Phenotypic variation and sexual dimorphism of the Madeiran wall lizard (*Tiera dugesii*)

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A thesis submitted in partial fulfilment of the requirement of Liverpool John Moores University for the degree of Master of Philosophy

October 2022

Abstract

The Madeiran wall lizard, *Teira dugesii* (Milne-Edwards, 1829) is an endemic lizard of the Madeiran archipelago and is widely dispersed throughout different environments. The previous reports of morphological variation of *T.dugesii* within Madeira have not provided clear patterns but prompted this research into sexual and environment-related differences in morphology. For this study, geometric morphometrics (GMM) techniques combined with phenotypic trajectory analysis were applied to investigate the dorsal and lateral head shape morphology of *T. dugesii*. Univariate and multivariate statistical analyses were conducted to assess sexual dimorphism within the species and identify if ecological adaptations towards intertidal and terrestrial habitats occurred in the *T. dugesii* populations across four different localities within Madeira.

Sexual dimorphism accounted for the largest proportion of size and shape variation in head morphology. Males exhibited a larger and more robust head shape compared to that of females which displayed relatively more petite and slender head shapes. Intertidal/terrestrial habitats were associated with head shape variation between sexes. Specimens from terrestrial environments also consistently had larger heads compared to intertidal specimens from the same locality. Additionally, phenotypic trajectory analysis revealed habitat differences in head morphology, again supporting parallel phenotypic divergence across localities between lizards from terrestrial and intertidal habitats.

KEYWORDS

Sexual dimorphism, phenotypic variation, geometric morphometrics, ecomorphology and phenotypic trajectory analysis.

Contents

1. Introduction.

The Madeiran archipelago consists of 4 islands, situated approximately 900km southwest of Portugal and 700km west of Africa's Moroccan coast (Brehm *et al*., 2001; Clemens and Allain, 2020; Czajkowski, 2002). The islands were created by giant volcanic hotspots beneath the Atlantic and the larger of the four islands formed are Madeira and Porto Santo (Bowler, 2018; Santos *et al*., 2004; Silva-Rocha *et al*., 2016). The Atlantic Ocean surrounding Madeira moderates the climate, leading to a Mediterranean climate that remains relatively constant most of the year (Santos *et al*., 2004). Temperatures range from 14 to 28˚C and decline with elevation, with southern slopes subject to warmer temperatures exceeding 28˚C compared to the more north-facing slopes (Bowler, 2018; Brehm *et al*., 2001; Capelo *et al*., 2005; Davenport and Dellinger, 1995; Rusu *et al*., 2008). Madeira consists of various ecological habitats due to its topography: it reaches 1862 m asl and comprises many ridges and gullies (Bowler, 2018; Santos *et al*., 2004).

Intertidal habitats consist of steep rocky inshore profiles and rockpools forged by volcanic rock and ocean waves weathering rock faces. Other parts of the island consist of extensive narrow dark pyroclastic pebble beaches (Bowler, 2018; Davenport and Dellinger, 1995; Pereira *et al*., 2013; Silva-Rocha *et al*., 2016). Inlets have been found to harbour species that employ and display different characteristics compared to terrestrial counterparts (Bowler, 2018; Brehm *et al*., 2001; Capelo *et al*., 2005).

Terrestrial habitats of Madeira are comprised of land forged by the volcanically porous bedrock with steady streams that help to maintain sources of water. Harsher environments within the island consist of arid scrubs and deserts. Such environments are subject to elevated daytime temperatures (Bowler, 2018; Capelo *et al*., 2005). The ground is covered by a few species of shrubby plants, various sized rocks, and boulders supporting vast insect and animal activity, especially in the summer months (Bowler, 2018; Capelo *et al*., 2005).

Madeira is home to endemic, invasive and introduced species of fauna and flora (Silva-Rocha *et al*., 2016). There are an estimated 3340 species of animals, the majority being invertebrates, including 1226 vascular plant species. Madeira provides ideal habitats to three introduced reptile species: Common wall gecko (*Tarentola mauritanica*) (Harris *et al*., 2004), Tropical house gecko (*Hemidactylus mabouia*) (Rato *et al*., 2021), and the Flowerpot snake (*Ramphotyphlops braminus*) (Clemens and Allain, 2020) The Madeiran wall lizard (*Tiera dugesii*) is the only endemic reptile species. It is a polymorphic lizard belonging to the order Squamata, family Lacertidae (Davenport and Dellinger, 1995; Jesus, 2012). It has a wide distribution across Madeira and is found to thrive in most habitats within the island and can be found in extremely high numbers (Davenport and Dellinger, 1995; Koleska *et al.*, 2017; Sá-Sousa, 1995; Silva-Rocha *et al*., 2016).

T.dugesii appears to be quite polymorphic which already inspired investigation into its general morphology (Báez and Brown 1997; Brehm *et al*., 2001). Sexual dimorphism is found across the animal kingdom and is displayed in three ways: (1) primary sexual characteristics, that are reproductive organs, (2) secondary characteristics that aid in an organism's reproductive success, e.g., weaponry or behavioural traits (Kratochvíl and Frynta, 2002), and (3) morphological features that do not directly correspond to reproduction, for example, related morph changes (Richards and Hawley, 2011; Rico-Guevara and Hurme, 2019). In addition to sexually dimorphic patterns, numerous morphological papers propose that environmental factors are essential in explaining adaptive characteristics (Báez and Brown, 1997; Shine, 1989; Stayton, 2005).

Modern Geometric Morphometrics (GMM) techniques have been broadly applied to study lizard morphological variation (Kaliontzopoulou, 2011). GMM has been a powerful fundamental tool in herpetological research and when used with mathematical procedures is important for quantifying morphological variation. It relies on biometric values such as linear distances, ratios, and angles to provide greater insight into patterns and causes of phenotypic diversification (Cardini, 2013; Kaliontzopoulou *et al*., 2008; Kaliontzopoulou, 2011; Klingenberg, 2016; Zelditch, 2012).

GMM requires placement of two-dimensional or three-dimensional landmarks or semi-landmarks on homologous regions/points of a specimen of interest (Buser *et al*., 2018; Cardini, 2013; Kaliontzopoulou, 2011; Stayton, 2005). GMM helps understand the physical size, homology, and shape variation and is undoubtedly a crucial technique for understanding biological diversification (Cardini, 2013; Zelditch, 2012).

Kaliontzopoulou (2007) investigated head scalation patterns in two species of *Podarcis* lizards from three locations in Portugal (Kaliontzopoulou *et al*., 2007). By orienting the head to obtain dorsal and lateral views, and using homologous points on the reptile's head, she found sexual dimorphism in head scalation. Kaliontzopoulou and collaborators later investigated intraspecific ecomorphological variation within *Podarcis bocagei* (Kaliontzopoulou *et al*., 2010). This research examined the ecomorphological variation of head scales. The results identified a significant impact of habitat selection on head scale shape in dorsal and lateral orientations (Kaliontzopoulou *et al*., 2007; Kaliontzopoulou *et al*., 2010). Interestingly, males and females from the same habitat displayed similar phenotypic shape patterns yet differed between locations. This suggests that shape change diverges between locations and converges within habitat (Kaliontzopoulou *et al*., 2010).

Davenport and Dellinger (1995) investigated melanism in *T. dugesii* to determine variation between different ecological habitats. Intertidal and terrestrial habitats were compared in Canico, SE Madeira. Field recordings of dorsal colour and linear body measurements were taken to investigate variation between neighbouring habitats and phenotypic variation in colour was detected. Intertidal lizards were distinctively darker and larger than their terrestrial neighbours (Davenport and Dellinger, 1995). The findings suggested that strong selection might have caused divergence between the habitats, but the findings were only preliminary as they were limited to just one beach-inland pair of sites

The possible finding that the same pattern of morphological divergence was repeated at the different sites would provide greater support for the pattern found in *T. dugesii* at Canico. Considering its relatively short evolutionary colonisation time (early Pleistocene, Brehm *et al.*, 2001), this would in turn support a rapid and consistent morphological differentiation concerning ecological adaptation.

This thesis aims to explore beach-inland divergence in *T. dugesii* using geometric morphometric (GMM) techniques and statistical procedures to evaluate sexual dimorphism and phenotypic variation. It is predicted that *T.dugesii* head shape and size will vary in a sexually dimorphic manner and within habitat in a consistent manner.

The hypotheses tested are:

1. As in other reptiles, there is sexual dimorphism in head size and shape.
2. Both male and female head size and shape will show geographical variation among localities.
3. Morphological divergence in head size/shape of *T. dugesii* is repeated across different pairs of beach and inland sites.

To statistically explore the third proposed hypothesis, I will take advantage of a novel statistical method proposed by Adams and Collyer (2009, see also Collyer and Adams 2013): the phenotypic trajectory analysis (PTA). Work by Meloro *et al.* (2014) and Charters *et al.* (2022) have demonstrated that PTA can be successfully applied to geometric morphometrics data of skulls and teeth. Here PTA will be used to detect changes in evolutionary trajectories magnitude, direction, and shape within the multivariate shape space identifiable by the head morphology of *T. dugesii*. If habitat adaptation provides a consistent constraint in the morphology of the Madeira wall lizard, it is expected that phenotypic trajectories defined by shape changes between terrestrial and intertidal specimens are parallel across separated locations within Madeira.

2. Materials & Methods

2. I. Sites and Specimens

Photographs of *T. dugesii* were available from four locations in Madeira, Portugal. The four study locations were Canico in SE Madeira, Paul do Mar in the southwest, Porto da Cruz in the north-east and São Vicente, located north-west of the island (see Fig. 1). At each location, samples were available from an intertidal site and an adjacent inland site 0.2-1km away. Sample sizes were large for males at all sites (range 36 – 60) and slightly smaller for females (range 22-41) (Table 2). In this thesis, I will refer to each sample of individuals having come from a beach or inland sampling as “intertidal” and “terrestrial” within one of the four locations i.e. Canico terrestrial, Canico intertidal.

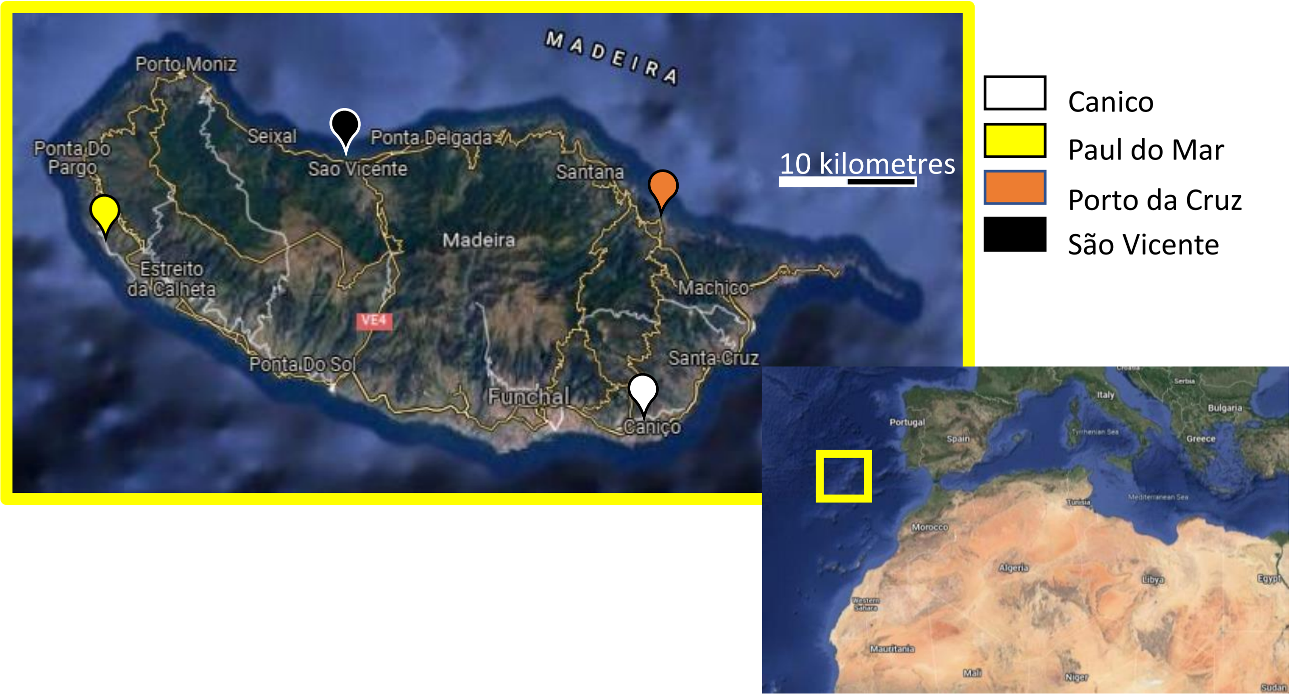

Fig. 1. Map of Madeira with 10-kilometre scale bar with location pins for specimen sites, colour coded respectively, Bottom right image of northern Africa for perspective.

Locations	Canico	Paul do Mar	Porto da Cruz	São Vicente	Total
Latitude	32.642678	32.758408	32.765237	32.804844	
Longitude	-16.830090	-17.231095	-16828818	-17.045862	
Dorsal					
Terrestrial	40	42	46	44	172
Intertidal	35	47	36	39	157
Total	75	89	82	83	329
Lateral					
Terrestrial	39	42	42	43	166
Intertidal	32	43	34	39	148
Total	71	85	76	82	314

Table 1. The number of specimens per location and environment with geographical coordinates.

The dorsal orientation was available for 329 specimens, of which 203 were males and 126 were females. 314 high quality photographs were available for the lateral orientation (192 males and 122 females). Images were provided by Prof Richard Brown and Dr Carlo Meloro. All individuals had been photographed near a scale bar providing a calibration point for use with Two-dimensional software TpsDIG2 version 2.3.1 (Rohlf, 2015).

2. II. Image control and landmarking

Specimen images that were subject to distortion, obscure angle, containing biological damage to the individual's scales or individuals that could not be definitively sexed were excluded (Loy and Slice, 2010; Buser *et al.*, 2018). Images of the specimens were organised into the correct location and environment along with a specimen specific number and sex symbol to ensure correct categorisation (see Table S1). All images were digitally rotated to the same angle to ensure the correct landmark configuration (Loy and Slice, 2010).

Landmark configurations within this study (Fig. 2) are described as two-dimensional x,y cartesian coordinates (coordinates contain non-shape information) (Buser *et al*., 2018; Loy and Slice, 2010; Mitteroecker and Gunz, 2009). The advantage of using this type of geometric morphometrics is that working with 2D landmarks gains greater ease to generate data recorded from digital pictures through accessible software, i.e., TpsDig2 (ver.2.3.1) (Buser *et al*., 2018; Loy, A. and Slice, DE, 2010).

