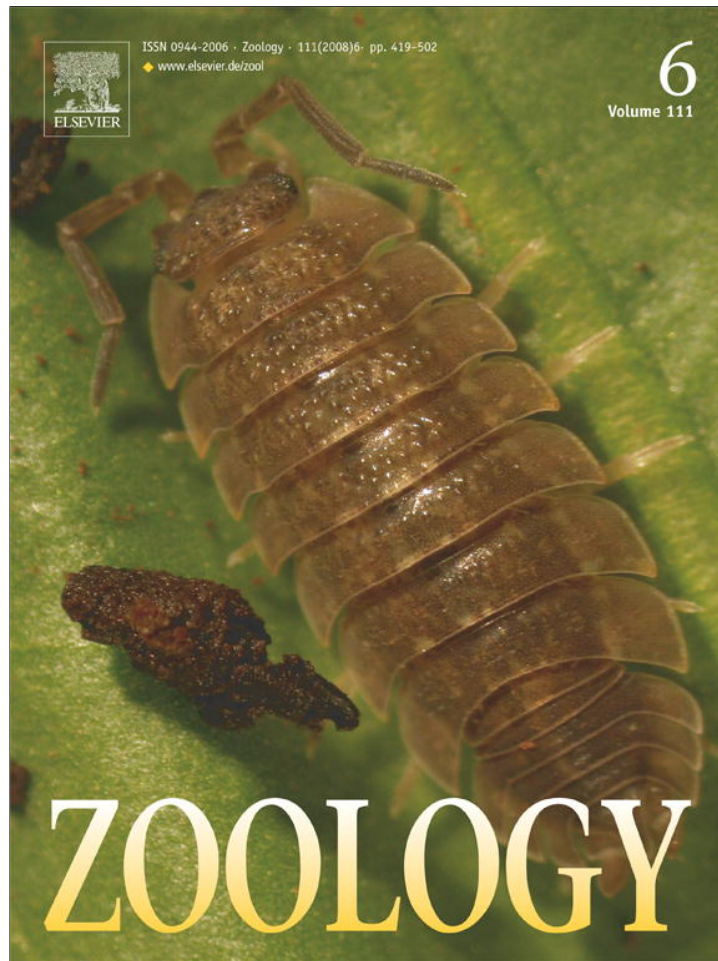


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## Cranial morphology and bite force in *Chamaeleolis* lizards – Adaptations to molluscivory?

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### Abstract

*Anolis* lizards have become a model system for the study of adaptive radiations as species with similar morphologies occupying similar habitats have arisen independently on all the larger islands in the Caribbean. However, on both, Cuba and Hispaniola unique forms have evolved that seemingly have no counterparts on any of the other Caribbean islands. Anoles of the genus *Chamaeleolis* comprise such a unique form and have been termed ‘twig giants’ because of their cryptic life style, slow locomotor mode, and short limbs. However, some of the most unusual features of these lizards are their large heads and molluscivorous diet. Here, we compare head shape, bite force, and muscle structure among sexes and age classes of *Chamaeleolis* lizards with *Anolis* crown giants. Our data show that *Chamaeleolis* lizards have a dramatically different head shape characterized by tall heads with a pronounced temporal ridge and long snouts. Analyses of bite force, surprisingly, show no differences between adult *Chamaeleolis* and *Anolis* crown giants. Juveniles of *Chamaeleolis*, however, have very tall heads for their size and bite harder than *Anolis* juveniles do. This can be related to the propensity of juveniles of this genus to eat snails, food items for which high bite forces are crucial. This observation is corroborated by the presence of well-developed jaw adductors in juveniles. Thus, our data suggest that the unusual phenotype of adults with large and tall heads may be due to selection on the juvenile life history stages.

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**Keywords:** Head shape; Bite force; Feeding; *Anolis*


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### Introduction

In the past couple of decades, *Anolis* lizards have become one of the model systems to study adaptive radiations and evolutionary diversification (Schluter 2000). On the different islands of the Greater Antilles,

similar forms that occupy similar habitats (termed ecomorphs) have arisen independently (Williams 1972; Losos 1995; Losos et al. 1998; Langerhans et al. 2006). *Anolis* lizards are a taxonomically ( $\pm 370$  species; Poe 2004) and phenotypically diverse group of lizards that have occupied a great diversity of niches in the Caribbean, ranging from terrestrial over arboreal to even aquatic species (Schwartz and Henderson 1991). Interestingly, while morphological convergence across islands is great for ground-dwelling and arboreal forms other ecotypes such as the aquatic anoles appear to

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show little or no convergence in morphology (Leal et al. 2002).

Interestingly, Cuba and Hispaniola are characterized by the presence of unique anoles typically not found on any of the other Greater Antillean islands (Rodríguez-Schettino 1999; Beuttell and Losos 1999). A striking example is the lizards of the genus *Chamaeleolis* which have been characterized as 'twig giants' (Hass et al. 1993; but see Beuttell and Losos 1999). *Chamaeleolis* lizards are animals of large body size that move slowly and deliberately around their habitat (Leal and Losos 2000). These animals are typically cryptic, slow, and have relatively short limbs (Wilson 1957; Beuttell and Losos 1999). Unexpectedly, and despite their unique morphology, this monophyletic clade is deeply nested within the genus *Anolis* and is most closely related to a group including a series of crown giants among which are *Anolis cuvieri* from Puerto Rico and *Anolis barahonae* from the Dominican Republic (Hass et al. 1993; Nicholson et al. 2005).

Besides their short limbs, one of the most striking features of these lizards is their head morphology (Rodríguez-Schettino 1999). Not only do they have relatively big heads, they also have a casque-like extension at the back of their head and molariform teeth in adults (Estes and Williams 1984; Schwartz and Henderson 1991). These features have often been associated with their reported snail-eating habits (Estes and Williams 1984; Rodríguez-Schettino 1999, 2003; Lee 1997, 2003).

