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The role of bite force in the evolution of head shape and head shape dimorphism in *Anolis* lizards

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Abstract

1. Patterns of convergent evolution in head shape, combined with performance measures, provide ideal opportunities to understand the processes driving its evolution. Anole lizards represent an excellent subject to test this, as recurrent habitat specialists or ecomorphs evolved independently across different islands.
2. We show that phenotypic similarity corresponds to both phylogenetic similarity and similarity in habitat, indicating that there is convergent evolution in head shape among ecomorphs. Moreover, we show that the evolution of tall, wide heads correlate with the evolution of higher bite forces, driving head shape variation among and within ecomorphs.
3. In addition, the processes affecting head shape variation can differ between sexes, leading to sexual head shape dimorphism. These processes might, however, still depend on the habitat. Consequently, there could also be convergent evolution in head shape dimorphism among ecomorphs.
4. We found no evidence for convergent evolution in sexual head shape dimorphism. Moreover, the sexual head shape dimorphism correlates poorly with bite force, suggesting that intersexual head shape differences are related to other functions. Different processes are thus driving the evolution of head shape and head shape dimorphism.

KEYWORDS
bite force, convergent evolution, ecomorph, head shape, phylogenetic signal, sexual dimorphism

1 | INTRODUCTION

Adaptive convergent evolution occurs when species independently evolve similar features, as species evolve similar phenotypes in response to similar local environments or ecological niches (Kolbe, Revell, Szekely, Brodie, & Losos, 2011; Losos, 2009). Such phenotypic convergence often correlates with similarities in whole-organism performance (Irschick & Higham, 2016). A typical example is the fusiform body shape of aquatic animals, such as fish and marine mammals, which is assumed to allow high-speed swimming in high drag environments (McGhee, 2011). Studies on convergent evolution should ideally examine both convergence in morphology and in performance (Donley, Sepulveda, Konstantinidis, Gemballa, & Shadwick, 2004; Herrel, Vanhooydonck, & Van Damme, 2004; Müller, 1996), as the inclusion of performance is essential to understand the morphology–ecology relationship. One of the most complex biological systems is the vertebrate head, which plays a role in feeding, breathing, brain protection, locomotion, display, defensive behaviour and sensory perception (Bels, Chardon, & Kardong, 1994; Cooper & Vitt, 1993; Herrel, Meyers, & Vanhooydonck, 2001; Lappin & Husak, 2005). Understanding the relation between head morphology, ecology and performance is therefore complex, as the cranial system is exposed to a mixture of (possibly conflicting) selective pressures. Selective pressures do not only differ among species, however, but also between sexes of a single species, possibly resulting in sexually dimorphic heads (Wittorski, Losos, & Herrel, 2016). Moreover, the factors driving head shape differences among species and between sexes are not necessarily the same. Convergent evolution in head shape and head shape dimorphism represents a unique opportunity to identify the main drivers of the variables. In addition, understanding convergence in head shape and associated performance traits such as bite force can play a vital role in understanding the interplay of morphology, function and ecology.

Prior studies have shown that *Anolis* lizards represent an ideal clade to study these issues, as convergent evolution in both size and shape dimorphism has occurred within this clade. On each of the Greater Antillean islands, independent radiations have taken place, producing the same set of habitat specialists – termed 'ecomorphs' – that are morphologically and behaviourally adapted to different parts of the environment: trunk, trunk-ground, trunk-crown, twig, grass-bush and crown-giants (Losos, 2009). Each ecomorph is characterized by a particular set of traits, which provide functional advantages in their environment, such as body size, limb length and the number of lamellae on their toepads (Losos, 2009). These traits are also sexually dimorphic, with the degree of dimorphism depending on the ecomorph. For example, convergent evolution in relative limb length among ecomorphs has been related to a trade-off between running and jumping capabilities versus manoeuvrability in dense, irregular environments (Butler, Sawyer, & Losos, 2007; Irschick & Losos, 1998, 1999; Losos, 2009). The degree of sexual dimorphism, on the other hand, depends on the intersexual variation in perch height and diameter within each ecomorph, with higher variation resulting in a higher degree of dimorphism (Butler, Schoener, & Losos, 2000). Unexpectedly, while convergent evolution is also observed in head shape among ecomorphs (Beuttell & Losos, 1999; Harmon, Kolbe, Cheverud, & Losos, 2005), little is known about how this is associated with convergence in performance. For example, trunk and trunk-ground anoles have the broadest heads, which has been hypothesized to be related to high size-corrected bite forces (Harmon et al., 2005), but this hypothesis remains untested. Moreover, Sanger et al. (Sanger et al., 2013) found evidence for convergent evolution in sexual dimorphism in facial length among *Anolis* clades, but it remains untested whether there is convergent evolution in sexual head shape dimorphism among ecomorphs and how this would relate to intersexual differences in performance.

An important and widely used performance measure is bite force, which plays a pivotal role in key functions, such as feeding and agonistic interactions related to territory or mate defence (Fabre, Andrade, Huyghe, Cornette, & Herrel, 2014; Herrel, Damme, Vanhooydonck, & Vree, 2001; Herrel & Holanova, 2008; Huyghe, Vanhooydonck, & Scheers, 2005; Lailvaux & Irschick, 2007; Verwaijen, Van Damme, & Herrel, 2002) and in the evolution of vertebrate head shape (Herrel, Schaerlaeken, Meyers, Metzger, & Ross, 2007; Kohlsdorf, Grizante, Navas, & Herrel, 2008). The magnitude of bite force is indeed strongly related to head shape, as bite force depends on jaw muscle size or the length of the jaw closing in-lever. In turn, these variables are associated with variation in head width and height (Herrel, Damme, et al., 2001; Herrel, De Grauw, & Lemos-Espinal, 2001; Vanhooydonck, Herrel, & Van Damme, 2007). Bite force is thus an excellent performance measure that could drive both ecomorph-specific differences in head shape and variation in the degree of head shape dimorphism. Bite force itself is potentially under the influence of both viability and sexual selection. Bite force can influence diet, as it directly impacts which prey items can be consumed (Herrel, Damme, et al., 2001; Herrel, Schaerlaeken, et al., 2007; Verwaijen et al., 2002). While low bite forces can constrain dietary preferences, high bite forces can either increase the dietary range of potential prey items or lead to a more specialized diet on larger, harder prey items. Because the encountered prey types and their variety are likely to differ among habitats, dietary differences can result in ecomorph-specific differences in bite performance. Bite force can, however, also be influenced by the degree of territoriality, as more territorial species are more likely to engage in agonistic interactions for which higher bite forces are beneficial (Lailvaux, Herrel, Vanhooydonck, Meyers, & Irschick, 2004a; Lailvaux & Irschick, 2007). Territoriality cannot only vary at the species level, but also at the ecomorph level (Johnson, Revell, & Losos, 2010). Consequently, ecomorph-specific differences in territoriality can result in ecomorph-specific differences in bite force and associated head shape differences. Finally, higher bite forces increase the success of males in competition for mates (Anderson & Vitt, 1990; Lappin & Husak, 2005) and are thus potentially under sexual selection (Lappin & Husak, 2005). Directional selection for high bite forces in males can thus lead to intersexual differences in bite force and head shape. Because male–male competition can be expected to be more pronounced in territorial species, the degree of sexual dimorphism in head shape might be ecomorph-dependent as well. By including bite forces in a comparative analysis of head shape, we aim to investigate whether there is convergent evolution in head shape and head shape dimorphism among ecomorphs and determine the potential role of bite force in these processes.

