Unexpected Morphological Diversity in New Zealand’s Large Diplodactylidae Geckos

Lachie Scarsbrook (lachiescarsbrook@gmail.com)
University of Otago

Emma Sherratt
University of Adelaide

Rod Hitchmough
Department of Conservation

R. Ewan Fordyce
University of Otago

Nicolas J. Rawlence
University of Otago

Research Article

Keywords: Diplodactylidae, ecomorphology, geometric morphometrics, Hoplodactylus duvaucelii, taxonomy

DOI: https://doi.org/10.21203/rs.3.rs-209257/v1

License: © Creative Commons Attribution 4.0 International License. Read Full License
Abstract

Prehistoric anthropogenically-mediated extinctions have impacted global biodiversity; however, effects on herpetofauna are poorly-documented. New Zealand’s Diplodactylidae geckos exhibit high species-level diversity, largely independent of discernible osteological changes (cryptic). Consequently, taxonomic affinities of isolated skeletal elements (fossils) are primarily determined by relative size, particularly in the identification of *Hoplodactylus duvaucelii*, New Zealand’s largest extant gecko species. Here, three-dimensional geometric morphometrics of maxillae (a common fossilized element) was used to determine whether consistent shape and size differences exist between genera, and if cryptic extinctions have occurred in ‘*Hoplodactylus cf. duvaucelii*’. Sampling included 13 Diplodactylidae species from five genera, and 11 Holocene ‘*H. cf. duvaucelii*’ subfossil individuals. We found phylogenetic history was the most important predictor of maxilla morphology among extant Diplodactylidae genera. Relative size comparisons could only differentiate *Hoplodactylus* from other genera, with the remaining genera exhibiting variable degrees of overlap. Six subfossils were positively identified as *H. duvaucelii*, confirming their proposed Holocene distribution throughout New Zealand. Conversely, five subfossils showed no affinities towards any modern Diplodactylidae genera, implying either increased morphological diversity in mainland ‘*H. cf. duvaucelii*’ or the presence of at least one extinct, large, broad-toed Diplodactylidae species. These results highlight the impact of anthropogenic disturbances on insular reptile diversity.

Background

The late Quaternary has been characterized by an intensifying wave of global species extinctions and population declines, with severity strongly correlated with hominin paleobiogeography (1–4). Anthropogenic overexploitation, habitat destruction, climate-change and introduction of non-native species (and diseases) collectively underpin these contemporary reductions in biodiversity; which are typified by island ecosystems (5–8). Both avifaunal and mammalian species extinctions (particularly megafauna) are well-characterized across oceanic islands globally (e.g. Hawaii (9), New Zealand (10)); whereas similar effects on herpetofaunal lineages remain poorly constrained (e.g. New Zealand (11,12)).

New Zealand’s lizard fauna is characteristic of isolated archipelagos, exhibiting high species endemism, extensive in-situ radiations (13,14) and insular gigantism (15). However, species diversity is considered osteologically cryptic, reflecting metabolic constraints of ectotherms, especially nocturnal Diplodactylidae gecko species under New Zealand’s cool, stable climate (14,16). Osteological comparisons have been further challenged by considerable taxonomic fluidity over the last 65 years (17–19). For example, allozyme (19,20) and mitochondrial DNA (21,22) analyses recognized three ‘super-species’ complexes within the genus *Hoplodactylus*, corresponding to two broad morphological groupings: narrow-toed (*H. granulatus* and *H. pacificus*) and broad-toed (*H. maculatus*) clades (23). Further taxonomic revision (14) separated *Hoplodactylus* ‘super-species’ into five genera (*Dactylocnemis*, *Mokopirirakau*, *Toropuku*, *Tukutuku* and *Woodworthia*), with *Hoplodactylus* reserved for *H. duvaucelii* and the extinct giant *H. delcourti* (12). Morphological descriptions of these revised genera were based exclusively on external characters (e.g. colouration and scalation (14)), with skeletal differences remaining largely unknown (with the exception of the frontal bone of the skull; (25,26)). Consequently, classification of isolated subfossil bones has been restricted to relative size comparisons in reference to outdated ‘super-species’ complexes (27,28); particularly in the identification of ‘*H. cf. duvaucelii*’, New Zealand’s largest extant Diplodactylid.

*Hoplodactylus duvaucelii* (‘Duvaucel’s gecko’) is a large, nocturnal species, with a pseudoendemic (realized) distribution on predator-free islands in the Cook Strait and off the north-eastern coast of the North Island (Figure 1;
Prior to Polynesian (~1280 AD; (30)) and European (effectively the late 1700's) arrival, ‘H. cf. duvaucelii’ was widely distributed throughout the North Island (31), and the northwest and eastern South Island ((27,28,32–34); Figure 1). Subsequent range contractions occurred through the synergistic effects of competitive exclusion and direct predation by introduced mammals, and degradation of forest habitat (31,35). Given elevated species diversity in other Diplodactylidae genera (14), combined with an extensive distribution across multiple biogeographic regions (27,36), unrecognized diversity may exist within ‘H. cf. duvaucelii’.

Herein, three-dimensional geometric morphometrics was used to characterise and quantify both shape and size variation in the maxilla of modern Diplodactylidae genera (Dactylocnemis, Hoplodactylus, Mokopirirakau, Naultinus and Woodworthia), for comparison with Holocene ‘H. cf. duvaucelii’ subfossils. Three main research questions were tested: (a) can revised Diplodactylidae genera be distinguished based on maxilla shape; (b) is relative-size a reliable method for generic-level identification of isolated cranial elements; and (c) have cryptic extinctions occurred in the Diplodactylidae (with a focus on ‘H. cf. duvaucelii’)?