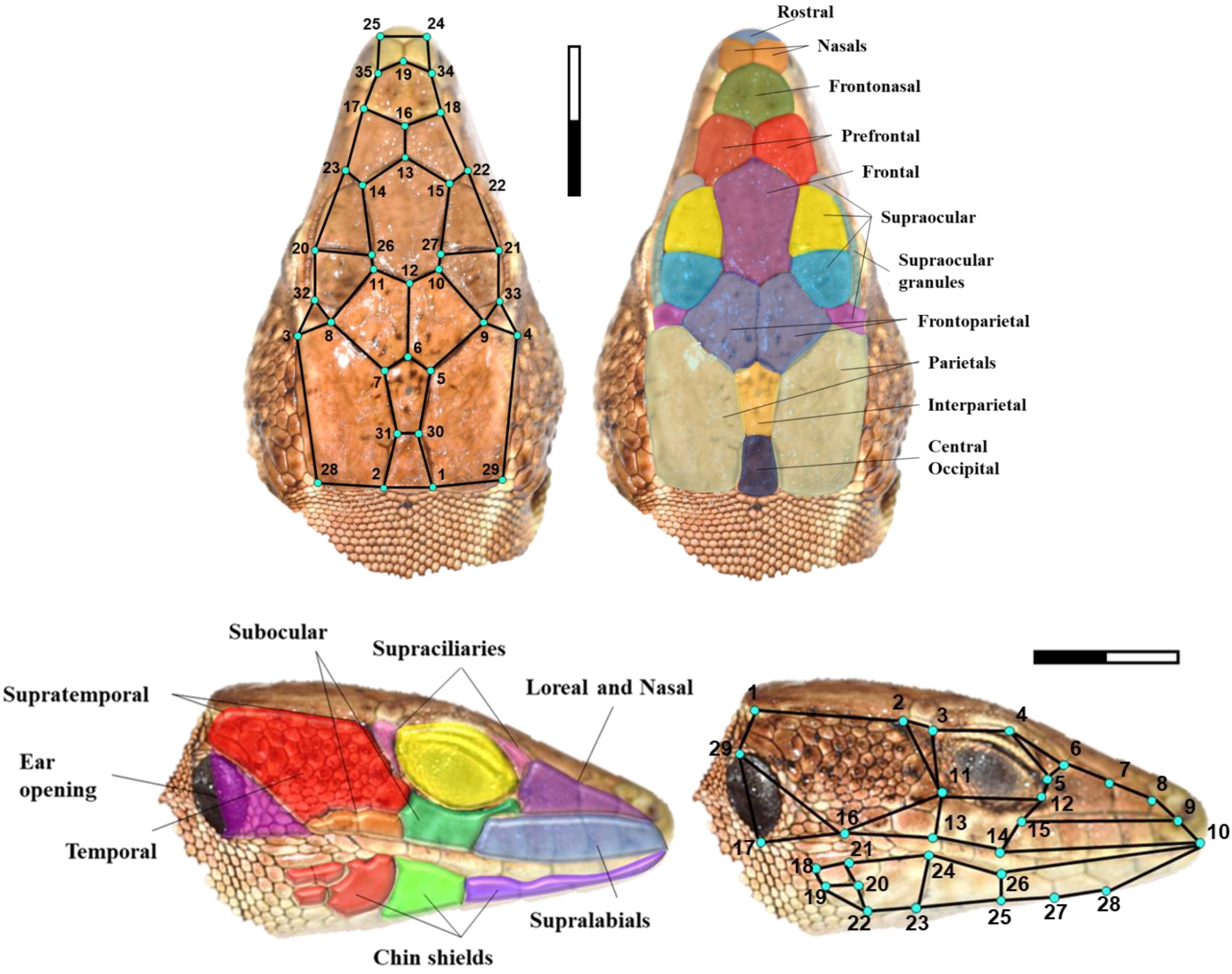

Fig. 2. Two-dimensional landmark configuration on homologous points visually reflecting shape pattern, specimen displayed was *T.dugesii* 7.02 female, *scale bar*: 1cm. Wireframes are derived from MorphoJ ver.1.07a.

Utilising TpsDIG2 (ver.2.3.1, Rohlf, 2015), the landmarks selected were placed on anatomically homologous points of the reptile's head to outline full-scale structure (Fig. 2.). Thirty-five individual landmarks were placed on the Dorsal orientated images and 28 landmarks for the lateral orientation. Dorsal landmarks positioned for this study were configured across the whole specimen aiding natural biological asymmetry to increase the understanding of shape variation within the species (Klingenberg *et al*., 2002; Kaliontzopoulou *et al*., 2008).

2. III. Geometric Morphometrics (GMM) analysis.

Statistical analyses of the data was conducted to quantify shape, allometric and size variation to understand if ecological divergence and sexual dimorphism were present. Analyses were primarily performed within R (ver.4.0.3) using the Geomorph (ver.4.0) and RRPP (ver.1.0) packages that carry out significance testing using randomisation (1,000 permutations were used here)(Adams *et al*., 2015; Adams and Otárola-Castillo, 2013; Collyer and Adams, 2018) and MorphoJ 1.07a (Klingenberg, 2011). PCA scatter plots and wireframes depicting shape changes based on thin-plate spline were produced in MorphoJ (ver.1.07a). Three datasets were analysed: males, females, and all specimens. Location and environments were added as adjacent factors to investigate the pattern of variation on both dorsal and lateral orientated datasets.

After successfully landmarking individuals to generate cartesian coordinates (cartesian coordinates possess non-shape information such as size, position, orientation) (Rohlf, 1999), the landmark configurations were superimposed using Generalised Procrustes Analysis (GPA) to provide shape variables (Goodall, 1991; Gower, 1975; Kaliontzopoulou, 2011; Rohlf and Bookstein, 2003). This procedure performs a Procrustes superimposition, a corrective orientation, translation and scaling to obtain a new set of coordinates, known as

Procrustes coordinates (Rohlf and Bookstein, 2003; Rohlf, 1999). Procrustes coordinates are the shape variables for landmarks projected within Kendall's shape space (the space tangent to the mean shape) (Kaliontzopoulou, 2011; Rohlf and Bookstein, 2003). Superimposition methods rely on specific points, the landmarks, to describe the aspects of shape variation (Adams *et al*., 2013; Buser *et al*., 2018; Cardini, 2013; Mitteroecker and Gunz, 2009). Size was extracted from each landmark configuration using centroid size and subsequently log-transformed to ensure normality (LogCS) (Mitteroecker and Gunz, 2009; Mitteroecker *et al*., 2013; Zelditch *et al*., 2012). Centroid size is the square root of the sum of squared distances of a set of landmarks from their centroid or, equivalently, the square root of the sum of the variances of the landmarks about that centroid in x- and y-directions (Mitteroecker *et al*., 2013; Kaliontzopoulou, 2011; Zelditch *et al*., 2012).

The Procrustes coordinates data matrix was transformed into a covariance matrix suitable for Principal Component Analysis (PCA). MorphoJ (ver.1.07a) can generate a covariance matrix from datasets of shape after Procrustes superimposition (Pavlinov and Mikeshina, 2002). The covariance matrix is a square symmetric matrix that provides the covariances between pairs of variables as off-diagonal entries and the individual variable variances as the diagonal elements (Jaadi, 2021; Mitteroecker and Gunz, 2009; Polly *et al*., 2013). Centroid size is not treated as a covariate and was extrapolated and analysed adjacent to the data exported. Covariates are the variables that provide quantitative information about the specimens that will be used to relate to morphological variance within morphometric analyses, e.g., PCA (Mestre, 2008; Roff and Mousseau, 2005).

PCA is a descriptive data reduction technique. When variables are correlated, it is able to reduce the dimensionality of a multivariate dataset containing these variables by creating a new set of variables in which most of the between-individual variation is expressed by a small number of them (Jaadi, 2021; Rao, 1964; Richardson, 2009; Ringnér, 2008).

Dimensionality is reduced by the identification of orthogonal (uncorrelated) vectors called principal components. A PCA is calculated by an eigenvalue-decomposition of the squared covariance matrix and is a rigid orthogonal rotation of the data from the PC origin (Abdi, 2007; Holland, 2008; Mitteroecker and Gunz, 2009; Polly *et al.*, 2013; Richardson, 2009). Ultimately, the principal components explain the greatest amount of variation between the average squared distance from each point in relation to the origin of the PC axis.

The first principal component (PC1) is oriented to explain the largest amount of variation in the dataset, while the second component (PC2) is orthogonal to the first and explains the next largest variation, and so forth until all the variance among individuals is represented (Abdi, 2007; Holland, 2008; Mitteroecker and Gunz, 2009; Ringnér, 2008). Additionally, PCA provides a way to show how shape changes occur along each PC vector relative to the mean (Klingenberg, 2016; Ringnér, 2008). If there are equal amounts of variation in all directions of shape space, this variance will have its minimum value of 0 on a PC axis (Klingenberg, 2016).

Visual interpretation of the two-dimensional shape variation of *T. dugesii* was conducted using PCA. In conjunction with the PCA, deformation wireframes were added to indicate the expansion and contraction of the homologous data points on the reptile's head across the dorsal and lateral datasets. For this study, PCA scatterplots form a powerful and informative way of visually understanding the shape variation between whole specimen data for sexual dimorphism and ecological purposes.

2. IV. Procrustes ANOVA

Procrustes ANOVA is an analysis of variance that allows testing of individual or within-group variation (Pairwise analysis) (Daboul *et al.*, 2018; McHugh, 2011). The Procrustes ANOVA analysis was employed to test the impact of sex, environment and location on shape (multivariate, dependent variable) and size (univariate dependent variable) (Goodall, 1991; Julien, 2013; Klingenberg *et al.*, 2002; McHugh, 2011). The null hypothesis tested was that location and environmental niches impact shape, and size variation in the total samples and sexes once separated. The interaction of these two factors was tested to assess if phenotypic variation responds differently to environments.

Allometry coherently describes how specific characteristics (portions of anatomy) of living creatures change with size (Gould, 1968, 1971; Klingenberg, 2016). This terminology initially referred to the scaling relationship between the size of an appendage relative to the whole body. More recently, the meaning of the term allometry has become slightly modified, referring to biological scaling relationships (Gould, 1968, 1971; Klingenberg, 2016). Allometric testing was conducted to understand the relationship between shape and log centroid size (LogCS) variation of head scale patterns for sexual dimorphic and ecomorphological purposes (if location and environment affect head scale patterns). Shape and size analyses were conducted using the R (ver.4.0.3) packages Geomorph and RRPP (Adams *et al.*, 2015; Adams and Otárola-Castillo, 2013; Collyer and Adams, 2018).

2.V. Phenotypic trajectory analysis

Phenotypic trajectory analysis is a method of quantifying the size, orientation, and shape of trajectory paths produced by average phenotypes within a multivariate shape space by examining the data to determine whether sets of trajectories are similar or different between one another (Adams and Collyer, 2009; Collyer and Adams, 2013). This can be tested across (for example) temporal or ecological gradients. This analysis is applied to investigate the impact of ecomorphological shape change between groups of specimens to understand if ecological morphology has evolved in parallel at different sites across Madeira (Adams and Collyer, 2009; Collyer and Adams, 2013) (i.e., the shape changes between intertidal and terrestrial lizards from one location [e.g., Canico] are similar to those observed from another location [e.g., Sao Vincente]). Note that this analysis produces fitted phenotypic values differing from a traditional shape PCA, which requires (in our case) the model shape~location+environment+location:environment to be significant for all the tested variance components (location, environment and their interaction). If no interaction occurs between location and environment, PTA is not applicable.

Trajectory size quantifies the path length of the phenotypic trajectory expressed by *T.dugesii* across environmental levels (Adams and Collyer, 2009; Collyer and Adams, 2013) that uses Euclidean distances between each factor. The vector connecting the means of phenotypic shape between two evolutionary levels will quantify the amount of change for this data set. If two phenotypic trajectory path lengths only specifically vary in trajectory size (i.e., their orientation/direction are identical) (Adams and Collyer, 2009; Collyer and Adams, 2013), the differences in phenotypic shape change can be described as one location exhibiting greater or shorter amounts of phenotypic shape change between environments than another location.

Trajectory direction provides the orientation/direction within the multivariate trait space in which phenotypic shape change occurs. Statistical comparisons of trajectory direction will indicate if specimens exhibit convergence, divergence, or parallelism between different locations across the investigated gradient [in our case intertidal vs terrestrial] (Adams and Collyer, 2009; Collyer and Adams, 2013). The trajectory orientation is the direction of the first principal component (PC1) from the covariance matrix (Adams and Collyer, 2009; Collyer and Adams, 2013). Pairwise differences provide the angle statistic (in degrees) of one vector to another, from the first principal component of differing trajectories (Adams and Collyer, 2009; Charters *et al*., 2022; Collyer and Adams, 2013). Large angles between principal components of compared groups indicate directional differences. Here, a directional difference will imply ecological shape convergence or divergence between specimens from different localities. Collyer and Adams (2013) state that when visually interpreting trajectory analysis, the analysis is calculated using all dimensions (x,y,z) of data space (i.e. shape space). The projection of vectors can be distorted by the angles (directions), therefore incurring a visually reduced angle and vector length due to projection onto an x, y dimensional shape space (Collyer and Adams, 2013).

Investigating the phenotypic shape change between four locations and two environments means that the datasets have two levels due to the two comparative variables, i.e. terrestrial v intertidal (Adams and Collyer, 2009). For instance, if the data had three factors, i.e. terrestrial, intertidal and "marine" environments, that would constitute a multilevel phenotypic change (see Adams and Collyer, 2009 for multilevel analysis). The summary statistics for trajectory analysis provide an estimate of the similarity of phenotypic shape change within this study. Statistical significance was assessed using a permutation procedure to evaluate pairwise differences between locations (Adams and Collyer, 2009; Collyer and Adams, 2013. If trajectories are significantly different in one [i.e., localities] or both factors, the summary statistic will be greater than that expected by chance alone (Adams and Collyer, 2009).

3. Results.

3. I. Dorsal shape and size variation, Total sample

The PCA scatterplot generated describes shape variation in the total sample of 329 specimens extracted 66 Principal Component vectors, of which the first two explain collectively 33.99% of variance. In total, 37 principal component vectors explained 95% of variance. A scatterplot of PC1 vs PC2 (Fig. 3a) visually displays sexual dimorphism showing marginal overlap but distinctive clustering between genders. Positive PC1 wireframes show deformation towards the posterior region of the lizard's head. Specifically, the parietal, frontoparietal and central occipital scales show shape expansion more significant than the consensus (PC scores = 0.00, in light blue, Fig. 3). Positive PC1 scores exhibit a shape reduction towards the nasal and rostral scales. In contrast, negative PC1 wireframes visually show the opposite, with evident contraction towards the posterior region of the head relative to an expansion of the anterior rostral scales.