Therefore, we first explore how head shape varies among ecomorphs to determine whether there is convergent evolution in head shape. Subsequently, we determine how head shape variation is related to bite force. Specifically, we predict that ecomorphs with taller and wider heads will show higher bite forces than ecomorphs with narrow, shallow heads leading to differences in bite force between ecomorphs. Next, we test the hypothesis that sexual head shape dimorphism is related to sexual bite force dimorphism. Finally, we test whether the degree of sexual head shape and bite force dimorphism differs among ecomorphs.

By testing these hypotheses, we will be able to provide crucial insights in the role of bite force in the convergent evolution of head shape, the evolution of head shape dimorphism and the interplay of bite force with head shape and ecology.

2 | MATERIALS AND METHODS

2.1 | Data collection

We collected data on 2,439 adult *Anolis* lizards belonging to 32 different species measured in the field or in the collection of the Museum for Comparative Zoology at Harvard; all measured by the same person (AH). The number of specimens per sex per species can be found in Table S1 (in Supporting Information), as well as the ecomorph assignation of each species. For each specimen, the following morphological measurements were taken: snout–vent length (SVL), head length (HL), head width (HW), head height (HH), lower jaw length (LJL), the distance from the quadrate to the tip of the lower jaw (quadrate length; QL), and the distance from the back of the jugal to the tip of the lower jaw (coronoid length; CL). All measurements, except for SVL, are further referred to as head size measurements. Head length was defined as the length from the anterior end of the premaxillary to the posterior edge of the parietal bone. The highest part of the head, just posterior to the orbita, was used for measuring head height. Head width was determined at the widest part of the head (Figure 1).

The bite force of 2,407 specimens, belonging to 27 different species, was measured in vivo at the natural ambient temperature of each species within 24 hr of capture by the same observer (AH). To do so, an isometric Kistler force transducer (type 9203, Kistler Inc.) was mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058A, Kistler Inc.), according to the protocol described in Herrel, Spithoven, Damme, and Vree (1999). During biting, the upper plate pivots around the fulcrum and exerts a pull on the transducer. The point of application of the bite force was standardized for each specimen, and gape angle was maintained equivalent at 30° by adjusting the distance between the bite plates. This measurement was repeated five times per lizard, and the maximum value obtained was used as our estimate of the maximal bite force (BF) of the lizard and is used in further analysis.

2.2 | Data analysis

Before analysis, all measurements were $\log_{10}$-transformed. To distinguish size from shape, we regressed each of the $\log_{10}$-transformed head size measurements and $\log_{10}$-transformed bite force against $\log_{10}$-transformed SVL and subsequently calculated the residuals. These residuals were used for further analysis and are referred to as head shape variables and size-corrected bite forces.

Rather than a phylogenetic PCA, which determines the major axes of non-phylogenetic shape variation, we performed a between-group principal component analysis (BG-PCA) in order to determine the major axes of head shape variation among ecomorphs. The residuals were used for two BG-PCAs using PAST3 (Hammer, Harper, & Ryan, 2001): a first BG-PCA on correlation matrix, which included all head shape variables and size-corrected BF (dataset of 27 species; 2,407 specimens) and a second BG-PCA on a variance–covariance matrix containing the head shape variables only, using the total dataset of 32 species. Furthermore, to explore whether species of the same ecomorph have a similar head shape, a UPGMA (unweighted paired-group method using arithmetic averages) was performed in PAST3 (Hammer et al., 2001) on a dataset containing the species means of each head shape variable. Next, we tested whether ecomorphs differ significantly in shape and whether this is sex-dependent by performing phylogenetic MANOVAs on datasets containing the species means of each head shape variable, both of the sexes combined and separated. When a MANOVA showed significant differences in head shape between ecomorphs, we performed phylogenetic ANOVAs (Holm-correction; 1,000 simulations) on the species means of the shape variables to determine which shape variables actually differ between ecomorphs. Additionally, a phylogenetic ANOVA was performed on

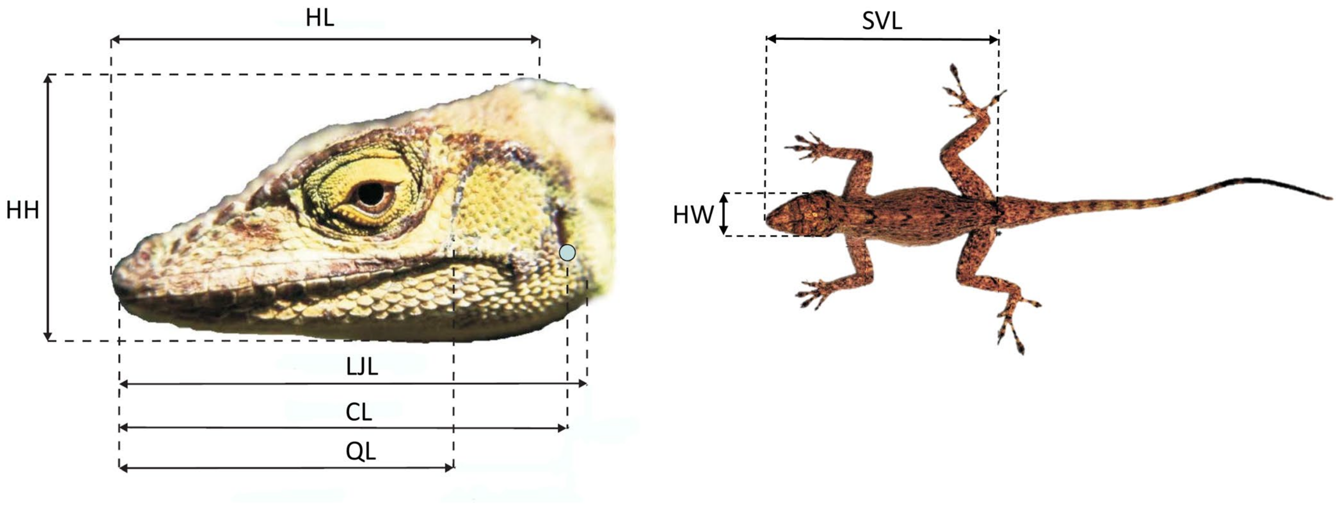

FIGURE 1 Figure of the taken head and body measurements, adapted from Herrel and Holanova (2008). CL, coronoid length; HH, head height; HL, head length; HW, head width; LJL, lower Jaw Length; QL, quadrate length; SVL, snout–vent length

