Contribution to the special issue on
REPTILE COGNITION:

Lizards as models to explore the ecological and neuroanatomical correlates of miniaturization

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Abstract
Extreme body size reductions bring about unorthodox anatomical arrangements and novel ways in which animals interact with the environment. Drawing from studies of vertebrates and invertebrates, we provide a theoretical framework for miniaturization to inform hypotheses using lizards as a study system. Through this approach, we demonstrate the repeated evolution of miniaturization across 11 families and a tendency for miniaturized species to occupy terrestrial microhabitats, possibly driven by physiological constraints. Differences in gross brain morphology between two gecko species demonstrate a proportionally larger telencephalon and smaller olfactory bulbs in the miniaturized species, though more data are needed to generalize this trend. Our study brings into light the potential contributions of miniaturized lizards to explain patterns of body size evolution and its impact on ecology and neuroanatomy. In addition, our findings reveal the need to study the natural history of miniaturized species, particularly in relation to their sensory and physiological ecology.

1. Introduction

Very small animals reside their entire lives encompassed by physical and sensory challenges disparate from our own. A parasitoid wasp struggles to break the water's surface tension (Shih et al., 2013), and a tiger beetle moves so rapidly that it becomes functionally blind (Zurek & Gilbert, 2014). By simply changing the scale of the surrounding environment, body size can have profound effects on an organism's ecology (LaBarbera, 1989), and as a consequence, the cognitive processes necessitated to interpret and respond to stimuli in the periphery (Martens et al., 2015). Because of the high diversity of life histories and anatomical forms in the animal kingdom, it is difficult to identify the ecological and cognitive correlates of small body size, even more so to establish the latter as a causative agent. Comparing closely related taxa that vary in body size is useful to minimize the confounding effect of phylogeny, and accordingly, many studies involve thorough sampling within clades spanning a wide range of body sizes (e.g., Jablonski, 1997; Hone et al., 2008; Cooper & Purvis, 2010; Collar et al., 2011; Feldman et al., 2016). As a result, there is a predominance of work examining evolutionary changes in body size, but less often a focus specifically on the small extremes — a phenomenon called 'miniaturization' (Hanken & Wake, 1993).

The bulk of research on miniaturization has been done in arthropods, where exquisite anatomical and functional correlates are well documented (reviewed in Polilov, 2015). Vertebrate bauplans differ dramatically in fundamental organization and offer a second taxonomic group to examine traits that accompany extreme reductions of body size. Yet, to date studies on miniaturized vertebrates are scant. We argue that lizards are a fruitful group to study miniaturization for several reasons: they exhibit high lability in body size, diminutive exemplars are found across the phylogeny (Feldman et al., 2016), and osteological traits have provided a basis for defining miniaturization (Rieppel, 1984). Together, this provides the building blocks for subsequent ecological, behavioural, and cognitive associations. In the present study, we have four aims: (1) provide a review of miniaturization as it relates to ecology and neuroanatomy, (2) identify clades of miniaturized lizards throughout the squamate phylogeny as well as close relatives that are non-miniaturized, (3) gather ecological data from the literature for these species and perform a meta-analysis to determine whether miniaturized lizards converge in microhabitat use and habitat aridity, and (4) explore differences in gross brain morphology between one miniaturized and one

non-miniaturized species, illustrating potential evolutionary patterns in brain morphology that accompany miniaturization. Very few ecological data exist for miniaturized squamates, and even less is known about the intersection of brain morphology, sensory systems, and cognition. Through identifying miniaturized lizards in light of body size variation in the phylogeny and examining ecological and neuroanatomical correlates, we offer a starting point in characterizing a syndrome (or suite of traits) associated with miniaturization.

1.1. Trends in body size and defining miniaturization

There is a strong propensity for animals to increase in body size over evolutionary time, termed Cope's Rule (Rensch, 1948; Brown & Maurer, 1986). A number of selective advantages associated with this trend include a shift in diet to resources of higher availability (Damuth, 1993), increased physical ability in predator-prey and competitive interactions (Stanley, 1973), more stable metabolic and thermoregulatory processes (Speakman, 2005), an increase in longevity and reproductive success (Brown & Sibly, 2006), and enhanced cognitive ability (Rensch, 1956; Sol et al., 2005). Body size increase is far more common than the opposite trend because the fitness benefits frequently outweigh the costs associated with large body size (but counterbalancing selective pressures may impose limits for large body size; see Blanckenhorn, 2000). In addition, size increases within clades tend to occur gradually (Newell, 1949; Hallam, 1978; Alroy, 1998), whereas evolutionary decreases in body size may be relatively rapid (Hanken & Wake, 1993; Caruso et al., 2014). For example, when exposed to acidic freshwater conditions, fish undergo strong selection for early maturation, high growth rates, and stress-mediated metabolic shifts, resulting in drastic reductions in body size (MacColl et al., 2012; Esin et al., 2020).

Body size decrease is typical in the evolution of extremely small taxa, often referred to as 'miniaturization', but it also occurs within clades of large-bodied animals. In discussions of size reductions, it is important to delineate these two intertwined processes. The more general, 'phyletic size decrease' or 'phyletic dwarfism', is defined as a proportional decrease in body size within a lineage (Gould & MacFadden, 2004). Early studies of extant and fossil mammals attracted attention to this phenomenon, illustrating the evolution of substantially smaller body sizes from a larger-bodied ancestor, e.g., in primates (Ford, 1980; Shea & Gomez, 1988; Montgomery

& Mundy, 2013), mammoths (Vartanyan et al., 1993; Herridge & Lister, 2012), elephants (Hooijer, 1951; Lyras, 2018), rhinoceroses (Prothero & Sereno, 1982), hippos (Simmons, 1988; Weston & Lister, 2009), horses (MacFadden, 1986; Gould & MacFadden, 2004), sloths (Anderson & Handley, Jr., 2002), sauropods, (Sander et al., 2006; Stein et al., 2010; Grellet-Tinner et al., 2012), and emus (Thomson et al., 2018). Hypotheses for size reductions of these large animals include adaptive changes in response to resource limitation, reduced levels of interspecific competition and predator release — all common but not exclusive to island habitats (Heaney, 1978; Lomolino, 1985; Palkovacs, 2003, Meiri et al., 2011). However, the very same selective pressures have been invoked to explain gigantism, presumed to act differently on organisms of differing body sizes and ecologies (Case, 1978; Marquet & Taper, 1998; Anderson & Handley, Jr., 2002).

In comparison to dwarfism in large-bodied taxa, transitions from the small to the extremely small can more easily go unnoticed. Taxonomic groups with small body size comprise a greater number of undescribed species (Diamond, 1985; Gaston, 1991; Cooper et al., 2006; Jones et al., 2009) despite smaller animals having higher diversification rates (Mooers & Harvey, 1994; Bromham et al., 1996; Fontanillas et al., 2007; Feldman et al., 2016). Second, in phylogenies based on morphology, homoplasies contribute to errors in species placement (Hanken & Wake, 1993; Rüber et al., 2007; Fröbisch & Schoch, 2009; Gamble et al., 2011), further exacerbated by similarities between diminutive adults of one species with juveniles of another (Pérez-Ben et al., 2018). By the late twentieth century, taxonomic work on small-bodied species had for instance revealed over 30 independent origins of significant body size reductions in fishes (Weitzman & Vari, 1988; Costa & Le Bail, 1999) and at least 10 in plethodontid salamanders (Wake, 1992). Although unquantified, body size decreases are widespread in insects, the smallest and largest of which differ in body size by more than three orders of magnitude (Grebennikov, 2008; Polilov, 2016).

At very small body sizes, developmental and anatomical constraints impose accentuated or novel selective pressures shaping biological processes (Polilov, 2015). Under this rationale, we define a second phenomenon, 'miniaturization' as an extreme reduction in body size that is accompanied by anatomical or ecological changes that deviate from scaling patterns across larger body sizes (Hanken & Wake, 1993; Doughty, 1996; Yeh, 2002; Maglia et al., 2007). Miniaturization is a subset of phyletic dwarfism, involving a

decrease in body size beyond a certain threshold at which marked changes occur to maintain organismal function, i.e., constraints owing to small absolute body size. Such a threshold likely varies across clades due to fundamental differences in anatomical organization or bauplan (Hanken & Wake, 1993). Formalizing an explicit framework for miniaturization is essential to examine the process in a phylogenetic context and across disparate clades of animals. By our definition, the objective changes from determining whether ecological or biological correlates with miniaturization exist, to identifying those correlates as evidence for miniaturization. Paradoxically, studies yet to uncover patterns with respect to miniaturization will entail the a priori assumption that miniaturization in a lineage has already occurred. However, unless scaling patterns support the hypothesis that a certain taxonomic group is miniaturized, the term will be inconclusive for even the most diminutive animals.

