

Unexpected Morphological Diversity in New Zealand's Large Diplodactylidae Geckos

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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;

(29)). 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 \pm 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.

		<i>Typicality Probabilities</i>					<i>Posterior Probabilities</i>				
		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	0.019	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	WO333	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 Eugongyline 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 Diplodactylidae genera: *Dactylocnemis*, *Hoplodactylus*, *Mokopirakau*, *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.).

(b) 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

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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.

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Figures

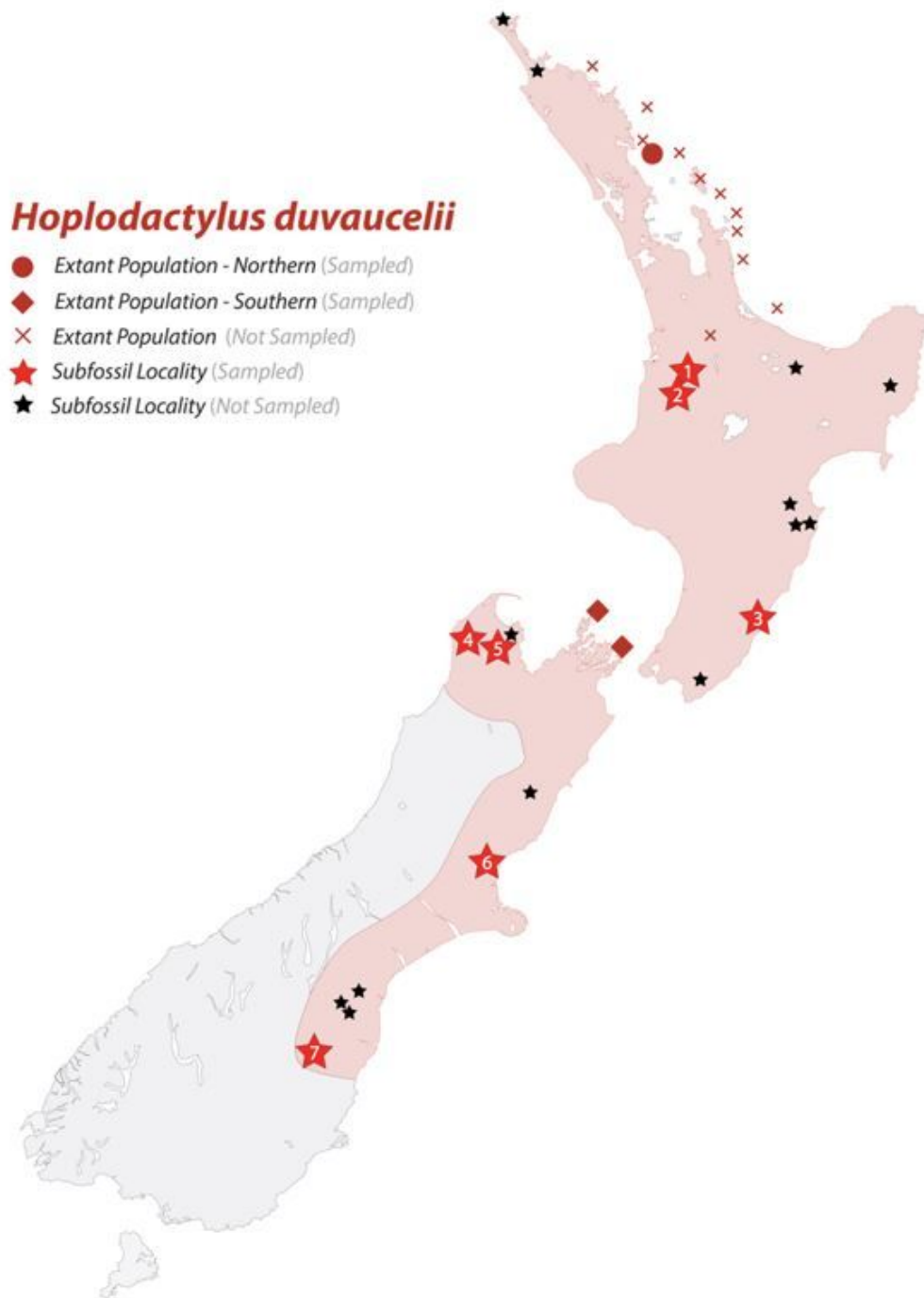


Figure 1

Assumed Holocene distribution (red fill) of *Hoplodactylus duvaucelii*, showing extant modern northern/southern populations (circles, crosses and triangles) and subfossil collection localities (stars). Numbers denote sampled 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); Goulard Downs, Tasman (4 - G); Takaka Hill, Tasman (5 - H); Ardenest, North Canterbury (6 - B/C/D/E/F); Earthquakes, North Otago (7 - J).