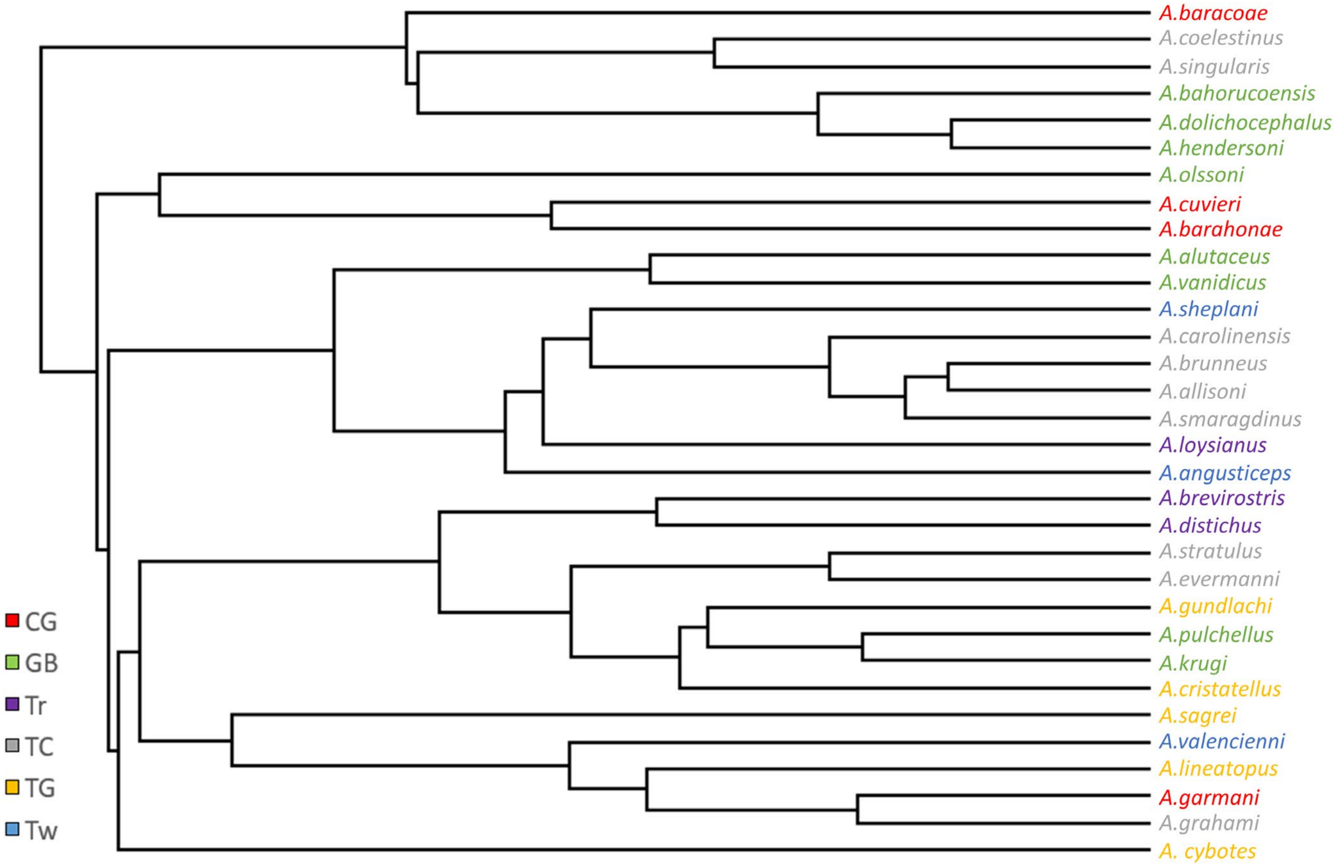

FIGURE 2 Phylogeny of the *Anolis* species included in our study and their ecomorph, according to Poe et al. (2017). CG, crown-giant; GB, grass-bush; TC, trunk-crown; TG, trunk-ground; Tr, trunk; Tw, twig

BF and size-corrected BF to test for significant differences between ecomorphs, again on datasets containing both sexes and each sex separately. All these analyses were performed in R, using the 'GEIGER'-package for the phylogenetic MANOVAs (Harmon, Weir, Brock, Glor, & Challenger, 2008), and the 'PHYTOOLS'-package (Revell, 2012) for the phylogenetic ANOVAs. In order to test whether there is convergent evolution in overall head shape, first, a regular PCA was performed on the head shape variables to minimize the number of shape variables. The first two principal components of this analysis were significant according to the broken-stick method and together explained 87.84% of the total shape variation. Of these two PCs, the means were calculated per species and per sex per species, which were then used to determine whether there is statistical support for convergent evolution in head shape with the 'CONVEVOL'-package in R (Stayton, 2015). Afterwards, convergent evolution for each head shape variable was quantified by calculating the wheatsheaf index (Arbuckle, Bennett, Speed, & Münkemüller, 2014) using the 'WINDEX'-package in R (Arbuckle & Minter, 2015), also for sexes combined and separately. Finally, to determine the relation between head shape and size-corrected BF, we calculated the Pearson correlation between the species mean of each head shape variable and the mean size-corrected BF. In addition, to correct for phylogeny, the phylogenetic independent contrasts (Felsenstein, 1985) of these variables were obtained using the 'APE'-package in R (Paradis & Schliep, 2018), and linear regressions were performed between the obtained contrasts of each head shape variable against those of size-corrected BF.

Subsequently, the degree of sexual dimorphism was determined by calculating mean[(Var_male)] − mean[(Var_female)], with Var being each of the head shape variables, as well as size-corrected BF. Similar as with head shape, we determined whether ecomorphs differ in the degree of head shape dimorphism by first performing a phylogenetic MANOVA, followed by phylogenetic ANOVAs to test which head shape and size dimorphism differ between ecomorphs. The same approach was used for sexual dimorphism in bite force. To determine whether sexual head shape dimorphism is related to sexual bite force dimorphism, we then calculated the Pearson correlation between each head shape dimorphism degree and the bite force dimorphism degree. Also, the phylogenetic independent contrasts of the dimorphism degrees were calculated and analysed as described above. A UPGMA was performed on the degree of dimorphism of each head shape variable to explore whether species of the same ecomorph are similar in head shape and their degree of dimorphism.

Finally, Blomberg's *K* (Blomberg, Garland, & Ives, 2003) was calculated for the species means of all head shape variables and size-corrected bite force, as well as for the degree of head shape and bite force dimorphism using the phylosignal function of the 'PICANTE'-package in R (Kembel et al., 2010). This describes whether