1.2. Constraints of miniaturization on the brain

In conjunction with miniaturization is the implication that there is a lower limit for how small an animal can become, a point at which the costs of further reductions in anatomy supersede the advantages of small size through impeding functionality (Beutel & Haas, 1998; Grebennikov, 2008; Polilov, 2008). For the smallest parasitic wasps, many of which are eclipsed in size by some *Paramecium* at under 300 μm (Polilov, 2015), small size occurs near the minimum theoretical thresholds of neuron size, axon diameter, and dendritic complexity within the brain (Makarova & Polilov, 2013a, b, 2017a, b). At this scale, ion-channel noise and energy consumption pose significant problems for information processing and signal transmission (Faisal et al., 2005; Niven & Farris, 2012), which are alleviated by the use of graded depolarizations (Chittka & Niven, 2009), multifunctional neurons (Niven & Chittka, 2010), 'matched filters' (Wehner, 1987), and anucleate neurons (Polilov, 2012). Though changes in neuronal features have been described in miniaturized tetrapods (e.g., Hanken, 1983; Roth et al., 1995), it would be ill-conceived to posit that molecular and cellular mechanisms limit size in the same fashion as in the smallest insects. Thus, a critical component of miniaturization is that limiting aspects are not ubiquitous in their constraints across clades of varying body sizes and bauplans.

Nevertheless, morphological changes in the brain remain relevant to both insects and vertebrates alike. Considering the entirety of body sizes within

closely related groups of animals, brain mass varies predictably with body mass in a trend known as Haller's rule, with smaller animals having relatively larger brains (Rensch, 1948; Striedter, 2005). Interestingly, Haller's rule seems to hold irrespective of whether taxa have undergone a size increase and/or decrease. That is, a shark that fluctuates in body size throughout its evolutionary history will have a brain/body mass ratio that exhibits coordinated changes along the trend line for sharks (Yopak et al., 2010). Robust patterns of negative allometry between body and brain mass were postulated to be the result of a trade-off between the metabolic costs of nervous tissue and functional output (Eberhard & Wcislo, 2011), and some explanatory power was afforded to comparisons of the relative proportions of brain regions, e.g., the expansion of the mammalian neocortex and its role in higher cognition (Riling & Insel, 1999). Still, a major assumption was that brain regions are comparable per unit of mass, yet concurrent histological studies indicated this was not the case (Tower, 1954; Haug, 1987; Stolzenburg et al., 1989).

Miniaturized animals tend to follow the same clade-specific scaling rules governing larger body sizes, and relative brain size increases as body size decreases (Striedter, 2005; Eberhard & Wcislo, 2011; Polilov & Makarova, 2017). Differences in the allometric coefficients and intercepts likely enable certain groups of animals to become smaller than others, described as grade changes in brain-body allometry (Eberhard & Wcislo, 2011). Hence, clades that allocate a small proportion of body mass to the brain, together with a lesser relative gain in brain mass per reduction in body size, reach smaller absolute body sizes. Tardigrades and kinorhynchs, with brains occupying as little as 1% of the body volume, reach significantly smaller sizes than the smallest arthropods (Barnes et al., 2009; Gross et al., 2019; Eberhard & Wcislo, 2011). Among tetrapods, salamanders devote a smaller fraction of total body mass to the brain than mammals and have a smaller allometric coefficient, facilitating more diminutive absolute body sizes (Hill & Smith, 1981; Hanken & Wake, 1994; Eberhard & Wcislo, 2011; Roth-Alpermann & Brecht, 2016). Only two genera of parasitic wasps have been found to deviate from clade-specific allometries. Intraspecific variation within *Trichogramma evanescens* revealed an isometric brain-body size relationship, and in *Nasonia vitripennis* as body size decreases, wasps switch from allometric to isometric scaling (van der Woude et al., 2013; Groothuis & Smid, 2017). In other words, smaller wasps had less neural tissue than expected for

their body size, suggesting that the energetic costs of increased relative brain size outweigh its potential cognitive surplus (van de Woude et al., 2018).

For very small species to adhere to the strict allometric scaling rules of their clades, drastic changes in gross morphology ensue. It is often in the interaction between brains and the surrounding structural architecture that both counterparts assume novel configurations for organisms to accommodate proportionally larger brains in smaller head capsules. In vertebrates, miniaturized species exhibit changes in ossification of the skull and an expanded braincase. Evidence includes a fused premaxilla and braincase bones in gekkotans (Daza, 2008; Gamble et al., 2011), deossification and more spherical braincases in hummingbirds (Ocampo et al., 2018), fused nasal bones, reduced palatines, and unfused prootics and exoccipitals in anurans (Yeh, 2002; Maglia et al., 2007), absence of ossified skull elements in salamanders (Hanken, 1984), widely-spaced dermal elements and retention of cartilaginous elements in caecilians (Wake, 1986), and resorption of cranial dermal bones in fishes (Weitzman & Vari, 1988; Rosa et al., 2014). Whereas changes in conformation of the braincase directly influence the volume of the cavity where the brain sits, why various elements of the skull undergo deossification is more difficult to explain. Reduction of skeletal elements throughout the body, such as the carpals and phalanges (Hanken, 1985; Yeh, 2002), have given credence to the hypothesis that deossification is a consequence of miniaturization, arising from truncated development or stunted growth rate (Hanken, 1993; Hanken & Wake, 1993). Alternatively, skull deossification could provide greater cranial kinesis and space for enlarged jaw adductor musculature to achieve adequate gape and bite force in feeding (Rieppel, 1984; Bhullar & Bell, 2008; Handschuh et al., 2019). Hyperossification, on the other hand, might be a compensation for structural weakening of the skeleton due to reduced ossification (Hanken, 1993; Maglia et al., 2007; Fröbisch & Schoch, 2009). Generally, these changes in skeletal morphology are convergent across extremely small vertebrates, and they are frequently used to classify taxa as miniaturized.

As skulls become smaller and take on new forms, brain morphology is not unvarying. With increasing relative metabolic costs of neural tissue and decreasing available space, many miniaturized species have brains that take on different shapes and positions. In very small plethodontid salamanders, the forebrain is located more posteriorly and becomes more triangular due to close contact with proportionally large eyes and nasal capsules (Roth et

al., 1990). Other vertebrate groups probably have analogous changes, but the majority of studies on miniaturized taxa have been devoted to skeletal anatomy. The brains of miniaturized arthropods have received more attention and feature extreme accommodations. In insects, the brain invades the thoracic and abdominal regions, ganglia become more concentrated and oligomerized, and various aspects of the nervous system are asymmetrical (reviewed in Polilov, 2015). The central nervous system of miniaturized spiders also overflows from its ancestral position, extending from the cephalothorax into the coxae and pedipalps (Quesada et al., 2011). To minimize spatial constraints, the brains of both vertebrates and arthropods more tightly fills the available volume within the head cavity (Hanken, 1983; Beutel & Haas, 1998; Randolf & Zimmermann, 2019).

1.3. *Miniaturization and sensory systems*

In evolutionary reductions in body size, two opponent processes are thought to govern relative brain size: the energetic requirements for maintaining and operating excess neural tissue, and an organism's information processing and behavioural capabilities (Burns et al., 2011; Niven & Farris, 2012). Regions of the brain responsible for processing sensory information, critical to an organism's life history, follow conservative negative allometries, in contrast to other brain regions which may be comparatively atrophied. In bolitoglossine salamanders, visual and visuomotor centres such as the thalamus, pretectum, and the optic tectum are 25% larger in miniaturized species at the expense of a reduced forebrain and tegmentum (Roth et al., 1990). Large eye size, extensive retinotectal projections, and higher tectal neuron densities are also present in bolitoglossines, all of which rely on visual acuity to direct their projectile tongues when capturing prey (Roth et al., 1988, 1997). Maintenance of sensory systems is evident in miniaturized insects as well, where certain sensory systems are retained while others degenerate. Insect parasitoids provide remarkable examples of this trade-off, because they have highly specific tasks during a short-lived imago life stage. In strepsipterans, visuomotoric centres are preserved at the loss of mouthparts and antennae, allowing them to perform coordinated jumps to enter their hosts, but rendering them unable to feed and smell (Beutel et al., 2005). Conversely, parasitic wasps have a large lateral protocerebrum and antennae, which play an important role in processing olfactory stimuli and locating hosts, but they have smaller relative volumes of the optic

lobes (Makarova & Polilov, 2013b). Although sensory systems relevant to an organism's essential behaviours are relatively large in miniaturized animals, they are still smaller in absolute size, prompting the question of whether behavioural capacity or precision is reduced (the 'size limitation hypothesis'; Eberhard, 2007). Fewer neurons, reduced dendritic complexity, and smaller sensory organs may negatively affect behavioural performance, and loss of redundancy of neural circuits may cause behaviours to be less reliable under a wider array of conditions (Chittka & Niven, 2009; Niven & Farris, 2012). Behavioural work has revealed relationships between brain size and behavioural output (Cole, 1985; Changizi, 2013; Snell-Rood et al., 2009; Palavalli-Nettimi & Narenda, 2018; van der Woud et al., 2018). However, there are numerous examples of minute taxa performing comparable complex behaviours as in their larger relatives (Greenspan & van Swinderen, 2004; Beutel et al., 2005; Eberhard, 2007; Makarova & Polilov, 2013b; Randolf et al., 2017). Evidence to support the size limitation hypothesis remains equivocal due to the difficulty in establishing objective criteria to characterize behavioural complexity and the limited scope of metrics used thus far (Healy & Rowe, 2006; Eberhard, 2007; Eberhard & Wcislo, 2011).