As snails are hard and brittle food items, changes in cranial morphology leading to increased bite forces have been suggested to be important features for lizards exploiting snails as a dietary resource (Dalrymple 1979; Rieppel and Labhardt 1979). For instance, the snail-crushing teiid lizard genus *Dracaena* is characterized by enlarged blunt molariform teeth and enlarged jaw muscles (Dalrymple 1979). Similar features have been reported for a snail-eating amphisbaenid lizard (*Amphisbaena ridleyi*; Pregill 1984) and Nile monitors (*Varanus niloticus*) which as adults incorporate snails into their diet (Lonnberg 1903; Mertens 1942; Rieppel and Labhardt 1979). Clearly, blunt molariform teeth are important to avoid tooth breakage and increase the contact area with the food. An increase in bite force, however, could be achieved in multiple, not mutually exclusive ways. The easiest way to increase bite force would be to increase overall body size, or head size relative to body size. Additionally, an increase in the mass or architecture (i.e. more pennate muscles with shorter fibers) of the jaw adductors, or changes in the mechanics of the lever system (i.e. increased jaw closing in-lever relative to the jaw out-lever) could improve bite performance (Herrel et al. 2007).

Here we compare *Chamaeleolis* lizards with *Anolis* crown giants to test for differences in cranial size

and shape that could improve bite performance and may allow these lizards to exploit hard dietary items such as snails. Where possible we specifically chose *A. barahonae* to compare *Chamaeleolis* lizards to as *A. barahonae* is of similar body size and is also a member of the sister group to the *Chamaeleolis* clade, making it an ideal species for comparison. Because sample sizes of juveniles for this species were small, we decided to add data for other crown giants (see Statistical analyses). In addition to comparing morphological traits, we also measured bite forces in lizards of different sex and age classes to test for differences in performance. Finally, we observed feeding behavior and quantified cranial morphology to investigate how *Chamaeleolis* lizards handle snails.

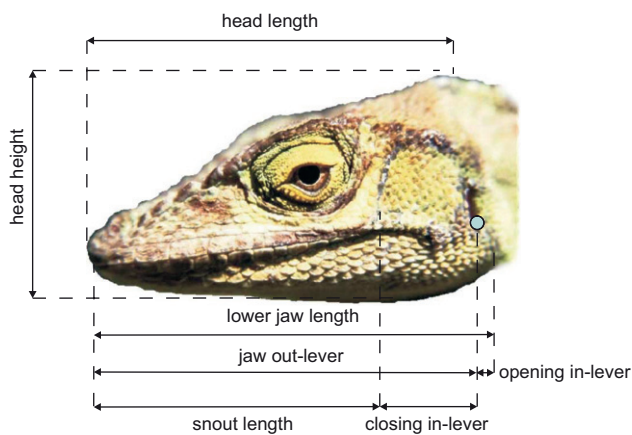
## Materials and methods

### Specimens

*Anolis equestris* specimens ( $N = 13$ ) were captured on the grounds of the University of Miami and surrounding neighborhood. The *A. cuvieri* specimens were captured in Cambalache ( $N = 17$ ) and El Yunque ( $N = 2$ ) National Forests in Puerto Rico, and the *A. barahonae* specimens ( $N = 39$ ) were captured in the vicinity of Polo on the Barahona peninsula in the Dominican Republic. *Anolis baracoae* ( $N = 3$ ), *A. equestris persparsus* ( $N = 6$ ), *Anolis luteogularis* ( $N = 3$ ), *Anolis noblei* ( $N = 2$ ), *Anolis smallwoodi* ( $N = 6$ ), *Chamaeleolis barbatus* ( $N = 13$ ), *Chamaeleolis chamaeleonides* ( $N = 5$ ), *Chamaeleolis guamuhaya* ( $N = 6$ ), and *Chamaeleolis porcus* ( $N = 17$ ) specimens were measured in the private collection of Veronika Holanova and Jan Hribal in Prague, Czech Republic. Although *Chamaeleolis* should technically be merged with the genus *Anolis*, we will use the genus name *Chamaeleolis* to indicate members of this clade throughout the manuscript for the sake of clarity.

### Morphometrics

The snout–vent length (SVL) of all individuals was measured from the tip of the snout to the posterior edge of the anal scale; head length was measured from the back of the parietal bone to the tip of the upper jaw; head width was measured at the widest part of the head (at the level of the jugal bones); head height was measured just posterior to the orbits; lower jaw length was measured from the back of the retroarticular process to the tip of the lower jaw (Fig. 1). Bony elements used to delineate morphological segments could be detected easily through palpation. Additionally, three morphological variables (Fig. 1) reflecting the biomechanics of the jaw system were estimated by



**Fig. 1.** Picture of the head of an adult *Anolis cuvieri* to illustrate the morphometric data gathered. See Materials and methods for a detailed explanation. The circle represents the quadrato-mandibular joint.

measuring: (1) the distance from the jaw articulation to the tip of the lower jaw, and (2) the distance from the posterior edge of the jugal (as an indicator of the position of the coronoid) to the tip of the lower jaw. By subtracting distance (1) from the lower jaw length we calculated the length of the jaw in-lever for opening (i.e. distance from the articulation to the back of the retroarticular process where the jaw-opener muscles insert). Subtracting distance (2) from distance (1) gave the in-lever for jaw closing (i.e. the distance from the articulation to the coronoid where the jaw-closing muscles attach). Distance (1) from the articulation to the tip of the jaw is the jaw out-lever. All measurements were taken using digital callipers (Mitutoyo CD-20DC, Sakato, Japan; precision: 0.01 mm).