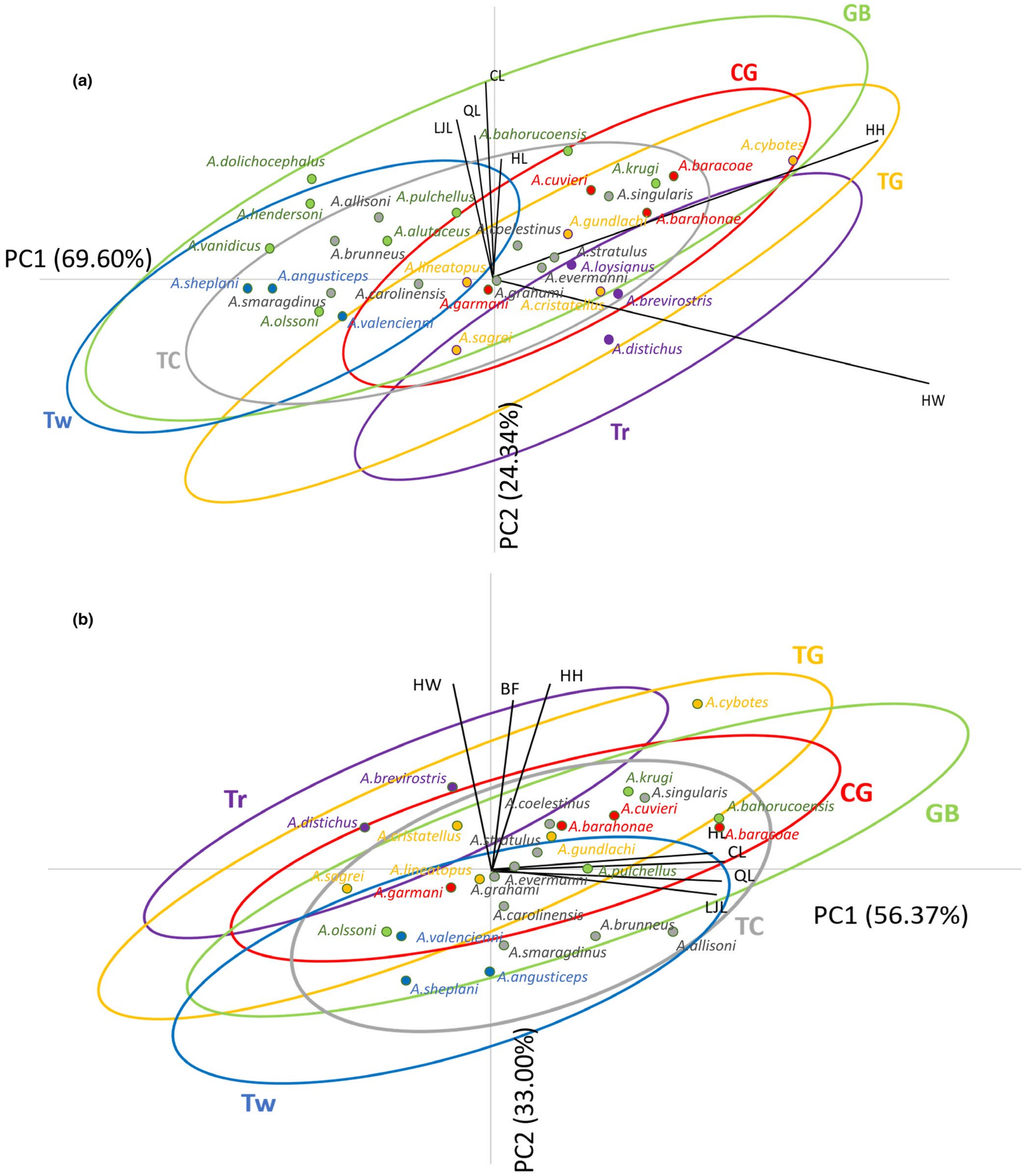

FIGURE 3 Plots of the BG-PCAs on the head shape variables only (a) and with size-corrected bite force (b). For the former, 32 species were used ($N = 2,439$), for the latter 27 species ($N = 2,407$). The percentage explained by each PC is mentioned in parentheses. The morphospace of each ecomorph is represented by 95% confidence ellipses. Dots represent the mean PC-scores per species, coloured according to ecomorph (CG, crown-giant; GB, grass-bush; TC, trunk-crown; TG, trunk-ground; Tr, trunk; Tw, twig)

a phylogenetic signal is present in our data, that is whether related species have the tendency to resemble each other. For the phylogenetic analyses, the phylogeny of Poe et al. (2017) was used (Figure 2).

The average ± standard deviation of all raw measurements, size-corrected measurements and the dimorphism degrees can be found in Tables S1-S3.

3 | RESULTS

3.1 | Head shape variation between ecomorphs

Principal Component 1 (PC1) of the BG-PCA on head shape variables explains 69.6% of the total shape variation and is positively correlated with variation in head height and width. Principal Component 2 (PC2), explaining 24.3% of the total variation, correlates positively with variation in head length (HL, LJL, QL and CL) and, to a lesser extent, also with head height, whereas it negatively correlates with head width (Figure 3a; Table S4). Within each ecomorph, there is a wide range of head shape variation (Figure 3b). Despite the overlap in morphospace among ecomorphs, the phylogenetic MANOVA on the shape variables shows that ecomorphs differ in head shape, and this holds true for both sexes combined ($F = 2.11$; $p < .01$) and separately ($F_{\text{male}} = 2.68$; $p_{\text{male}} < .01$; $F_{\text{female}} = 2.93$; $p_{\text{female}} < .01$). Post hoc phylogenetic ANOVAs show, however, that, with the exception of head width, most head shape variables did not differ significantly between ecomorphs, and this holds true for both the sexes combined and separated (Table 1). In males, twigs and grass-bush anoles differed significantly in head width from the other ecomorphs. In females, significant differences are only found between twig anoles and trunk-ground, trunk-crown and crown-giants (Table S5).

While the above-described results demonstrate that there is at least some degree of convergent evolution in head shape among ecomorphs, significant support for convergent evolution in overall head shape was only found for species belonging to the trunk-ecomorph, independent of sexes (p_{male} and $p_{\text{female}} = .01$) and for species belonging to the twig anoles, but only in females ($p = .01$). Support for convergent evolution among male twig anoles was only close to significant ($p = .09$; Table S6). While there is convergent evolution in overall head shape, none of the separate head shape variables showed (strong) convergent evolution in these latter two ecomorphs (Table S7). Significant wheatsheaf indices were only found for head height in both sexes of trunk-ground anoles (p_{male} and $p_{\text{female}} = .04$) and lower jaw length in female grass-bush anoles ($p = .01$; Table S7), indicating that convergent evolution in these aspects is stronger than would be expected at random.

The little support for convergent evolution might be due to the high interspecific variation within a single ecomorph, as observed in the BG-PCA. Accordingly, the UPGMA on the species means shows that, while most species of an ecomorph cluster closely together, exceptions exist within each ecomorph (Figure 2). *Anolis krugi* and *A. bahorucoensis*, for example, differ extensively in head shape from the other grass-bush anoles (Figure 3a).

Finally, a significant phylogenetic signal is detected for all head shape variables, with the exception of head length, for both sexes combined and separately (Table 2). Phylogenetic signal is strong ($K > 1$) in all head shape variables, except for head length and head width, in males. In both the female dataset and the sexes combined dataset, only head height had a K-value > 1. These high K-values indicate that more closely related species are more likely to resemble

TABLE 1 Overview of the calculated *p*-values (see footnote) according to the phylogenetic ANOVAs, used to test for significant differences in head shape and size-corrected bite force between ecomorphs

	HL	HW	HH	LJL	QL	CL	BF
Male	0.50	**	0.07	0.20	0.30	0.20	0.21
Female	0.33	**	0.14	0.21	0.18	0.08	0.19
Male + female	0.47	**	0.11	0.22	0.26	0.10	0.21
Dimorphism	0.41	0.45	0.27	0.20	0.27	0.10	0.18

Note: ANOVAs were performed for each head shape variable and size-corrected bite force, based on the means per species (male + female), the means per sex per species and the dimorphism degree ($N = 32$ for head shape variables; $N = 27$ for bite force).
**<.01.

TABLE 2 Overview of the calculated Blomberg's *K*-values for each head shape variable and size-corrected bite force, based on the means per species (male + female), the means per sex per species and the dimorphism degree ($N = 32$ for head shape variables; $N = 27$ for bite force)

	HL	HW	HH	LJL	QL	CL	BF
Male	0.83 (**)	0.86 (**)	1.16 (***)	1.21 (***)	1.16 (***)	1.05 (***)	1.01 (**)
Female	0.57 (.36)	0.90 (**)	1.08 (***)	0.75 (*)	0.84 (**)	0.99 (***)	0.98 (***)
Male + female	0.70 (.03)	0.88 (**)	1.15 (***)	0.98 (***)	0.99 (***)	0.99 (***)	1.02 (**)
Dimorphism	0.61 (.23)	0.63 (.14)	0.72 (*)	0.85 (**)	0.85 (**)	1.05 (***)	0.67 (.20)

Note: Values <1 indicate weak phylogenetic signal, values >1 strong phylogenetic signal. *p*-values are given in parentheses.
*<.05
**<.01
***<.001.