As alluded to previously, reduction in brain size and the surrounding cranial architecture that constrains it does not evolve in isolation. An organism's ecology and life history are important factors driving brain evolution and sensory organ elaboration. The shape, size, and composition of major brain regions have been linked to locomotor mode, microhabitat, diet, cognition, and sociality in many taxonomic groups (Pérez-Barbería, 2007; Olkowicz et al., 2016; Hoops et al., 2017; DeCasien et al., 2017; Macrí et al., 2019). Miniaturization adds an extra dimension to this evolutionary association. Size reductions can allow exploitation of highly specialized niches, such as in meiofaunal organisms that inhabit the spaces between sediment grains (Rundell & Leander, 2010; Gross et al., 2019), small bats that roost inside pitcher plants in a putative mutualism (Schöner et al., 2017), and the evolution of parasitic lifestyles (Poulin, 2005; Minelli & Fusco, 2019). Morphological novelty is another common result of developmental changes in miniaturized animals, which may be co-opted for modified or new behaviours (Britz & Conway, 2009; Lautenschlager et al., 2018; Polilov et al., 2019). However, just as changes in body size can promote niche expansion and morphological innovation, it can also have the opposite effect. For instance, miniaturized terrestrial amphibians may be restricted to humid environments due to a

greater susceptibility to desiccation (Lourenço-de-Moraes et al., 2018), and small body size inhibits the use of many sensory modalities in oceanic environments (Martens et al., 2015). In sum, miniaturization simultaneously imposes constraints on brain evolution and influences the assemblage of stimuli that an organism is exposed to. Certain morphologies and sensory systems may only be functionally relevant at extremely small body sizes, while others lose their utility. Because cognitive processes are dependent on a species' ecology and sensory systems, miniaturization is therefore intimately linked to animal cognition.

1.4. Squamates as models to study miniaturization

Squamates are good candidates to explore the interface of miniaturization, ecology, and the brain. Approximately 15.5% of lizards, comprising more than 900 species, exceed the minimum body mass threshold of the smallest mammals and birds currently known (Hill & Smith, 1981; de la Hera, 2009; Roth-Alpermann & Brecht, 2016; Feldman et al., 2016). There is also substantial variation throughout the squamate phylogeny. Lizards range from under 33 mm in total length and 0.14 g in dwarf geckos (*Sphaerodactylus ariasae*; Hedges & Thomas, 2000) to over 3 m and 81.5 kg in the Komodo dragon (*Varanus komodoensis*; Jessop et al., 2006). Snakes have a similar size disparity, the smallest threadsnakes being under 10 mm and 0.5 g (*Leptotyphlops* spp.; Hedges, 2008) to sizes upwards of 6 m and 75 kg in wild reticulated pythons (*Malayopython reticulatus*; Shine et al., 2006). Body size reductions are pervasive in many squamate lineages, which indicates a strong possibility for repeated miniaturization events (Feldman et al., 2016). Furthermore, studies have already described convergent changes in skull ossification and the relative positions of bones, spanning across at least 21 squamate families (Vallejo Pareja, 2018). Osteological rearrangements include closure of post-temporal fenestrae, a posterior shift of the occipital condyles, and a change in overall skull shape involving proportionally large otic capsules and braincase, the latter aligning adjacent to the skull roof (Rieppel, 1984; Vallejo Pareja, 2018). Although these features are not all present together in a given taxon, extremely small squamates usually have one or a combination of novel skull morphologies, supporting the notion that osteology is a reliable trait for characterizing squamate species as miniaturized. The conceptual scope of miniaturization in squamates is thus far limited to skeletal morphology, and questions remain as to how extreme size

reductions impact brain anatomy and ecology. For example, do miniaturized squamates exhibit shifts in microhabitat use as in amphibians or changes in brain shape akin to salamanders? More generally, does the evolution of miniaturization across different vertebrate groups entail convergent trait changes due to size constraints? Our study contributes data to address this gap in lizards, testing for ecological correlates through phylogenetic comparative methods, and touching upon neuroanatomy using micro-CT scans of two gecko species that have a large size disparity.

2. Methods

2.1. Literature review

To quantify ecological differences between miniaturized and non-miniaturized squamates, we first chose a threshold of body size below which a taxon is considered miniaturized. Existing osteological data of squamates indicate that at skull lengths less than 15 mm, the diameter of the neurocranium increases disproportionately along with rearrangements of the surrounding skull bones (Rieppel, 1984; Vallejo Pareja, 2018). This characteristic has been used in defining miniaturization in squamates (Rieppel, 1984). In a study that collected head and body lengths of 610 lizard species, all taxa with head lengths less than 15 mm had a corresponding snout–vent length (hereafter referred to as SVL) less than 40 mm (Scharf & Meiri, 2013). Therefore, an SVL of 40 mm was designated as the upper threshold for a lizard species to be miniaturized. Although body sizes above 40 mm do not abide by our conservative threshold for miniaturization, we cannot surmise that all such taxa do not share similar constraints and anatomical characteristics with miniaturized taxa. The lower threshold for a non-miniaturized species was instead set at 100 mm SVL, a body size greater than the average for all lizards (96.7 mm; Feldman et al., 2016). Because snakes and limbless lizards exhibit high variation in head to body proportion (Pough & Groves, 1983; Brandley et al., 2008), we chose to restrict the scope of our study to limbed lizards. The most comprehensive study on squamate body sizes includes body lengths of 6275 lizard species, 8% of which (a total of 501 species) have a maximum SVL less than or equal to 40 mm (Table 1; Feldman et al., 2016). We matched taxa in this dataset with those in the squamate phylogeny produced by Tonini et al. (2016), resulting in 6197 total species of lizards with known body sizes and phylogenetic relationships. We then mapped the continuous trait of maximum SVL across the squamate

phylogeny, calculating maximum likelihood estimates of ancestral states at internal nodes and interpolating intermediate states using the function *contMap* in the package *phytools* (Felsenstein, 1985; Revell, 2011, 2013).

Because we are interested in testing whether miniaturized lizards have undergone convergence with respect to ecological traits, it would not be informative to focus within diverse clades of miniaturized species which have likely descended from a single miniaturized ancestor. Instead, we produced a list of species pairs that include one miniaturized species and its closest non-miniaturized relative. First, for every miniaturized species, we determined its closest non-miniaturized relative, that is, a taxon with a maximum SVL $\geqslant$ 100 mm. If multiple non-miniaturized species were of equal patristic distance from a miniaturized species, the non-miniaturized species with the smallest SVL, and therefore closest to 100 mm, was chosen. We opted against choosing the largest non-miniaturized species to avoid including taxa that have experienced an evolutionary increase in body size. Next, miniaturized species that shared the same non-miniaturized outgroup were grouped together, and only the miniaturized species with the smallest SVL was selected. This does not preclude species pairs from being nested within other pairs. By choosing the smallest miniaturized species, we ensured sampling of taxa that are the outcomes of the most drastic body size reductions in evolutionary history of lizards. Through this methodology, we arrived at 44 pairs of miniaturized and non-miniaturized species, broadly spanning the lizard phylogeny (Figure 1). Moreover, due to the selection criteria, body size variation was low within our sampled miniaturized (32.4 ± 6.0 mm) and non-miniaturized (109.2 ± 15.4 mm) species.

We conducted a literature review to characterize ecological traits of the 88 selected species. Two categorical variables were created: microhabitat and aridity. Microhabitat was described as (1) arboreal; perching on vegetation above the ground, (2) rupicolous; residing on rocky substrates, (3) surface-dwelling; may be on a variety of substrates, (4) fossorial; burrowing under the ground, and (5) semi-aquatic. The last category, semi-aquatic, was given to species that have evidence of inhabiting or exclusively residing immediately adjacent to aquatic environments. Aridity reflects the moisture content and habitat type of the large-scale surrounding environment. Four categories were chosen: (1) humid; e.g., tropical, evergreen, cloud, mangrove, palm grove, and riparian forests, wetlands and marshes, (2) mesic; e.g., bushland, woodland, deciduous, temperate, and dry forests, (3) semi-arid; e.g., savannas, grasslands, mulga, plains, shrubland, and rocky habitats
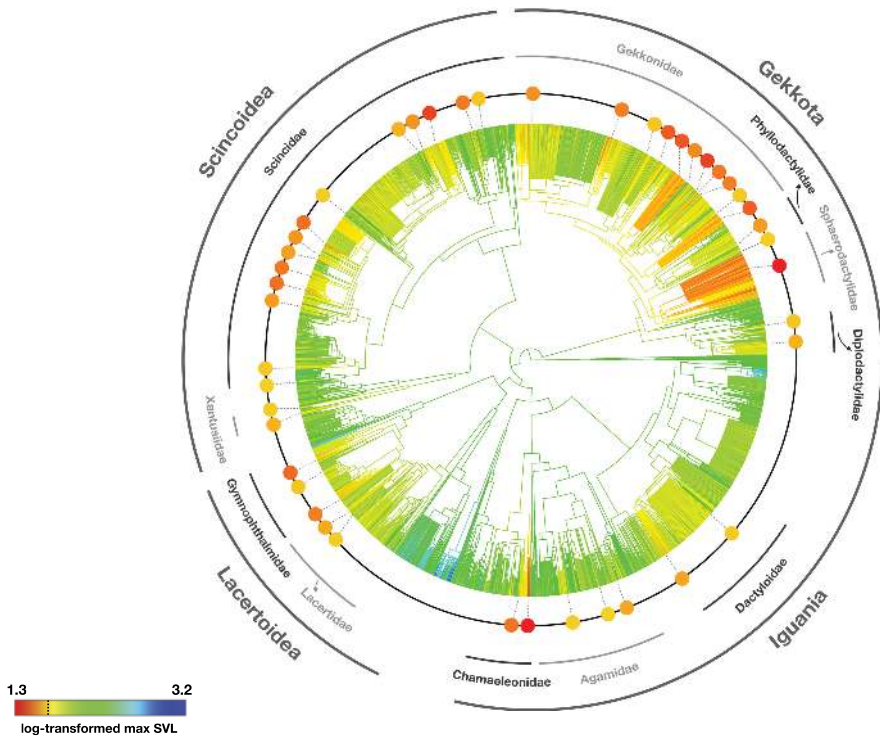
Figure 1. Lizard phylogeny showing log-transformed maximum SVL for 6197 species. Body size data were drawn from Feldman et al. (2016), phylogenetic relationships were obtained from Tonini et al. (2016), and ancestral state reconstruction was performed using the R package *phytools* (Revell, 2011, 2013). The dotted line along the colour scale represents a cut-off value of 40 mm, which was used in the criteria for species selection. Coloured circles denote miniaturized species, a total of 44, included in our phylogenetic model.