**Results**

(a) **Principal axes of Diplodactylidae maxillae variation**

Principal component (PC) analysis (Figure 2A; Supplementary Figure 4) reveals the majority (71.5%) of maxilla shape variability among extant New Zealand Diplodactylidae is concentrated in four dimensions. Subsequent PC contributions (PC5 - PC54) are either small or negligible (< 5.0%), and thus not considered further.

PC1, the primary axis of shape variation (39.7%), largely pertains to morphological changes in the nasal and orbital margins (Supplementary Figure 5). Shifting from positive to negative values describes an elongation of the nasal margin and adjacent medial flange, with corresponding shortening and increased concavity of the prefrontal and orbital margins. Additionally, the palatal shelf becomes more convex with increasingly negative values along this axis. Naultinus and Mokopirirakau (excluding the M. ‘southern North Island’ specimen – see below) form distinct clusters in the negative region of PC1, whereas Dactylocnemis, Hoplodactylus and Woodworthia primarily occupy overlapping intermediate-positive regions (Figure 2A).

PC2 (16.7% of variance) describes changes associated with overall element robustness, with dorsoventrally shallow, laterally slender maxillae at more negative values contrasting dorsoventrally deep, laterally broad maxillae at more positive values. Two morphologically distinct, generic clusters form along this axis: gracile maxillae (Naultinus-Woodworthia) and robust maxillae (Dactylocnemis-Hoplodactylus-Mokopirirakau; Supplementary Figure 5).

PC3 (8.0% of variance) describes morphological shifts in both the anterolateral lappet and prefrontal margin (Supplementary Figure 5). In the negative direction, the width of the anterolateral lappet reduces moving towards the terminus (which increases in dorsal extent), and the prefrontal margin forms a broad plateau, markedly separating it from the orbital margin. Moving in the positive direction, the anterolateral lappet becomes dorsoventrally flatter and laterally broader, and the prefrontal margin forms a near-continuous curve with the adjacent orbital margin. Shape change along PC4 (7.2%) is primarily associated with increased curvature of the tooth row towards more negative values (Supplementary Figure 5).

Visually, Holocene subfossil specimens cluster in the intermediate-positive regions of PC1, PC2 and PC4; overlapping multiple extant genera morphospaces (Figure 2A; Supplementary Figure 4). Conversely, Holocene
subfossil specimens (excluding H) occupy increasingly positive regions of PC3, with some individuals (B, E, I, J) exhibiting no overlap with extant genera (Supplementary Figure 4). Procrustes distances of the Holocene subfossil specimens (Supplementary Table 4) across all PC axes suggest shape similarities with Dactylocnemis (E, K), Hoplodactylus (A, C, D, G, I, J) and Woodworthia (B, F, H), with no affinities towards Mokopirirakau or Naultinus.

(b) Predictors of shape and size

Procrustes ANOVA (Supplementary Table 5) revealed that phylogenetic affiliation (i.e. genus) is a highly significant predictor ($F_{(4,38)} = 9.01$, $p < 0.001$) of maxillae shape, accounting for 45.2% of the shape variation. Multivariate pairwise post-hoc tests found differences to be significant between most genera ($p < 0.05$), excluding Dactylocnemis-Hoplodactylus ($p = 0.229$), and Hoplodactylus-Mokopirirakau ($p = 0.056$) comparisons (Supplementary Table 6). A weak but significant relationship also exists between maxillae shape and centroid size ($F_{(1,41)} = 5.39$, $p = 0.020$), and their interaction ($F_{(4,38)} = 1.35$, $p = 0.023$; Supplementary Table 5), suggesting a small proportion of the shape diversity (6.8%) is due to allometry.

One-way ANOVA (Supplementary Table 7) identified significant differences in maxillae centroid size between genera ($F_{(4,38)} = 32.22$, $p < 0.001$), with Hoplodactylus (1690 ± 228.1; mean ± sd) being significantly larger under all HSD post-hoc comparisons (Supplementary Table 8). Additionally, Woodworthia (968 ± 100.9) was significantly smaller than most other genera (Supplementary Figure 6; Supplementary Table 8), excluding the Naultinus-Woodworthia comparison ($p = 0.253$). Conversely, Dactylocnemis (1198 ± 142.9), Mokopirirakau (1241 ± 115.6) and Naultinus (1093 ± 104.0) were indistinguishable from each other based on centroid size alone. Subfossil specimens show no overlap with the error bars of non-Hoplodactylus maxillae, with some (G = 2042, H = 2086, I = 2024, K = 2316) extending beyond the maximum extant Hoplodactylus maxillae centroid size (Supplementary Figure 6).

(c) Phylogenetic shape differences

Canonical variate (CV) analysis (Figure 2C) and Mahalanobis distance probabilities (Supplementary Table 9) show all genera form significantly different groups, with a cross-validation accuracy of 100%. Canonical function 1 (CV1; 53.9% among-group variance) clearly distinguishes Naultinus and Woodworthia, which occupy opposite extremes of the morphospace (Figure 2C). A shift towards positive values describes shortening of the nasal margin and adjacent medial flange, with corresponding shortening in the prefrontal margin (similar to PC1; Figure 2D). Hoplodactylus occupies the extreme positive end of canonical function 2 (CV2; 30% among-group variance), characterized by a relative slope decrease of the nasal margin and consequent shortening of the orbital margin (Figure 2C/D).