TABLE 3 Results of the correlation analyses

	HL	HW	HH	LJL	QL	CL
Pearson						
Shape	0.24 (.23)	**0.39 (.04)**	**0.65 (<.01)**	0.29 (.14)	0.36 (.07)	0.20 (.32)
Dimorphism	0.25 (.21)	**0.38 (.05)**	0.22 (.27)	0.30 (.13)	0.33 (.09)	0.24 (.23)
PIC						
Shape (PIC)	0.08 (.68)	0.13 (.51)	**0.44 (.02)**	0.29 (.15)	0.32 (.11)	0.07 (.71)
Dimorphism (PIC)	0.03 (.89)	0.34 (.08)	0.12 (.56)	0.09 (.66)	0.12 (.56)	0.04 (.86)

Note: Pearson correlation values were calculated between the head shape variables and size-corrected bite force, calculated on the species mean level and the dimorphism degree ($N = 27$); the *r*-values were obtained from the linear regression between the phylogenetic independent contrasts (PIC) of both the species means and the dimorphism degrees of all head shape variables against those of size-corrected bite force. *p*-values are given in parentheses. Significant results are shown in bold.

each other's morphology. *Anolis barahonae* and *A. cuvieri* are, for example, the most similar of all crown-giants and are the most closely related. Similarly, the trunk-crown anoles of the *A. carolinensis*-clade have a comparable head shape, but differ from the other trunk-crown species (Figure 3a).

3.2 | Bite force variation between ecomorphs and the link with head shape

To explore the role of bite force (BF) in head shape variation, a second BG-PCA was performed on the correlation matrix of all head shape variables and size-corrected BF. PC1 (56.37% of the variation) is related to variation in head length, with higher PC1 scores being associated with long heads and vice versa. Principal Component 2 (33.00%) is related to variation in head height, width and bite force, with higher PC2 scores being associated with wider, taller heads and higher size-corrected bite forces (Figure 3b). This relation between head shape and size-corrected bite force is confirmed by the results of the Pearson correlation analyses, as bite force correlates best with head height, followed by head width (Table 3). However, according to the linear regressions of the independent contrasts, only head height correlates significantly with bite force (Table 3). Again, there is strong overlap in morphospace between ecomorphs. Accordingly, no significant differences are found in size-corrected bite force between the ecomorphs ($p_{\text{male+female}} = .21$; $p_{\text{male}} = .21$; $p_{\text{female}} = .20$).

3.3 | Sexual dimorphism in ecomorphs

Figure 4 illustrates the variation in the degree of head shape dimorphism within ecomorphs. Ecomorphs do not differ significantly in head shape dimorphism ($p = .29$) and dimorphism in size-corrected bite force ($p = .20$). Accordingly, the UPGMA based upon the dimorphism degrees shows that species of the same ecomorph do not cluster together (Figure 5). A weak, but significant phylogenetic signal in the degree of dimorphism was found for coronoid length, quadrate length, lower jaw length and head height (Table 2). No significant signal was found for dimorphism in head length ($p = .23$), head width ($p = .14$) and bite force ($p = .18$). Finally, we found no significant correlation between head shape dimorphism and bite force dimorphism, with the exception of the Pearson correlation between head width and bite force (Table 3).

4 | DISCUSSION

4.1 | Convergent evolution in head shape and its link with bite force

Understanding the evolution of head shape variation is a complex task as the head plays a key role in many vital functions, such as feeding, breathing, display, brain protection, locomotion, defensive behaviour and sensory perception (Bels et al., 1994; Cooper & Vitt, 1993; Herrel, Meyers, et al., 2001; Lappin & Husak, 2005). On a macroevolutionary time-scale, viability selection is expected to drive head shape in relation to a variety of environmental variables. Cases of convergent evolution in head shape therefore represent unique opportunities to understand the link between head shape and ecology. Moreover, by including ecologically relevant performance measures, one can gain crucial insights into the relation among head shape morphology, ecology and performance. While convergent evolution has been documented in several traits in *Anolis* lizards including limb length and body size, relatively little attention has been given to head shape and the possible functional consequences of head shape variation. Here, we included bite forces in a comparative morphological analysis between anole ecomorphs to assess whether and how they differ in head shape and how this is related to differences in bite force.

Our analysis demonstrates that anole ecomorphs can differ in head shape, corroborating the results of previous research (Harmon et al., 2005; Sanger, Mahler, Abzhanov, & Losos, 2012). Still, there is overlap in head shape among ecomorphs as well, and the differences in head shape between ecomorphs are thus not strongly pronounced. In addition, we only found evidence that the similarity in head shape among trunk and twig anoles is due to convergent evolution. For the remaining ecomorphs, no statistical support for convergent evolution was found, even though the cluster analysis shows that most species of a single ecomorph cluster together according to head shape. However, within each ecomorph, there are also species that exhibit a head shape that differs

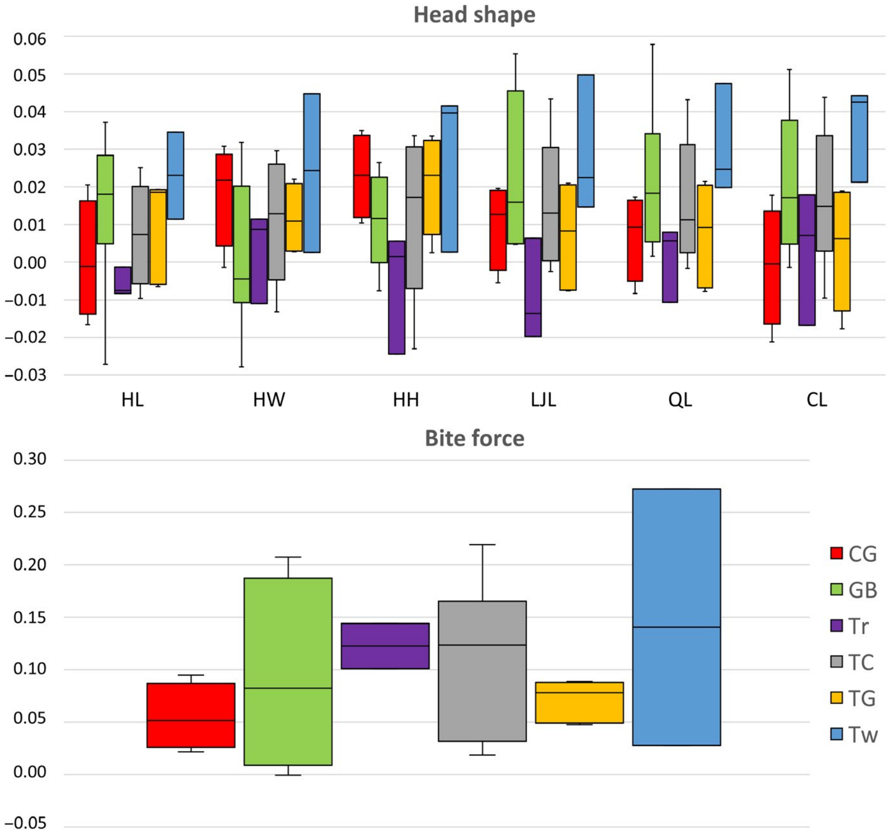

FIGURE 4 Box-and-whisker plots of the dimorphism degree of the head shape variables (up) and size-corrected bite force (down). The boxes represent the interquartile range, with the central line being the median, the whiskers the minimum and maximum dimorphism degrees per ecomorph (CG, crown-giant; CL, coronoid length; GB, grass-bush; HH, head height; HL, head length; HW, head width; LJL, lower jaw length; QL, quadrate length; TC, trunk-crown; TG, trunk-ground; Tr, trunk; Tw, twig)

strongly from those of the same ecomorph members. *Anolis cybotes*, for example, exhibits a much taller head compared to the other trunk-ground anoles. Because of such exceptions, it is not possible to distinguish ecomorphs as completely different morphological entities. Consequently, statistically significant patterns of convergent evolution in head shape of particular ecomorphs often do not occur. Still, there are indications of convergent evolution among all ecomorphs. For example, we observe that trunk-crown anoles on three islands (*A. grahami*, *A. evermanni*, *A. coelestinus* and *A. stratulus*) converged in head shapes, even though they are not closely related. Similar examples, in which most members of an ecomorph converged in head shape, can be found among the other ecomorphs as well.