### Muscle mass

Jaw muscles were removed unilaterally in one adult male specimen of *A. cuvieri*, one adult female of *A. barahonae*, one adult and one juvenile of *A. garmani*, and one adult female and one hatchling of *C. chamaeleonides*. All specimens used for the analysis of muscle mass were preserved in a 10% aqueous formaldehyde solution for 24–48 h, depending on the size of the specimen. After fixation, specimens were rinsed in water and transferred to a 70% aqueous ethanol solution. The *Chamaeleolis* were preserved directly in a 70% aqueous ethanol solution. All specimens were kept in 70% ethanol for at least 2 months before dissection thereby assuring a similar degree of dehydration of tissue. All cranial muscle bundles were removed individually from specimens and stored in 70% ethanol until weighed. Muscles were blotted dry and weighed on a Mettler MT5 electronic balance (accuracy:  $\pm 0.01$  mg).

### Bite force

*In vivo* bite forces were measured using an isometric Kistler force transducer (type 9203, range  $\pm 500$  N; Kistler, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995A, Kistler, Switzerland; see Herrel et al. 1999, for a more detailed description of the setup). When the free end of the holder was placed between the jaws of the animal, prolonged and repeated biting resulted. The place of application of bite forces was standardized for all animals. Gape angle was standardized by moving the bite plates away from each other for larger animals. Measurements were repeated five times for each animal, with an inter-trial interval of at least 30 min. The maximal value obtained during such a recording session was considered to be the maximal bite force for that individual.

### Feeding behavior

Juvenile and adult *C. chamaeleonides*, *C. porcus*, *C. barbatus*, and *C. guamuhaya* as well as one adult *A. baracoae* were filmed with a Redlake Imaging MotionPro 500 camera set at 200 frames  $s^{-1}$  and a Sony camcorder while eating snails. Recordings were reviewed to identify bite positions and the way animals handled and crushed snails.

### Statistical analyses

All data were  $\log_{10}$ -transformed before analyses. To explore overall head shape differences between *Chamaeleolis* lizards and crown giants in general, we assembled a data set including all the species listed above. Data on head dimensions in these animals were recorded and used as input for a factor analysis. However, as head dimensions co-vary with body size, and the first factor would therefore be simply an indicator of overall size, all variables were regressed against snout–vent length and unstandardized residuals were saved. These were used as input for a factor analysis with Varimax rotation and factor scores were saved (Table 1). A multivariate analysis of variance was conducted on the factor scores to test for overall differences in head shape between *Chamaeleolis* lizards and *Anolis* crown giants.

Next, the data set was separated according to age and sex classes (including both *Anolis* and *Chamaeleolis*). For adults, comparisons of head dimensions and bite force were restricted to a comparison of the different *Chamaeleolis* species lumped together (due to limited within-species sample sizes) to *A. barahonae*. For juveniles, additional data on *A. cuvieri* and *A. equestris* were added to the data set to increase the sample size. Head

**Table 1.** Results of a factor analysis performed on the residual cranial morphometric data

Residual cranial morphometric data	Factor		
	1 (60.11)	2 (14.60)	3 (14.04)
Residual head length	<b>0.934</b>	0.004	-0.124
Residual head width	<b>0.839</b>	-0.235	-0.176
Residual head height	0.693	-0.149	-0.242
Residual lower jaw length	<b>0.968</b>	0.085	0.157
Residual out-lever	<b>0.972</b>	0.086	-0.141
Residual opening in-lever	-0.134	-0.016	<b>0.981</b>
Residual snout length	<b>0.919</b>	-0.306	-0.109
Residual closing in-lever	-0.078	<b>0.991</b>	-0.016

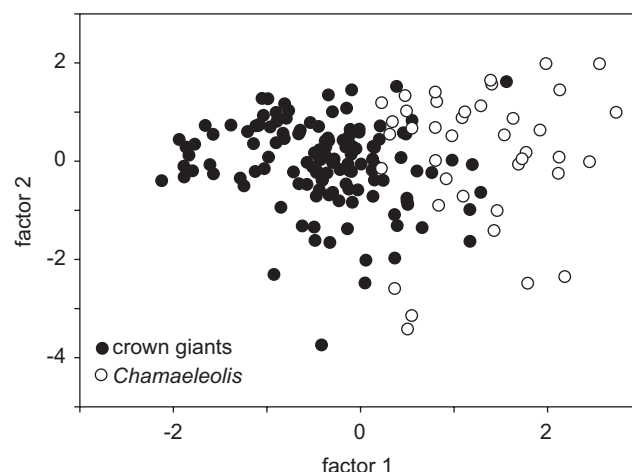
Loadings higher than 0.7 are indicated in bold. The percentage of variance explained by each factor is indicated in brackets.

dimensions and bite forces were compared between the two groups using analyses of co-variance. Stepwise multiple regression models within each sex and age class were run with  $\log_{10}$ -transformed bite force as the dependent variable and the  $\log_{10}$ -transformed morphometric variables as independent variables to explore which cranial variables best explained variation in bite force.

## Results

### Head shape

All head dimensions were highly correlated with snout–vent length (all  $P < 0.001$ ) across the entire data set as well as within groups. A factor analysis on the residual morphometric variables yielded three axes together explaining 88.7% of the variation in the data set. While the first factor was most strongly correlated with residual head length and residual head width, the second factor was determined by the residual in-lever for jaw closing and the third axis by the residual in-lever for jaw opening (Table 1). A MANOVA on the factor scores indicated significant differences between the two groups, one group containing all *Chamaeleolis* individuals and another one containing the crown giants (Wilks' lambda = 0.5,  $F = 55.62$ ,  $P < 0.001$ ; see Fig. 2). Subsequent univariate  $F$ -tests indicated that differences were significant on the first axis only ( $F_{1,169} = 162.63$ ,  $P < 0.001$ ) with *Chamaeleolis* lizards having significantly longer and wider heads. Stepwise multiple regression with residual bite force as independent variable and residual morphometric variables as dependent factors/variables yielded a model with residual head height as only predictor. Thus, lizards with relatively taller heads bite harder compared to their body size.



