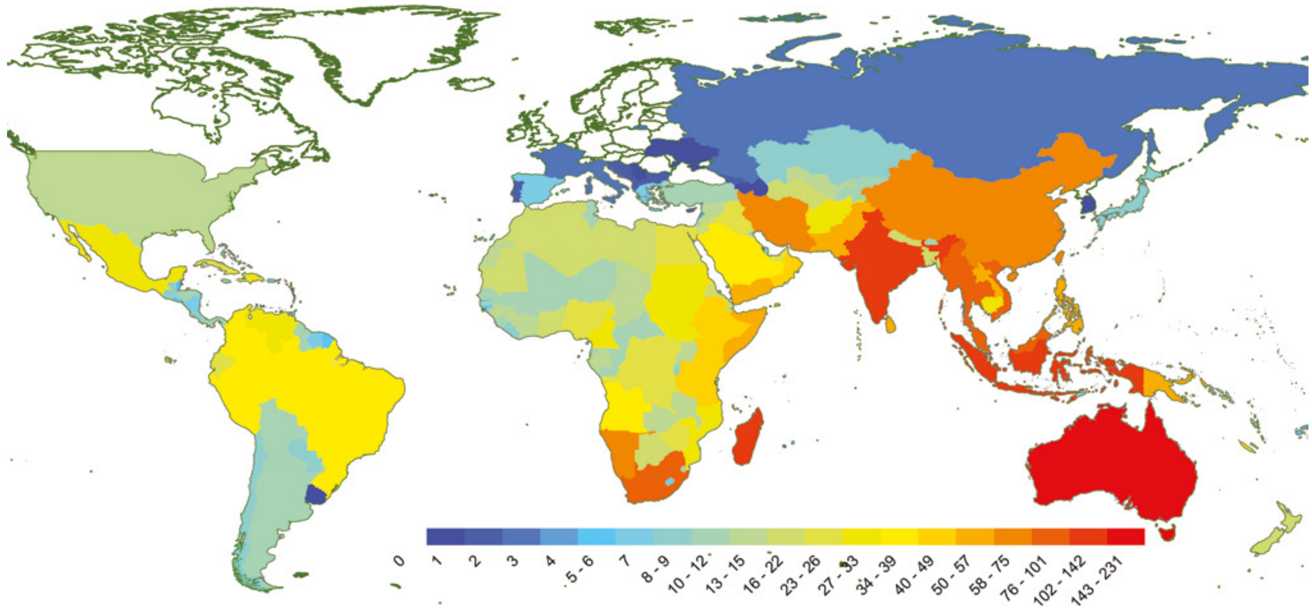

Figure 5. Number of gecko species per country. Geckos are concentrated in the areas surrounding the Indian Ocean. Compare to species richness map in Meiri (2020, this issue).

Table 4. 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	136
Madagascar	121
Malaysia	105
Indonesia	97
Vietnam	90
South Africa	85
Thailand	85
Namibia	70
Iran	69

countries, have relatively few geckos (Meiri 2020, this volume, and Fig. 5), 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 and 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 and Sanders 2009). Subsequently, gecko lineages have colonized or re-colonized additional landmasses including oceanic islands via dispersal, often across wide barriers (e.g. Gamble et al. 2008b; Nielsen et al. 2011; Heinicke et al. 2011, 2014; Novosolov and Meiri 2013; Skipwith et al. 2016; Oliver et al. 2018). The old age of the clade and high dispersal abilities of geckos results in members of the families Eublepharidae, Gekkonidae, Phyllodactylidae, and Sphaerodactylidae, occurring across multiple continents. Also as a result of this history of dispersals, as many as four families of geckos may occur in sympatry. While the otherwise Australian family Diplodactylidae is also found on New Caledonia and New Zealand — probably due to dispersal after those three land masses split from each other — the Carphodactylidae is entirely restricted to Australia. Only two pygopodids (both species of *Lialis*) occur elsewhere – in nearby New Guinea.

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.

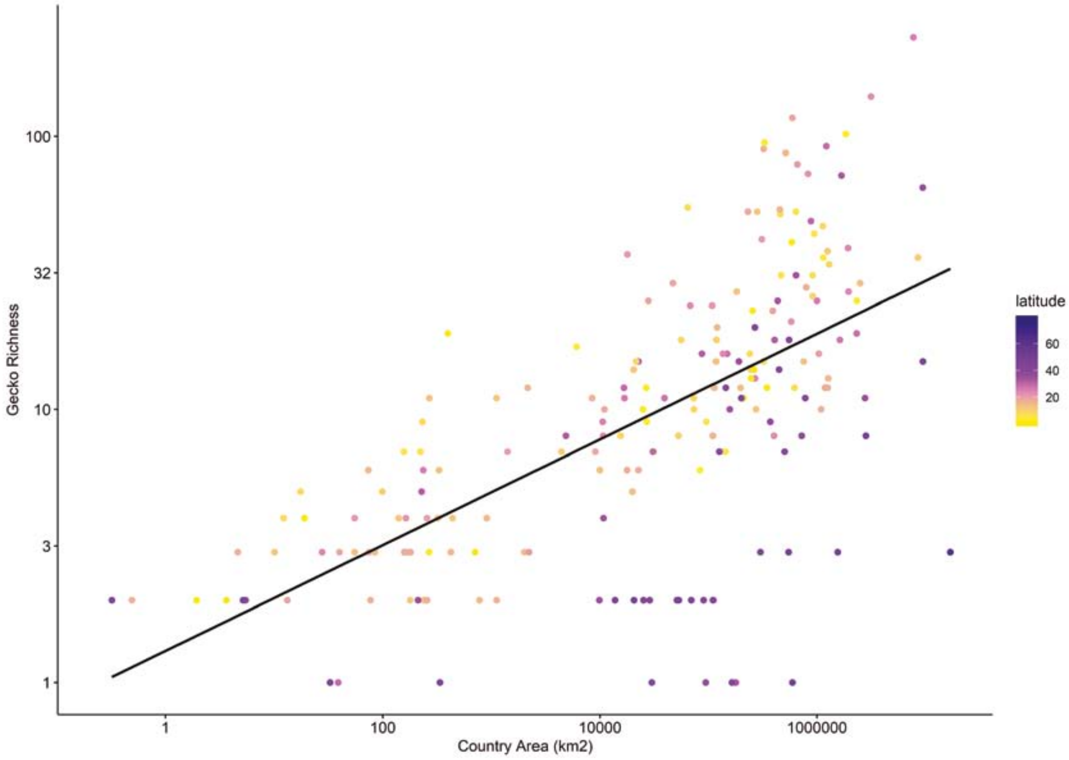

Figure 6. The larger a country is, the more geckos it has. As expected, countries outside the tropics (purple-blue) have fewer species (latitude of the geographical centroids of each country encoded by color), but the effect of area is stronger. Country sizes and species numbers are given on a log-10 scale. Bottom right: Russia (3 species).

Materials and methods

Species and author data were derived from the December 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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