While there is at least some degree of convergent evolution among ecomorphs, most head shape variables also show a strong phylogenetic signal, indicating that more closely related species will have more similar head shapes. There indeed seems to be a trend that, even when species of a single ecomorph cluster together in morphospace, the more closely related species will be more similar in head shape than less related ecomorph members. The crown-giants *A. barahonae* and *A. cuvieri* are, for example, the most similar in head shape and the most closely related. Also, the trunk-crown anoles of the *A. carolinensis*-clade have a very similar head shape, distinct from the other trunk-crown anoles. So, while the occupation of similar habitats can result in the evolution of similar head shapes among ecomorphs due to convergent evolution, the degree of similarity also depends on the degree of phylogenetic similarity.

Convergent evolution in head shape could be correlated with evolution in bite force, as the relation between head shape and bite force has already been established in previous studies (Donihue, Brock, Foufopoulos, Herrel, & Grindstaff, 2016; Herrel, De Grauw, et al., 2001; Herrel & Holanova, 2008). Indeed, here, we show that this relation can explain differences both at the ecomorph and species levels. Relatively wider and taller heads are correlated with higher size-corrected bite forces, resulting in differences among ecomorphs, but also among species within ecomorphs. This suggests that the evolution of taller, wider heads is driven by selection for higher bite forces relative to body size in *Anolis* lizards. However, our study does not allow to identify the underlying mechanisms driving selection for higher bite forces. In general, differences in bite force can be related to three primary factors, each of which deserves further study: (a) dietary differences (Herrel, Damme, et al., 2001; Herrel, Joachim, Vanhooydonck, & Irschick, 2006; Herrel et al., 1999) with higher bite forces allowing the consumption of larger, harder prey items; (b) territorial defence (Lailvaux, Herrel, Vanhooydonck, Meyers, & Irschick, 2004b; Lailvaux & Irschick, 2007) with higher bite forces allowing anoles to better occupy or defend territories; and (c) defence against predators (Leal & Rodríguez-Robles, 1995; Vanhooydonck, Herrel, Damme, & Irschick, 2005). Determining which mechanism(s) underlie differences in head shape and bite force between species and ecomorphs requires more research. By linking the similarity observed in ecology and behaviour among ecomorphs with their similarity in head shape and performance, future studies should

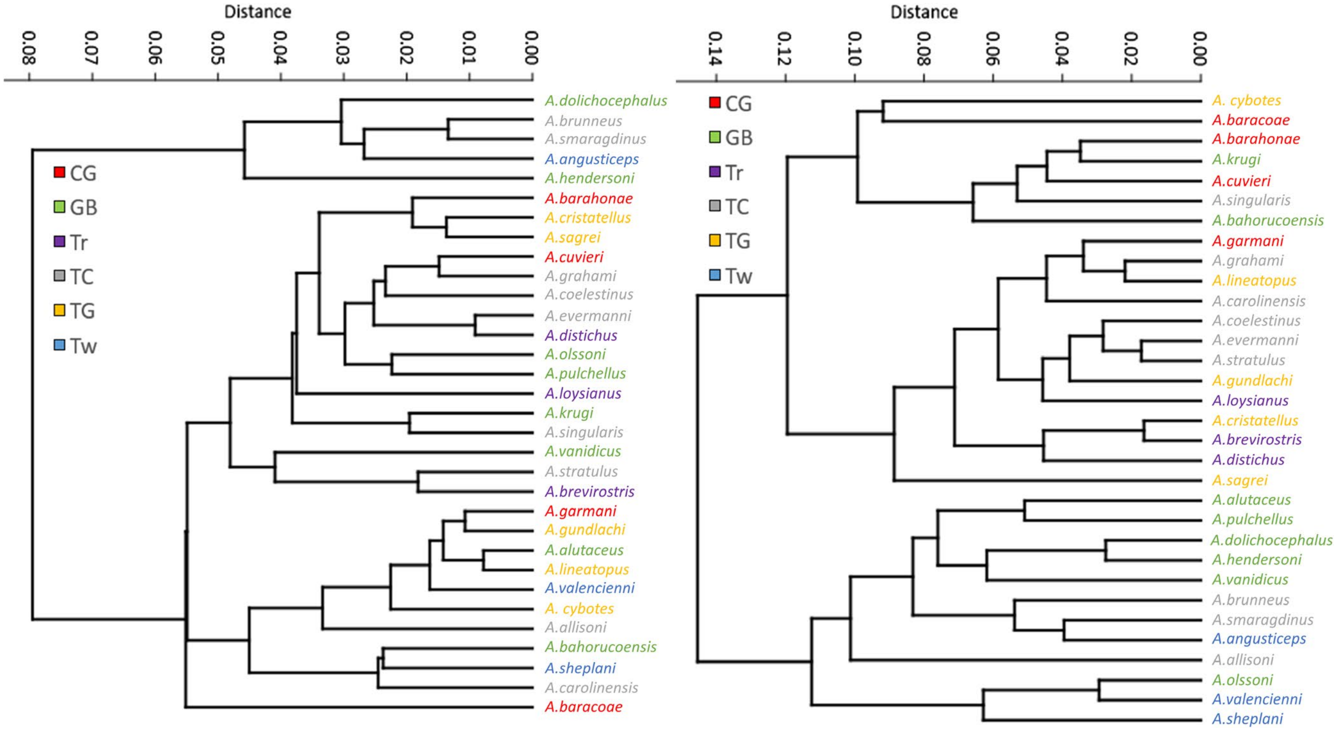

FIGURE 5 UPGMA phenogram on the head shape dimorphism degrees (left) and the species means of each head shape variable (right), with the species being coloured according to ecomorph (CG, crown-giant; GB, grass-bush; TC, trunk-crown; TG, trunk-ground; Tr, trunk; Tw, twig)

be able to identify the proper mechanisms behind head shape and bite force variation.

4.2 | Convergent evolution in head shape dimorphism and its link with bite force

Selective pressures on head shape can differ not only among species and ecomorphs but also between sexes of the same species, resulting in sexual head shape dimorphism. Males in several lizard species tend to have relatively larger heads than females (Fabre, Cornette, Huyghe, Andrade, & Herrel, 2014; Herrel, De Grauw, et al., 2001; Herrel et al., 2006; Herrel, Mcbrayer, & Larson, 2007). This phenomenon has been related to either resource partitioning, in which males and females differ in diet (Herrel, Damme, et al., 2001; Herrel, Mcbrayer, et al., 2007), and sexual selection, in which larger male heads increase the success in male–male competition for mates (Gvozdík & Van Damme, 2003; Lailvaux et al., 2004b; Lailvaux & Irschick, 2007). Independent of the possible underlying mechanisms, the relatively larger heads allow them to generate higher bite forces than females, taking into account potential differences in body size (Fabre, Andrade, et al., 2014; Herrel, Damme, et al., 2001; Herrel, De Grauw, et al., 2001; Herrel, Mcbrayer, et al., 2007). Consequently, the degree of sexual head shape dimorphism could be associated with the degree of sexual dimorphism in size-corrected bite force. More specifically, based on the comparative analysis between ecomorphs, we expected that sexual differences in head height and width would have the largest impact on sexual dimorphism in size-corrected bite force.