with sparse vegetation, and (4) arid; e.g., deserts, semi-deserts, and dunes. If a species inhabits several aridity zones or utilizes multiple microhabitats, the category most often documented in the literature was used. If microhabitat and aridity data were unavailable for a given species, we selected the next candidate species that upholds our sampling criteria and adheres to the two size thresholds. Extinct species were excluded when gathering trait data.

2.2. Statistical analysis

Our objective was to determine whether miniaturized and non-miniaturized species have different assemblages of ecological traits. Prior to analysis, we combined surface-dwelling, fossorial, rupicolous, and semi-aquatic cat-

egories of microhabitat use into one category: terrestrial. This decision was made for the purposes of increasing statistical power given our sample size, and because the relatively few observations cited for many species afforded little confidence in discrimination between those categories (see Table S1). The four aridity categories remained unchanged. Thus, our model included a two-level variable for microhabitat (terrestrial vs. arboreal) and a four-level variable for aridity. Statistical analysis was conducted using a Bayesian inference framework, performed in R version 4.0.2 (R Core Team, 2020). Using the function *brm* in the *brms* package, we ran a zero-intercept model with aridity and microhabitat as predictors of a binary variable indicating whether or not a taxon was miniaturized (Bürkner, 2017). All summary statistics for Bayesian models were performed using the *bayestestR* package (Makowski et al., 2019a).

Bayesian models generate posterior distributions of parameter estimates by constructing Markov chains (MCMC) conditioned on priors, which entail distributions of the initial values for each parameter. For measures of uncertainty, we summarized posterior distributions using medians and 89% highest posterior density intervals (*HDI*s), thought to be more stable than 95% intervals (Kruschke, 2014). Effect existence was quantified through the probability of direction (*pd*), which represents the certainty of an effect being positive or negative (Makowski et al., 2019a). As an index for significance, we report the percentage of the 89% HDI that falls within a range of negligible effect size, the latter termed the region of practical equivalence (ROPE). There is currently a lack of consensus for defining ROPE range limits. As suggested by Kruschke & Liddell (2018), we select a standardized difference of $\pm\, 0.1$ multiplied by $\sqrt{3}/\pi$, appropriate for logistic models that contain parameters expressed in log odds ratios. Percentages of HDIs that cover the ROPE are used in hypothesis teting, such that values less than 2.5% are significant and reject the null hypothesis, and values greater than 97.5% indicate a negligible magnitude and acceptance of the null hypothesis (Makowski et al., 2019b). Percentages in between the two thresholds are of undecided significance.

To account for phylogenetic nonindependence between species, we pruned the phylogeny (Tonini et al., 2016) to the 88 species of interest, resolved polytomies using the *multi2di* function in the *phytools* package (Revell, 2011), then inputted a variance-covariance matrix into the model generated through the *vcv* function in the *ape* package (Paradis & Schliep,

2019). Uninformative priors were specified using a normal distribution with a mean of zero and a standard deviation of one. The model was first run with four chains of 1000 MCMC iterations and 50% burn-in to assess adequate sampling, normality of posterior distributions, and convergence of chains. After checking diagnostics, we ran the model again with four chains of 200 000 iterations, half of which were burn-in, resulting in posterior distributions of 100 000 samples per parameter as well as their 89% HDIs. An interaction between microhabitat and aridity was initially incorporated; however, all posterior distributions of the interaction terms were nonsignificant, so the model was re-run with additive predictor variables. The full model with additive predictor variables yielded one divergent transition after warm-up. To prevent post-warmup divergences, we coerced smaller step sizes by increasing the *adapt_delta* value from 0.8 to 0.99 (Bürkner, 2017). All data and R code for models and analysis can be accessed at doi:10.17605/OSF.IO/US6P9.

2.3. Brain morphology

Diffusible iodine-based contrast-enhanced computed tomography (diceCT) is at the forefront of techniques for high-resolution characterization of soft tissues (Gignac et al., 2016). Using scans of two geckos, *Sphaerodactylus nicholsi* (RT 14402) and *Gekko smithii* (FMNH 267868), we created visualizations of the brain-skull interface to explore preliminary differences in gross brain morphology between miniaturized and non-miniaturized lizards. These two gekkotans were selected because their SVLs and skull lengths are compatible with our sampling criteria for miniaturized and non-miniaturized species and also on the basis of availability of scans. SVL was measured as the length from the tip of the snout to the cloaca, and skull length was defined as the length from the anterior tip of the premaxilla to the posterior end of the braincase. Each lizard underwent two scans, the first pertaining to osteology and the second of the iodine-stained soft tissues. All scans were performed at the University of Texas High-Resolution X-ray CT Facility in Austin, Texas in July–October 2018 and May–July 2019. To increase resolution, each was scanned in six to eight parts, then stitched together in Xradia. Both specimens were stained in 2.5% Lugol's iodine, *S. nicholsi* for two days and *G. smithii* for approximately 32 days.

Using the software Avizo Lite (version 2019.3), we first registered the skeletal and iodine scans together through iterative optimization algorithms

for alignment in 3D space. Primarily owing handling time and exposure to air, slight changes in the relative positions of a specimen's internal structures between scans obviates perfect alignment. Nevertheless, to maintain integrity of shape, we only used rigid transformations, i.e., solely translation and rotation. We then segmented the skull, cranial endocast, and brain of each gecko, using voxel intensity thresholds and manual boundary limits as needed (see Figure S1 that can be accessed at 10.6084/m9.figshare. 14797800). Skull bones were taken into consideration from the tip of the snout until the superior process of the first cervical vertebra, and cranial endocasts were defined as the entire cavity within the braincase. Brain tissue included the three primary brain vesicles (prosencephalon, mesencephalon, and rhombencephalon), and the following subdivisions were also isolated: olfactory bulbs and tracts, telencephalon, diencephalon, optic tecta, and cerebellum. Optic nerves of the diencephalon and cranial nerves of the hindbrain were severed along the contours of adjacent brain regions, and brain segmentation terminated at the junction of the brain stem and spinal cord. We calculated the volumes of each brain vesicle, their subdivisions, and the cranial endocasts. We also report the proportion of the cranial endocast volume occupied by the brain and each brain region as a percentage of total brain volume. Volumetric measurements of other subdivisions within the midbrain and hindbrain (e.g., pons and medulla oblongata) were not quantified due to limitations of scan resolution. For visualization, we rendered isosurfaces for brains, and skulls were superimposed at low opacity, all of which underwent unconstrained smoothing, which reduces the variability of triangle orientation on the exterior surface of the polygonal mesh.

3. Results

Ancestral state reconstruction revealed substantial lability in body size throughout the lizard phylogeny, with miniaturized species present in four out of the five lizard superfamilies and 11 of 37 lizard families (Table 1; taxonomy based on Uetz et al., 2020). Miniaturized species spanned the majority of the phylogeny, notable exceptions being Anguimorphs and non-dactyloid iguanian pleurodonts (Figure 1). Gekkonidae and Sphaerodactylidae had the greatest numbers of miniaturized species, 178 and 154, respectively, followed by Scincidae with 100 species. Among genera, *Sphaerodactylus* exhibited the greatest diversity of miniaturized taxa, comprising

Table 1.

Representation of miniaturized lizard species across various taxonomic levels.