The negative PC2 wireframe describes widening of the posterior head region, including supraocular scales. The posterior head widening creates a significant contraction of the central occipital and elongation of the interparietal. The positive PC2 wireframe showed a slender shape with an expansion of rostral scale. The posterior of the head showed an apparent contraction of the interparietal scale. The PCA indicates that a greater percentage of males cluster towards positive PC1 scores and then spread from negative PC2 into positive PC2, indicating males have greater shape expansion in regards to the posterior region of the head. A high concentration of females are distributed between negative PC1 and positive PC2, showing that females tend to present a slender head with posterior shape contraction, a more elongated central occipital, and a reduced interparietal.

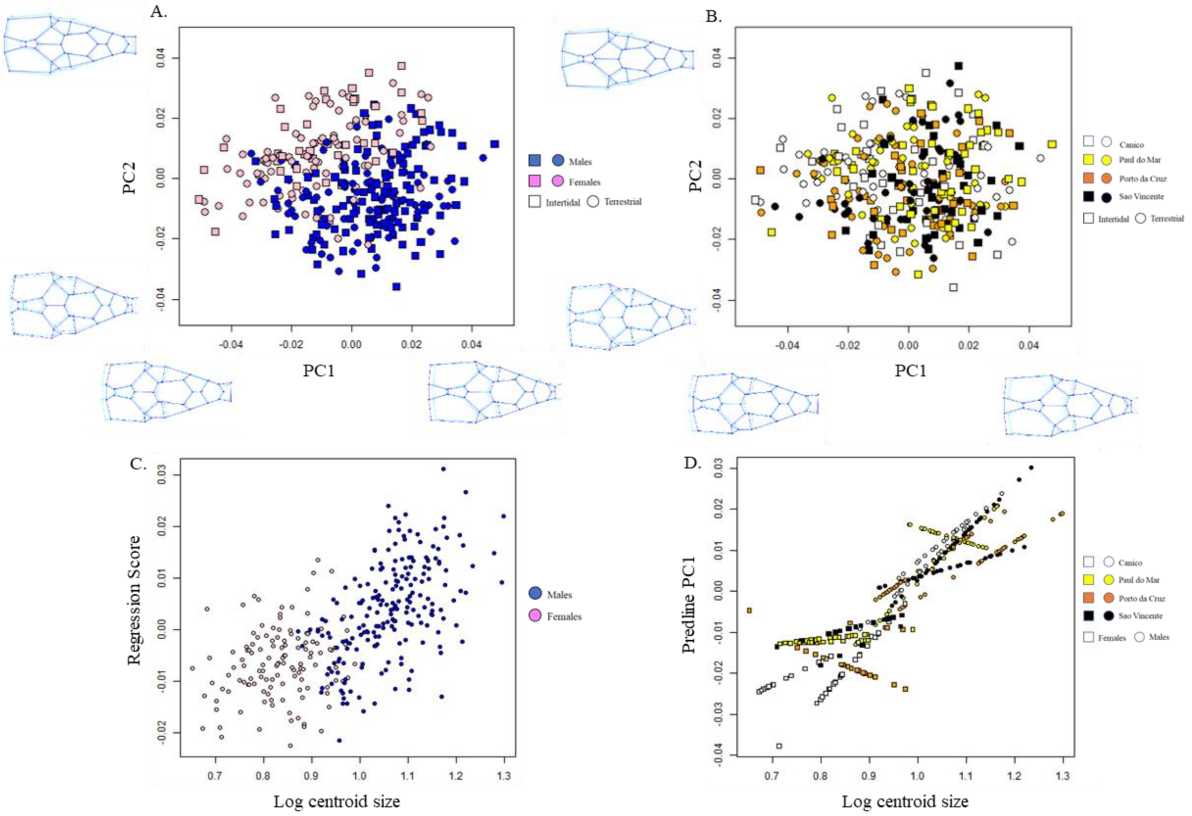

Fig. 3. Scatter plots of whole sample analyses: (A) PC1 and PC2 with sexes labelled. (B) PC1 and PC2 with localities labelled. (C) Sexual dimorphism allometric regression (D) Allometric regression of PC1 fitted values to log centroid size. Wireframes of dorsal scale patterns are used along the PC1 and PC2 axis as a visual representation of phenotypic variation.

Procrustes ANOVA significantly identified sex as the main factor explaining shape variation (8.4%) compared to that of location (3.5%) and then environment (2.5%) (Table 2). The interaction terms sex:location and environment:location was also significant. When analysing size, sex is again the factor explaining most of the variation in the total sample (66%), followed by location (9.8%) and then environment (1.7%, Table 2). Environment:location was significant among the interaction terms and when sex was added as a covariate. Allometric shape variation is present in this sample, with size explaining 9.2 % of shape variation. This pattern differs between sexes and locations but not between environments (Table 2).

All specimens		*F*	*Z*	*df*	r^2	*P*
Dorsal Shape Variation	Sex	30.046	7.1919	1	0.08415	**0.001**
	Environment	8.4738	4.342	1	0.02526	**0.001**
	Location	3.9251	4.8479	3	0.03496	**0.001**
	Sex x Location	1.5151	1.8475	3	0.01201	**0.032**
	Sex x Environment	1.1422	0.5867	1	0.00302	0.277
	Location x Environment	1.8513	2.7088	3	0.01468	**0.003**
	Sex x Location x Environment	1.2421	1.0977	3	0.00985	0.144
Dorsal Allometry	Log Centroid Size	34.3577	6.7992	1	0.09283	**0.001**
	LogCS x Sex	2.7648	2.6692	1	0.00747	**0.006**
	LogCS x Environment	1.3639	1.073	1	0.00369	0.138
	LogCS x Location	1.9246	2.6574	3	0.01547	**0.005**
	LogCS x Environment x Location	1.6422	2.3759	3	0.01233	**0.011**
Dorsal Log Centroid Size	Sex	643.67	9.9889	1	0.66312	**0.001**
	Environment	21.3189	3.3898	1	0.01782	**0.001**
	Location	11.854	4.2863	3	0.09863	**0.001**
	Sex x Environment	0.3745	-0.0553	1	0.00031	0.539
	Sex x Location	0.5016	-0.4856	3	0.00126	0.676
	Environment x Location	10.4102	4.1409	3	0.02611	**0.001**
	Sex x Environment x Location	5.2679	2.8435	3	0.01321	**0.001**

Table 2. Procrustes ANOVA statistics for dorsal shape, dorsal allometry and log centroid size variation of pooled groups, including factor interactions (significance in **bold**).

3. II. Dorsal shape and size variation, Males.

The PCA scatter plot (Fig. 4a) describes shape variation for the first two PC vectors of males (n = 203) that collectively explain 28.7% of the total variation. The plot shows extensive overlap between locations with PC1 wireframes showing distinctive deformation in the posterior region of the lizard's head (Fig. 4a). Specifically, the parietal and frontoparietal scales of positive PC1 visually show shape contraction, whereas negative PC1 show expansion (consensus, with PC scores = 0.00, light blue). Positive PC1 scores represent relative expansion of shape towards the nasal and rostral scales, while negative PC1 scores represent relative contraction in this region.

Negative PC2 scores represent small contraction to parietal and supraocular scales with a significant elongation of the central occipital and extension of the interparietal. Positive PC2 wireframes show a slender overall shape with an expansion of parietal and rostral scales. The posterior of the head shows an apparent contraction of the interparietal scale, this contraction is near the point of scale deletion, effectively expanding the surrounding scales.

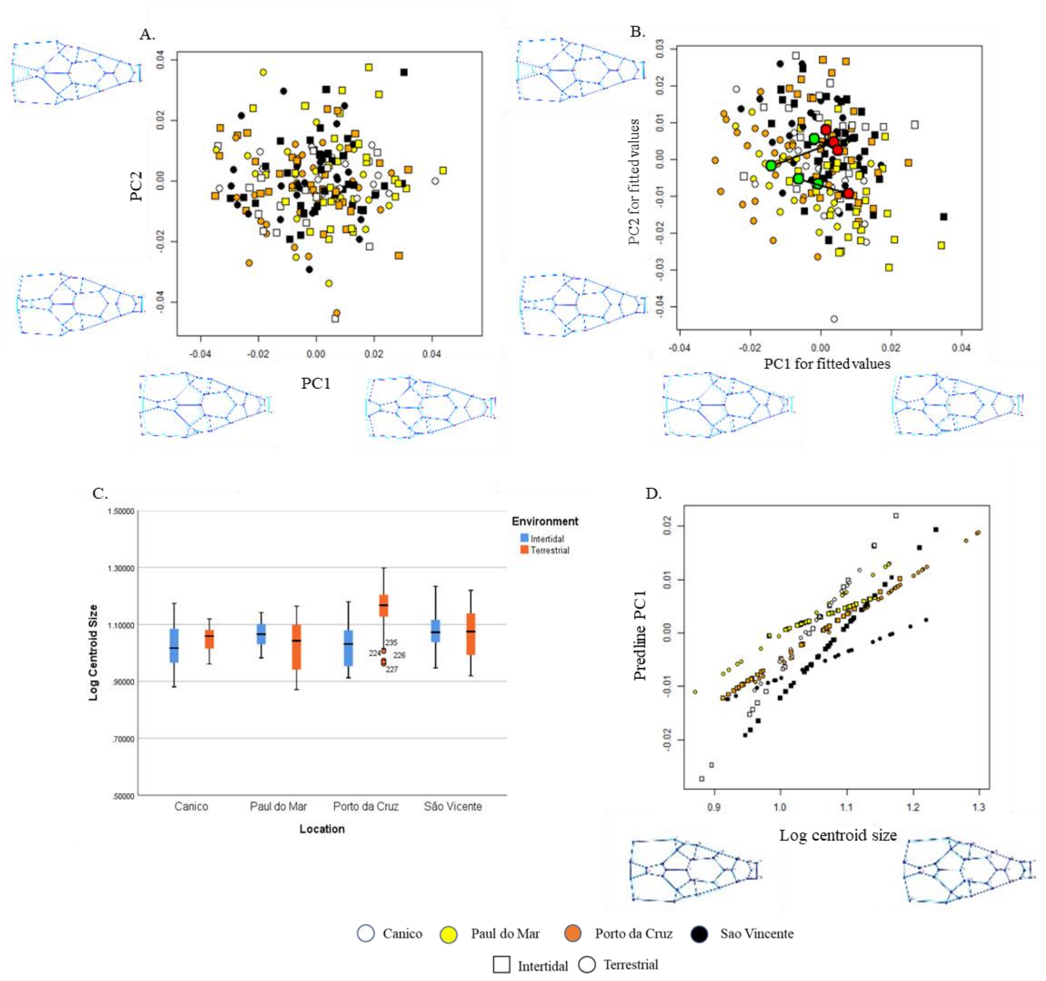

Fig. 4. PC1 and PC2 scatterplots of male shape variation between locations, (A) PCA scatterplot of shape coordinates together with wireframes of dorsal scale pattern deformation., (B) phenotypic trajectory estimated fitted coordinates with wireframes of dorsal scale pattern deformation., (C) boxplot comparing log centroid size from intertidal (blue) and terrestrial (orange), (D) Allometric regression of PC1 fitted values to log centroid size, with deformation wireframes for size.

The Procrustes ANOVA significantly identified location as the main factor explaining shape variation (3.5%), followed by environment (2.7%) (Table 3). The locations;environment interaction term was significant for males. Males showed similar levels of variation between factors for LogCS, yet again location explained 3.8% variance and environment 3.5% (Table 3). The interaction term between environment:location was also significant, explaining 13.9% of the variation. Males from the terrestrial environment within Porto da Cruz appear to be larger than the comparable locations (Fig. 4c). Allometry is equally present in this sample, explaining 2.1% variance between locations. The interaction term LogCS:environment:location, was significant, explaining 2.3% of variation (Table 3). Fig 4d allometric regression shows differences in allometric trajectories between localities and possibly environments with intertidal Paul do Mar and Terrestrial Sao Vincente exhibiting a quite divergent allometric slope.

Males		*F*	*Z*	*df*	r^2	*P*
Shape	Environment	4.8007	4.1959	1	0.02333	**0.001**
	Location	2.4074	4.7571	3	0.03502	**0.001**
	Location x Environment	1.9421	3.2684	3	0.02733	**0.001**
Dorsal Allometry	Log Centroid Size	7.7585	5.5307	1	0.03644	**0.001**
	LogCS x Environment	1.4145	1.14	1	0.00664	0.119
	LogCS x Location	1.4967	1.9506	3	0.02088	**0.025**
	LogCS x Environment x Location	1.7327	2.7472	3	0.02322	**0.004**
Dorsal Log Centroid	Environment	7.3557	2.2508	1	0.0353	**0.004**
	Location	2.593	1.5993	3	0.03762	0.054
	Environment x Location	11.4506	4.2326	3	0.13896	**0.001**

Table 3. ANOVA statistics of dorsal shape, dorsal allometry and log centroid size variation within pooled groups of males only. Location and environment, including factor interactions (significance in **bold**).

The phenotypic trajectory scatter plot displays the first two PC scores for scale shape deformation of male dorsal specimens: PC1 represents 35.5% of male shape variation, while PC2 represents 26.25% (Fig. 4b). The pairwise phenotypic comparison of trajectories (Table 4) identified significant trajectory size changes between Canico and Porto da Cruz against Sao Vicente. Vector angles of all locations against Canico significantly support divergent phenotypic changes only for this locality relative to the others.

	$MD_{1,2}$				$\theta_{1,2}$			
Males Dorsal Location	Canico	Paul do Mar	Porto da Cruz	São Vicente	Canico	Paul do Mar	Porto da Cruz	São Vicente
Canico	-	0.006597	0.007283	0.006959	-	91.79229	75.22358	91.2565
Paul do Mar	0.296	-	0.005947	0.005666	**0.004**	-	57.38777	56.67442
Porto da Cruz	0.802	0.399	-	0.005321	**0.045**	0.369	-	71.97715
São Vicente	**0.017**	0.072	**0.006**	-	**0.002**	0.395	**0.028**	-

Table 4. Summary statistics for differences in phenotypic trajectory pairwise, size ($MD_{1,2}$) and direction ($\Theta_{1,2}$) for all males pooled across the two environments between locations. Parameter statistics and P-values (significance in **bold**)

3. III. Dorsal shape and size variation, Females.

The PCA scatter plot for females (n = 126) showed the first two axes explained collectively 39.6%. 95% of the variance was achieved in 31 PC vectors (Fig. 5a). Wireframes show deformation towards the posterior region of the reptile's head, as represented by positive PC1 scores. The parietal, frontoparietal and central occipital scales visually exhibit shape expansion, this expansion noticeably leads to a more anterior positioning of distal scales. Positive PC1 scores are associated with a shape reduction towards the nasal and rostral scales. In contrast, negative PC1 wireframes visually show the opposite, with evident contraction to the posterior region of the head relative to an expansion of the rostral scales.