The Holocene subfossil specimens are broadly distributed throughout the morphospace (Figure 2C), with some individuals visually falling within the 95% confidence-interval of extant genera (Hoplodactylus: D, E, J, K; Woodworthia: B) for CV1-CV2. Typicality probabilities of Mahalanobis distances across all CVs (Table 1) find that while many Holocene subfossil specimens strongly associate with Hoplodactylus (A, D, E, F, J, K), other specimens (B, C, G, H, I) show no clear phylogenetic affinities, indicating Holocene subfossil specimens display greater variation in maxillae than that encompassed by the extant genera. Conversely, despite posterior probabilities (Table 1) showing similar significant support for Holocene subfossil Hoplodactylus classification (A, C, D, E, F, H, J, K), unique specimens were assigned to Woodworthia (B, G, I).
Table 1  Typicality and posterior probabilities of Holocene subfossil specimens belonging to extant genera, calculated using Mahalanobis distances. Highest typicality ($p > 0.20$) and posterior probabilities for each Holocene subfossil specimen are indicated in bold.

| Typicality Probabilities | Posterior Probabilities |
|--------------------------|-------------------------|
|                         | D | H | M | N | W | D | H | M | N | W |
| A  AU7700                | 0.026 | 0.215 | 0.020 | 0.018 | 0.033 | <0.001 | 1 | <0.001 | <0.001 | <0.001 |
| B  S.33703.2             | 0.013 | 0.030 | 0.021 | 0.013 | 0.041 | <0.001 | <0.001 | <0.001 | <0.001 | 0.999 |
| C  S.33703.3             | 0.031 | 0.110 | 0.046 | 0.026 | 0.070 | <0.001 | 0.999 | <0.001 | <0.001 | <0.001 |
| D  S.33703.4             | 0.257 | 0.688 | 0.096 | 0.046 | 0.122 | <0.001 | 1 | <0.001 | <0.001 | <0.001 |
| E  S.33703.7             | 0.570 | 0.819 | 0.133 | 0.072 | 0.120 | <0.001 | 0.999 | <0.001 | <0.001 | <0.001 |
| F  S.33703.8             | 0.157 | 0.557 | 0.125 | 0.060 | 0.286 | <0.001 | 0.999 | <0.001 | <0.001 | <0.001 |
| G  S.38813.2             | 0.031 | 0.060 | 0.054 | 0.024 | 0.061 | <0.001 | 0.19 | 0.004 | <0.001 | 0.809 |
| H  S.39086               | 0.041 | 0.167 | 0.043 | 0.020 | 0.114 | <0.001 | 0.999 | <0.001 | <0.001 | <0.001 |
| I  S.46528.1             | 0.028 | 0.091 | 0.044 | 0.016 | 0.090 | <0.001 | 0.049 | <0.001 | <0.001 | 0.512 |
| J  VT791a                | 0.078 | 0.205 | 0.027 | 0.022 | 0.038 | <0.001 | 1 | <0.001 | <0.001 | <0.001 |
| K  W0333                 | 0.177 | 0.742 | 0.088 | 0.050 | 0.105 | <0.001 | 1 | <0.001 | <0.001 | <0.001 |

Discussion

(a) Variation and morphological convergence in Diplodactylidae maxillae.

Phylogenetic position is a highly significant predictor of maxilla shape diversity in New Zealand Diplodactylidae, with all genera (*Dactylocnemis, Hoplodactylus, Mokopirirakau, Naultinus* and *Woodworthia*) being morphologically distinct. These results contrast previous long-held notions of skeletal conservatism in New Zealand’s geckos (e.g. (27,37)) through identification of taxonomically informative morphological variation within a single skeletal element. This retention of genus-level phylogenetic signal is remarkable given pronounced ecological species radiations since the early Miocene (14). However, similar trends of reduced disparity in maxillae (relative to rate of evolution) are observed across both extant and extinct squamates (excluding snakes; (38)), suggesting constrained evolution in this cranial region.

Diplodactylidae maxilla shape is predominantly characterized by two character-states, described by the first two axes of both PCA and CVA: (1) posterior extension/reduction of the nasal margin; and (2) increase/decrease in dorsoventral extent of the facial process. The separation of genera along PC1 appears to reflect broad habitat use of the New Zealand Diplodactylidae, with terrestrial-arboreal (*Dactylocnemis, Hoplodactylus* and *Woodworthia*) and exclusively arboreal (*Naultinus*) genera occupying positive and negative regions respectively (39,40). This morphological signature of habitat use extends to species-level comparison, most notably in the discrimination of
the terrestrial-arboreal *M. 'southern North Island' from the arboreal *M. granulatus* (41), characterized by a shift to more positive values.