(Super-)Family	Miniaturized species	Genera
Gekkota		
Diplodactylidae	3	*Dierogekko, Strophurus*
Gekkonidae	178	*Afroedura, Alsophylax, Altiphylax, Cnemaspis, Cryptactites, Cyrtodactylus, Cyrtopodion, Dixonius, Ebenavia, Gekko, Gehyra, Goggia, Hemidactylus, Hemiphyllodactylus, Lepidodactylus, Luperosaurus, Lygodactylus, Matoatoa, Mediodactylus, Microgecko, Nactus, Narudasia, Pachydactylus, Phelsuma, Stenodactylus, Tropiocolotes, Trigonodactylus, Urocotelydon*
Phyllodactylidae	5	*Asaccus, Garthia, Homonota, Phyllodactylus*
Sphaerodactylidae	154	*Coleodactylus, Gonatodes, Lepidoblepharis, Pristurus, Pseudogonatodes, Saurodactylus, Sphaerodactylus, Quedenfeldtia*
Iguania		
Agamidae	3	*Ceratophora, Diporiphora, Sitana*
Chamaeleonidae	16	*Brookesia, Palleon, Rhampholeon*
Dactyloidae	15	*Anolis*
Lacertoidea		
Gymnophthalmidae	20	*Alopoglossus*, Amapasaurus, Arthrosaura, Cercosaura, Colobosauroides, Gymnophthalmus, Leposoma, Loxopholis, Procellosaurinus, Psilops, Vanzosaura*
Lacertidae	3	*Eremias, Ophisops*
Scincoidea		
Scincidae	100	*Ablepharus, Amphiglossus, Calyptotis, Cryptoblepharus, Ctenotus, Emoia, Eroticoscincus, Eutropis, Flexiseps, Geomyersia, Janetaescincus, Lygisaurus, Lampropholis, Leptosiaphos, Lerista, Lipinia, Lygosoma, Madascincus, Menetia, Morethia, Nannoscincus, Notoscincus, Panaspis, Paracontias, Parvoscincus, Proablepharus, Pygmaeascincus, Ristella, Saproscincus, Scelotes, Scincella, Sphenomorphus, Tribolonotus, Tropidophorus, Tytthoscincus*
Xantusiidae	4	*Cricosaura, Lepidophyma, Xantusia*

Number of miniaturized species listed is with regard to the family level. The asterisk for *Alopoglossus* indicates that the genus, together with *Ptychoglossus*, has been elevated to family status (Alopoglossidae: Goicoechea et al., 2016; Hernández Morales et al., 2020).
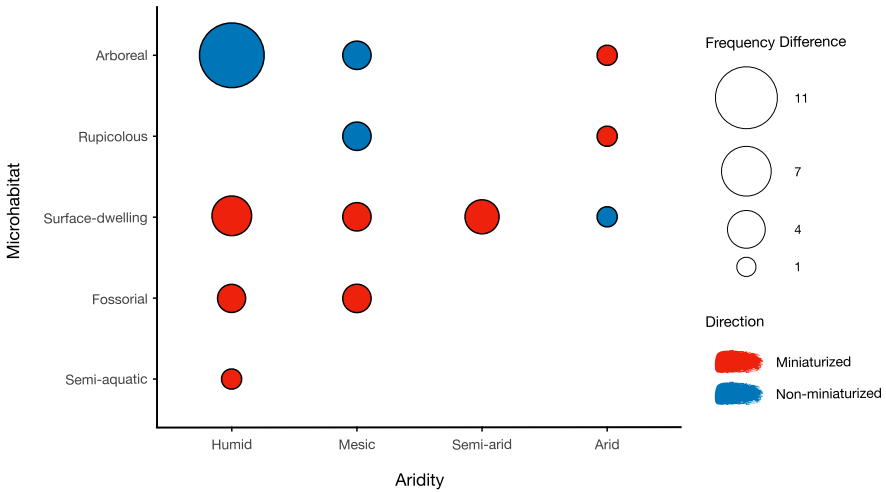
Figure 2. Differences in frequency between 44 miniaturized and 44 non-miniaturized lizard species, categorized by ecological traits (microhabitat and aridity). Circle size represents the magnitude of the difference. Red indicates a greater number of miniaturized species, and blue indicates a greater number of non-miniaturized species.

101 miniaturized species which accounts for over one fifth of all miniaturized lizards (Table 1). As previously stated, through generating one-to-one pairings of miniaturized and non-miniaturized species, we arrived at 44 species pairs as a phylogenetically-informed pool of species for our subsequent model. Data collection of ecological traits from the literature revealed a dearth of natural history data for miniaturized species. The majority of those data was found in descriptions of a few individuals encountered in biodiversity surveys and at times, solely in taxonomic descriptions of type specimens or citations thereof. The lack of data likely reflects both the apparent rarity of miniaturized species and the collection challenges associated with extremely small body sizes. Classification of miniaturized and non-miniaturized species illustrated variation in ecology across both groups (Figure 2; detailed descriptions provided in Table S1, that can be accessed at 10.6084/m9.figshare.14797800).

Due to the high resolution of our two ecological variables given our sample size, with 20 possible combinations, the intersection of many microhabitat and aridity categories lacked representation in both miniaturized and non-miniaturized groups. Therefore, for modelling we reduced the five-level microhabitat variable into two levels: arboreal and terrestrial. In the additive

Bayesian linear model, terrestrial microhabitat yielded a 0.988 probability of being positive (median = 0.891, SD = 0.403, 89% HDI [0.249, 1.532]), a significant predictor of miniaturization (0% in ROPE). Considering arboreal microhabitat as a reference level, mesic (*pd* of 0.806, median = −0.434, SD = 0.507, 89% HDI [−1.246, 0.370]; 22.05% in ROPE), semi-arid (*pd* of 0.677, median = −0.218, SD = 0.476, 89% HDI [−0.979, 0.540]; 30.24% in ROPE), and arid (*pd* of 0.699, median = −0.330, SD = 0.635, 89% HDI [−1.349, 0.679]; 22.14% in ROPE) environments were all of uncertain directionality and undecided significance. Among the four aridity conditions, only the humid category showed a trend, though a non-significant one, having 0.944 probability of being negative (median = −0.645, SD = 0.408, 89% HDI [−1.295, −0.005]; 8.02% in ROPE). In sum, miniaturized species occupied terrestrial microhabitats more often than non-miniaturized species, and there may be a tendency for arboreal non-miniaturized species to reside in humid environments (Figure 2).

Micro-CT scans of the brains of one miniaturized gecko species (*Sphaerodactylus nicholsi*, SVL: 18.26 mm, skull length: 5.153 mm) and one non-miniaturized species (*G. smithii*, SVL: 142.6 mm, skull length: 39.46 mm) revealed many dissimilarities in gross brain morphology (Figure 3). Volumetric measurements of brain regions are reported in Table 2. Due to limited sample size ($N = 2$), rather than statistically evaluating whether differences exist, we instead enumerate distinctions in overall brain architecture between the two species. As expected, the brain of *S. nicholsi* occupied a greater proportion of the cranial endocast than in *G. smithii*, filling 26.8% more volume of the available endocranial space (Figure 4). The brain of *S. nicholsi* is markedly thicker, extending further in the coronal and sagittal planes, and overall, it is more rectangular, constrained by the surrounding soft and hard tissues. For one, the dorsal surface of the telencephalon and optic tectum is flattened due to contact with the skull roof. In contrast to *G. smithii*, the optic tectum projects above the telencephalon in *S. nicholsi*, owing to a downward slope of the parietal bones. The telencephalon of *S. nicholsi* in particular is shaped differently, following the contours of the eyes anteriorly and of the musculus pseudotemporalis superficialis of the jaw adductor muscles posteriorly. This results in a wider anterior portion of the telencephalon than in *G. smithii*. Considering the relative volumes of brain regions, the primary brain vesicles are similar between *S. nicholsi* and *G. smithii* (Table 2).
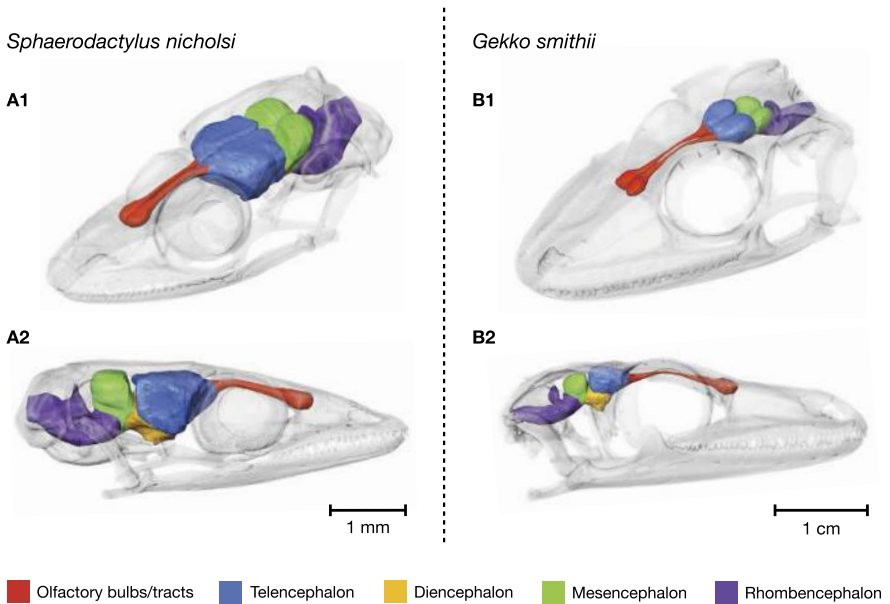
Sphaerodactylus nicholsi

A1

A2

Gekko smithii

B1

B2

1 mm

1 cm

■ Olfactory bulbs/tracts ■ Telencephalon ■ Diencephalon ■ Mesencephalon ■ Rhombencephalon

Figure 3. The brain-skull interface of one miniaturized (*Sphaerodactylus nicholsi*: A1, A2) and one non-miniaturized (*Gekko smithii*: B1, B2) gecko species, rendered from diceCT scans. Notches between the sclerotic ossicles of *S. nicholsi* were not discernible in the scans due to their small size and thinness; the entire sclerotic rings were smoothed for visualization purposes.

