# **Supplementary Material for:**

Skeletal variation in extant species enables systematic identification of New Zealand's large, subfossil diplodactylids.

Lachie Scarsbrook<sup>1</sup>, Emma Sherratt<sup>2</sup>, Rodney A. Hitchmough<sup>3</sup>, Nicolas J. Rawlence<sup>1</sup>

<sup>1</sup> Otago Paleogenetics Laboratory, Department of Zoology, University of Otago, Dunedin, New Zealand

<sup>2</sup> School of Biological Sciences, The University of Adelaide, Adelaide, South Australia, Australia

<sup>3</sup> Department of Conservation, Wellington, New Zealand

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## **Supplementary Methods**

### (a) Study specimens

To capture extant morphological variation, we examined both left and right maxilla (*sensu* (1)) from 43 adult skeletal specimens (Supplementary Table 1) representing 13 species from five diplodactylid genera: *Dactylocnemis, Hoplodactylus, Mokopirirakau, Naultinus* and *Woodworthia* (Supplementary Figure 1). Maxillae were utilized as they were known to be taxonomically informative in fossil lizards (2,3) and relatively abundant in subfossil collections given preservation (paired structure) and identification (characteristic Gekkonidae morphology; (4)) biases. Samples were chosen based on availability in museum collections, resulting in limited sample sizes and absence of rarer genera, namely *Toropuku* and *Tukutuku* (e.g. (5)). Species-level determination was based on collection locality (Hitchmough, pers. comm. 2020) given classification prior to significant taxonomic revisions (6). Accordingly, most statistical analyses were restricted to inter-genera, with differences between species visualized through species specific notation on plots. Additionally, northern and southern Duvaucel's gecko (*Hoplodactylus duvaucelii*) populations were distinguished with similar notations, given extensive genetic distance (e.g. (7)).

Despite being observed in other squamates (8–10), morphological diversity attributable to sexual dimorphism was not examined, as sex was not recorded for the majority (63%) of specimens. To determine how maxilla shape influences juxtaposing cranial elements (prefrontal, frontal and nasal), whole-skull micro-computed tomography (micro-CT) scans of a representative individual from each genus analysed were downloaded (with author permission; Paluh et al. 2018) from MorphoSource (Identifiers: S15380; S15404; S15417; S15420; S15463; https://www.morphosource.org/). In addition, we examined 11 wellpreserved, Holocene subfossil maxillae identified as '*Hoplodactylus cf. duvaucelii*' (Supplementary Table 1), covering the majority of their assumed prehuman range (Figure 1). Lack of sampling from known Holocene subfossil localities (e.g. Figure 1) reflected either an absence of maxillae (in museum collections), or poor morphological preservation of recovered elements. Maxilla morphology (Supplementary Figure 2) was characterized following Evans (11), Gray et al. (2) and Ledesma and Scarpeta (12).

#### (b) Imaging

3D rendered surface models were generated from X-ray micro-Computed Tomography (micro-CT) reconstructions of both extant and Holocene subfossil maxilla. Specimens were micro-CT scanned at a resolution of  $\sim$ 16 μm (typically 50 kV, 200 μA), using a Skyscan 1172 (Bruker micro-CT) at the Otago Micro and Nanoscale Imaging facility (OMNI). Scattering artefacts were reduced using a 0.5 mm aluminium filter. The raw X-ray images (shadowgrams) were reconstructed into volumes using the NRecon software interface (Skyscan, Aartselaar, BE) and sliced transversely, producing image stacks (.TIFF), from which individual maxilla were digitally isolated using the grayscale threshold method in FIJI v. 2.0.0 (13).

(c) Landmark acquisition and morphometric analysis

Maxilla shape was characterized using 3D Cartesian coordinates of 15 fixed landmarks (representing equivalent anatomical loci) and 40 equally spaced semi-landmarks (demarcating four major homologous curves; Figure 1B; Supplementary Table 2), manually digitized using Checkpoint v. 2019.03.04.1102 (Stratovan Corporation, Davis, CA). Landmark digitization was duplicated, and the specimen order randomized to minimize measurement and systematic errors respectively (14). Coordinate data were exported as individual Morphologika files, with reflected copies of each left maxilla generated through reversing the sign of the x-coordinates (for symmetric analysis below). All subsequent statistical analyses were performed in the R statistical environment v. 3.6.1 (15) using the packages *geomorph* v. 3.1.2 (16) and *Morpho* v. 2.7 (17).