Negative PC2 scores represent a significant contraction of the central occipital area of the posterior head region, (see wireframe in Fig. 5). Positive PC2 scores reflect a slender overall shape with a relative expansion of the rostral scale. The posterior region of the head shows an apparent contraction of the interparietal scale, in conjunction with an increase in the surrounding scales.

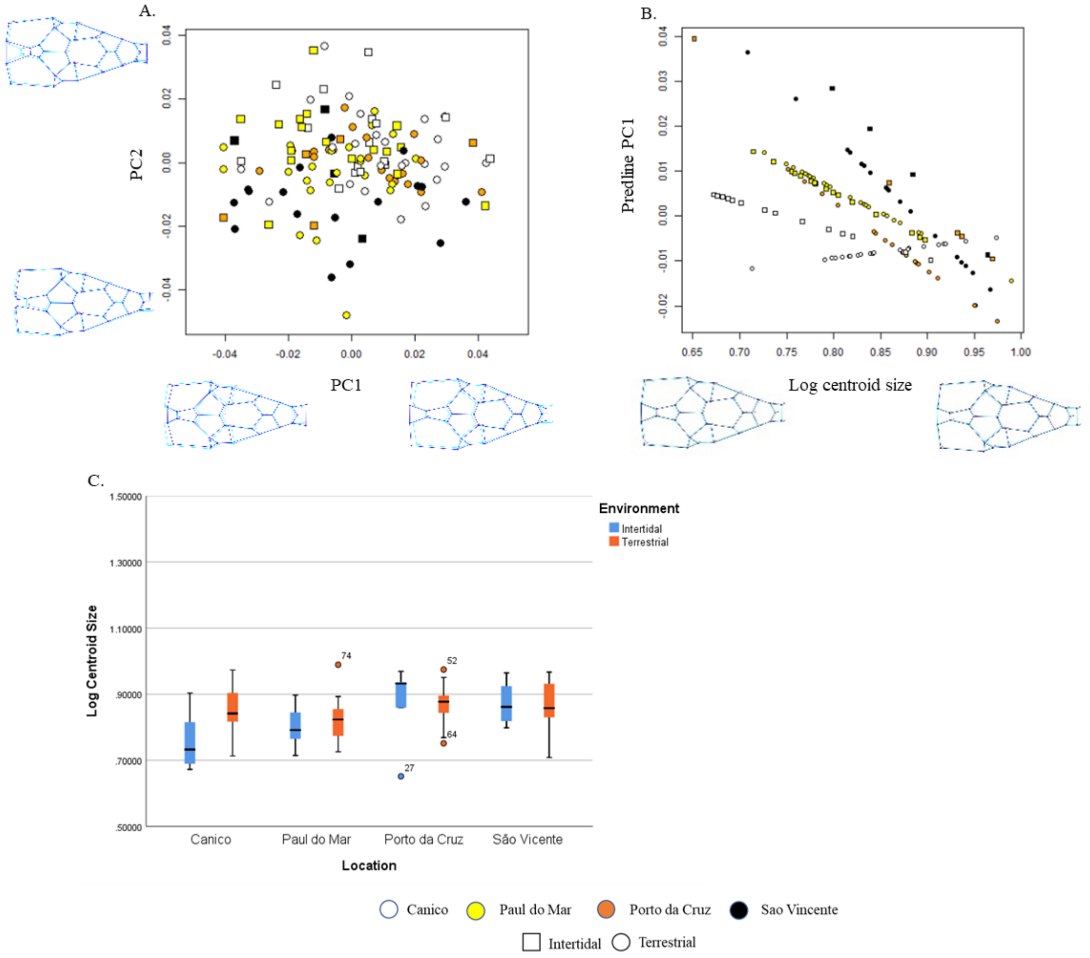

Fig. 5. PC1 and PC2 scatterplots of female shape variation between locations, (A) PCA scatterplot of shape coordinates together with wireframes of dorsal scale pattern deformation., (B) Allometric regression of PC1 fitted values to log centroid size, with deformation wireframes for size (C) boxplot comparing log centroid size from intertidal (blue) and terrestrial (orange).

In the female subsample, Procrustes ANOVA identified location as the factor explaining the highest percentage of shape variation (6.5%), followed by environment (2.9%) (Table 5). Interestingly the interaction term between locations and environments was non-significant (Table 5), and so PTA analysis was not carried out on this subsample.

Similar levels of variation in LogCS occur between factors, with location explaining (11.7%) and environment (9.6%) (Table 5). The interaction term, environment:location was equally significant (Table 5). This can be seen within the boxplot (Fig. 5c), where terrestrial specimens within Canico appear to be larger than their intertidal counterparts. Meanwhile, Porto da Cruz displays the opposite. Allometric variation explains 4.9% of variation (Table 5) and Fig (5b) distinctive allometric trajectory for Canico terrestrial specimens.

Females		*F*	*Z*	*df*	r^2	*P*
Shape	Environment	3.7507	3.1631	1	0.02936	**0.001**
	Location	2.8491	3.7765	3	0.06547	**0.001**
	Location x Environment	1.1499	0.6498	3	0.02583	0.267
Dorsal Allometry	Log Centroid Size	6.5519	3.755	1	0.04947	**0.001**
	LogCS x Environment	0.8285	-0.1965	1	0.00626	0.577
	LogCS x Location	1.4793	1.7814	3	0.03206	**0.036**
	LogCS x Environment x Location	1.0739	0.4223	3	0.02255	0.333
Dorsal Log centroid	Environment	13.122	2.7308	1	0.0957	**0.001**
	Location	5.3844	2.8366	3	0.11692	**0.004**
	Environment x location	3.7961	2.2146	3	0.07266	**0.012**

Table 5. ANOVA statistics of dorsal shape, dorsal allometry and log centroid size variation within pooled groups of females only. Location and environment, including factor interactions (significance in **bold**).

3. IV. Lateral shape and size variation, Total sample.

A scatterplot of PC1 vs PC2 (Fig. 6a) generated for 314 specimens collectively explained 34.81% of head shape variation in lateral view and displayed sexual dimorphism. The negative PC1 scores represent shape enlargement of the supratemporals scales, with a slight enlargement of the ear opening and noticeable shape broadening of the chin shields. The positive PC1 scores represent an elongation of the subocular and supraciliary scales, the temporal area and chin shields display contraction, creating a smaller shape area than negative PC1 deformation.

The negative PC2 scores identify an expansion of the temporal region accompanied by subocular and ear-opening shape expansion. Chin shields showed a contracted elongation giving rise to a slender lower jaw shape. In comparison, positive PC2 scores represent a contraction of temporal and subocular scales with an expansion of the chin shield creating a more robust lower jaw deformation. Male shape variation indicates that males display greater lateral shape robustness with greater lower jaw expansion (Fig. 6a and b). Meanwhile, females show lateral narrowing with relatively smaller chin shields. Interpretation of Fig (6b) of shape change between locations shows clustering of Sao Vincente females central of the PCA whereas Canico shape variation clusters extensively across both PC2 scores and negative PC1, Porto da Cruz and Sao Vincente are more central, suggesting shape variation within Canico.

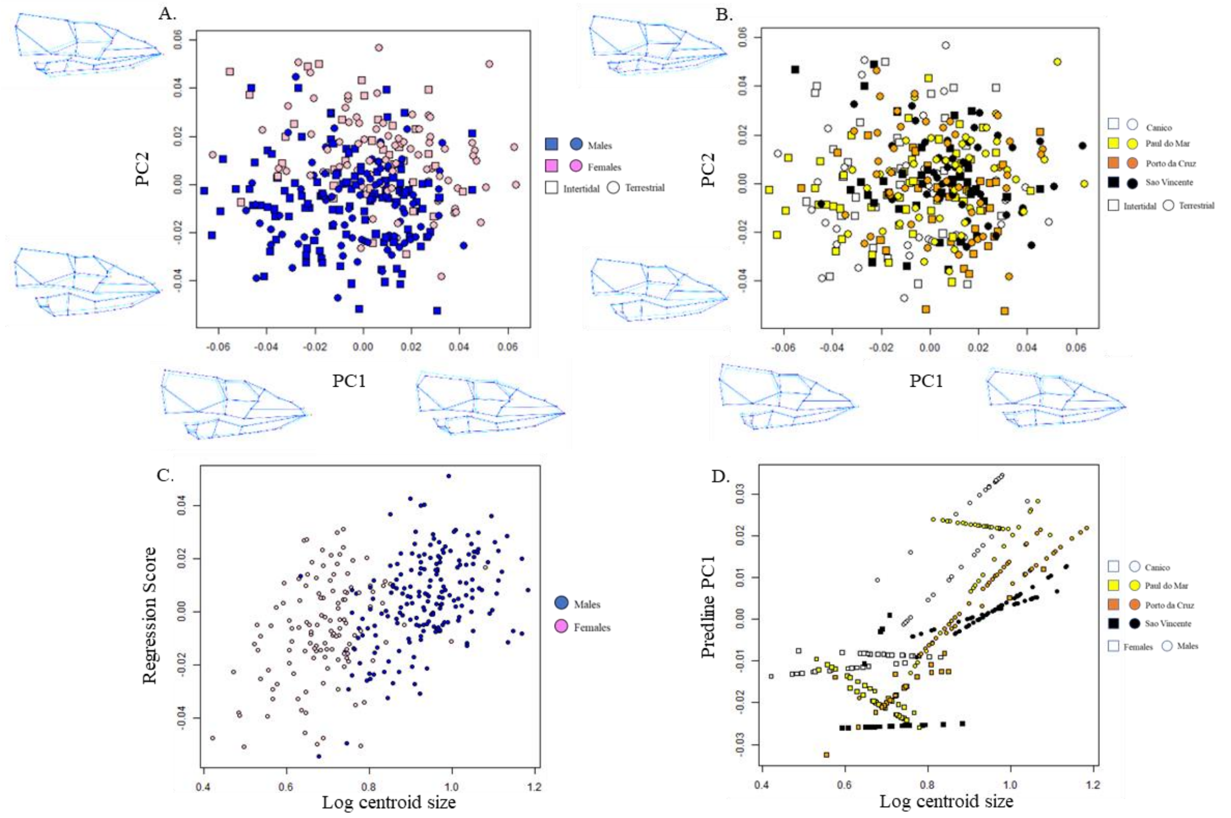

Fig. 6. Scatter plots of whole sample analyses: (A) PC1 and PC2 with sexes labelled. (B) PC1 and PC2 with localities labelled. (C) Sexual dimorphism allometric regression (D) Allometric regression of PC1 fitted values to log centroid size. Wireframes of lateral scale patterns are used along the PC1 and PC2 axis as a visual representation of phenotypic variation.

Procrustes ANOVA significantly identified sex as the main factor explaining lateral shape variation (5.8%), followed by location (5.4%) and then environment (2.4%) (Table 6). The interaction terms sex:location and location:environment was also equally significant (Table 6). When analysing size, sex again explains most of the variation in the total sample (60%), followed by location (12%) (Table 6). The interaction term, environment:location is significant (Table 6). The allometric variation presented within the total sample showed significant LogCS:location and LogCS:environmental choice (Table 6).

All specimens		F	Z	df	r^2	P
Lateral Shape Variation	Sex	19.226	6.002	1	0.05804	**0.001**
	Environment	7.6517	4.3817	1	0.02394	**0.001**
	Location	5.9156	6.86	3	0.05415	**0.001**
	Sex x Location	1.6311	2.198	3	0.01321	**0.017**
	Sex x Environment	1.1595	0.6273	1	0.00313	0.259
	Location x Environment	3.5476	5.1469	3	0.02874	**0.001**
	Sex x Location x Environment	1.3099	1.3087	3	0.01061	0.099
Lateral Allometry	Log Centroid Size	24.4731	6.7348	1	0.07112	**0.001**
	LogCS x Sex	1.6112	1.4947	1	0.00468	0.068
	LogCS x Environment	2.2564	2.3035	1	0.00654	**0.012**
	LogCS x Location	1.8807	2.6541	3	0.01578	**0.004**
	LogCS x Environment x Location	0.9307	-0.1889	3	0.00721	0.58
Lateral Log centroid Size	Sex	469.91	8.3671	1	0.60098	**0.001**
	Environment	0.9625	0.54144	1	0.00308	0.318
	Location	14.059	4.76	3	0.11976	**0.001**
	Sex x Environment	2.0901	1.1004	1	0.00225	0.14
	Sex x Location	0.2293	-1.2084	3	0.00074	0.893
	Environment x Location	4.6821	2.5416	3	0.01511	**0.006**
	Sex x Environment x Location	2.5383	1.5173	3	0.00819	0.069

Table 6. ANOVA statistics for lateral shape, lateral allometry and log centroid size variation of pooled groups, including factor interactions (significance in **bold**).

3.V. Lateral shape and size variation, Males.

The PCA scatterplot of males in lateral view (n =192) shows the first two PC collectively explaining 31.28% of variance (Fig. 7a). Negative PC1 scores represent shape enlargement of the supratemporal scales and slight enlargement of the ear opening, this enlargement forces the supraciliary and subocular scales to a more anterior position. Positive PC1 scores represent elongation of the subocular and supraciliary scales, while the temporal area and chin shields display contraction, creating a smaller shape area compared to negative PC1 scores. Negative PC2 identifies an expansion of the temporal region accompanied by subocular and ear-opening shape expansion. Chin shields are more elongated, forming a slenderer shape yet contracting to create a shallower lower jaw. Positive PC2 displays a contraction of temporal and subocular scales with an expansion of the chin shield creating a more robust visualisation (Fig. 7a).