However, the subdivisions revealed three principal discrepancies. The miniaturized gecko, *S. nicholsi*, has smaller olfactory bulbs and tracts, a smaller cerebellum, and a larger telencephalon — 8.2% smaller, 3.4% smaller, and 9.0% larger in relative size, respectively (Table 2; Figure 3). Lastly, the entire brain of *S. nicholsi* is oriented differently relative to the body axis, rotated forward in the sagittal plane, and the eyes are displaced anteriorly within the skull, likely to accommodate a proportionally large volume of neural tissue in the forebrain.

4. Discussion

Although the phenomenon of miniaturization has received wide attention, the term has been used loosely to describe the evolution of extremely small body size or a generalized evolutionary decrease in body size (Avaria-Llatureo et al., 2012; Lee et al., 2014; Gross et al., 2019). In accordance with Hanken & Wake (1993), we argue that the term should exclusively refer to

Table 2.

Comparison of the relative volumes of brain regions between one miniaturized (*Sphaerodactylus nicholsi*) and one non-miniaturized (*Gekko smithii*) gecko species.

	Sphaerodactylus nicholsi		*Gekko smithii*	
	Volume (mm^3)	Percentage	Volume (mm^3)	Percentage
Cranial endocast	$2.079 \cdot 10^0$	–	$3.152 \cdot 10^2$	–
Brain	$1.269 \cdot 10^0$	61.0%	$1.147 \cdot 10^2$	36.4%
		(of endocast)		(of endocast)
Prosencephalon	$6.856 \cdot 10^{-1}$	54.0%	$6.103 \cdot 10^1$	53.2%
Mesencephalon	$2.729 \cdot 10^{-1}$	21.5%	$2.214 \cdot 10^1$	19.3%
Rhombencephalon	$3.103 \cdot 10^{-1}$	24.5%	$3.157 \cdot 10^1$	27.5%
Olfactory bulbs & tracts	$3.499 \cdot 10^{-2}$	2.8%	$1.266 \cdot 10^1$	11.0%
Telencephalon	$4.977 \cdot 10^{-1}$	39.2%	$3.465 \cdot 10^1$	30.2%
Diencephalon	$1.529 \cdot 10^{-1}$	12.0%	$1.371 \cdot 10^1$	12.0%
Optic tecta	$1.914 \cdot 10^{-1}$	15.1%	$1.578 \cdot 10^1$	13.8%
Cerebellum	$8.770 \cdot 10^{-3}$	0.7%	$4.649 \cdot 10^0$	4.1%

The percentages for total brain volume represent the proportion of cranial endocast volume occupied by the brain, whereas the percentages for brain subdivision volumes are calculated as each brain region divided by total brain volume. The three brain vesicles (prosencephalon, mesencephalon, and rhombencephalon) constitute the entirety of the brain, and the olfactory bulbs and tracts, telencephalon, and diencephalon account for all neural tissue within the prosencephalon. The optic tecta and cerebellum were the only subdivisions quantified from the mesencephalon and prosencephalon, respectively, due to resolution limitations of the micro-CT scan data.

taxa that undergo novel or accentuated changes in anatomy and/or ecology due to the constraints imposed by body size reduction. A central tenet of this definition is that compensatory changes alleviate the detrimental effects of small body size in the face of traits tightly constrained by evolutionary history or organismal function (Wake, 1986; Griffith, 2016). For example, metabolic rate scales predictably with cell size and body mass (Kozłowski & Konarzewski, 2004; Glazier, 2008; Starostová et al., 2009), but relative investment in tissues and heterochronic processes are highly labile, resulting in structural simplification in many miniaturized species (Hanken & Wake, 1993; Smith, 2003; Polilov, 2015; Ferreira Marinho, 2017). It is common for studies to choose a threshold of maximum body size for species to be considered miniaturized (e.g., Yeh, 2002; Toledo-Piza et al., 2014). However, these clade-specific thresholds are not necessarily biologically meaningful nor are they comparable across distantly related groups of animals. Anatomical data
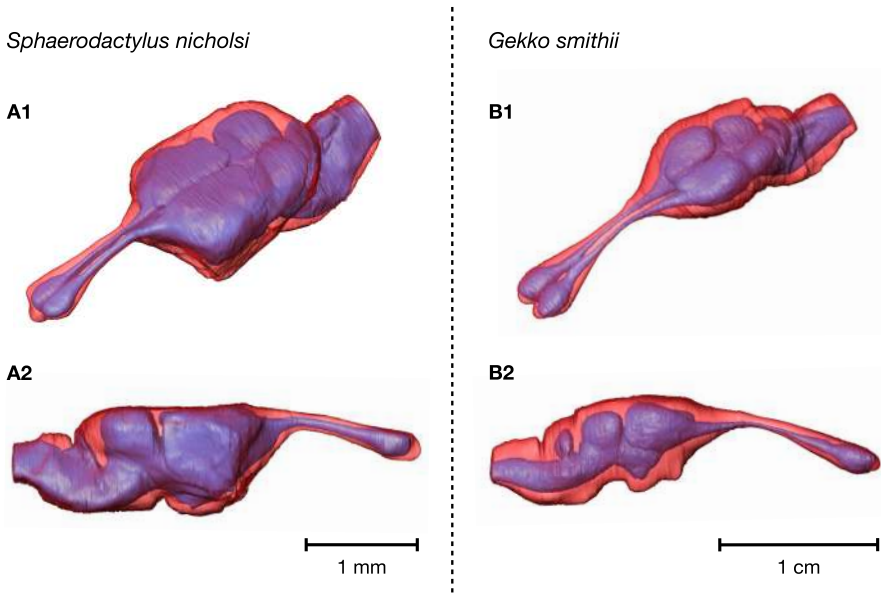
Sphaerodactylus nicholsi

A1

A2

1 mm

Gekko smithii

B1

B2

1 cm

Figure 4. Relative volumes of brains (blue) and cranial endocasts (semi-transparent red) of one miniaturized (*Sphaerodactylus nicholsi*: A1, A2) and one non-miniaturized (*Gekko smithii*: B1, B2) gecko species, rendered from diceCT scans.

are needed to support the hypothesis that a species is miniaturized, yet such data are only available for a small number of species. In this study, we use osteological evidence to inform a body size threshold for miniaturized lizards to explore ecological and neuroanatomical correlates.

Trait mapping and ancestral state reconstruction of body size across the lizard phylogeny provide strong evidence for the repeated evolution of miniaturization (Figure 1). Lizards have representation of miniaturized taxa in numerous lineages across the phylogeny and high diversity within miniaturized clades (Table 1), making this group fertile ground to evaluate the mechanisms driving miniaturization at different evolutionary time scales. Historically, studies of miniaturization in vertebrates have primarily focused on fish and salamanders, providing a foundation for the effect of extreme size reductions on anatomy, physiology, and life history (Weitzman & Vari, 1988; Roth et al., 1990; Hanken & Wake, 1993). We encourage the study of squamates as a parallel system to fish and salamanders for testing hypotheses about processes associated with miniaturization. If small body size is achieved via similar mechanisms, perhaps a syndrome (or suite of convergent

trait changes) exists for miniaturized vertebrates. Alternatively, differences in the evolutionary lability of traits between taxonomic groups may allow miniaturization to arise through distinct compensatory changes. In the era of genomics, it is now also feasible to conduct comparative studies on the genetic basis for miniaturization in these three vertebrate clades and whether the underlying mechanisms of body size reductions are intertwined with those of paedomorphosis (Voss & Shaffer, 1997) or more generally, genome size (Decena-Segarra, 2020).