The 3D landmark coordinates for extant maxillae  $(n = 83)$  were aligned using a generalized least-squares Procrustes superimposition (effectively removing differences in size, position and orientation; (18)), taking into account both matching symmetry and replicate, resulting in shape variables for the symmetric component of shape (19). To minimize Procrustes distance between specimens, semi-landmarks were permitted to slide along their tangent directions during Procrustes superimposition (20). As snout-vent length measurements were not available for most skeletal specimens, centroid size (calculated as the square root of the sum of squared distances of each landmark prior to Procrustes superimposition) was used as a proxy for body size (21). Procrustes mean square estimates for individual variation and fluctuating asymmetry (of both shape and size) exceeded measurement error under initial Procrustes ANOVA,

suggesting effects of measurement error are negligible ((19); Supplementary Table 3). The resulting symmetric shape data (averaged left and right shape configurations; (19)) were used in all subsequent analyses.

#### (d) Principal component analysis

Principal component analysis (PCA) was performed on the extant dataset to visualize maxilla shape variation among genera. Holocene subfossil specimens were later projected into this morphospace through matrix multiplication with the PCA eigenvectors (e.g. (22)). To interpret shape differences described by the major axes of shape variation identified by the PCA, a twodimensional morphospace was plotted with points identified by species. To visualize shape differences throughout the PCA morphospace, 3D surface warps (23) representing shape change along principal component (PC) axes were generated using the thin-plate spline (TPS) method (24). Specifically, a triangular surface mesh closely resembling the mean shape (*Hoplodactylus cf. duvaucelii*, S.33703.3) was warped into the mean configuration of all symmetric shape coordinates using TPS (e.g.  $(25)$ ). This reference mesh was subsequently warped into the shapes represented by the minima and maxima of the first four PC axes, in addition to the mean shape of each genus. Additionally, Procrustes distances for inter-genera and genera-subfossil comparisons were calculated as Euclidean distances in tangent space (21).

#### (e) Comparative statistical analysis

Procrustes analysis of variance (ANOVA) was performed on the extant dataset (using the '*procD.lm*' function; (26)) to determine whether genera occupy different regions of the morphospace (thus exhibiting distinct maxilla morphologies), in addition to testing the effect of size on maxilla shape. Statistical significance of shape differences (*p* < 0.05) was assessed using Goodall's F-ratio (27) and a randomized residual permutation procedure using 10,000 iterations (28,29).

A Bartlett's test of homogeneity of variances (between genera) was performed on centroid size data (Bartlett's  $K^2 = 7.232$ ,  $p = 0.124$ ) to ensure assumptions of ANOVA were satisfied. Once validated, one-way ANOVA was used to examine differences in centroid size between genera, with statistical significance  $(p < 0.05)$  assessed using Tukey's honestly significant difference (HSD) *post-hoc* test (30).

#### (f) Phylomorphospace

Phylogenetic signal in maxilla shape was calculated using  $K_{mult}$  (31), a generalization of Blomberg's K-statistic appropriate for high-dimensional and multivariate data (32). Under a Brownian motion model of trait evolution,  $K_{mult}$  has an expected value of 1.0, with higher  $K_{mult}$ values indicating increasing phylogenetic signal, thus greater morphological variance between, rather than within clades  $(32)$ . Statistical significance of K<sub>mult</sub> was determined using phylogenetic permutation with 1,000 iterations; calculated by permuting the mean symmetric shape data of each extant species among all tips of the phylogenetic tree (using the '*physignal*' function; (16)) inferred from (33) and (6). Phylogeny-associated shape variation (between species) was visualized using the '*phylomorphospace*' function (16) across the first two PC axes.