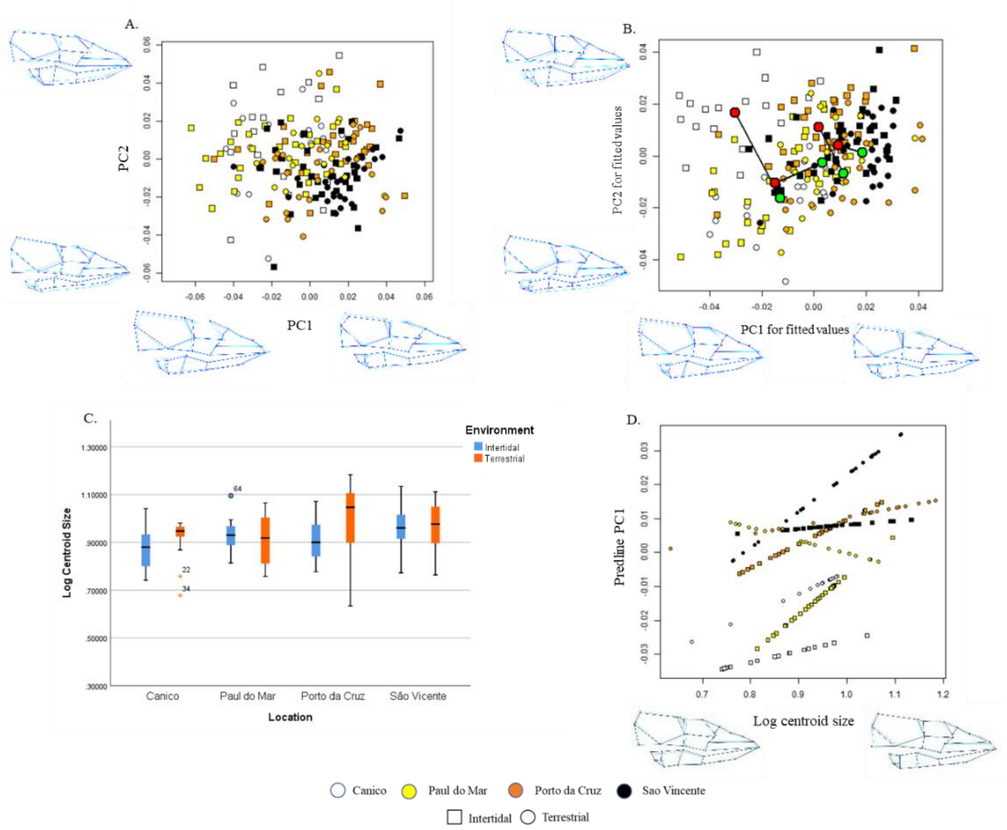

Fig. 7. PC1 and PC2 scatterplots of male shape variation between locations, (A) PCA scatterplot of shape coordinates together with wireframes of lateral scale pattern deformation., (B) phenotypic trajectory estimated fitted coordinates with wireframes of lateral scale pattern deformation., (C) boxplot comparing log centroid size from intertidal (blue) and terrestrial (orange), (D) Allometric regression of PC1 fitted values to log centroid size, with deformation wireframes for size.

For the lateral shape of males, Procrustes ANOVA significantly identified location as the main factor (8.1%), followed by environment (2.5%) (Table 7). The interaction term location:environment was also significant (Table 7). Size analysis shows again that location explains most of the variation in the male subsample (6.3%), followed by environment (Table 7). Environment: location is significant among the interaction terms (Table 7).

Porto da Cruz terrestrial males display larger heads compared to other locations (Fig. 7c). Interestingly size variation between environments within each location display minor amounts of variation. The allometric variation presented within the male subsample showed significant results between location and the interaction term LogCS:location:environment (Table 7). Allometric variation is described in Fig 7d with Sao Vincente intertidal showing a quite divergent trajectory.

Males		*F*	*Z*	*df*	r^2	*P*
Lateral shape	Environment	4.9119	3.9404	1	0.0252	**0.001**
	Location	5.5605	7.4514	3	0.0815	**0.001**
	Location x Environment	3.1493	4.8402	3	0.04351	**0.001**
Lateral Allometry	Log Centroid	9.6459	5.79	1	0.04746	**0.001**
	LogCS x Environment	1.2676	0.8491	1	0.00624	0.192
	LogCS x Location	1.7119	2.3963	3	0.02378	**0.01**
	LogCS x Environment x Location	1.4738	1.931	3	0.01912	**0.026**
Lateral Log centroid	Environment	3.6125	1.5725	1	0.01866	**0.044**
	Location	4.2441	2.4075	3	0.06343	**0.005**
	Environment x Location	3.9496	2.2259	3	0.05537	**0.01**

Table 7. ANOVA statistics of lateral shape, allometry and log centroid size variation within pooled groups of males only. Location and environment, including factor interactions (significance in **bold**).

The phenotypic trajectory scatter plot displays the first two PC scores for scale shape deformation of male dorsal specimens. PC1 represents 48.54% of shape variation in males, while PC2 represents 21.5% (Fig. 7b). Pairwise phenotypic comparison of trajectories (Table 8) identified significant trajectory size differences for all locations against Canico. Vector angles approach 90 degrees when the Canico sample is compared to Paul do Mar and Sao Vicente. Sao Vincente equally shows a divergent trajectory direction compared to Porto da Cruz.

	$MD_{1,2}$				$\theta_{1,2}$			
Lateral Males Location	Canico	Paul do Mar	Porto da Cruz	São Vicente	Canico	Paul do Mar	Porto da Cruz	São Vicente
Canico	-	0.010179	0.009776	0.010715	-	85.17512	68.87095	73.55939
Paul do Mar	**0.003**	-	0.008518	0.00869	**0.007**	-	93.35809	66.23356
Porto da Cruz	**0.002**	0.983	-	0.008194	0.089	**0.001**	-	73.58038
São Vicente	**0.001**	0.094	0.087	-	**0.035**	0.075	**0.014**	-

Table 8. Summary statistics for differences in phenotypic trajectory pairwise, size ($MD_{1,2}$) and direction ($\Theta_{1,2}$) for all males pooled across the two environments between locations. Parameter statistics and P-values (significance in **bold**)

3.V1. Lateral shape and size variation, Females

A PCA was carried out to describe shape variation of females (n = 122), the first two principal components explained collectively 38.27% variation, 28 principal component vectors explained 95% of variance. Fig. (8a) shows negative PC1 scores associated with a shape enlargement of the supratemporals scales, with a minor enlargement of the ear opening. Positive PC1 scores reflect an elongation of the subocular and supraciliary scales. The temporal area contracts and chin shields display shortening yet more robust shape deformation, creating a smaller shape area than for negative PC1 scores. Negative PC2 scores are related to an expansion of the temporal region accompanied by subocular and ear-opening shape expansion. Chin shields show elongation forming a slenderer shape yet contracting to create a shallow lower jaw. Positive PC2 describes a contraction of temporal and subocular scales with an expansion of the chin shield creating a more robust visualisation.

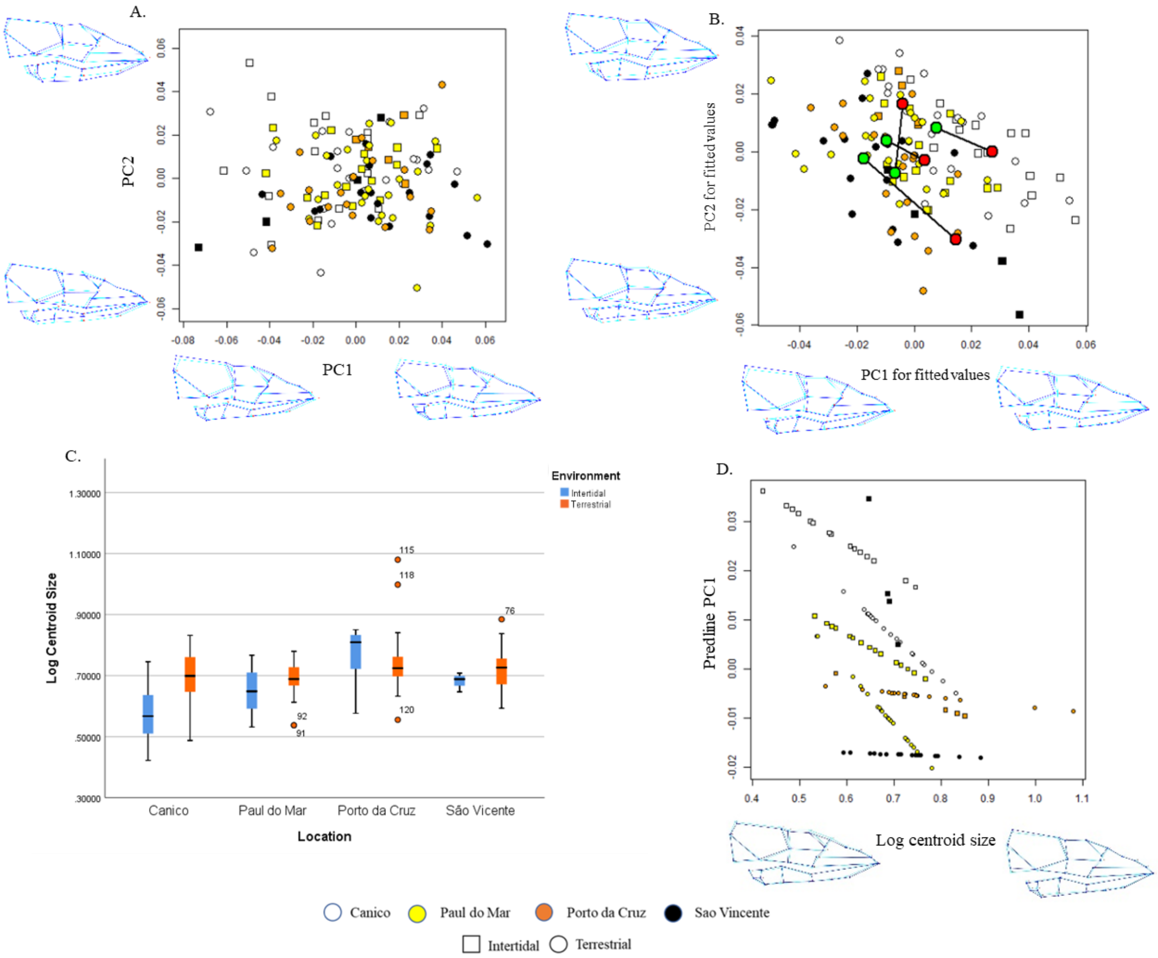

Fig. 8. PC1 and PC2 scatterplots of female shape variation between locations, (A) PCA scatterplot of shape coordinates together with wireframes of dorsal scale pattern deformation., (B) phenotypic trajectory estimated fitted coordinates with wireframes of dorsal scale pattern deformation., (C) boxplot comparing log centroid size from intertidal (blue) and terrestrial (orange), (D) Allometric regression of PC1 fitted values to log centroid size, with deformation wireframes for size.

Procrustes ANOVA significantly identified location as the driving factor explaining lateral shape variation (6.6%) again, followed by environment (3.6%)(Table 9). The interaction term between location:environment was also significant (Table 9). LogCS analysis resulted in location being the highest percentage of variation in the female subsample (16.4%), closely followed by environment (12.4%) (Table 9). The size interaction term, environment:location was marginally non-significant (Table 9).

A boxplot (Fig. 8c) shows that females from terrestrial environments display larger heads than intertidal females, except for Porto da Cruz. The Canico terrestrial sample appears to show greater size variation than the corresponding Canico intertidal sample. The allometric variation presented within the female sample is significant explaining only 3.7% of variance with no interaction occurring.

Females		*F*	*Z*	*df*	r^2	*P*
Lateral shape	Environment	4.5361	3.739	1	0.03642	**0.001**
	Location	2.7771	3.8789	3	0.06595	**0.001**
	Location x Environment	1.7127	2.1068	3	0.039	**0.017**
Lateral Allometry	Log Centroid Size	4.746	3.4675	1	0.03735	**0.001**
	LogCS x Environment	1.42	1.0813	1	0.01117	0.156
	LogCS x Location	1.1545	0.7339	3	0.02665	0.239
	LogCS x Environment x Location	0.9478	-0.0837	3	0.02124	0.537
Lateral Log centroid	Environment	17.021	3.1714	1	0.12422	**0.001**
	Location	7.7241	3.5326	3	0.16414	**0.001**
	Environment x Location	2.5918	1.5679	3	0.04833	0.059

Table 9. ANOVA statistics of lateral shape, allometry and log centroid size variation within pooled groups of females only. Location and environment, including factor interactions (significance in **bold**).

The phenotypic trajectory scatter plot shows that the first two PCs represent 67.25% of shape variation (Fig. 8b). Pairwise phenotypic comparison of trajectories (Table 10) identified significant trajectory size differences between Paul do Mar against Sao Vicente which is more significant than expected by chance. Vector angles indicated highly divergent trajectories for the Porto da Cruz sample relative to Canico and Sao Vicente (Table 7).

	$MD_{1,2}$				$\theta_{1,2}$			
Lateral Females Location	Canico	Paul do Mar	Porto da Cruz	São Vicente	Canico	Paul do Mar	Porto da Cruz	São Vicente
Canico		0.011702	0.018147	0.021741		53.94324	84.25924	66.42196
Paul do Mar	0.057		0.018359	0.021548	0.42		96.52029	49.6587
Porto da Cruz	0.671	0.104		0.01797	**0.039**	0.339		108.7246
São Vicente	0.137	**0.017**	0.156		0.339	0.811	**0.002**	

Table 10. Summary statistics for differences in phenotypic trajectory pairwise, size ($MD_{1,2}$) and direction ($\Theta_{1,2}$) for all females pooled across the two environments between locations. Parameter statistics and P-values (significance in **bold**)

4. Discussion

For this study, GMM and PTA supported the original hypotheses by demonstrating that morphological changes occur between distinct *T.dugesii* populations from Madeira. In the dorsal and lateral orientation of males, location had a much greater impact on the shape, allometry and size variation of head scalation. Analysis of dorsal head shape in females showed location is more significant than environments within the shape and allometric variation. Female size variation was significant for both orientations for locations and environments. Lateral female variation between locations and environments was not significantly important to allometric change.

No research has investigated morphological modifications of lacertids using two-level PTA through different environments and localities for comparison. I found that phenotypic trajectory pairwise comparisons presented phenotypic change in males across environments in both dorsal and lateral orientations. Dorsal phenotypic paths displayed differences in males from Sao Vincente compared to Porto da Cruz and Canico, indicating increased or decreased levels of shape change between environments. Again, males from Sao Vincente showed differing phenotypic vector angles when compared to Porto da Cruz and Canico. Interestingly vector angles of Canico were significant when compared with Paul do mar, Porto da Cruz and Sao Vincente, indicating that Canico males display phenotypic shape change that diverges from the rest (Table 4). Male lateral phenotypic paths showed further phenotypic change in Canico with an increased shape change. The largest lateral phenotypic path length showed that the greatest shape variance is between Canico and Sao Vincente (Table 8).

Canico consistently showed significant shape variation between environments supporting previous research conducted by Davenport and Dellinger (1995) and was also divergent compared to other localities. PTA analysis showed Canico specimens have ecologically diverged in shape. Size variation further supported Davenport and Dellinger's (1995) finings, Canico lizards indicated similar-sized lizards but by investigating the regression plot (Fig. 4d) and error bars (Fig. 4c), the intertidal lizards were indeed larger than terrestrial lizards. However, larger intertidal specimens were less abundant. Numerous reasons could cause this divergence, dietary shifts, predation and intraspecific competition could drive variation between environments of Canico (Carretero, 2004). Canico is situated south on Madeira, with potentially hotter temperatures, this could increase raptor and seabird numbers, thus forcing greater predation upon the species. Human activity and increased tourism may dictate available environmental space, food resources and behavioural traits that influence their phenotypic adaptations (Cook, 1979; Davenport and Dellinger, 1995; Des Roches *et al.*, 2018; Donoghue, 1998).