In gekkotans, arboreal forms tend towards broad, pointed and dorsoventrally shallow skulls, enabling faster climbing speeds on non-horizontal surfaces (42,43). While cranial modifications associated with habitat use are undocumented in the New Zealand Diplodactylidae, extension of the nasal margin in arboreal species appears to be linked to two superficial morphological changes in the adjacent prefrontal margin: (1) a reduction in anterior extent (observed in other Gekkota; (44)); and (2) formation of a thickened ridge along the prefrontal orbital margin (Supplementary Figure 7). While the function of these structures remains unclear, association with arboreality provides strong evidence for ecomorphological convergence between phylogenetically independent lineages. Despite describing similar shape change, separation of genera along CV1 reflects broad phylogenetic relationships, distinguishing broad (*Hoplodactylus, Woodworthia*) and narrow (*Dactylocnemis, Mokopirirakau, Naultinus*) toed clades at positive and negative values respectively; supporting previous morphological classification (20).

In addition to habitat use, skull-shape evolution in lizards is strongly influenced by diet, with shape variation concentrated in the premaxilla, nasal and jaw joint, reflecting their roles in rostral prey capture and feeding biomechanics (38,42). Herbivorous lizard skulls tend towards reduced snouts and high temporal regions relative to carnivorous lizards, contributing to an increased bite strength required for processing fibrous and tough foliage (45–47). Conversely, omnivorous gekkotans represent intermediate forms not specialized to particular feeding behaviors, and consequently lack unique morphological adaptations (48). New Zealand geckos are predominantly omnivorous, consuming a wide variety of food items including plant matter (fruit, honeydew and nectar) and arthropods (40). Such extensive dietary overlap effects the performance of diet as an explanatory variable of maxilla shape diversity, given categories (omnivorous and insectivorous) are not discrete.

**(b) Efficacy of size-based discrimination**

Maxilla size was significantly correlated with phylogenetic affinity, however, only *Hoplodactylus* could be fully differentiated (under post-hoc comparisons), with the remaining Diplodactylidae genera exhibiting variable degrees of overlap. This highlights the inefficiency of previous size-based taxonomic identification of non-*Hoplodactylus* Holocene subfossil geckos, especially intermediate-sized genera (*Dactylocnemis, Mokopirirakau* and *Naultinus*), which exhibit complete size overlap. Similarly, while large relative size proves reliable in discriminating extant *H. duvaucelii*, applications in Holocene subfossil identification are limited given assumptions of temporal taxonomic homogeneity (or “covert biases”; (49)).

Previous analyses of squamate genera including *Anolis* (50,51) and *Iguana* (52) have shown maxillae to be effective predictors of snout-vent length (SVL). Our results exhibit similar trends both between and within Diplodactylidae genera, with mean genus centroid size reflecting relative SVL (53), and larger species (*N. punctatus, D. 'three kings') having increased centroid sizes relative to congeners (*N. elegans, D. pacificus; (54,55)).

**(c) Increased Holocene diversity of large geckos**

Our results provide evidence for increased morphological diversity of large geckos during the Holocene in New Zealand, with declines in both shape and size variation following Polynesian and European colonization.

Combined Procrustes and Mahalanobis distance comparisons provide support for previous size-based classification of five Holocene subfossils (A, D, E, J, K) as *H. duvaucelii*, confirming assumed prehuman distribution
across both the North and South Islands. The remaining six Holocene subfossil specimens (B, C, F, G, H, I) exhibited classification discrepancies and/or reduced assignment probabilities (below relevant thresholds), reflected in their unique position across CV1/CV2. These distinct Holocene subfossil maxillae (“unknown taxa”) are not reflective of differential adaptation to mainland and island habitats (see above), therefore reflecting either increased morphological diversity of mainland large species (not encompassed by extant populations) or the presence of at least one extinct, large, broad-toed Diplodactylidae species.

Based on digit morphology, the extinct giant *H. delcourti* was positioned within the broad-toed clade, sister to *H. duvaucelii* (24), suggesting these “unknown taxa” could potentially represent small or even juvenile *H. delcourti* (with respect to the latter hypothesis). However, this seems unlikely given the paucity of reported subfossil remains of *H. delcourti* (56), despite extensive collections of other Diplodactylidae taxa (37). Accurate phylogenetic affinities of both *H. delcourti* and “unknown taxa” could be determined through future ancient DNA analysis.

During the Holocene, mainland *H. duvaucelii* (and “unknown taxa”) reached larger sizes than extant populations, reflected in a reduction in maximum maxilla size (a proxy for body size; e.g. (50)). Such sized-biased extinction is well-documented in Quaternary lizards globally (51,57–59), including the extinction of two large-bodied Eugongylinae skink species (*Oligosoma northlandi* and *Oligosoma sp.*) in northern New Zealand (12,31,60). This reflects the inherent vulnerability of New Zealand’s large-bodied, nocturnal herpetofauna towards high-predation rates and ecological displacement by exotic mammals (including the Pacific rat (kiore); (61,62)), particularly in forest-cleared environments (63). Smaller lizards can escape predation during periods of inactivity through utilizing narrow retreats, given limited overlap in body diameter with small mammalian predators (39). Conversely, refugia utilized by large-bodied lizards can be accessed by mammalian predators, evidenced by reductions in body weight, tail width and recruitment of *H. duvaucelii* on kiore-inhabited islands (35,64).

Similar to extant *H. duvaucelii* populations (65), Holocene subfossil *H. duvaucelii* also exhibit a latitudinal cline in maxilla size opposing Bergmann’s rule (i.e. increased size at high latitudes), with individuals from northern localities being noticeably larger than those from southern localities. For diurnal lizards, reduced body size appears to be an advantageous thermoregulatory strategy in cooler climates, with high surface-area to volume ratio permitting rapid heat gain whilst sun-basking (66,67). Despite being nocturnal, *H. duvaucelii* occasionally emerge from retreats to thermoregulate through cryptic sun-basking (68,69), suggesting small body size provided an adaptive advantage at high latitudes.