Our meta-analysis revealed that miniaturized lizards tend to occupy terrestrial microhabitats, compatible with previous work suggesting a correlation between miniaturization and fossoriality (Rieppel, 1984; Lee, 1998; Vallejo Pareja, 2018). We posit that this pattern may be the outcome of an adaptive shift driven by the interaction between body size and physiology. As body size decreases, an organism's surface area to volume ratio increases (Heatwole & Veron, 1977). Consequently, desiccation risk is intensified in small animals on account of higher cutaneous evaporative rates of water loss (EWL) and lower absolute water content (Le Lagadec et al., 1998; Allen et al., 2012; Dias et al., 2013; Bujan et al., 2016). Biophysical models in anurans support this hypothesis, with larger bodies conferring greater water retention and prolonged survival (Tracy et al., 2010). To deal with hydration problems, small animals exhibit physiological adaptations, especially in environments where humidity levels are unfavourable (Cox & Cox, 2015), but moisture is also limiting in humid ecosystems, e.g., tropical forests (Bujan et al., 2016). Examples include lower cutaneous permeability (Bentley & Schmidt-Nielsen, 1966; Gunderson, 2011; Allam et al., 2016), decreased cutaneous blood flow (Burggren & Vitalis, 2005), production of secretions (Lillywhite, 1971), differences in body shape (Spight, 1968; Broly et al., 2015), all of which reduce EWL, and enhanced tolerance to low hydration levels (Ray, 1958; Heatwole & Veron, 1977). Behavioural and ecological adjustments can also help minimize water loss, such as changes in activity patterns (Le Lagadec et al., 1998), the adoption of compact resting postures (Pough et al., 1983), and a shift to local microclimates that have greater moisture (Pintor et al., 2016). The latter is frequently tied with terrestriality, which allows the exploitation of higher humidity levels through active site selection within heterogeneous substratum (Morritt, 1987; Hood & Tschinkel, 1990; Villani et al., 1999; Dias et al., 2013). In the miniaturized

gecko genus *Sphaerodactylus*, high EWL rates and vulnerability to desiccation due to high surface area to volume ratios are thought to be offset by terrestrial refuges that fulfill the hydration requirements of their tiny bodies (Dunson & Bramham, 1981; MacLean, 1985; Steinberg et al., 2007; Turk et al., 2010). In our data, given that miniaturized lizards inhabit both humid and arid environments (Figure 2; Table S1), an ecological shift to terrestrial microhabitats may allow them to persist in areas of lower ambient humidity levels.

Body size also greatly affects thermoregulation. Smaller organisms equilibrate quickly to the conditions of the surrounding environment, retaining heat less efficiently and losing heat more rapidly (Bell, 1980; Bittner et al., 2002). For ectotherms, this problem is exacerbated by the reduced capability of homeostatic mechanisms to regulate body temperatures (Abram et al., 2017). Miniaturized squamates are thus less tolerant to thermal fluctuations and succumb more easily to heat stress (Levinton, 2020). That is not to say that classical measures of thermal tolerance necessarily differ in small animals (i.e., critical thermal limits; Ospina & Mora, 2004), but that low thermal inertia causes those extrema to be reached more rapidly (Calder, 1984). Surface-dwelling and semi-fossorial habits can counteract thermoregulatory deficits by limiting exposure to sunlight and providing insulation (Stevenson, 1985; Kearney et al., 2009). In fact, the ability to use shaded pockets in the understory and interstitial terrestrial spaces is in part enabled by extremely small body size (Farji-Brener et al., 2004; Vitt et al., 2005). Miniaturized lizards likely complement a terrestrial microhabitat preference with behavioural responses, including activity patterns, thermoregulatory behaviours, and microhabitat selection, that coincide with favourable environmental conditions to maintain stability with regard to both humidity and temperature (Allen & Powell, 2014). They may either engage in periodic retreats to remain active during warmer parts of the day or assume a more crepuscular or nocturnal lifestyle. Although the same behaviours are widespread among squamates, higher susceptibility to physiological changes in miniaturized taxa calls for an integral role of behavioural regulation (Huey & Slatkin, 1976; Fraser & Grigg, 1984). At present, descriptions of the natural history of miniaturized species are nearly non-existent, limiting our ability to determine whether general behavioural patterns are present independent of body size and principally driven by evolutionary history. Thus,

we highlight the need for studies that characterize the time budgets and functional habitat use of miniaturized species, in aims of understanding how they overcome the hydrothermal challenges imposed by their size.

Ecological differences often manifest in changes in neuroanatomy that are size dependent. Microhabitat (Corfield et al., 2015; Hoops et al., 2017), habitat complexity (Safi & Dechmann, 2005; Park & Bell, 2010), locomotor mode (Iwaniuk & Hurd, 2005; Barks et al., 2015), diet (Louail et al., 2019), predation risk (Liao et al., 2015), social interactions (Pollen et al., 2007), sensory systems (Kotrschal et al., 1998; O'Donnell et al., 2018), and body size reductions (Roth et al., 1990) have all been implicated in mosaic brain evolution, whereby selection acts differentially across brain regions and reflects sensory and cognitive specialization (Barton & Harvey, 2000; DeCasien & Higham, 2019). The brain of the miniaturized gecko, *S. nicholsi* features reduced olfactory bulbs in comparison to non-miniaturized *G. smithii* and a comparable relative volume of the optic tecta (Table 2; Figure 3), which indicates *S. nicholsi* may rely on vision as its primary sensory modality at the expense of olfaction. These results are in opposition of the hypothesis that size reductions are accompanied by a predominance of brain regions associated with sensory input to maintain functional efficiency (Hanken, 1983). Indeed, structural simplification of the brain may ensue when absolute brain size is reduced (Roth et al., 1997; Hanken & Wake, 1993). However, the most prominent distinction between the two brains lies in the telencephalon, which is proportionally enlarged in the miniaturized *S. nicholsi*. The telencephalon in reptiles is responsible for sensory integration and other complex cognitive functions such as decision-making and spatial memory (Rodríguez et al., 2012; Naumann et al., 2015; Pessoa et al., 2019). In miniaturized lizards, increased investment in telencephalic volumes may preserve the cognitive machinery responsible for integration of sensory information to compensate for deficits due to reductions of the visual or chemosensory centers. Small nervous systems also experience greater noise, a higher density of energy consumption, and a reduction in parallel processing of neural circuits, limiting the capability to rapidly and accurately interpret information (Chittka & Niven, 2009; Niven & Farris, 2012). Integration of stimuli from multiple sensory modalities provides a mechanism to improve the efficacy of perceiving stimuli through increasing redundancy and utilizing the advantages of distinct sensory pathways under varying environmental conditions (Partan & Marler, 2005; Bro-Jørgensen, 2010; Fischer et al., 2017; Metaxakis et al.,

2018). A relative increase relative increase in size of the telencephalon may then confer advantages in computational power for multimodal integration in miniaturized species.

Volumetric comparisons between brains and endocasts demonstrated that the brain of *S. nicholsi* fills a greater proportion of the endocranial space than in *G. smithii* (Figure 4; Table 2), supporting the hypothesis that body size reductions result in tighter packing of neural tissue inside smaller head capsules (Beutel & Haas, 1998; Ocampo et al., 2018). In particular, the dorsal surfaces of the telencephalon and mesencephalon, and ventral surface of the rhombencephalon lie near the outermost edges of the cranial endocast in the miniaturized species (Figure 4). Spatial constraints are further supported by differences in brain orientation (Figure 3), consistent with changes in the braincase positioning to lie at the same level as the dermatocranium in miniaturized squamates (Rieppel, 1984; Vallejo Pareja, 2018) and a more triangular telencephalon fitted against the contours of large eyes as in *Thorius* salamanders (Hanken, 1983; Roth et al., 1990). The pronounced affinity of brain structure to the surrounding cranial endocast suggests there are significant constraints on proportional increases of the brain relative to the braincase at small body sizes. Because of the conserved negative allometry brain and body mass (Eberhard & Wcislo, 2011), brain size may therefore delimit the minimum body size a lizard can theoretically attain. One solution to accommodate proportionally larger brains may be to increase the volume of the endocranial cavity at the expense of skeletal and muscular elements that provide neurocranial reinforcement or increased gape and bite force. However, musculature constrains brain-endocast morphology due to biomechanical constraints (Challands et al., 2020), and miniaturized species of several squamate families are characterized by an increase in jaw adductor muscles and changes in ossification (Rieppel, 1984; Daza et al., 2008; Vallejo Pareja, 2018). We suggest these novel musculoskeletal rearrangements in miniaturized squamates preclude unprecedented increases in endocranial volume.

Sphaerodactylus nicholsi and congeneric *Gekko* species are both known to use visual and chemosensory signals (or cues) in a variety of contexts such as courtship and predation (Loew, 1994; DePerno et al., 1996; Röll, 2000; Regalado, 2012; 2015). Perception of stimuli from these two modalities and their importance in eliciting behaviours provide a biologically and ecologically relevant framework to our comparisons of sensory regions between the

two brains. However, the two species differ in aspects of their ecology; *S. nicholsi* is terrestrial and diurnal (Genet et al., 2001; López-Ortiz & Lewis, 2004), and *G. smithii* is arboreal and nocturnal (Shahrudin, 2013; 2016). Because ecological differences influence neuroanatomy, we are unable to confidently generalize the effect of miniaturization on the lizard brain. Brain volume data of various lizard species across the phylogeny, as in our analysis using ecological traits, are needed to distinguish the effect of size reductions on brain morphology from those of ecology and evolutionary history. Furthermore, although the functional significance of brain shape is poorly understood, geometric morphometrics would help evaluate whether miniaturized lizards converge in brain shape and whether particular brain regions are more strongly restricted by the available endocranial space.