**Fig. 2.** Results of a factor analysis performed on the residual head measures. Note how the two groups are separated on the first factor indicating strong differences in head shape between *Chamaeleolis* and *Anolis* crown giants. Filled circles represent *Anolis* crown giants, and empty circles represent *Chamaeleolis* lizards.

As a MANOVA on the raw morphometric variables indicated significant differences between the sexes (Wilks' lambda = 0.71,  $F = 5.15$ ,  $P < 0.001$ ) and age classes (Wilks' lambda = 0.34,  $F = 30.35$ ,  $P < 0.001$ ), data were further analyzed by sex and age class separately.

### Bite force and head shape

A MANCOVA on the morphometric data for males indicated significant differences in head shape between *A. barahonae* and *Chamaeleolis* (Wilks' lambda = 0.13,  $F = 21.61$ ,  $P < 0.001$ ). Univariate ANCOVAs indicated that these differences were significant for all variables (Figs. 3 and 4) with the exception of the residual in-lever for jaw opening ( $F_{1,40} = 1.66$ ,  $P = 0.21$ ) and head height ( $F_{1,40} = 2.95$ ,  $P = 0.09$ ). In general, *Chamaeleolis* lizards had bigger heads than *A. barahonae*. A univariate analysis of variance indicated no differences in bite force between the two groups ( $F_{1,40} = 2.39$ ,  $P = 0.13$ ). Stepwise regression with bite force as independent variable yielded a significant model with head height and snout length as only predictors ( $r = 0.90$ ,  $P < 0.001$ ) indicating that male lizards with greater head height and longer snouts bite harder.

Results for females were similar to those for males; whereas a MANCOVA indicated significant differences in head shape (Wilks' lambda = 0.09,  $F = 9.55$ ,  $P = 0.002$ ), univariate ANCOVAs indicated that the in-lever for jaw opening was not different between *Chamaeleolis* and *A. barahonae* ( $F_{1,16} = 0.63$ ,  $P = 0.44$ ). As in males, female *Chamaeleolis* have relatively bigger heads than female *A. barahonae*. A univariate ANCOVA

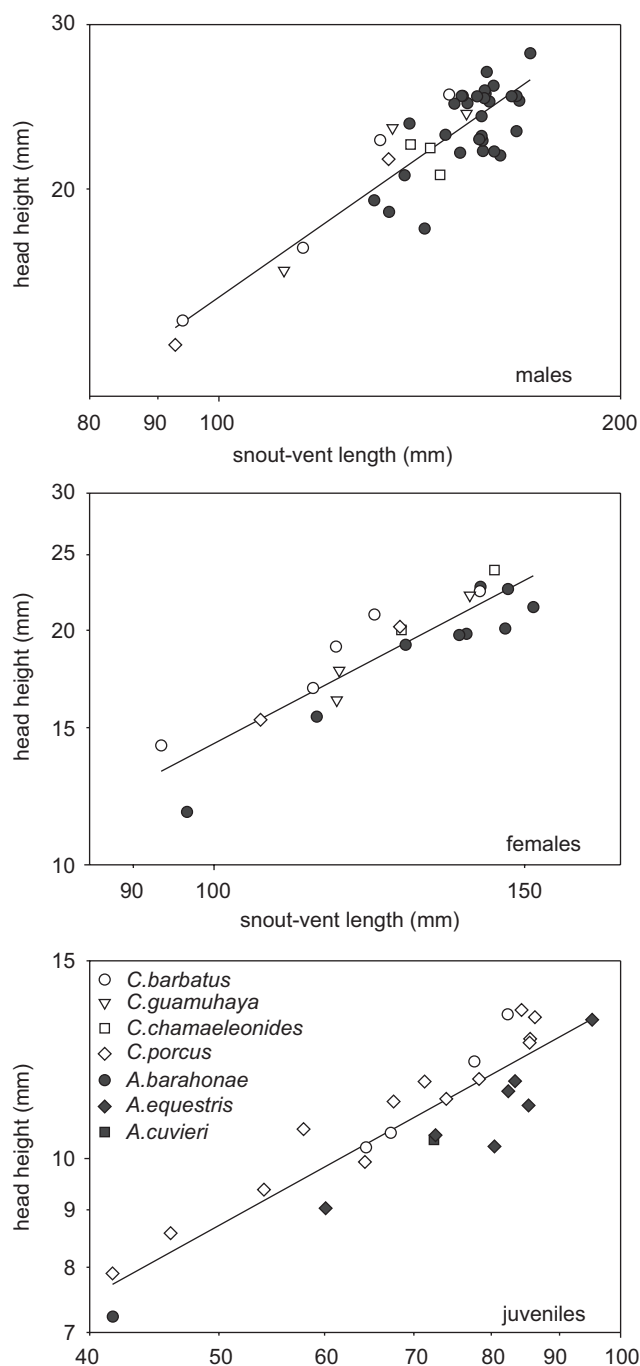
indicated that there were no significant differences in bite force between groups ( $F_{1,16} = 0.09$ ,  $P = 0.78$ ). Stepwise regression with bite force as independent variable and the morphometric variables as dependent factors yielded a significant model with head height as

only predictor ( $r = 0.82$ ,  $P < 0.001$ ) indicating that female lizards with greater head height bite harder.