**Conclusions**

New Zealand Diplodactylidae genera can be fully differentiated based on maxilla shape, which exhibits strong correlations with phylogenetic history. Additional species-level discrimination based ecomorphological adaptations highlights the potential application of geometric morphometrics to more functionally variable elements (or whole skulls) in taxonomic descriptions of extant Diplodactylidae species. Previous sized-based identification of Holocene subfossils is ineffective and grossly underestimates extinct diversity, suggesting global assemblages of insular reptiles are depauperate in comparison to prehuman diversity.

**Methods**

(a) Specimen Selection
To capture extant morphological variation, we examined both left and right maxillae (sensu (70)) from 43 adult skeletal specimens (Supplementary Table 1) representing 13 species from five Diplodactyliidae genera: *Dactylocnemis, Hoplodactylus, Mokopirirakau, Naultinus* and *Woodworthia* (Supplementary Figure 1; Supplementary Table 1). In addition, we examined 11 well-preserved Holocene subfossil maxillae identified as ‘*Hoplodactylus cf. duvaucelii*, covering the majority of their prehuman (assumed) range (Figure 1; Supplementary Table 1). Maxillae were utilized primarily due to their relative abundance in subfossil deposits (for additional specimen selection details see Supplementary Methods.).

**Geometric morphometrics**

Geometric morphometric analyses were performed on a total of 94 maxillae (see Supplementary Methods for additional analytical details). Three-dimensional rendered surface models were generated from micro-CT reconstructions of maxillae, with shape characterized by 15 landmarks and 40 sliding semi-landmarks (Supplementary Figures 2, 3; Supplementary Table 2) digitized in Checkpoint (Stratovan Corporation, Davis, CA). Landmark coordinates were aligned using a generalized least-squares Procrustes superimposition (71), with semi-landmark position optimized using the Procrustes distance criterion (72) and paired elements symmetrized (following mirroring of left maxillae coordinates; Supplementary Table 3).

Shape variation in maxillae of the extant species was assessed using principal component analysis (PCA); with intergeneric differences (shape \~ genus * size) tested using a Procrustes analysis of variance (ANOVA; (73)), and visualized using canonical variate analysis (CVA; (74)) with cross-validations, based on a reduced set of PC scores (75,76). Three-dimensional surface warps (77) representing minimum and maximum shapes along both principal component (PC) and canonical variate (CV) axes were generated using the thin-plate spline (TPS) method (76,78). Holocene subfossil maxillae were then projected into these two-dimensional morphospaces (i.e. PCA and CVA) through matrix multiplication with respective eigenvectors (e.g. (79)). Phylogenetic classification of Holocene subfossil specimens was performed through Procrustes and Mahalanobis distance comparisons (to the mean maxilla shape of each genus), with the latter used to calculate typicality (80,81) and posterior (82) probabilities.

Variation in size of the maxilla (represented as centroid-size of the landmark configuration) between genera was examined using a one-way ANOVA and Tukey's honestly significant difference (HSD) *post-hoc* tests (83), and visualised using a barplot. All statistical analyses were performed in the R statistical environment v. 3.6.1 (84) using the packages *geomorph* v. 3.1.2 (85) and *Morpho* v. 2.7 (86).

**Declarations**

**Ethics approval and consent to participate:** Not applicable

**Consent for publication:** Not applicable

**Availability of data and materials:** The dataset (i.e. raw landmark coordinates and R-code) supporting the conclusions of this article is included within the article (and its additional files).

**Competing interests:** Not applicable

**Funding:** This work was supported by the Departments of Geology and Zoology, University of Otago; and the Royal Society of New Zealand Marsden FastStart Grant (16-U00-096).
Authors’ contributions: LS and NR conceived the study; LS carried out data collection and analyses with assistance from ES; ES, RH and NR assisted with data interpretation; LS drafted the manuscript, and all authors edited the manuscript; NR and REF provided funding. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Acknowledgements: We thank the following New Zealand institutions: Auckland Museum (Ruby Moore and Matt Rayner), Otago Museum (Cody Phillips), Museum of New Zealand Te Papa Tongarewa (Alan Tennyson and Tom Schultz) and Waitomo Caves Museum (Bridget Mosely), for access to comparative specimens. We are also very grateful to Andrew McNaughton (Otago Micro and Nanoscale Imaging) for assistance with micro-CT scanning; Ludovic Dutoit (University of Otago) for coding assistance; and both Aaron Bauer (Villanova University) and Daniel Paluh (University of Florida) for access Diplodactylidae cranial scans. In addition, we would like to thank both Alexander Verry (University of Otago) and Kerry Walton (University of Otago) for manuscript review.