(g) Canonical variate analysis

Canonical variate analysis (CVA) with cross-validations (for dataset calibration) was used to reveal the morphological shape variables that maximize intergeneric variance relative to intrageneric variance, and to predict the potential phylogenetic position of Holocene subfossil specimens (22,34). CVA was performed on a reduced set of PC scores (representing 95% of the cumulative variation) to ensure the dimensionality of shape variables  $(n = 19)$  was less than the number of specimens  $(n = 43)$ , in addition to removing minor components of non-shape (i.e. measurement error) variation (35,36). 95% confidence intervals were generated around each of the extant genera within the CVA morphospace. Holocene subfossil specimens were then projected into this morphospace using the canonical variates. As CVA ordinations do not preserve Procrustes geometry, Mahalanobis distances were used in subsequent analyses to correct for shape-space distortions from Euclidean space (36).

Typicality and posterior probabilities concerning Holocene subfossil phylogenetic classification were calculated using generalized distances (D): the Mahalanobis distance of Holocene subfossil specimens to the mean of each genus, adjusted by the standard deviation (37). The squared distance  $(D^2)$  was used to calculate chi-square (typicality) probabilities with p (number of discriminating variables) degrees of freedom, assuming multivariate normal within-group distribution (38). Typicality (or 'unrestricted') probabilities are a multivariate extension of the univariate t-test, which evaluates whether a single observation belongs to a group, enabling Holocene subfossils to be classified as outliers (*p* < 0.20) with respect to the extant dataset (39–41). Conversely, posterior (or 'restricted') probabilities, which require additional standardization through comparison to intrageneric distances (resampled 10,000 times), force Holocene subfossil specimens to belong to an existing genus (38). If the distance between a Holocene subfossil specimen and a genus mean was greater than 95% (*p* = 0.05) of the within-genera differences, the null hypothesis: that the Holocene subfossil belongs to that genus, was rejected (e.g. (22)). Partial warps, representing the maximum and minimum shape along canonical variate (CV) axes, were generated by regression analysis of CV scores against maxilla shape variation and visualized using TPS (36).

# **Supplementary Figures (S1-S8)**



**Supplementary Figure 1** Collection localities of diplodactylid specimens (circles, diamonds and triangles), with concatenated species distributions shown for each genera [39]. For *Hoplodactylus duvaucelii*, extant pseudoendemic island populations (crosses) and subfossil collection localities (numbered stars) are shown, with the illustrated range reflecting prehuman distribution (assumed). Numbers denote Holocene subfossil collection localities (1-7), with letters corresponding to subfossil specimens (A-J): Little Lost World, Waitomo (1 - A); Companionway Cave, Waitomo (2 - K); Mataikona River, Wairarapa (3 - I); Gouland Downs, Tasman (4 - G); Takaka Hill, Tasman (5 - H); Ardenest, North Canterbury (6 – B/C/D/E/F); Earthquakes, North Otago (7 - J).





**Supplementary Figure 2** Surface model of a representative diplodactylid skull (A) highlighting position of maxilla; and maxilla shown in anterior (B), medial (C) and lateral (D) views highlighting anatomical features associated with landmarks (abbreviations explained in the table).



**Supplementary Figure 3** Principal component (PC) analysis of maxilla shape showing PC3 versus PC4 (which represent 15.2% of variation in maxilla shape). Points are modern individuals (symmetric component of left-right maxilla shape) coloured by genus (*Dactylocnemis*: blue-grey, *Hoplodactylus*: red, *Mokopirirakau*: yellow, *Naultinus*: green, *Woodworthia*; purple) and bounded by convex hulls, with shapes (circle, diamond, triangle) corresponding to species (shown in Figure 1B). Holocene subfossil individuals are shown as red circles (A-J): Waitomo (A: AU7700, K: WO333), Wairarapa (I: S.46528.1), Tasman (G: S.38813.2; H: S.39086), North Canterbury (B: S.33703.2, C: S.33703.3, D: S.33703.4, E: S.33703.7, F: S.33703.8) and North Otago (J: VT791a).