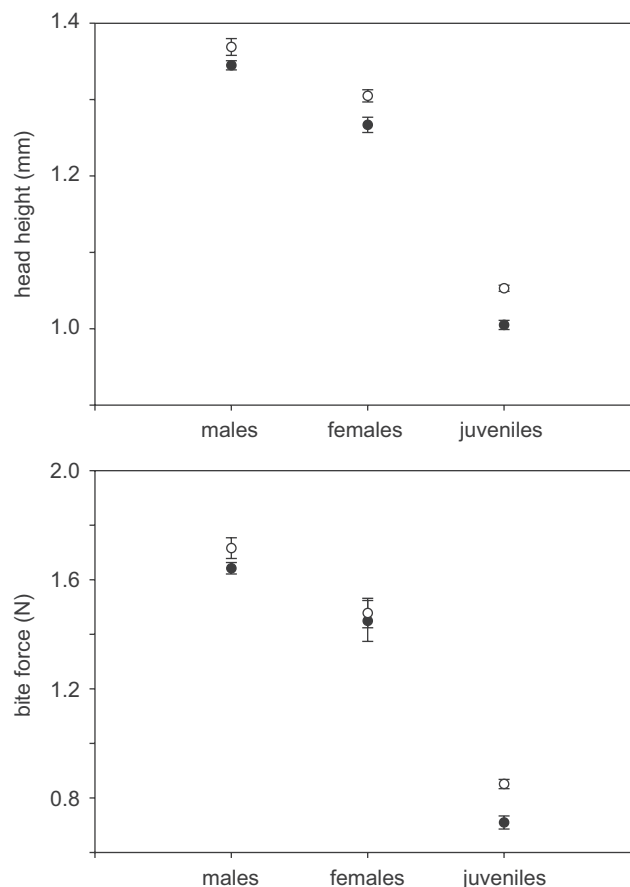
Juveniles of both groups were also significantly different in overall head shape (Wilks' lambda = 0.07,  $F = 22.87$ ,  $P < 0.001$ ). Subsequent ANCOVAs showed that differences were significant in all head dimensions (Figs. 3 and 4) with the exception of the in-levers for jaw opening ( $F_{1,23} = 0.03$ ,  $P = 0.86$ ) and jaw closing ( $F_{1,23} = 2.72$ ,  $P = 0.11$ ). In contrast to the data for adults, an ANCOVA on residual bite force demonstrated significant differences ( $F_{1,23} = 23.26$ ,  $P < 0.001$ ). Thus, juvenile *Chamaeleolis* have relatively bigger heads and also bite harder than *Anolis* crown giants. Stepwise multiple regression yielded a model with snout length as only predictor ( $r = 0.95$ ,  $P < 0.001$ ). Thus, juveniles with longer snouts bite harder.

### Cranial morphology

Inspection of the tooth rows in juvenile and adult *Chamaeleolis* indicates that in accordance with previous



**Fig. 3.** Plots of head height against snout–vent length for male (top), female (middle), and juvenile (bottom) lizards. Filled symbols represent *Anolis* crown giants, empty symbols represent *Chamaeleolis* lizards. Note how especially juvenile *Chamaeleolis* have much taller heads than *Anolis* crown giants. Different symbols represent different species. Note the log-scale on X- and Y-axes.



**Fig. 4.** Plots showing the adjusted means of the  $\log_{10}$ -transformed head height and bite force for adult males, adult females, and juveniles. Error bars represent one standard deviation. Filled circles: *Anolis* crown giants, empty circles: *Chamaeleolis* lizards.

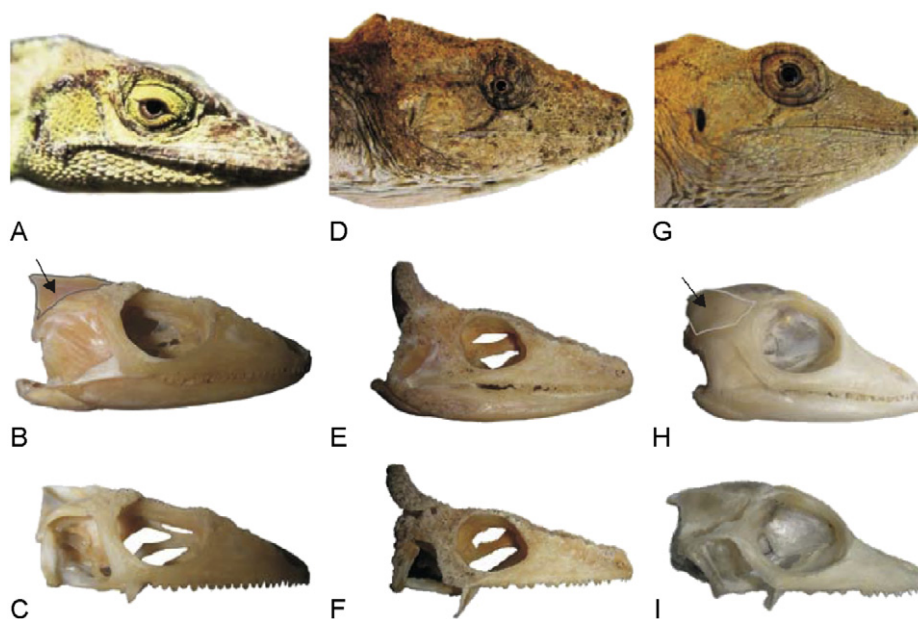
reports (Estes and Williams 1984) the tooth morphology changes from typical tricuspid anteriorly to blunt and molariform at the posterior part of the tooth row. None of the crown giants examined showed the presence of molariform teeth, neither in juveniles nor in adults. The cranial morphology of *Chamaeleolis* lizards changed dramatically throughout ontogeny. Whereas an open upper temporal window allowing the jaw adductors to bulge and attach to the parietal crest is typical of the skulls in juveniles, this window closes completely in adults (Fig. 5). In *Anolis* crown giants no marked changes in cranial morphology appeared to take place and the upper temporal window remains open throughout life (Fig. 5).