References

1. Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, et al. Has the Earth’s sixth mass extinction already arrived? Nature. 2011;471(7336):51–7. doi:10.1038/nature09678.
2. Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Sci Adv. 2015;1(5):e1400253. doi:10.1126/sciadv.1400253.
3. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. Defaunation in the Anthropocene. Science. 2014;345(6195):401–6. doi:10.1126/science.1251817.
4. Sandom C, Faurby S, Sandel B, Svenning J-C. Global late Quaternary megafauna extinctions linked to humans, not climate change. Proc R Soc B Biol Sci. 2014;281(1787):20133254. doi:10.1098/rspb.2013.3254.
5. Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. Human predators outpace other agents of trait change in the wild. Proc Natl Acad Sci U S A. 2009;106(3):952–4. doi:10.1073/pnas.0809235106.
6. Mendenhall CD, Daily GC, Ehrlich PR. Improving estimates of biodiversity loss. Vol. 151, Biological Conservation. Elsevier; 2012. p. 32–4.
7. Koch PL, Barnosky AD. Late Quaternary extinctions: State of the debate. Annu Rev Ecol Evol Syst. 2006;37:215–50. doi:10.1146/annurev.ecolsys.34.011802.132415.
8. Purvis A, Gittleman JL, Cowlishaw G, Mace GM. Predicting extinction risk in declining species. Proc R Soc London Ser B Biol Sci. 2000;267(1456):1947–52. doi:10.1098/rspb.2000.1234.
9. Walther M, Hume J. Extinct birds of Hawaii. Honolulu, HI: Mutual Publishing; 2016.
10. Tennyson A, Martinson P. Extinct Birds of New Zealand. Wellington: Te Papa Press; 2006.
11. Easton LJ, Rawlence NJ, Worthy TH, Tennyson AJD, Scofield RP, Easton CJ, et al. Testing species limits of New Zealand’s leiopelmatid frogs through morphometric analyses. Zool J Linn Soc. 2018;183(2):431–44. doi:10.1093/zoolinnean/zlx080.
12. Worthy TH. Fossil skink bones from Northland, New Zealand, and description of a new species of Cyclodina, Scincidae. J R Soc New Zealand. 1991;21(4):329–48. doi:10.1080/03036758.1991.10420831.
13. Chapple DG, Hitchmough RA. Biogeography of New Zealand lizards. In: New Zealand Lizards. Springer International Publishing; 2016. p. 109–31. doi:10.1007/978-3-319-41674-8_5.
14. Nielsen S V, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH. New Zealand geckos (Diplodactylidae): Cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol. 2011;59(1):1–22.

15. Daugherty CH, Gibbs GW, Hitchmough RA. Mega-island or micro-continent? New Zealand and its fauna. Vol. 8, Trends in Ecology and Evolution. Elsevier Current Trends; 1993. p. 437–42.

16. Skipwith PL, Bi K, Oliver PM. Relicts and radiations: Phylogenomics of an Australasian lizard clade with east Gondwanan origins (Gekkota: Diplodactyloidea). Mol Phylogenet Evol. 2019;140:106589.

17. McCann C. The lizards of New Zealand. Dom Museum Bull. 1955;17:1–127.

18. Hitchmough RA, Patterson GB, Chapple DG. Putting a name to diversity: Taxonomy of the New Zealand lizard fauna. In: New Zealand Lizards. Springer International Publishing; 2016. p. 87–108. doi:10.1007/978-3-319-41674-8_4.

19. Daugherty CH, Patterson GB, Hitchmough RA. Taxonomic and conservation review of the New Zealand herpetofauna. New Zeal J Zool. 1994;21(4):317–23. doi:10.1080/03014223.1994.9518002.

20. Hitchmough RA. A systematic revision of the New Zealand Gekkonidae. Victoria University of Wellington; 1997.

21. Chambers GK, Wee Ming Boon, Buckley TR, Hitchmough RA. Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: Three case studies. Aust J Bot. 2001;49(3):377–87. doi:10.1071/BT00021.

22. Chong N. Phylogenetic analysis of the endemic New Zealand gecko species complex Hoplodactylus pacificus using DNA sequences of the 16S rRNA gene. Victoria University, Wellington, New Zealand; 1999.

23. Bauer A. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonn Zool Bull. 1990;30:1–218.

24. Russell AP, Bauer AM. The giant gecko Hoplodactylus delcourtii and its relations to gigantism and insular endemism in the Gekkonidae. Bull Chicago Herpetol Soc. 1986;26:26–30.

25. Daza JD, Bauer AM, Snively ED. On the fossil record of the Gekkota. Anat Rec. 2014;297(3):433–62. doi:10.1002/ar.22856.

26. Lee MSY, Hutchinson MN, Worthy TH, Archer M, Tennyson AJD, Worthy JP, et al. Miocene skinks and geckos reveal long-term conservatism of New Zealand’s lizard fauna. Biol Lett. 2009;5(6):833–7. doi:10.1098/rsbl.2009.0440.

27. Worthy TH, Holdaway RN. Quaternary fossil faunas from caves on Mt Cookson, North Canterbury, South Island, New Zealand. J R Soc New Zeal. 1995;25(3):333–70. doi:10.1080/03014223.1995.9517494.

28. Worthy TH. Quaternary fossil fauna of South Canterbury, South Island, New Zealand. J R Soc New Zeal. 1997;27(1):67–162. doi:10.1080/03014223.1997.9517528.

29. Morgan-Richards M, Hinlo AR, Smuts-Kennedy C, Innes J, Ji W, Barry M, et al. Identification of a rare gecko from North Island New Zealand, and genetic assessment of its probable origin: A novel mainland conservation priority? J Herpetol. 2016;50(1):77–86. doi:10.1670/13-128.

30. Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proc Natl Acad Sci U S A. 2008;105(22):7676–80. doi:10.1073/pnas.0801507105.