Recent work has called into question the reliability of soft tissue volume quantification from diceCT scans. Specimen preparation for scanning such as formalin fixation and exposure to iodine-based solutions results in tissue shrinkage, the latter in a concentration-dependent manner (Vickerton et al., 2013; Buytaert et al., 2014). Long-term storage in ethanol, typical of museum specimens, also contributes to tissue deformation, hindering comparability with freshly collected specimens (Hedrick et al., 2018; Leonard et al., 2021). There is evidence that variable fixation times, on the other hand, do not significantly affect the degree of shrinkage (Powell & Leal, 2012). Although our volumetric measures of lizard brains likely represent underestimates owing to tissue shrinkage, the cross-specimen comparisons of the relative volumes of brain regions are not necessarily compromised because both geckos were preserved and prepared in a similar manner. The specimens of *S. nicholsi* and *G. smithii* were collected in 2003 and 2004, respectively, fixed in formalin, stored in ethanol for approximately the same amount of time, then exposed to solutions with the same I_2KI concentration. Moreover, the brain-endocast disparities we observe cannot be solely attributed to tissue shrinkage as squamate brains generally do not fill the entire endocranial space (Kim & Evans, 2014; Allemand et al., 2017). It is worth noting, however, that tissues vary in their susceptibility to shrinkage due to differences in cellular composition and fluid content (Buytaert et al., 2014; Hedrick et al., 2018). Specifically, within the brain, the cerebellum may therefore retain a closer resemblance to its original form on account of smaller cell sizes and higher neuronal densities (Weisbecker, 2012). It remains unclear whether such differences in shrinkage across brain regions are also characteristic of

brains that are not isolated from the surrounding connective tissues which may confer structural support and shape integrity (Vickerton et al., 2013).

In the field of comparative neuroscience, cognitive performance has long been correlated with measures such as absolute and relative brain size, resting on the assumption that there is little variation in neuronal composition within and across clades (Jerison, 1985; Deaner et al., 2007). With the advent of isotropic fractionation, a rapid method to measure neuronal and nonneuronal cell numbers, evolutionary neurobiologists greatly increased the taxonomic breadth of data concerning neural mass, neuronal density, neuron cell size, and glia/neuron ratios across various regions of the brain (Herculano-Houzel & Lent, 2005). While there appears to be a single relationship between non-neuronal cell numbers and brain mass, neuronal densities follow distinct trajectories across clades and brain regions (Herculano-Houzel et al., 2006, 2007; Azevedo et al., 2009; Sarko et al., 2009; Gabi et al., 2010; Herculano-Houzel, 2011a; Kazu et al., 2014; Riberio et al., 2014). Glia/neuron ratios were found to covary with neuronal cell size as opposed to brain mass (Mota & Herculano-Houzel, 2014), and the spurious notion that energetics of the brain scales with brain mass could finally be dismissed, with the former instead scaling linearly with total number of neurons (Herculano-Houzel, 2011b). Differences in cellular scaling rules across clades were then juxtaposed with behavioural data, providing new insights into the origins of cognitive processes. For example, songbirds and parrots have high numbers of neurons and neuronal densities in the telencephalon, a mechanism underlying primate-like cognitive abilities in brains that are smaller in absolute size (Olkowicz et al., 2016). Higher neuron numbers in primate brains than in rodent brains of the same size similarly offered an explanation for why brain size is not always a good predictor of cognition (Herculano-Houzel et al., 2007; Dicke & Roth, 2016). Our comparative data on gross brain morphology may be indicative of a broader pattern of increased investment in sensory integration and higher cognitive functions in miniaturized taxa, though finer level data are needed to understand neuroanatomy in the context of cognitive performance. Characterization of neuronal numbers and densities in squamates has been largely neglected in comparison to mammals (Herculano-Houzel et al., 2015). With data currently available for only three lizard species (Kverková et al., 2020; Storks et al., 2020), it is difficult to generalize the scaling rules across squamates and evaluate whether miniaturized taxa conform to or deviate from these patterns. Hypothetically, scaling

patterns for neuronal densities may be robust among squamates, while relative enlargement of the telencephalon in *S. nicholsi* is chiefly responsible for maintaining cognitive capabilities in brains smaller in absolute size. On the other hand, miniaturized squamates may have undergone selection for neuronal densities that are higher than expected as per scaling patterns despite increased metabolic costs.

To begin to understand the perceptual world as it is experienced by the sensory systems of miniaturized vertebrates (their *umwelten*; von Uexküll, 1926; Otálora-Luna & Aldana, 2017), it can be informative to look to other taxonomic groups that have similar ecologies and body size. An organism's ecology determines the transmission efficacy of stimuli in various sensory modalities (Dusenbery, 2001), and body size likewise structures sensory hierarchies by limiting or enabling detection of those sensory modalities through physical and physiological means (Martens et al., 2015). Perpetually dark environments underground and in caves limit the use of vision (Schlegel et al., 2009; Emerling & Springer, 2014), eusocial behaviour in insects is rapidly and reliably mediated by olfactory signals (Zhou et al., 2015; d'Etorre et al., 2017), and small body size sets limits on sensing modes in oceanic animals (Martens et al., 2015). For miniaturized squamates, arthropods of similar size are appropriate ecological analogues, filling comparable ecological niches, sharing similar assemblages of predators and prey, and having high population densities (Rodda et al., 2001; Vitt et al., 2005). Among arthropods, the use of substrate-borne vibrations is widespread (Barth, 1982; Cocroft & Rodríguez, 2005; Cividini & Montesanto, 2020), functioning in prey localization (Casas et al., 1998), predator avoidance (Roberts, 2017), assessment of habitat (Evans et al., 2005), and intraspecific communication, the latter including advertisement of food resources (Yadav et al., 2017) and predatory threats (Hunt & Richard, 2013), parent–offspring communication (Savoyard et al., 1998), territory defence (Yack et al., 2001), and courtship (Uetz & Roberts, 2002). However, this sensory modality has received less attention in vertebrates. As stated in a review of vibrational communication by Hill (2001) and Hildebrand (1995), much of the body surface of tetrapods is in contact with the substrate, and the presence of a stapes makes them well suited to detecting low frequency vibrations. Moreover, the use of vibrations for locating prey and intraspecific communication has already been described in several squamates (Hetherington, 1989; Barnett et al., 1999; Young et al., 2003). Being anatomically

equipped to perceive substrate-borne stimuli and thriving in environments where arthropods extensively use vibrations, miniaturized squamates are primed for the use of this sensory modality. Whether they detect vibrations during prey-predator interactions or can discriminate between vibrational signals generated by conspecifics merits exploration.

4.1. Concluding remarks

Extreme size reductions bring about unorthodox anatomical arrangements and novel ways in which miniaturized animals interact with the environment. In this study, we provide a comprehensive assessment of lizard body sizes and identify taxa that have independently evolved to be miniaturized using phylogenetic tools, setting the stage for comparative work using those species. The data collected as part of this review begin an exploration of ecological, neuroanatomical, and sensory correlates with miniaturization. This includes performing a meta-analysis that reveals a tendency for miniaturized taxa to occupy terrestrial microhabitats. We also quantify the volumes of major brain regions and endocasts of two species of geckos (*S. nicholsi* and *G. smithii*), illustrating the feasibility of diceCT imaging for the study of brain morphology in miniaturized lizards. Baseline neuroanatomical data, when integrated with animal behaviour, have been instrumental in establishing relationships between brain morphology and cognition. Future work evaluating whether miniaturized lizards have undergone convergence in the relative proportion of brain regions and neuronal organization will help explain how cognitive processes are achieved in brains of reduced size.

Lastly, studies of natural history have become increasingly rare over the past several decades, potentially due to the false premise that observational studies are not rigorous and lack a theoretical framework (Greene, 2005; Schmidly, 2005). Our review exemplifies the shortcomings of this trend, as the majority of natural history data for miniaturized species were obtained from one or two literature sources, often from chance encounters during biodiversity surveys or descriptions of type specimens. If we are to understand the interface of ecology, neuroanatomy, sensory perception, and cognition, we must first set out to acquire an intimate understanding of the habits and behaviours of these animals in a natural context. In other words, it is critical to understand species' *umwelten* in order to develop a cohesive framework to describe evolutionary patterns and inform biologically sound hypotheses.

Acknowledgements

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Supplementary Table S1. Ecological trait data gathered from the literature for miniaturized and non-miniaturized taxa. This table can be accessed at 10.6084/m9.figshare.14797800.

Supplementary Figure S1. Representative coronal sections from diceCT scans of *Sphaerodactylus nicholsi* (left) and *Gekko smithii* (right), shown through the olfactory tracts (A1, B1), transition between the olfactory tracts and telencephalon (A2, B2), telencephalon (A3, B3), mesencephalon (A4, B4), and rhombencephalon (A5, B5). Segmentations are illustrated by the brain outlined in blue and cranial endocast in red. Within the blue boundaries, areas with neural tissue absent (i.e., unstained dark regions) were excluded from brain volumetric measurements via thresholding, whereas the cranial endocast included all voxels encompassed by the braincase. This figure can be accessed at 10.6084/m9.figshare.14797800.