An analysis of the jaw closer muscle mass shows that juvenile *Chamaeleolis* lizards have a relatively large jaw adductor for their size compared to *Anolis* crown giants. Whereas a juvenile *C. chamaeleonides* with a head length of only 17.76 mm had a total adductor mass of 36.52 mg, *A. garmani* with a head length of 21.29 mm had a comparatively small adductor mass of 41.39 mg (Fig. 6). This is most pronounced in the extension of the musculus pseudotemporalis pars superficialis, which takes up most of the upper temporal window and attaches to the enlarged parietal crest. As a consequence

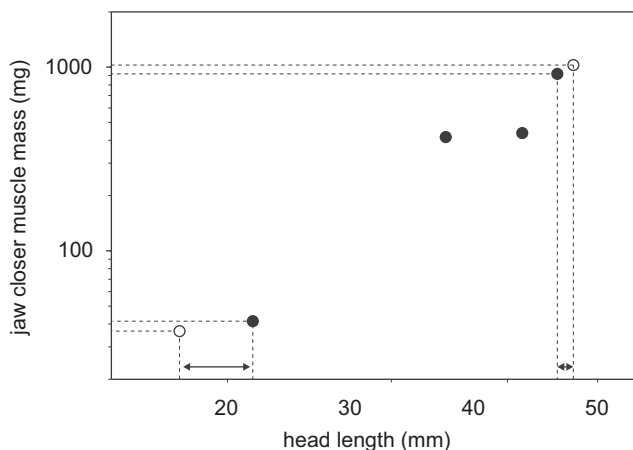
of the change in cranial morphology characterized by the closing of the upper temporal window, adult *Chamaeleolis* lizards do not have disproportionately large jaw adductors compared to closely related *Anolis* crown giants (Fig. 6).

### Feeding behavior

Both adult and juvenile *Chamaeleolis* readily approached snails when presented with them and picked them up from the substrate using their tongue. One-week-old juveniles already recognized and ate snails of appropriate size when presented with them (Fig. 7A). Hatchlings could not be tested due to the lack of snails small enough for feeding them. Snails were manipulated in the oral cavity and repositioned several times before being crushed. Crushing took place either unilaterally at the posterior aspect of one of the mandibles or bilaterally with the snails being positioned in between the tooth rows of the lower jaw (Fig. 7B). Multiple bites (five to six) were often used to crush the shell. Shell fragments were removed from the mouth by the tongue before swallowing. Animals were able to crush snails with a diameter of up to roughly half the length of the



**Fig. 5.** Photographs of the head and skull of a typical crown giant and a *Chamaeleolis* lizard. (A) Lateral view of the head of *A. cuvieri*; (B) lateral view of the jaw adductor musculature in *A. cuvieri*. Note how the jaw adductors run under the upper temporal bar and attach at the parietal crest (arrow); (C) lateral view of the skull of *A. cuvieri*; (D) lateral view of the head of *C. chamaeleonides*; (E) lateral view of the jaw adductor muscles in *C. chamaeleonides*. Note how the upper temporal window has been covered completely by the outgrowth of the parietal; (F) lateral view of the skull of *C. chamaeleonides*; (G) lateral view of the head of a juvenile *C. chamaeleonides*; (H) lateral view of the jaw adductor musculature in a hatchling *C. chamaeleonides*. In contrast to the adults, juveniles have an open temporal fenestra and pronounced parietal crest allowing for the attachment of the jaw adductors; (I) lateral view of the skull of a hatchling *C. chamaeleonides*. The arrows in (B) and (H) indicate the adductor musculature which can be seen bulging through the upper temporal window in both juvenile *C. chamaeleonides* and adult *A. cuvieri*. The window has been outlined to improve clarity.



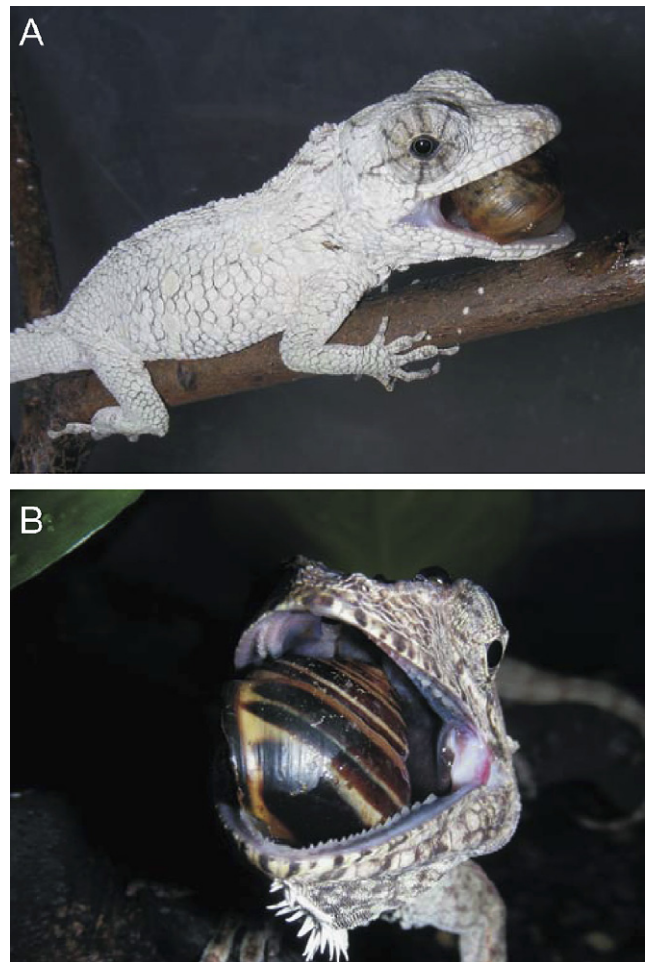
**Fig. 6.** Plot of jaw closer muscle mass against head length illustrating how juvenile *Chamaeleolis* lizards (empty symbols) have relatively large jaw adductors compared to *Anolis* crown giants (filled symbols) for their head size. This appears not to be the case for adults.

tooth row. One *A. baracoae* which was willing to eat a snail crushed the snail once at the posterior tooth row and swallowed it whole without removing the shell fragments.