While sexual dimorphism in all head shape variables was generally poorly correlated with bite force dimorphism, surprisingly, the lowest correlation value was found for dimorphism in head height, whereas the highest correlation value was found for head width. Intersexual differences in bite performance have been related to differences in jaw muscle size (Herrel, Mcbrayer, et al., 2007). This is notable for superficial muscles which tend to be larger and more important for bite force generation in males compared to females (Fabre, Andrade, et al., 2014; Wittorski et al., 2016). Consequently, intersexual differences in the size of these muscles can be expected to be most closely correlated to differences in relative head width, rather than in head height or length. The low correlation values of sexual head shape dimorphism with size-corrected bite force dimorphism, and the more pronounced sexual difference in size-corrected bite force could be due to variation in the underlying musculoskeletal system. Indeed, Lappin and Husak (2005) found little correlation between external head dimensions and bite performance in the collared lizard (*Crotaphytus collaris*), suggesting that differences in internal structure are more important in determining bite force within a species. Variation in the architecture and physiology of the jaw muscles including muscle arrangement, pennation angle, relative jaw muscle size and the skeletal lever system can all potentially cause differences in bite force that cannot be observed by external morphology (Fabre, Andrade, et al., 2014; Fabre, Cornette, et al., 2014; Herrel, Mcbrayer, et al., 2007). A comparative musculoskeletal analysis between sexes, and among species and ecomorphs could allow one to determine how external head shape variation results in variation in the musculoskeletal system, and to evaluate whether additional changes in the musculoskeletal system can be observed, independent of head shape.

While previous research showed that the degree of dimorphism in limb shape differs among ecomorph (Butler et al., 2007), we found that this is not the case for sexual head shape dimorphism. Rather, we observe that the degree of sexual dimorphism varies more among species than among ecomorphs. The grass-bush anoles *A. olssoni* and *A. vanidicus*, for example, differ more substantially from each other in dimorphism degree compared to trunk-crown versus twig anoles. Moreover, as dimorphism in head shape and size-corrected bite force is poorly correlated, selection for relatively higher bite forces in one sex, independent of the underlying mechanism, is expected to be only poorly related to sexual head shape differences. The weak correlation between bite force and head shape dimorphism also suggests that sexual differences in head shape are likely related to other functions. For example, the relatively broader head of males, caused by larger superficial muscles, has been related to visual signalling in the context of male–male competition and/or female choice (Fabre, Andrade, et al., 2014; Fabre, Cornette, et al., 2014; Herrel et al., 1999; Huyghe et al., 2005). Alternatively, subtle differences in head shape can have an impact on climbing abilities or prey capturing efficiency (Losos, 2009; Vanhooydonck et al., 2007). Because head shape plays a role in such a variety of functions, dimorphism degrees could be influenced by intersexual differences in one or multiple environmental variables, such as diet or the degree of intraspecific competition. Butler et al. (2007) indeed showed that there is a high correlation between intersexual differences in habitat use and the dimorphism degree. The interplay of head shape with the environment could explain why the degree of dimorphism depends on the species, rather than the ecomorph. Males and females of *A. olssoni* could, for example, differ more substantially in diet than for *A. vanidicus*, despite belonging to the same ecomorph. Consequently, more research is required to determine the functional consequences and implications of sexual head shape differences and to evaluate the variability of the mechanisms underlying sexual head shape dimorphisms among anole species.

5 | CONCLUSIONS

While there is overlap in head shape among ecomorphs, we still found that species of the same ecomorphs generally have the same head shape. As such, there is at least some degree of convergent evolution in head shape among ecomorphs, for which statistical support was found in trunk and twig anoles. In the other ecomorphs, no significant support is found due to the presence of species with a strongly differing head shape compared to most other ecomorph members. In addition, we found that more closely related species will be more similar in head shape than less related ecomorph members. As such, both similarity in habitat and similarity in phylogeny are associated with similarity in head shape. Moreover, we found evidence that the development of taller, wider heads is associated with higher bite forces, resulting in differences in size-corrected bite force within and among ecomorphs. Selection for higher bite force thus seems to be an important driver of head shape evolution in anoles. While convergent evolution in head shape does occur, this was not the case for head shape dimorphism. Moreover, sexual dimorphism in head shape was a poor predictor of intersexual differences in bite force, highlighting that head shape and head shape dimorphism have evolved largely independently. Future research is required to identify these selective pressures and their relative importance at both the species level and the ecomorph level.

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AUTHORS' CONTRIBUTIONS

A.H., D.J.I., B.V. and J.B.L. were responsible for the collection of the data and the in vivo bite force measurements. J.D.M. performed all analyses, guided by the other authors. J.D.M. wrote the first version of the manuscript and rewrote the manuscript according to the guidelines of all other authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.1v26h11 (De Meyer et al., 2019).

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REFERENCES

Anderson, R. A., & Vitt, L. J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia*, *84*, 145–157. https://doi.org/10.1007/BF00318265

Arbuckle, K., Bennett, C. M., Speed, M. P., & Münkemüller, T. (2014). A simple measure of the strength of convergent evolution. *Methods in Ecology and Evolution*, *5*, 685–693. https://doi.org/10.1111/2041-210X.12195

Arbuckle, K., & Minter, A. (2015). windex: Analyzing convergent evolution using the Wheatsheaf index in R. *Evolutionary Bioinformatics Online*, *11*, 11–14.

Bels, V. L., Chardon, M., & Kardong, K. V. (1994). Biomechanics of the hyolingual system in squamata. In V. L. Bels, M. Chardon, & P. Vandewalle (Eds.), *Biomechanics of feeding in vertebrates* (pp. 197–240). Berlin, Germany: Springer Verlag.

Beuttell, K., & Losos, J. B. (1999). Ecological Morphology of Caribbean Anoles. *Herpetological Monographs*, *13*, 1–28. https://doi.org/10.2307/1467059

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*, 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Butler, M. A., Sawyer, S. A., & Losos, J. B. (2007). Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature*, *447*, 202–205. https://doi.org/10.1038/nature05774

Butler, M. A., Schoener, T. W., & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in greater antillean *Anolis* lizards. *Evolution*, *54*(1), 259. https://doi.org/10.1554/0014-3820(2000)054[0259:TRBSSD]2.0.CO;2

Cooper, W. E., & Vitt, L. J. (1993). Female mate choice of large male broad-headed skinks. *Animal Behaviour*, *45*, 683–693. https://doi.org/10.1006/anbe.1993.1083

De Meyer, J., Irschick, D. J., Vanhooydonck, B., Losos, J. B., Adriaens, D., & Herrel, A. (2019). Data from: The role of bite force in the evolution of head shape and head shape dimorphism in *Anolis* lizards. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.1v26h11.

Donihue, C. M., Brock, K. M., Foufopoulos, J., Herrel, A., & Grindstaff, J. (2016). Feed or fight: Testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. *Functional Ecology*, *30*, 566–575. https://doi.org/10.1111/1365-2435.12550

Donley, J. M., Sepulveda, C. A., Konstantinidis, P., Gemballa, S., & Shadwick, R. E. (2004). Convergent evolution in mechanical design of lamnid sharks and tunas. *Nature*, *429*, 61–64. https://doi.org/10.1038/nature02435

Fabre, A.-C., Andrade, D. V., Huyghe, K., Cornette, R., & Herrel, A. (2014). Interrelationships between bones, muscles, and performance: biting in the lizard *Tupinambis merianae*. *Evolutionary Biology*, *41*, 518–527. https://doi.org/10.1007/s11692-014-9286-3

Fabre, A. C., Cornette, R., Huyghe, K., Andrade, D. V., & Herrel, A. (2014). Linear versus geometric morphometric approaches for the analysis of head shape dimorphism in lizards. *Journal of Morphology*, *275*, 1016–1026. https://doi.org/10.1002/jmor.20278

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist*, *125*, 1–15. https://doi.org/10.1086/284325

Gvozdík, L., & Van Damme, R. (2003). Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootoca vivipara*: A test of two hypotheses. *Journal of Zoology*, *259*, 7–13. https://doi.org/10.1017/S0952836902003308

Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological statistics software package for education and data analysis. *Palaeo Electronica*, *4*, 1–9.