**Supplementary Figure 4** Four principal axes of maxilla shape variation visualized as surface warps in medial, dorsal and lateral view (from left to right). PC axes were derived from a PCA of the symmetric component of extant diplodactylid maxilla shape. Surface warps represent the extreme maximum (+) and minimum (-) shape differences along each PC axis. Position of mean shapes for each genus are indicated (coloured circles) along each axis.



**Supplementary Figure 5** Barplot of extant maxilla centroid size (coloured by genera) showing means ± SE, with points coloured by species. Genera that are significantly different are represented by a different lowercase letter (a-c). Holocene subfossil individuals are shown as red circles (A-J): Waitomo (A: AU7700, K: WO333), Wairarapa (I: S.46528.1), Tasman (G: S.38813.2; H: S.39086), North Canterbury (B: S.33703.2, C: S.33703.3, D: S.33703.4, E: S.33703.7, F: S.33703.8) and North Otago (J: VT791a).



**Supplementary Figure 6** Phylomorphospace representing maxilla shape variation (PC1 versus PC2) of mean symmetric shape data. Points represent described/undescribed species (mean symmetric component of left-right maxilla shape for all individuals) coloured by genus (*Dactylocnemis*: blue-grey, *Hoplodactylus*: red, *Mokopirirakau*: yellow, *Naultinus*: green, *Woodworthia*; purple). White nodes represent hypothetical maxilla shape of shared ancestors.



**Supplementary Figure 7** Maxilla surface warps (in medial view) representing the extreme maximum and minimum shape differences along canonical variate (CV) axes 1 and 2 (see Figure 2C).



**Supplementary Figure 8** Comparative surface models of diplodactylid genera skulls (in dorsal view; (42)) highlighting relative position of prefrontal (yellow), maxilla (blue-grey) and nasal (pink). Arrows indicate location of a thickened ridge along the prefrontal orbital margin (present in *Mokopirirakau* and *Naultinus*).

# **Supplementary Tables (S1-S8)**

**Supplementary Table 1** List of modern/Holocene subfossil specimens in morphometric analyses with ID (museum accession number), species-level identification, institution and collection locality. Institution abbreviations are as follows: AM: Auckland Museum; AUM: Auckland University Museum; NMNZ: Museum of New Zealand Te Papa Tongarewa; OM: Otago Museum; WCM: Waitomo Caves Museum. References associated with subfossil collection localities (of '*H.* cf. *duvaucelii*' material) are shown as superscript values:  $(43)$ ,  $(44)$ ,  $(45)$ ,  $(46)$ ,  $(47)$ ; with estimates for deposit ages reported (where available) in thousands of years (ka).





**Supplementary Table 2** Anatomical definitions of fixed (1-15) landmarks and curves comprising semi-landmarks (C1-C4).



**Supplementary Table 3** Examining fluctuating asymmetry: Procrustes ANOVAs of diplodactylid maxilla centroid size (A) and shape (B) by individual, side, replicate and their interaction terms, with statistical significance assessed through 10,000 permutations. Significant results (*p < 0.05*) are indicated in bold.





**(B)**



**Supplementary Table 4** Procrustes distances resulting from Procrustes superimposition of the extant dataset after projection of Holocene subfossil individuals into the morphospace. Shortest Procrustes distances for each Holocene subfossil individual to extant genera (conferring shape similarity) are indicated in bold.



**Supplementary Table 5** Procrustes ANOVA of maxilla shape by genus, centroid size and their interaction, with statistical significance assessed through 10,000 permutations. Significant results (*p < 0.05*) are indicated in bold.



**Supplementary Table 6** Significance values for post-hoc pairwise comparison between genera maxilla shape. Significant results (*p < 0.05*) are indicated in bold.



**Supplementary Table 7** One-way ANOVA of maxilla centroid size. Significant results (*p < 0.05*) are indicated in bold.



**Supplementary Table 8** Significance values for HSD post-hoc comparison between genera maxilla size. Significant results  $(p < 0.05)$  are indicated in bold.



**Supplementary Table 9** Posterior probabilities of extant genera comparisons based on Mahalanobis distance using 10,000 permutations. Significant results ( $p < 0.05$ ) are indicated in bold.



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