## Discussion

The radiation of *Anolis* lizards has been characterized by recurrent adaptive changes in morphology in response to the invasion of novel niches (Losos et al. 1998). The demands imposed by the micro-habitats occupied have led to strong natural selection on limb morphology such that animals perform best in the habitat they live in (Irschick and Losos 1999). For example, although short-limbed anoles are relatively slow on all substrates, they perform relatively better on the narrowest perches (Losos and Sinervo 1989; Vanhooydonck et al. 2006; Calsbeek and Irschick 2007). Interestingly, it has recently been demonstrated that convergence in habitat specialists is not restricted to limb size and shape, but also occurs in other aspects of morphology such as sexual size dimorphism and head shape (Harmon et al. 2005). Although it has been suggested that the functional demands imposed by the prey (i.e. prey hardness and elusiveness) may select for certain head shapes (Herrel et al. 2006) in different sexes and age classes, it remains currently unknown which aspects of the trophic niche may select for convergence in head shape in different ecomorphs.

Our data for *Chamaeleolis* lizards show that they are morphologically different from closely related crown giants by having bigger and differently shaped heads. Given the supposed molluscivorous diet of *Chamaeleolis* lizards, it is tempting to interpret these head shape



**Fig. 7.** (A) Ten-day-old *Chamaeleolis porcus* eating a snail. (B) Adult *C. guamuhaya* crushing a snail in between the mandibular tooth rows.

differences as the result of natural selection for improved bite force capacity. Indeed, having longer and wider heads should allow for more jaw muscle and should thus increase bite force as has been demonstrated for lizards and other vertebrates that specialize on molluscs (Dalrymple 1979; Rieppel and Labhardt 1979; Pregill 1984; Fisher Huckins 1997; Herrel et al. 2002). However, our results are paradoxical as the difference in head morphology in adult *Chamaeleolis* is not translated into a difference in bite performance. Thus, these data would, at first sight, suggest that the observed changes in head size and shape are non-adaptive and may be the result of, for example, sexual selection on head size for display purposes. Juvenile *Chamaeleolis*, on the other hand, have bigger heads and do have bigger bite forces. This suggests that selection on bite force capacity may be stronger in juveniles.

Unfortunately, no ecological data on the diet of *Chamaeleolis* are available, and we can only speculate about the relative importance of hard prey such as snails in the diet of both juvenile and adult lizards. One



argument against the importance of snails in the diet of juveniles is the lack of molariform teeth, often considered crucial in allowing lizards to exploit hard and brittle prey (Estes and Williams 1984). However, behavioral experiments with just 1-week-old juvenile lizards indicate that they readily recognize and capture snails if presented with them. Moreover, and in contrast to other anoles that occasionally eat snails (e.g. *A. baracoae* will swallow snails whole and never remove shell fragments before swallowing), juvenile *Chamaeleolis* crush the snails and remove shell fragments from the mouth before swallowing. This suggests the presence of an innate behavioral pattern specifically associated with eating snails. Clearly, there is a great need for quantitative dietary data in these animals to verify the importance of snails in their diet (see also Estes and Williams 1984).

Interestingly, our data thus suggest that selection has operated on the juvenile life-history stages in *Chamaeleolis* lizards, resulting in large heads and large bite forces. Since adults do not differ in bite force from *Anolis* crown giants but do have larger heads this suggests that the adult phenotype may be the result of selection on juveniles. Adults have large bite forces in absolute terms which may allow them to crush snails without the need for an additional increase in head dimensions and bite force. Although adult crown giants do not appear to specialize on hard prey, they do eat relatively large prey such as other vertebrates and fruits (Brach 1976; Dalrymple 1980; Schwartz and Henderson 1991; Bowersox et al. 1994; Herrel et al. 2004; Holanová and Hribal 2005) and do include a significant proportion of hard prey such as large beetles into their diet (Herrel, personal observation). Our morphological data show why adult *Chamaeleolis* lizards do not bite harder than *Anolis* crown giants: the upper temporal window is completely covered by bone, thus preventing the jaw adductors from growing into that space. Juvenile *Chamaeleolis*, on the other hand, have an open temporal window, an enlarged parietal crest and a strongly hypertrophied m. pseudotemporalis. These features explain why juvenile *Chamaeleolis* lizards have stronger bites than juvenile *Anolis* crown giants. Why the upper temporal window is covered during ontogeny remains unclear at this point and needs to be investigated further.

In summary, our data suggest morphological and behavioral specializations of *Chamaeleolis* lizards to a diet of snails. As these lizards are cryptic, have short limbs and move about slowly, snails may be a profitable prey resource. As adult *Chamaeleolis* have large bite forces in absolute terms because of their large heads, hard prey such as snails are potential dietary items. Juvenile lizards in general, however, have small heads and thus low bite forces. In *Chamaeleolis*, selection appears to have operated on juveniles and has resulted in an increase in head size and bite force compared to closely related *Anolis* crown giants. This may provide

juvenile *Chamaeleolis* with a relatively unexploited dietary resource as most other small lizards are not able to crush these prey items. Interestingly, twig *Anolis* lizards such as *Anolis sheplani* also have a relatively strong bite force and appear to include hard prey into their diet (i.e. beetles; see Huyghe et al. 2007). Although it is tempting to interpret the presence of big heads and high bite forces as a convergent trait in slow moving and cryptic anoles, this needs to be tested. At least in *Chamaeleolis* lizards, the small size of juveniles appears to have led to strong selection on head size to increase bite force and to allow these animals to exploit a free niche. The adult phenotype in these animals, on the other hand, appears largely the result of selection on juveniles rather than adaptively related to diet.