Surprisingly, phenotypic trajectory pairwise comparison within the female dorsal subsample was redundant due to the interaction term environment:location being non-significant for shape. The female lateral subsample showed a single significant path length between Paul do Mar and Sao Vincente indicating greater amounts of phenotypic shape variation between environments, but the vector angle indicated non-significance with a relatively small angle, suggesting greater levels of change with a somewhat similar shape

(Table 10). Porto da Cruz showed significant angular differences when compared to Sao Vincente, the comparison showed an extremely large angle difference, the obtuse angle distinctively indicates phenotypic shape divergence environmentally between the two locations. The angular difference between Porto da Cruz and Canico indicated that the phenotypic change is apparent, further supporting the ecological differences at Canico (Davenport and Dellinger, 1995).

Porto da Cruz showed more discrepancies in shape variation when compared to other localities and environments. PTA indicates that Porto da Cruz females have diverged lateral scale shape, suggesting that ecological pressures/success have greater influence in one environment. Furthermore, the divergence shown could be caused by anomalies in specimens, potentially some lizards displayed an extreme phenotype that has been produced as an error or accident in developmental stages, intense environmental stresses during development or a fluke genotype (Voipio, 1991).

As Brehm *et al.*, (2001) investigated isolated island divergence and gene flow of *T.dugesii*. Brehm *et al*. (2001) suggested that *T.dugesii* populations have not been subject to an intense genetic bottleneck and that gene flow occurs. Although island isolation presented lower geneflow subject to more diverse environments, the environmental and geographic isolation caused has not led to differentiation. Brehm *et al*. (2001) further acknowledges that populations appear morphologically distinct from each other, yet genetically show no clear difference between geographic locations (Brehm *et al.*, 2001). From this genetic study, the divergence displayed by males of Canico and females of Porto da Cruz could be caused by natural and sexual selection. In addition, Canico is positioned directly south of Porto da Cruz with a mountainous ridge separating the two locations, this separation potentially intensifies local adaptations caused by environmental factors and random processes influencing morphology (Báez and Brown, 1997; Bellati *et al.*, 2015).

When the question of “what affects species morphological characteristics” arises, there cannot be a sole answer, numerous external and internal factors can form harmonious relationships, combining to create diverse changes and distinctive qualities (Hedrick and Temeles, 1989; Kaliontzopoulou *et al*., 2007, 2008). Phenotypic adaptations within lacertids are often hypothesized to have arisen through natural or sexual selection (Algar and López-Darias, 2016; Cox *et al.*, 2007).

Environmental partitioning may be the cause of variation within this study, both males and females displayed greater shape and size variation within the terrestrial environment. The morphological changes between locations and environments may be characterised as adaptive pressures caused by trophic competition, resource availability and/or the abundance of a specific resource (Butler *et al*., 2007; Gil *et al.*, 2020; Hedrick and Temeles, 1989; Herrel *et al*., 1999). Food resources are undoubtedly varied in Madeira from one location to the next due to environmental differences. Resource partitioning can directly affect and change morphological characteristics, for example, males can capitalise on various resources that females are simply unequipped for, this would reduce dietary competition between sexes (Law and Mehta, 2018; Sagonas *et al.*, 2014; Toft, 1985). The environmental changes and resources will be impacting foraging behaviour, additionally, reproductive requirements (ovulation) may shift some lizards to forage more plant matter or protein/vitamin-rich food (Carretero 2004; Cox *et al.*, 2007; Hierlihy *et al.*, 2013; Toft, 1985).

Abundant invertebrate species across Madeira will all have different levels of predation difficulty, past research has shown *T.dugesii* to devour and digest various sized prey items from large cockroaches to pupal cases, but mostly favouring isopods (Davenport and Dellinger, 1995; Herrel *et al*., 1999; Sagonas *et al.*, 2014). Castilla *et al*. (2009) noted that adult *Podarcis atrata* would utilise intertidal ranges to actively forage and feed on invertebrates, seabird regurgitates, carcasses and seabird egg remains. Whereas Matias (2009) documented a phenomenon that rarely occurs, *T.dugesii* was documented predating on Cory's Shearwaters (*Calonectris diomedea*) and numerous species of Petrel seabird chicks (*Bulweria bulwerii*, *Oceanodroma castro*, and *Pelagodroma marina*). Morphological changes in the shape and size of *T.dugesii* could be consequently caused by differing food resources and feeding behaviours (Araya-Donoso *et al*., 2017; Cox *et al.*, 2007; Koleska *et al.*, 2017).

Predation pressures may also be the cause for phenotypic variation between and within locations. Numerous avian species have been sighted across Madeira, whether this is for migration or nesting as mentioned earlier. Raptors such as kestrels, buzzards and barn owls inhabit the island with no limitation to hunting ranges, from towns to high mountain ranges predating the local population of mammals, birds and reptiles (Harcourt, 1851; Marshall *et al*., 2016). It is not uncommon for smaller songbirds and seabirds to predate juvenile lizards (Gil *et al.*, 2020; Harcourt, 1851; Marshall *et al*., 2016; Rocha *et al*., 2010). The terrestrial environment within this study showed males tended to be generally larger. However, dorsal orientated males of Paul do mar intertidal lizards and female Porto da Cruz intertidal specimens were larger than terrestrial lizards. The size difference in environments could be influenced by avian predation as *T.dugesii* may have adapted to become smaller in size to avoid detection or enable itself to fit into smaller crevices offered by intertidal ranges. More terrestrial dwelling lizards may find adequate cover in plants and man-made structures discouraging avian predation, therefore, allowing for larger growth.

I found that *T.dugesii* exhibited levels of sexual dimorphism within the total sample groups. The dorsal shape and allometric sexual dimorphism were discrete, while size attributed to greater variation between sexes. Research frequently shows that males often possess larger heads than females, typically for mating success, as males will bite and incapacitate a female to successfully reproduce (Kaliontzopoulou *et al*., 2007, 2008; Olsson *et al*., 2002; Salvador *et al*., 2008; Urošević *et al*., 2013). Sexual dimorphism of head size in lacertids is frequently suggested to have arisen due to intrasexual combat. Battles occur amongst males for territory and mating purposes, the larger head morphology has shown to house greater jaw muscles creating a more substantial bite force, thus imposing dominance over inferior males (Cox *et al.*, 2007; Cox and Kahrl, 2014; Herrel *et al*., 1999; Husak *et al*., 2006; Olsson *et al*., 2002). The victors of male-male fights have been found to have a slightly larger head and greater body mass in some lizards (Husak *et al*., 2006; Molina-Borja *et al*. 1998). Additionally, victorious males used bite force and displayed throat inflation as a form of intimidation, thus increasing perceived size and offering a more dominating stature, concluding that head size and bite force are key sexually selected properties for weapon performance in intraspecific encounters. Much of the literature reviewed provided evidence that sexual selection within lacertids drives males to develop larger heads, whereas females direct growth abdominally for reproductive purposes (Braña, 1996; Cox *et al.*, 2007; Hedrick and Temeles, 1989; Olsson *et al*., 2002; Scharf and Meiri, 2013).

Studies of cranial development of lacertids have provided information on why shape and size variation may occur between sexes. The posterior region of lacertid skulls is known to ossify last, generally developing in later stages of growth. Such growth would dorsally manifest within the parietal, inter and central parietals and frontoparietal scales. Laterally, the temporal region would predominately be affected (Bever *et al*., 2005; Barahona and Barbadillo, 1998; Costantini *et al*., 2010; Jesus *et al.*, 2006; Müller, 2002; Urošević *et al*., 2013). Male *T.dugesii* specimens have distinctively shown shape variation in parietal areas throughout this study as opposed to females (see Fig. S1 and S2 for size expansion). This overdevelopment of the posterior or parietal region of the head could be due to such intraspecific sexual selection (Butler *et al*., 2007; Herrel *et al*., 1999; Husak *et al*., 2006). Through visual shape interpretation of *T.dugesii*, males showed expansions to the posterior head regions, increasing the parietal scales with corresponding decreases to the central occipital and intraparietal scales. Females exhibited contracted interparietal and relatively consistent central occipital scales when dorsally orientated (Bruner *et al*., 2005; Jesus *et al*., 2006).

With the posterior region of male *T.dugesii* heads changing in shape and size, the increased mass and lateral head height would suggest greater housing of jaw muscles for intraspecific interactions as previously reviewed. Research indicates that lateral head height could influence bite force, as the larger jaw muscles would provide more extraordinary power transmission to the lower jaw, additionally increasing head height allowing lizards to possess a wider gape for various food items (Kaliontzopoulou *et al.*, 2008; Urošević *et al*., 2013). Laterally, males displayed shape expansion to the temporal scales and the chin shields to the posterior of the jaw. Females displayed a slender head shape, eye and ear openings, and a more contracted jaw shape. Terrestrial males showed more temporal and lower jaw size expansion to the posterior. In contrast, females showed contractions in these areas (see Fig. S1 and S2 for size expansion). Supporting deformations have been observed previously within other lacertids (see Kaliontzopoulou *et al*., 2007, 2008, 2010; Sagonas *et al.*, 2014; Urošević *et al*., 2013).

The dorsal and lateral allometry for the total sample showed a clear separation of sexes, further supporting sexual dimorphism within the species (see Fig. 3d and 6d). Males have different allometric slope trajectories than females with variation explained by size being smaller in dorsal view (3.64% of var.) than lateral (4.97% of var.). The opposite occurs in females where size variation explains 4.95% of shape variance in dorsal view and 3.7% of var. in lateral view. Interestingly, the allometric interaction terms were significant in males further supporting that phenotypic variation is different within environments at the same location. A larger dorsal allometric spread can be seen between Canico intertidal and terrestrial lizards, indicating larger intertidal specimens (Fig. 4d). Sao Vincente showed lizards of larger sizes, yet shape converges then diverges, indicating shape differences between environments. Lateral allometry of males showed that Canico was different to the compared locations (Fig. 7d) due to a smaller lateral size with negative PC shape.

Female allometric signalling was more inconsistent, with dorsal allometry changing only due to location (Table 5). The allometric data reveal only one significant interaction, suggesting that females show different allometric changes at different locations. Some similarities can be seen within the female allometric regression plot (Fig. 5b): as size increases, female allometric shape changes converge negatively toward a similar head shape on the predicted line PC regression plot. However, Canico terrestrial and Porto da Cruz intertidal females show divergence within the regression plot. Females show shape changes as size increases in different locations. Lateral female allometric regression has no significant differences between locations and environments. As size increased, the shape was forced negatively on the predicted line PC1 showing that females obtain similar lateral size with minor shape change (Fig. 8d). The allometric results support scaling relationships, that size modifications cannot occur without subsequent shape modification (Kaliontzopoulou *et al*., 2008; West *et al*., 2000). The male regression evidently shows that shape is intimately linked to size meanwhile females have similarities. This aids in pointing towards a sexually pressured developmental mechanism that is present in both sexes. Kaliontzopoulou *et al*. (2010) visually showed shape differences in male and female *P. bocagei* lizards from different environments and found distinctive ecological morphological changes (Kaliontzopoulou *et al*., 2008, 2010; Sagonas *et al.*, 2014 [*Lacerta trilineata*]). The allometric regression plots here showed differences between sexes and environments, this environmental differentiation supports Kaliontzopoulou *et al*. (2010) that ecological conditions can mutate head shape of lacertids. The results reinforce that sexually selected pressures can combine with naturally selected pressures resulting in adaptations.

5. Conclusion

This thesis has shown that both dorsal and lateral orientations of head scale morphology in shape, size and allometric signalling quantified by GMM, showing significant variation in relation to sex, location and environment choices of different *T.dugesii* populations. Following sexually selected predictions and scaling relationships, male lizards have larger heads (shape and size) when compared to females, displaying greater variation to the posterior of the head and lower jaw. Ecomorphological changes between locations and environments support past observations, the head shape and size variation discovered, somewhat merges sexual and natural selected pressures.

Males indicate consistent levels of variance across locations and environments. In contrast, females indicate the interaction term of location:environment is not as influential being significant only in lateral shape. PTA showed patterns of shape divergence of males from Canico environments and females of Porto da Cruz environments when compared to the remaining locations. Lizards of alternate sexes in different locations exhibited deformations favouring naturally selected pressures influencing variation, providing answers to phenotypic changes in this species. Further analysis could prove to be more advantageous in understanding shape divergence within *T.dugesii*, bioclimatic variables such as temperature, precipitation and elevation (see Báez and Brown 1997) could help diminish and support theories. In addition, the data provided could, in time, present evidence of rapid ecomorphological evolution.

6. Acknowledgements

I want to thank Dr Carlo Meloro and Prof Richard Brown for their time, effort, and support throughout this thesis, additionally for providing access to the specimens used in this study. I would further like to thank Daniel Charters for his overall support through all aspects of this thesis and Dr Peter Falkingham for ensuring well-being throughout my research. I want to dedicate this research to Mark Thomas for helping me pursue this achievement and career path.

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8. Supplementary

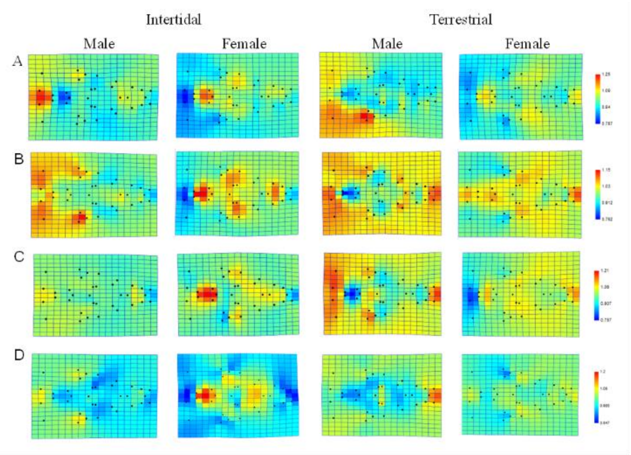

Fig. S1. Dorsal head scale variation associated with size showing consensus deformation of each site within each environment and sex from the group mean. (A) Deformation grids of Canico, (B) Deformation grids of Paul Do Mar, (C) Deformation grids of Porto Da Cruz, (D) Deformation grids of Sao Vincente. All deformation grids are assigned left to right, Intertidal - Male, Female; Terrestrial - Male, Female. Temperature related Jacobean expansion factors have been used as a visual aid on deformation grids. Blue shows contraction, red shows expansion.