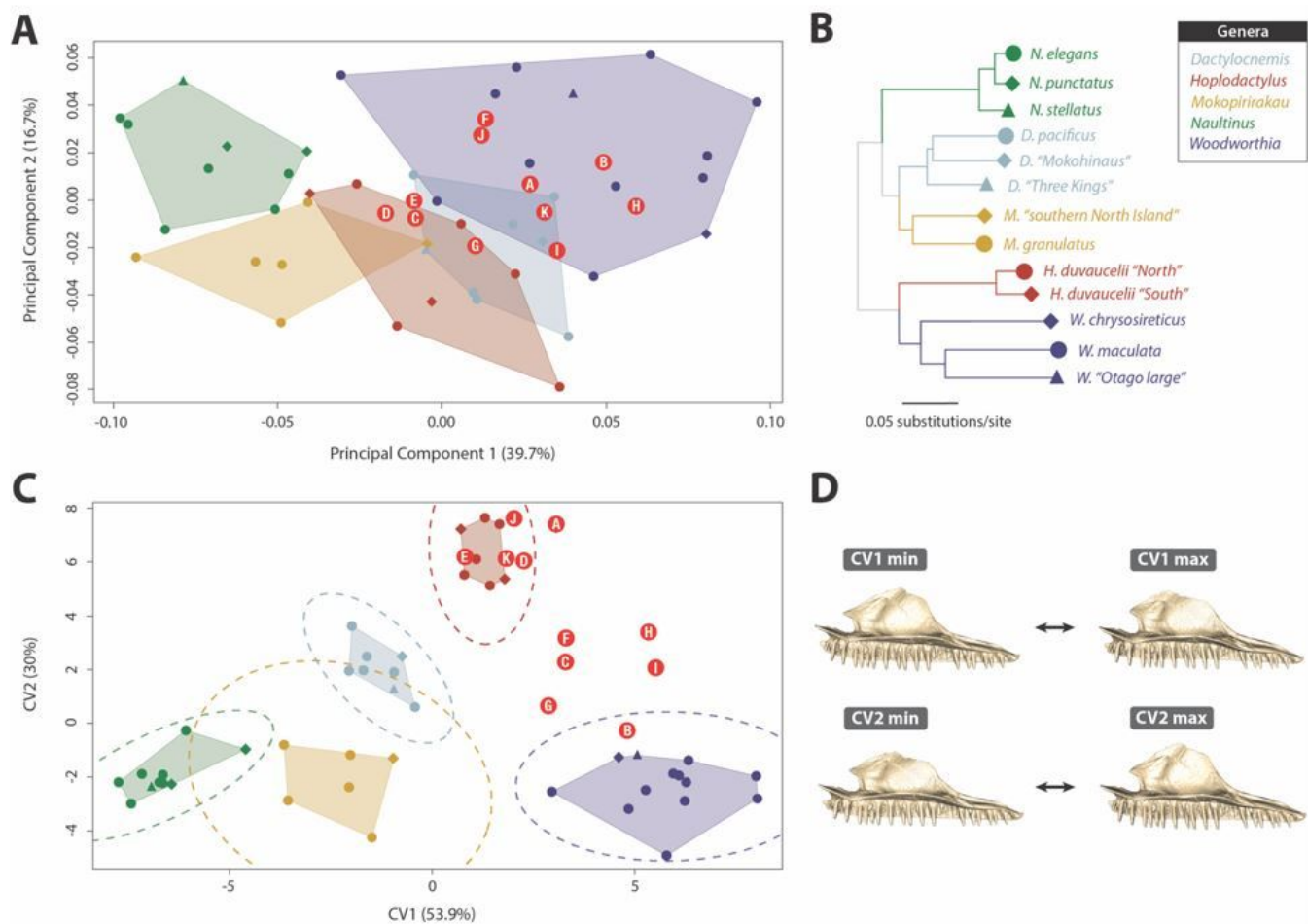


Figure 2

(A) Principal component (PC) analysis of maxillae shape showing PC1 versus PC2 (representing 56.4% of variation in maxillae shape). (B) Phylogenetic tree of described/undescribed Diplodactylidae species analysed (adapted from (14,22)). (C) Canonical variates (CV) analysis showing CV1 versus CV2 (representing 83.9% of the total among-group variance) with 95% confidence ellipses plotted for each genus. (D) Surface warps representing the maxima and minima of CV1/CV2 axes (see C). Points in (A) and (C) are modern individuals (symmetric component of left-right maxillae shape) coloured by genus (Dactylocnemis: blue, Hoplodactylus: red, Mokopirirakau: yellow, Naultinus: green, Woodworthia: purple) and bounded by convex hulls, with shapes (circle, diamond, triangle) corresponding to species shown in (B). Holocene subfossil individuals are shown as red circles (A-J): Waitomo (A: AU7700, K: W0333), 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).

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