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## References

- Beuttell, K., Losos, J.B., 1999. Ecological morphology of Caribbean anoles. *Herpetol. Monogr.* 13, 1–28.
- Bowersox, S.R., Calderon, S., Powell, R., Parmelee Jr., J.S., Smith, D.D., Lathrop, A., 1994. Nahrung eines Riesenanolis, *Anolis barahonae*, von Hispaniola, mit einer Zusammenfassung des Nahrungsspektrums westindischer Riesenanolis-Arten. *Salamandra* 30, 155–160.
- Brach, V., 1976. Habits and food of *Anolis equestris* in Florida. *Copeia* 1976, 187–189.
- Calsbeek, R., Irschick, D.J., 2007. The quick and the dead: locomotor performance and natural selection in island lizards. *Evolution* 61, 2493–2503.
- Dalrymple, G.H., 1979. On the jaw mechanism of the snail-crushing lizards, *Dracaena* Daudin 1802 (Reptilia, Lacertilia, Teiidae). *J. Herpetol.* 13, 303–311.
- Dalrymple, G.H., 1980. Comments on the density and diet of a giant anole *Anolis equestris*. *J. Herpetol.* 14, 412–415.
- Estes, R., Williams, E.E., 1984. Ontogenetic variation in the molariform teeth in lizards. *J. Vertebr. Paleontol.* 4, 96–107.
- Fisher Huckins, C.J., 1997. Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. *Ecology* 78, 2401–2414.
- Harmon, L.J., Kolbe, J.J., Cheverud, J.M., Losos, J.B., 2005. Convergence and the multidimensional niche. *Evolution* 59, 409–421.

- Hass, C.A., Hedges, S.B., Maxson, L.R., 1993. Molecular insights into the relationships and biogeography of West Indian *Anolis* lizards. *Biochem. Syst. Ecol.* 21, 97–114.
- Herrel, A., Spithoven, L., Van Damme, R., De Vree, F., 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* 13, 289–297.
- Herrel, A., O'Reilly, J.C., Richmond, A.M., 2002. Evolution of bite performance in turtles. *J. Evol. Biol.* 15, 1083–1094.
- Herrel, A., Vanhooydonck, B., Joachim, R., Irschick, D.J., 2004. Frugivory in polychrotid lizards: effects of body size. *Oecologia* 140, 160–168.
- 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*. *Biol. J. Linn. Soc.* 89, 443–454.
- 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. *Integr. Comp. Biol.* 47, 107–117.
- Holanova, V., Hribal, J., 2005. *Anolis baracoae*, the Baracoa Anole. *Reptilia* 40, 52–56.
- Huyghe, K., Herrel, A., Vanhooydonck, B., Meyers, J.J., Irschick, D.J., 2007. Microhabitat use, diet, and performance data on the Hispaniolan twig anole, *Anolis sheplani*. *Zoology* 110, 2–8.
- 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 Caribbean anoles. *Am. Nat.* 154, 293–305.
- Langerhans, R.B., Knouft, J.H., Losos, J.B., 2006. Shared and unique features of diversification in Greater Antillean *Anolis* ecomorphs. *Evolution* 60, 362–369.
- Leal, M., Losos, J.B., 2000. Behavior and ecology of the Cuban “chipojos bobos” *Chamaeleolis barbatus* and *C. porcus*. *J. Herpetol.* 34, 318–322.
- Leal, M., Knox, A.K., Losos, J.B., 2002. Lack of convergence in aquatic *Anolis* lizards. *Evolution* 56, 785–791.
- Lee, A.S., 1997. Cuba Natural. Pangaea, Saint Paul.
- Lee, A.S., 2003. Mi Libro de Lagartijas. Editorial Gente Nueva, Ciudad de La Habana.
- Lonnberg, E., 1903. On the adaptations to a molluscivorous diet in *Varanus niloticus*. *Arkiv Zool.* 1, 65–83.
- Losos, J.B., 1995. Community evolution in Greater Antillean *Anolis* lizards: phylogenetic patterns and experimental tests. *Philos. Trans. R. Soc. Lond. B* 349, 69–75.
- Losos, J.B., Sinervo, B., 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* 145, 23–30.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K., Rodriguez-Schettino, L., 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279, 2115–2118.
- Mertens, R., 1942. Die Familie der Warane (Varanidae). Teil 2. Schädel. *Abh. Senckenberg. Naturforsch. Ges.* 462, 1–391.
- Nicholson, K.E., Glor, R.E., Kolbe, J.J., Larson, A., Hedges, S.B., Losos, J.B., 2005. Mainland colonization by island lizards. *J. Biogeogr.* 32, 929–938.
- Poe, S., 2004. Phylogeny of anoles. *Herp. Monogr.* 18, 37–89.
- Pregill, G., 1984. Durophagous feeding adaptations in an amphisbaenid. *J. Herpetol.* 18, 186–191.
- Rieppel, O., Labhardt, L., 1979. Mandibular mechanics in *Varanus niloticus*. *Herpetologica* 35, 158–163.
- Rodriguez-Schettino, L., 1999. The Iguanid Lizards of Cuba. University Press of Florida, Gainesville.
- Rodriguez-Schettino, L., 2003. Anfibios y Reptiles de Cuba. Instituto de Ecología y Sistemática, Havana, Cuba.
- Schluter, D., 2000. The Ecology of Adaptive Radiation. Oxford University Press, Oxford.
- Schwartz, A., Henderson, R.W., 1991. Amphibians and Reptiles of the West Indies. University of Florida Press, Gainesville, FL.
- Vanhooydonck, B., Herrel, A., Irschick, D.J., 2006. Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. *J. Exp. Biol.* 209, 4515–4523.
- Williams, E.E., 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evol. Biol.* 6, 47–89.
- Wilson, E.O., 1957. Behavior of the Cuban lizard *Chamaeleolis chamaeleontides* (Dumeril and Bibron) in captivity. *Copeia* 1957, 145.