Harmon, L. J., Kolbe, J. J., Cheverud, J. M., & Losos, J. B. (2005). Convergence and the multidimensional niche. *Evolution*, *59*, 409–421. https://doi.org/10.1111/j.0014-3820.2005.tb00999.x

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics*, *24*, 129–131. https://doi.org/10.1093/bioinformatics/btm538

Herrel, A., Damme, R. V., Vanhooydonck, B., & Vree, F. D. (2001). The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology*, *79*, 662–670. https://doi.org/10.1139/z01-031

Herrel, A., De Grauw, E., & Lemos-Espinal, J. A. (2001). Head shape and bite performance in Xenosaurid lizards. *Journal of Experimental Zoology*, *290*, 101–107. https://doi.org/10.1002/jez.1039

Herrel, A., & Holanova, V. (2008). Cranial morphology and bite force in Chamaeleolis lizards–adaptations to molluscivory? *Zoology*, *111*, 467–475. https://doi.org/10.1016/j.zool.2008.01.002

Herrel, A., Joachim, R., Vanhooydonck, B., & Irschick, D. J. (2006). Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society*, *89*, 443–454.

Herrel, A., Mcbrayer, L. D., & Larson, P. M. (2007). Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society*, *91*, 111–119. https://doi.org/10.1111/j.1095-8312.2007.00772.x

Herrel, A., Meyers, J. J., & Vanhooydonck, B. (2001). Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): A population-level analysis. *Biological Journal of the Linnean Society*, *74*, 305–314. https://doi.org/10.1111/j.1095-8312.2001.tb01394.x

Herrel, A., Schaerlaeken, V., Meyers, J. J., Metzger, K. A., & Ross, C. F. (2007). The evolution of cranial design and performance in squamates: Consequences of skull-bone reduction on feeding behavior. *Integrative and Comparative Biology*, *47*, 107–117. https://doi.org/10.1093/icb/icm014

Herrel, A., Spithoven, L., Van Damme, R., & De Vree, F. (1999). Sexual dimorphism of head size in *Gallotia galloti*: Testing the nice divergence hypothesis by functional analyses. *Functional Ecology*, *13*, 289–297.

Herrel, A., Vanhooydonck, B., & Van Damme, R. (2004). Omnivory in lacertid lizards: Adaptive evolution or constraint? *Journal of Evolutionary Biology*, *17*, 974–984. https://doi.org/10.1111/j.1420-9101.2004.00758.x

Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-borja, M., & Van damme, R. (2005). Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology*, *19*, 800–807. https://doi.org/10.1111/j.1365-2435.2005.01038.x

Irschick, D. J., & Higham, T. (2016). *Animal athletes: An ecological and evolutionary approach*. Oxford, UK: Oxford University Press.

Irschick, D. J., & Losos, J. B. (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Carribean *Anolis* lizards. *Evolution*, *52*, 219–226.

Irschick, D. J., & Losos, J. B. (1999). Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Carribean anoles. *The American Naturalist*, *154*, 293–305.

Johnson, M. A., Revell, L. J., & Losos, J. B. (2010). Behavioral convergence and adaptive radiation: Effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution*, *64*, 1151–1159. https://doi.org/10.1111/j.1558-5646.2009.00881.x

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kohlsdorf, T., Grizante, M. B., Navas, C. A., & Herrel, A. (2008). Head shape evolution in Tropidurinae lizards: Does locomotion constrain diet? *Journal of Evolutionary Biology*, *21*, 781–790. https://doi.org/10.1111/j.1420-9101.2008.01516.x

Kolbe, J. J., Revell, L. J., Szekely, B., Brodie, E. D. 3rd, & Losos, J. B. (2011). Convergent evolution of phenotypic integration and its alignment with morphological diversification in Caribbean *Anolis* ecomorphs. *Evolution*, *65*, 3608–3624. https://doi.org/10.1111/j.1558-5646.2011.01416.x

Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J., & Irschick, D. J. (2004a). Fighting tactics differ in two distinct male phenotypes in a lizard: Heavyweight and lightweight bouts. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 2501–2508.

Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J., & Irschick, D. J. (2004b). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis* *carolinensis*). *Proceedings of the Royal Society B: Biological Sciences*, *271*, 2501–2508.

Lailvaux, S. P., & Irschick, D. J. (2007). The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *American Naturalist*, *170*, 573–586.

Lappin, A. K., & Husak, J. F. (2005). Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *The American Naturalist*, *166*, 426–436.

Leal, M., Rodríguez-Robles, J. A., & Rodriguez-Robles, J. A. (1995). Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia*, *1995*, 155–161. https://doi.org/10.2307/1446810

Losos, J. B. (2009). *Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles*. Berkeley and Los Angeles, CA: University of California Press.

McGhee, G. R. (2011). *Convergent evolution: Limited forms most beautiful*. Cambridge, MA: Massachusetts Institute of Technology.

Müller, A. (1996). Convergent evolution of morphological specializations in Central European bee and the honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera, Apoidea and Masaridae). *Biological Journal of the Linnean Society*, *57*, 235–252.

Paradis, E., & Schliep, K. (2018). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Poe, S., Nieto-Montes de Oca, A., Torres-Carvajal, O., de Queiroz, K., Velasco, J. A., Truett, B., … Latella, I. (2017). A phylogenetic biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae). *Systematic Biology*, *665*, 663–697. https://doi.org/10.1093/sysbio/syx029

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Sanger, T. J., Mahler, D. L., Abzhanov, A., & Losos, J. B. (2012). Roles for modularity and constraint in the evolution of cranial diversity among *Anolis* lizards. *Evolution*, *66*, 1525–1542.

Sanger, T. J., Sherratt, E., McGlothlin, J. W., Brodie, E. D., Losos, J. B., & Abzhanov, A. (2013). Convergent evolution of sexual dimorphism in skull shape using distinct developmental strategies. *Evolution*, *67*, 2180–2193. https://doi.org/10.1111/evo.12100

Stayton, C. T. (2015). The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution*, *69*, 2140–2153. https://doi.org/10.1111/evo.12729

Vanhooydonck, B., Herrel, A., & Van Damme, R. (2007). Interactions between habitat use, behavior, and the trophic niche of lacertid lizards. In S. M. Reilly, L. D. Mcbrayer, & D. B. Miles (Eds.), *Lizard ecology: The evolutionary consequences of foraging mode* (pp. 427–449). Cambridge, UK: Cambridge University Press.

Vanhooydonck, B., Herrel, A., Van Damme, R., & Irschick, D. J. (2005). Does dewlap size predict male bite performance in Jamaican *Anolis* lizards. *Functional Ecology*, *19*, 38–42. https://doi.org/10.1111/j.0269-8463.2005.00940.x

Verwaijen, D., Van Damme, R., & Herrel, A. (2002). Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology*, *16*, 842–850. https://doi.org/10.1046/j.1365-2435.2002.00696.x

Wittorski, A., Losos, J. B., & Herrel, A. (2016). Proximate determinants of bite force in *Anolis* lizards. *Journal of Anatomy*, *228*, 85–95.

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