31. Worthy TH. Osteological observations on the larger species of the skink Cyclodina and the subfossil occurrence of these and the gecko Hoplodactylus duvaucelii in the North Island, New Zealand. New Zeal J Zool. 1987;14(2):219–29. doi:10.1080/03014223.1987.10422992.
32. Worthy TH, Holdaway RN. Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. J R Soc New Zeal. 1996;26(3):275–361. doi:10.1080/03014223.1996.9517514.

33. Worthy TH. Quaternary fossil faunas of Otago, South Island, New Zealand. J R Soc New Zeal. 1998;28(3):421–521. doi:10.1080/03014223.1998.9517573.

34. Worthy TH, Holdaway RN. Quaternary fossil faunas from caves in Takaka Valley and on Takaka Hill, northwest Nelson, South Island, New Zealand. J R Soc New Zeal. 1994;24(3):297–391. doi:10.1080/03014223.1994.9517474.

35. Christmas E. Interactions between Duvaucel's gecko (Hoplodactylus duvaucelii) and kiore (Rattus exulans). University of Otago, Dunedin; 1995.

36. Wallis GP, Trewick SA. New Zealand phylogeography: Evolution on a small continent. Mol Ecol. 2009;18(17):3548–80. doi:10.1111/j.1365-294X.2009.04294.x.

37. Worthy TH. A review of the fossil record of New Zealand lizards. In: New Zealand Lizards. Springer International Publishing; 2016. p. 65–86. doi:10.1007/978-3-319-41674-8_3.

38. Watanabe A, Fabre AC, Felice RN, Maisano JA, Müller J, Herrel A, et al. Ecomorphological diversification in squamates from conserved pattern of cranial integration. Proc Natl Acad Sci U S A. 2019;116(29):14688–97. doi:10.1073/pnas.1820967116.

39. Tingley R, Hitchmough RA, Chapple DG. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv. 2013;165:62–8.

40. Hare KM, Chapple DG, Towns DR, van Winkel D. The ecology of New Zealand’s lizards. In: New Zealand Lizards. Springer International Publishing; 2016. p. 133–68. doi:10.1007/978-3-319-41674-8_6.

41. Tingley R, Hitchmough RA, Chapple DG. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv. 2013;165:62–8.

42. Gray JA, Sherratt E, Hutchinson MN, Jones MEH. Evolution of cranial shape in a continental-scale evolutionary radiation of Australian lizards. Evolution. 2019;73(11):2216–29. doi:10.1111/evo.13851.

43. Revell LJ, Johnson MA, Schulte JA, Kolbe JJ, Losos JB. A phylogenetic test for adaptive convergence in rock-dwelling lizards. Evolution. 2007;61(12):2898–912. doi:10.1111/j.1558-5646.2007.00225.x.

44. Rieppel O. The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). Zool J Linn Soc. 1984;82(3):291–318. doi:10.1111/j.1096-3642.1984.tb00645.x.

45. Herrel A, Aerts P, De Vree F. Ecomorphology of the lizard feeding apparatus: A modelling approach. Netherlands J Zool. 1998;48(1):1–25. doi:10.1163/156854298x00183.

46. Metzger KA, Herrel A. Correlations between lizard cranial shape and diet: A quantitative, phylogenetically informed analysis. Biol J Linn Soc. 2005;86(4):433–66. doi:10.1111/j.1095-8312.2005.00546.x.

47. Stayton CT. Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. Evolution. 2006;60(4):824–41. doi:10.1111/j.0014-3820.2006.tb01160.x.

48. Daza JD, Herrera A, Thomas R, Claudio HJ. Are you what you eat? A geometric morphometric analysis of gekkotan skull shape. Biol J Linn Soc. 2009;97(3):677–707. doi:10.1111/j.1095-8312.2009.01242.x.

49. Bell CJ, Mead JI. Not Enough Skeletons in the Closet: Collections-Based Anatomical Research in an Age of Conservation Conscience. Anat Rec. 2014;297(3):344–8. doi:10.1002/ar.22852.
50. Bochaton C, Kemp ME. Reconstructing the body sizes of Quaternary lizards using *Pholidoscelis* Fitzinger, 1843, and *Anolis* Daudin, 1802, as case studies. J Vertebr Paleontol. 2017;37(1):e1239626. doi:10.1080/02724634.2017.1239626.

51. Bochaton C, Bailon S, Herrel A, Grouard S, Ineich I, Tresset A, et al. Human impacts reduce morphological diversity in an insular species of lizard. Proc R Soc B Biol Sci. 2017;284(1857):20170921. doi:10.1098/rspb.2017.0921.

52. Bochaton C. Describing archaeological *Iguana laurenti*, 1768 (Squamata: Iguanidae) populations: Size and skeletal maturity. Int J Osteoarchaeol. 2016;26(4):716–24. doi:10.1002/oa.2463.

53. van Winkel D, Baling M, Hitchmough R. Reptiles and amphibians of New Zealand. Auckland University Press, NZ; 2018.

54. Robb J, Hitchmough RA. Review of the genus *Naultinus* Gray (Reptilia: Gekkonidae). Rec Auckl Inst Museum. 1979;16:189–200.

55. Parrish GR, Gill BJ. Natural history of the lizards of the three kings Islands, New Zealand. New Zeal J Zool. 2003;30(3):205–20. doi:10.1080/03014223.2003.9518339.

56. Bauer A, Russell A. Osteological evidence for the prior occurrence of a giant gecko in Otago, New Zealand. Cryptozoology. 1988;7:22–37.