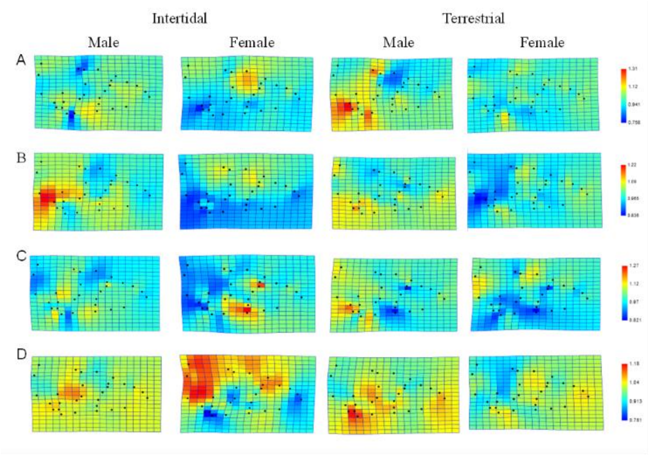

Fig. S2. Dorsal head scale variation associated with size showing consensus deformation of each site within each environment and sex from the group mean. (A) Deformation grids of Canico, (B) Deformation grids of Paul Do Mar, (C) Deformation grids of Porto Da Cruz, (D) Deformation grids of Sao Vincente. All deformation grids are assigned left to right, Intertidal - Male, Female; Terrestrial - Male, Female. Temperature related Jacobean expansion factors have been used as a visual aid on deformation grids. Blue shows contraction, red shows expansion.

Id	Sex	Environment	Sites	LogCS Dorsal	LogCS Lateral
1.01_F	Female	Intertidal	Canico	0.701061198	N/A
1.02_M	Male	Intertidal	Canico	1.005771837	0.879992817
1.03_M	Male	Intertidal	Canico	1.102085631	0.954491386
1.04_M	Male	Intertidal	Canico	1.1404819	1.041173445
1.05_M	Male	Intertidal	Canico	0.895869096	0.741162224
1.06_F	Female	Intertidal	Canico	0.76693435	0.643601
1.07_M	Male	Intertidal	Canico	1.073730256	0.973395493
1.08_M	Male	Intertidal	Canico	1.141283247	N/A
1.09_M	Male	Intertidal	Canico	0.952625111	0.750172673
1.10_M	Male	Intertidal	Canico	1.060846039	0.932945981
1.11_F	Female	Intertidal	Canico	0.795090634	0.628642497
1.12_F	Female	Intertidal	Canico	0.738085373	0.497394616
1.13_F	Female	Intertidal	Canico	0.903606	0.74568108
1.14_F	Female	Intertidal	Canico	0.681593851	0.567007675
1.15_M	Male	Intertidal	Canico	0.965057705	0.799975884
1.16_M	Male	Intertidal	Canico	1.174136966	N/A
1.17_M	Male	Intertidal	Canico	0.978056203	0.850093215
1.18_M	Male	Intertidal	Canico	0.958015507	0.813965919
1.19_M	Male	Intertidal	Canico	1.016629786	0.881331102
1.20_F	Female	Intertidal	Canico	0.691980763	0.522764541
1.21_F	Female	Intertidal	Canico	0.676329417	0.528867999
1.22_F	Female	Intertidal	Canico	0.701476867	0.472410172
1.23_M	Male	Intertidal	Canico	1.094909819	0.954809671
1.24_M	Male	Intertidal	Canico	1.04852652	0.911163071

1.25_M	Male	Intertidal	Canico	1.042466228	0.920619155
1.26_M	Male	Intertidal	Canico	1.00317787	0.858136817
1.27_F	Female	Intertidal	Canico	0.820376434	0.607310086
1.28_F	Female	Intertidal	Canico	0.81004901	0.616560558
1.29_F	Female	Intertidal	Canico	0.875114825	0.657665057
1.30_M	Male	Intertidal	Canico	0.88085603	0.745041252
1.31_M	Male	Intertidal	Canico	0.965287262	0.758280851
1.32_F	Female	Intertidal	Canico	0.876846456	0.724644167
1.33_F	Female	Intertidal	Canico	0.672543807	0.421970636
1.34_F	Female	Intertidal	Canico	0.687436084	0.484066951
1.35_F	Female	Intertidal	Canico	0.727002991	0.563049673
3.01_M	Male	Terrestrial	Canico	1.119412569	0.939668861
3.02_M	Male	Terrestrial	Canico	1.015107004	0.868267976
3.03_F	Female	Terrestrial	Canico	0.829083898	0.693215431
3.04_M	Male	Terrestrial	Canico	1.103217823	0.962565925
3.05_M	Male	Terrestrial	Canico	1.099481973	0.969689797
3.06_M	Male	Terrestrial	Canico	0.960973822	0.757888655
3.07_M	Male	Terrestrial	Canico	1.076375698	0.938918663
3.08_M	Male	Terrestrial	Canico	1.080600821	0.971469287
3.09_F	Female	Terrestrial	Canico	0.826054974	0.644599613
3.10_F	Female	Terrestrial	Canico	0.919102733	0.740258447
3.11_F	Female	Terrestrial	Canico	0.940546009	0.763834627
3.12_F	Female	Terrestrial	Canico	0.838987619	0.704998085
3.13_F	Female	Terrestrial	Canico	0.798419007	0.66132719
3.14_M	Male	Terrestrial	Canico	1.037494799	0.965010044
3.15_M	Male	Terrestrial	Canico	1.059779151	0.98040485
3.16_F	Female	Terrestrial	Canico	0.816268322	0.646999528
3.17_F	Female	Terrestrial	Canico	0.911554722	0.740054459
3.18_F	Female	Terrestrial	Canico	0.802183667	0.650702179
3.19_F	Female	Terrestrial	Canico	0.843285018	0.679063432

3.20_F	Female	Terrestrial	Canico	0.917947946	0.803046443
3.21_F	Female	Terrestrial	Canico	0.896101661	0.738437942
3.22_F	Female	Terrestrial	Canico	0.841675129	0.636347546
3.23_M	Male	Terrestrial	Canico	1.0740628	0.977600665
3.24_M	Male	Terrestrial	Canico	1.091943123	0.948942515
3.25_M	Male	Terrestrial	Canico	0.998904724	0.924506068
3.26_F	Female	Terrestrial	Canico	0.880179014	0.713094201
3.27_M	Male	Terrestrial	Canico	1.053567316	0.94755166
3.28_M	Male	Terrestrial	Canico	1.030654836	0.90162862
3.29_M	Male	Terrestrial	Canico	1.002091594	0.965687479
3.30_F	Female	Terrestrial	Canico	0.809479364	0.655592085
3.31_M	Male	Terrestrial	Canico	1.058793338	0.923858087
3.32_F	Female	Terrestrial	Canico	0.919285159	0.77976241
3.33_F	Female	Terrestrial	Canico	0.973266356	0.803722877
3.34_F	Female	Terrestrial	Canico	0.790726977	0.487453073
3.36_F	Female	Terrestrial	Canico	0.878794503	0.831819504
3.36_M	Male	Terrestrial	Canico	0.969918483	0.6782077
3.37_F	Female	Terrestrial	Canico	0.828824995	0.646434481
3.38_F	Female	Terrestrial	Canico	0.871085893	0.760493736
3.39_F	Female	Terrestrial	Canico	0.713033331	0.593677922
3.40_F	Female	Terrestrial	Canico	0.81765632	N/A
4.01_M	Male	Intertidal	Porto da Cruz	0.929328544	0.876129566
4.02_M	Male	Intertidal	Porto da Cruz	0.957220496	0.782964694
4.03_M	Male	Intertidal	Porto da Cruz	1.015698032	0.933707753
4.04_M	Male	Intertidal	Porto da Cruz	0.971089828	0.794036223
4.05_M	Male	Intertidal	Porto da Cruz	1.111413951	0.96299651
4.06_M	Male	Intertidal	Porto da Cruz	1.067744203	0.974233027
4.07_M	Male	Intertidal	Porto da Cruz	1.063958831	N/A
4.08_M	Male	Intertidal	Porto da Cruz	1.032904625	0.947515279
4.09_M	Male	Intertidal	Porto da Cruz	0.943856079	0.776490973

4.11_M	Male	Intertidal	Porto da Cruz	0.934506245	0.851626463
4.12_M	Male	Intertidal	Porto da Cruz	1.095125443	0.99198654
4.13_M	Male	Intertidal	Porto da Cruz	1.000339732	N/A
4.14_M	Male	Intertidal	Porto da Cruz	0.937166276	0.802879575
4.15_M	Male	Intertidal	Porto da Cruz	1.179307326	1.071317796
4.16_M	Male	Intertidal	Porto da Cruz	1.070209826	0.942758939
4.17_M	Male	Intertidal	Porto da Cruz	1.069942515	1.063290271
4.18_M	Male	Intertidal	Porto da Cruz	1.064521301	0.875730736
4.19_F	Female	Intertidal	Porto da Cruz	0.651506882	0.576522437
4.20_M	Male	Intertidal	Porto da Cruz	1.102896766	0.983146694
4.21_M	Male	Intertidal	Porto da Cruz	1.085484194	0.965868822
4.22_F	Female	Intertidal	Porto da Cruz	0.969167428	0.809275109
4.23_F	Female	Intertidal	Porto da Cruz	0.932212753	0.850371753
4.24_M	Male	Intertidal	Porto da Cruz	1.150040452	1.036853168
4.25_M	Male	Intertidal	Porto da Cruz	1.073070301	0.956715047
4.26_M	Male	Intertidal	Porto da Cruz	1.086312031	0.996759823
4.27_M	Male	Intertidal	Porto da Cruz	0.955415818	0.866758507
4.28_M	Male	Intertidal	Porto da Cruz	0.973684119	0.802544384
4.29_F	Female	Intertidal	Porto da Cruz	0.936382401	0.833430307
4.30_M	Male	Intertidal	Porto da Cruz	0.950888672	0.818580529
4.31_M	Male	Intertidal	Porto da Cruz	0.941381722	0.841033683
4.32_M	Male	Intertidal	Porto da Cruz	1.031394616	0.89939983
4.33_M	Male	Intertidal	Porto da Cruz	0.920868599	0.858508286
4.34_M	Male	Intertidal	Porto da Cruz	0.912597547	0.802677605
4.35_M	Male	Intertidal	Porto da Cruz	0.964860503	0.899882897
4.36_F	Female	Intertidal	Porto da Cruz	0.85904463	0.721910802
4.37_M	Male	Intertidal	Porto da Cruz	1.100363768	1.037808998
5.01_F	Female	Intertidal	Paul do Mar	0.791644524	0.557589048
5.02_M	Male	Intertidal	Paul do Mar	1.04233568	N/A
5.03_F	Female	Intertidal	Paul do Mar	0.799168608	0.729286586

5.04_M	Male	Intertidal	Paul do Mar	1.078012571	1.095084901
5.05_M	Male	Intertidal	Paul do Mar	1.141944146	N/A
5.06_M	Male	Intertidal	Paul do Mar	1.133613748	0.966043563
5.07_F	Female	Intertidal	Paul do Mar	0.758642649	N/A
5.08_M	Male	Intertidal	Paul do Mar	1.114078774	0.974014793
5.09_F	Female	Intertidal	Paul do Mar	0.891372348	0.714591428
5.10_M	Male	Intertidal	Paul do Mar	1.026925763	0.852822108
5.11_M	Male	Intertidal	Paul do Mar	1.03027698	0.92544562
5.12_F	Female	Intertidal	Paul do Mar	0.764938374	0.660341431
5.13_F	Female	Intertidal	Paul do Mar	0.735948588	0.53150633
5.14_F	Female	Intertidal	Paul do Mar	0.781041885	0.576584996
5.15_M	Male	Intertidal	Paul do Mar	1.075588135	0.943559516
5.16_M	Male	Intertidal	Paul do Mar	1.025535237	0.920710594
5.17_F	Female	Intertidal	Paul do Mar	0.755153704	0.606608179
5.18_M	Male	Intertidal	Paul do Mar	1.03394862	0.872443657
5.19_M	Male	Intertidal	Paul do Mar	1.072744927	0.994296284
5.20_M	Male	Intertidal	Paul do Mar	0.983258634	0.813959225
5.21_F	Female	Intertidal	Paul do Mar	0.897270127	0.742811439
5.22_M	Male	Intertidal	Paul do Mar	1.013627149	0.891286209
5.23_F	Female	Intertidal	Paul do Mar	0.780025503	0.630580597
5.24_M	Male	Intertidal	Paul do Mar	1.006924097	0.885564449
5.25_M	Male	Intertidal	Paul do Mar	1.042993276	0.925535233
5.26_M	Male	Intertidal	Paul do Mar	1.039143293	0.920184291
5.27_M	Male	Intertidal	Paul do Mar	1.125851701	0.969209605
5.28_M	Male	Intertidal	Paul do Mar	1.073017448	0.871684218
5.29_M	Male	Intertidal	Paul do Mar	1.087164716	0.949380253
5.30_M	Male	Intertidal	Paul do Mar	1.101719421	0.971991279
5.31_M	Male	Intertidal	Paul do Mar	1.134606696	0.982397968
5.32_F	Female	Intertidal	Paul do Mar	0.819866138	0.648689367
5.33_M	Male	Intertidal	Paul do Mar	1.109259638	0.955269554

5.34_M	Male	Intertidal	Paul do Mar	1.085835875	0.913757026
5.35_M	Male	Intertidal	Paul do Mar	1.104211537	0.90289793
5.36_M	Male	Intertidal	Paul do Mar	1.034675235	0.938952858
5.37_F	Female	Intertidal	Paul do Mar	0.891707941	0.705151142
5.38_M	Male	Intertidal	Paul do Mar	1.097121806	0.970661957
5.39_F	Female	Intertidal	Paul do Mar	0.844854587	N/A
5.40_M	Male	Intertidal	Paul do Mar	1.058578569	0.966581876
5.41_F	Female	Intertidal	Paul do Mar	0.883139741	0.766921062
5.42_M	Male	Intertidal	Paul do Mar	1.009372825	0.835909492
5.43_M	Male	Intertidal	Paul do Mar	0.98219417	0.934271447
5.44_F	Female	Intertidal	Paul do Mar	0.71454365	0.568046125
5.45_F	Female	Intertidal	Paul do Mar	0.804962176	0.672303969
5.46_F	Female	Intertidal	Paul do Mar	0.776097134	0.612824755
5.47_M	Male	Intertidal	Paul do Mar	1.03086648	0.847059431
6.01_M	Male	Intertidal	Sao Vincente	1.057662451	1.052520443
6.02_M	Male	Intertidal	Sao Vincente	1.107823714	0.977983667
6.03_M	Male	Intertidal	Sao Vincente	1.142335766	1.016250197
6.04_M	Male	Intertidal	Sao Vincente	1.209621823	1.134522354
6.05_M	Male	Intertidal	Sao Vincente	1.007541487	0.868513454
6.06_M	Male	Intertidal	Sao Vincente	1.070790946	0.978480938
6.07_M	Male	Intertidal	Sao Vincente	1.233950185	1.090499082
6.08_M	Male	Intertidal	Sao Vincente	0.954189891	0.77236214
6.09_F	Female	Intertidal	Sao Vincente	0.96424877	0.690040387
6.10_F	Female	Intertidal	Sao Vincente	0.838758	0.686763181
6.11_F	Female	Intertidal	Sao Vincente	0.798346602	0.647012421
6.12_F	Female	Intertidal	Sao Vincente	0.884301553	0.708135392
6.13_M	Male	Intertidal	Sao Vincente	1.110540506	0.963617954
6.14_M	Male	Intertidal	Sao Vincente	1.099123179	0.95638536
6.15_M	Male	Intertidal	Sao Vincente	1.157658724	1.13206591
6.16_M	Male	Intertidal	Sao Vincente	1.067547602	0.94654221