57. Kemp ME, Hadly EA. Extinction biases in Quaternary Caribbean lizards. Glob Ecol Biogeogr. 2015;24(11):1281–9. doi:10.1111/geb.12366.

58. Bailon S, Bochaton C, Lenoble A. New data on Pleistocene and Holocene herpetofauna of Marie Galante (Blanchard Cave, Guadeloupe Islands, French West Indies): Insular faunal turnover and human impact. Quat Sci Rev. 2015;128:127–37.

59. Bochaton C, Grouard S, Corette R, Ineich I, Lenoble A, Tresset A, et al. Fossil and subfossil herpetofauna from Cadet 2 Cave (Marie-Galante, Guadeloupe Islands, F. W. I.): Evolution of an insular herpetofauna since the Late Pleistocene. Comptes Rendus - Palevol. 2015;14(2):101–10.

60. Gill BJ. Subfossil bones of a large skink (Reptilia: Lacertilia) from Motutapu Island, New Zealand. Rec Auckl Inst Museum. 1985;22:69–76.

61. Whitaker AH. Lizard populations on islands with and without Polynesian rats *Rattus exulans*. Proc New Zeal Ecol Soc. 1973;20:121–30.

62. Towns DR, Daugherty CH. Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. New Zeal J Zool. 1994;21(4):325–39. doi:10.1080/03014223.1994.9518003.

63. Towns DR. Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: The kiore (*Rattus exulans*). J R Soc New Zeal. 1991;21(2):119–36. doi:10.1080/03036758.1991.10431400.

64. Hoare JM. Novel predators and naïve prey: how introduced mammals shape behaviours and populations of New Zealand lizards. Victoria University of Wellington; 2006.

65. Cree A. Low annual reproductive output in female reptiles from New Zealand. New Zeal J Zool. 1994;21(4):351–72. doi:10.1080/03014223.1994.9518005.

66. Ashton KG, Feldman CR. Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. Evolution. 2003;57(5):1151–63. doi:10.1111/j.0014-3820.2003.tb00324.x.

67. Pincheira-Donoso D, Hodgson DJ, Tregenza T. The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? BMC Evol Biol. 2008;8:68.
68. Barry M, Shanas U, Brunton DH. Year-round mixed-age shelter aggregations in Duvaucel’s geckos (Hoplodactylus duvaucelii). Herpetologica. 2014;70(4):395–406.

69. Whitaker AH. The lizards of the Poor Knights Islands, New Zealand. New Zealand J Sci. 1968;11:623–51.

70. Cardini A. Lost in the other half: Improving accuracy in geometric morphometric analyses of one side of bilaterally symmetric structures. Syst Biol. 2016;65(6):1096–106. doi:10.1093/sysbio/syw043.

71. Adams DC, Rohlf FJ, Slice DE. A field comes of age: Geometric morphometrics in the 21st century. Hystrix, Ital J Mammal. 2013;24(1):7–14. doi:10.4404/hystrix-24.1-6283.

72. Rohlf FJ, Slice D. Extensions of the procrustes method for the optimal superimposition of landmarks. Syst Zool. 1990;39(1):40. doi:10.2307/2992207.

73. Adams DC. A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. Evolution. 2014;68(9):2675–88. doi:10.1111/evo.12463.

74. Albrecht GH. Multivariate analysis and the study of form, with special reference to canonical variate analysis. Am. Zool. 1980;20:679–93. doi:10.1093/icb/20.4.679.

75. Strauss R. Discriminating groups of organisms. In: Elewa A, editor. Morphometrics for non morphometricians. Berlin, Germany: Springer; 2010. p. 73–91.

76. Mitteroecker P, Bookstein F. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. Evol Biol. 2011;38(1):100–14. doi:10.1007/s11692-011-9109-8.

77. Drake AG, Klingenberg CP. Large-scale diversification of skull shape in domestic dogs: Disparity and modularity. Am Nat. 2010;175(3):289–301.

78. Bookstein FL. Principal warps: Thin-plate splines and the decomposition of deformations. IEEE Trans Pattern Anal Mach Intell. 1989;11(6):567–85.

79. Dickson BV, Sherratt E, Losos JB, Pierce SE. Semicircular canals in Anolis lizards: ecomorphological convergence and ecomorph affinities of fossil species. R Soc Open Sci. 2017;4(10):170058. doi:10.1098/rsos.170058.

80. Klecka W. Discriminant Analysis. Newbury Park: Sage Publications; 1980.

81. Wilson SR. On comparing fossil specimens with population samples. J Hum Evol. 1981;10(3):207–14.

82. Albrecht GH. Assessing the affinities of fossils using canonical variates and generalized distances. Hum Evol. 1992;7(4):49–69. doi:10.1007/BF02436412.

83. Copenhaver M, Holland B. Computation of the distribution of the maximum studentized range statistic with application to multiple significance testing of simple effects. J Stat Comput Simul. 1988;30(1):1–15. doi:10.1080/00949658808811082.

84. R Development Core Team. R: a language and environment for statistical computing. Vienna; 2019.

85. Adams DC, Collyer M, Kaliontzopoulou A. geomorph: Software for geometric morphometric analyses. https://cran.r-project.org/web/packages/geomorph/index.html. 2020.

86. Schlager S. Morpho: calculations and visualizations related to geometric morphometrics. 2016.