6.17_M	Male	Intertidal	Sao Vincente	1.105819309	1.024647981
6.18_M	Male	Intertidal	Sao Vincente	1.072274022	0.925471847
6.19_M	Male	Intertidal	Sao Vincente	1.127336699	0.971474881
6.20_M	Male	Intertidal	Sao Vincente	1.080575623	1.008043728
6.21_M	Male	Intertidal	Sao Vincente	1.079694265	0.960275693
6.22_M	Male	Intertidal	Sao Vincente	1.067821268	0.925307203
6.23_M	Male	Intertidal	Sao Vincente	1.12189224	1.015231853
6.24_M	Male	Intertidal	Sao Vincente	1.039484445	0.922045627
6.25_M	Male	Intertidal	Sao Vincente	1.045879717	0.9417763
6.26_M	Male	Intertidal	Sao Vincente	1.129995108	1.01647032
6.27_M	Male	Intertidal	Sao Vincente	1.16741587	1.09697566
6.28_M	Male	Intertidal	Sao Vincente	1.094817169	1.018931035
6.29_M	Male	Intertidal	Sao Vincente	1.019781649	0.899201165
6.30_M	Male	Intertidal	Sao Vincente	1.035380721	0.932512215
6.31_M	Male	Intertidal	Sao Vincente	1.055781272	0.963500409
6.33_M	Male	Intertidal	Sao Vincente	1.035539789	0.896762199
6.34_M	Male	Intertidal	Sao Vincente	1.142313689	0.989743382
6.35_M	Male	Intertidal	Sao Vincente	1.015762392	0.899309054
6.36_M	Male	Intertidal	Sao Vincente	0.966446341	0.86625004
6.37_M	Male	Intertidal	Sao Vincente	1.075274595	0.921302153
6.38_M	Male	Intertidal	Sao Vincente	1.045042506	0.909236245
6.39_M	Male	Intertidal	Sao Vincente	0.998889807	0.893248787
6.40_M	Male	Intertidal	Sao Vincente	0.946655632	0.875842601
7.01_M	Male	Terrestrial	Sao Vincente	0.9899601	0.874099388
7.02_M	Male	Terrestrial	Sao Vincente	0.91910556	0.808132578
7.03_M	Male	Terrestrial	Sao Vincente	1.032560981	0.930907949
7.04_F	Female	Terrestrial	Sao Vincente	0.9668915	0.837676818
7.05_M	Male	Terrestrial	Sao Vincente	1.106386208	1.018178594
7.06_F	Female	Terrestrial	Sao Vincente	0.708589109	0.593100005
7.07_M	Male	Terrestrial	Sao Vincente	0.992554467	0.896224661

7.08_M	Male	Terrestrial	Sao Vincente	0.921047957	0.763620214
7.09_F	Female	Terrestrial	Sao Vincente	0.858878527	0.737811266
7.10_F	Female	Terrestrial	Sao Vincente	0.817679195	0.671636052
7.11_M	Male	Terrestrial	Sao Vincente	1.047062742	0.978306438
7.12_M	Male	Terrestrial	Sao Vincente	1.164894433	1.050688504
7.14_M	Male	Terrestrial	Sao Vincente	1.00144802	0.815540949
7.15_M	Male	Terrestrial	Sao Vincente	1.21967432	1.111097177
7.16_M	Male	Terrestrial	Sao Vincente	1.149277422	1.058778356
7.17_F	Female	Terrestrial	Sao Vincente	0.881924479	0.709048297
7.18_F	Female	Terrestrial	Sao Vincente	0.81465132	0.608092102
7.19_M	Male	Terrestrial	Sao Vincente	1.087587112	0.931945954
7.20_F	Female	Terrestrial	Sao Vincente	0.871174252	0.745333026
7.21_F	Female	Terrestrial	Sao Vincente	0.83912394	0.658986491
7.22_F	Female	Terrestrial	Sao Vincente	0.759384724	0.649437079
7.23_M	Male	Terrestrial	Sao Vincente	1.13866927	1.053354212
7.24_M	Male	Terrestrial	Sao Vincente	1.107264805	1.049212586
7.25_M	Male	Terrestrial	Sao Vincente	1.169085734	1.111463712
7.26_M	Male	Terrestrial	Sao Vincente	1.195130283	1.0338535
7.27_M	Male	Terrestrial	Sao Vincente	1.150044268	1.06453417
7.28_M	Male	Terrestrial	Sao Vincente	1.047446693	0.972072006
7.29_F	Female	Terrestrial	Sao Vincente	0.90789836	0.756012729
7.30_M	Male	Terrestrial	Sao Vincente	1.066556881	0.976233107
7.31_M	Male	Terrestrial	Sao Vincente	1.102641654	1.009070558
7.32_F	Female	Terrestrial	Sao Vincente	0.936612093	0.793405924
7.33_M	Male	Terrestrial	Sao Vincente	0.963878326	0.784802235
7.34_F	Female	Terrestrial	Sao Vincente	0.832132042	0.738979214
7.35_M	Male	Terrestrial	Sao Vincente	1.082628909	N/A
7.36_M	Male	Terrestrial	Sao Vincente	1.105810805	1.012235951
7.37_M	Male	Terrestrial	Sao Vincente	0.981107329	0.907942036
7.38_M	Male	Terrestrial	Sao Vincente	1.04007667	0.904644175

7.39_F	Female	Terrestrial	Sao Vincente	0.940661417	0.787565127
7.40_F	Female	Terrestrial	Sao Vincente	0.948546585	0.884524503
7.41_F	Female	Terrestrial	Sao Vincente	0.856749725	0.713046813
7.42_F	Female	Terrestrial	Sao Vincente	0.855586453	0.684676969
7.43_M	Male	Terrestrial	Sao Vincente	0.932512312	0.764788042
7.44_F	Female	Terrestrial	Sao Vincente	0.931467683	0.751526458
7.45_F	Female	Terrestrial	Sao Vincente	0.829821632	0.714614473
8.01_F	Female	Terrestrial	Paul do Mar	0.74939211	0.672835131
8.02_M	Male	Terrestrial	Paul do Mar	0.941148502	0.75761948
8.03_F	Female	Terrestrial	Paul do Mar	0.853321659	0.728359941
8.04_M	Male	Terrestrial	Paul do Mar	1.138439972	1.01868666
8.05_M	Male	Terrestrial	Paul do Mar	1.163918357	1.049076919
8.06_M	Male	Terrestrial	Paul do Mar	1.157485894	1.065231227
8.07_M	Male	Terrestrial	Paul do Mar	1.097271386	1.00398507
8.08_M	Male	Terrestrial	Paul do Mar	1.07290663	1.046225483
8.09_M	Male	Terrestrial	Paul do Mar	1.16315582	0.742166616
8.10_F	Female	Terrestrial	Paul do Mar	0.893047648	0.64406672
8.11_F	Female	Terrestrial	Paul do Mar	0.766625234	0.736566765
8.12_F	Female	Terrestrial	Paul do Mar	0.792483746	0.829066841
8.13_M	Male	Terrestrial	Paul do Mar	0.970010985	0.90372151
8.14_M	Male	Terrestrial	Paul do Mar	1.031176741	0.909041569
8.15_M	Male	Terrestrial	Paul do Mar	1.092792273	0.984026437
8.16_M	Male	Terrestrial	Paul do Mar	1.053450287	0.682563356
8.17_F	Female	Terrestrial	Paul do Mar	0.828807893	0.612685459
8.18_F	Female	Terrestrial	Paul do Mar	0.778827347	0.922264253
8.19_M	Male	Terrestrial	Paul do Mar	1.029014997	0.675459907
8.20_F	Female	Terrestrial	Paul do Mar	0.79595421	0.688181201
8.21_F	Female	Terrestrial	Paul do Mar	0.837523833	0.932642303
8.22_M	Male	Terrestrial	Paul do Mar	1.099041201	0.914158494
8.23_M	Male	Terrestrial	Paul do Mar	0.997857506	0.795543527

8.24_M	Male	Terrestrial	Paul do Mar	0.934909389	0.724298163
8.25_F	Female	Terrestrial	Paul do Mar	0.834130127	0.811576707
8.26_M	Male	Terrestrial	Paul do Mar	0.913023683	0.537144097
8.27_F	Female	Terrestrial	Paul do Mar	0.769746852	0.537434637
8.28_F	Female	Terrestrial	Paul do Mar	0.757168027	0.76965873
8.29_M	Male	Terrestrial	Paul do Mar	0.921849017	0.749506723
8.30_F	Female	Terrestrial	Paul do Mar	0.989196567	N/A
8.31_F	Female	Terrestrial	Paul do Mar	0.890245636	0.77607216
8.32_M	Male	Terrestrial	Paul do Mar	0.871037435	0.666467794
8.33_F	Female	Terrestrial	Paul do Mar	0.774656821	0.727018286
8.34_F	Female	Terrestrial	Paul do Mar	0.837426128	0.779564463
8.35_F	Female	Terrestrial	Paul do Mar	0.870696224	0.697700664
8.36_F	Female	Terrestrial	Paul do Mar	0.856896696	0.729499443
8.38_F	Female	Terrestrial	Paul do Mar	0.83299588	0.693139907
8.39_F	Female	Terrestrial	Paul do Mar	0.789312523	0.629481881
8.40_F	Female	Terrestrial	Paul do Mar	0.817990578	0.689107024
8.41_F	Female	Terrestrial	Paul do Mar	0.864673755	0.724704074
8.42_F	Female	Terrestrial	Paul do Mar	0.773249957	0.668417375
8.43_F	Female	Terrestrial	Paul do Mar	0.725962373	0.682254303
9.01_M	Male	Terrestrial	Porto da Cruz	1.214214898	0.961404223
9.02_M	Male	Terrestrial	Porto da Cruz	1.172658423	1.085795204
9.03_M	Male	Terrestrial	Porto da Cruz	1.220276267	1.107808242
9.04_M	Male	Terrestrial	Porto da Cruz	1.279017995	1.169518002
9.05_M	Male	Terrestrial	Porto da Cruz	1.129449303	1.169018325
9.06_M	Male	Terrestrial	Porto da Cruz	1.207680614	1.03371888
9.07_M	Male	Terrestrial	Porto da Cruz	1.295672611	1.046750902
9.08_M	Male	Terrestrial	Porto da Cruz	1.298146825	1.148652129
9.09_F	Female	Terrestrial	Porto da Cruz	0.950780484	1.183118145
9.10_F	Female	Terrestrial	Porto da Cruz	0.877275247	0.721362511
9.11_F	Female	Terrestrial	Porto da Cruz	0.886566057	0.724308843

9.12_F	Female	Terrestrial	Porto da Cruz	0.855386013	0.745638886
9.13_F	Female	Terrestrial	Porto da Cruz	0.862443821	0.742739527
9.14_M	Male	Terrestrial	Porto da Cruz	1.073437379	0.930393506
9.15_F	Female	Terrestrial	Porto da Cruz	0.873674541	0.749066866
9.16_F	Female	Terrestrial	Porto da Cruz	0.888770542	0.700631777
9.17_M	Male	Terrestrial	Porto da Cruz	1.177148648	N/A
9.18_F	Female	Terrestrial	Porto da Cruz	0.910944483	0.722353953
9.19_M	Male	Terrestrial	Porto da Cruz	1.200622294	1.102917447
9.20_M	Male	Terrestrial	Porto da Cruz	1.180054246	1.120926653
9.21_M	Male	Terrestrial	Porto da Cruz	1.124422077	1.033343619
9.22_M	Male	Terrestrial	Porto da Cruz	1.151459445	1.048660276
9.23_F	Female	Terrestrial	Porto da Cruz	0.886712871	0.774816237
9.24_M	Male	Terrestrial	Porto da Cruz	1.005874494	0.865460591
9.25_M	Male	Terrestrial	Porto da Cruz	1.131672732	1.051578162
9.26_F	Female	Terrestrial	Porto da Cruz	0.90152263	0.747375593
9.27_F	Female	Terrestrial	Porto da Cruz	0.950548748	0.808827607
9.28_M	Male	Terrestrial	Porto da Cruz	1.167342043	1.061723225
9.29_M	Male	Terrestrial	Porto da Cruz	1.162515258	1.035450974
9.30_M	Male	Terrestrial	Porto da Cruz	1.175797169	N/A
9.31_M	Male	Terrestrial	Porto da Cruz	1.172991749	N.A
9.32_M	Male	Terrestrial	Porto da Cruz	1.166049772	1.005205452
9.33_M	Male	Terrestrial	Porto da Cruz	1.014921234	0.844803321
9.34_M	Male	Terrestrial	Porto da Cruz	1.213020427	1.079843268
9.35_F	Female	Terrestrial	Porto da Cruz	0.84241772	0.694088972
9.36_M	Male	Terrestrial	Porto da Cruz	0.968382731	0.845456719
9.37_M	Male	Terrestrial	Porto da Cruz	0.96166594	0.858341309
9.38_F	Female	Terrestrial	Porto da Cruz	0.787688823	0.709893298
9.39_M	Male	Terrestrial	Porto da Cruz	1.14770212	0.998087376
9.40_F	Female	Terrestrial	Porto da Cruz	0.890498888	0.674368723
9.41_M	Male	Terrestrial	Porto da Cruz	0.973270143	0.810448812

9.42_F	Female	Terrestrial	Porto da Cruz	0.804564639	0.633863242
9.43_F	Female	Terrestrial	Porto da Cruz	0.768729325	0.555182335
9.44_F	Female	Terrestrial	Porto da Cruz	0.844834848	0.689241611
9.45_F	Female	Terrestrial	Porto da Cruz	0.974603771	0.840664592
9.46_F	Female	Terrestrial	Porto da Cruz	0.751367489	0.632563135

Table S1. Specimen list