

# Patterns of morphological variation in the skull and cephalic scales of the lacertid lizard *Algyroides nigropunctatus*

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We applied a geometric morphometrics approach to examine sexual size and shape dimorphisms (SSD and SShD) in dorsal and ventral skull portions and cephalic scales (pileus) in the lacertid lizard *Algyroides nigropunctatus*. We found significant sexual dimorphism in all three structures that are mostly attributable to allometry. Males and females share allometric trajectories for the pileus and dorsal portion of the skull, i.e. the significant differences in shape between sexes are due to differences in size. Regardless of sex, allometric shape differences between small and large individuals show negative allometry in the anterior parts and more pronounced positive allometry of the parietal region in the dorsal skull and pileus. We observed a marginally significant divergence in sex-specific allometric trajectories of the ventral skull. The similar patterns of covariation between the ventral skull and the dorsal skull portion and pileus indicate close relationships between the skull bones and cephalic scales. The stronger covariation between the ventral and dorsal skull portion in males compared to females raises the question whether sexual dimorphism in the structure of morphological variation of the lizard skull exists.

**Key words:** allometry, cranium, geometric morphometrics, pileus, sexual shape dimorphism, sexual size dimorphism

## INTRODUCTION

The lizard skull is a form–function complex that has been subjected to many anatomical, morphological, phylogenetic and functional studies (e.g. Estes et al., 1988; Barahona & Barbadillo, 1998; Herrel et al., 1998; Herrel et al., 2001; Metzger, 2002; Metzger & Herrel, 2005; Stayton, 2005; Arnold et al., 2007). The functional morphology of the lizard skull has become an active field of investigation due to relatively new techniques and approaches (micro-CT data analysis, multibody dynamics and finite element analyses, and geometric morphometrics) that allow for more detailed information to be obtained (Herrel et al., 2007; Moazen et al., 2008a,b; Costantini et al., 2010). Lacertid lizards are suitable objects for such studies because sexual size dimorphism (SSD) and sexual shape dimorphism (SShD) in head size and head shape are common (e.g. Braña, 1996; Herrel et al., 1999; Verwaijen et al., 2002; Kaliontzopoulou et al., 2006; Aleksić et al., 2009), and lacertid lizards are characterized by distinct cephalic scales covering the dorsal surface of the head (pileus), which could serve as a visible external reference to underlying cranial elements as a result of functional and structural relationships between them. The cranial osteodermal layer develops alongside the underlying dorsal bones of the skull, and is closely attached to them. It is laid down in discrete portions, each corresponding to an epidermal scute (Arnold, 1989), and

it is therefore assumed that changes in the size and shape of the pileus may reflect changes in the underlying bones and muscular anatomy. A recent study has indicated that the patterns of sexual shape differences in the ventral aspect of the lacertid skull (Ljubisavljević et al., 2010) are similar to those previously found for the pileus (Bruner et al., 2005; Kaliontzopoulou et al., 2007), but statistical comparisons of patterns of morphological covariation between skull elements and the pileus are as yet lacking. Further research on the structural relationships and biomechanical interactions between cephalic bones and scales within the framework of morphological integration is of special interest (see also Costantini et al., 2010).

To explore the morphological covariation between cephalic scales and skull in line with SSD and SShD, we examined both dorsal and ventral portions of the skull and the pileus of *Algyroides nigropunctatus* (Dalmatian *Algyroides*). The genus *Algyroides* has long been recognized as an evolutionarily distinct clade of four well-differentiated species of small lacertid lizards with disjunct distributions in southern Europe (Harris et al., 1999; Arnold et al., 2007), despite recent evidence for paraphyly of the genus (Pavlicev & Mayer, 2009). The Dalmatian *Algyroides* is restricted to the Balkan Peninsula, usually occupying degraded scrub and rocky cliff areas along the coastal region of the Adriatic and Ionian Seas (Bejaković et al., 1996; Chondropoulos, 1997). Pronounced sexual dimorphism in body size (Bejaković et al., 1996) provides an opportunity

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to explore patterns of sexual size and shape dimorphism in the ventral and dorsal skull and pileus as well as the pattern of covariation between these structures.

The skeletal elements of the ventral skull that are formed by the upper jawbones and palate (parts of the dermatocranium) as well as the skull base (the neurocranium) are directly involved in the mechanics of feeding, affecting the bite force through connection to the jaw musculature (Herrel et al., 2007). Muscle forces also act upon the dermal bones of the skull roof (Haas, 1973), whose elements are mostly influenced by the development of the brain and the sensory organs they support. These skeletal elements and their connections, such as the frontoparietal suture, also have important roles in cranial kinesis and reducing stresses during biting and feeding (Moazen et al., 2008a, 2009). Numerous anatomical landmarks on both aspects of the skull and well-defined cephalic scales allowed us to obtain information on specific patterns of sexual dimorphism in the size and shape of the skull and cephalic scales. More specifically, we explored the possible sexual differences in allometric slopes of the pileus, the dorsal and ventral skull shape, and the pattern of covariation between these cephalic structures.

## MATERIALS AND METHODS

### Sample size, skull preparation and landmarks

A total of 24 male and 23 female *A. nigropunctatus* from the Herpetological Collection of the Natural History Museum of Montenegro in Podgorica were used in this study; the specimens were collected on the island of Bisage in Lake Skadar in Montenegro (42°06'N, 19°21'E) under permits provided by the Ministry of Tourism and Environmental Protection, Republic of Montenegro (nos. 01-1519/4 and UPI-145/1). The maturity of each specimen was determined on the basis of reproductive characterizations previously used in other lacertid species (see, for example, Tomašević-Kolarov et al., 2010).

The images of the pileus were taken prior to the clearing and staining process using a Sony DSC-F828 digital camera (resolution 8.0 MP) with the scale bar placed beside the pileus. The camera set-up and the placement of the specimens relative to the camera lens were kept constant to minimize image aberration due to parallax (distorted images resulted from placing the camera too close to the specimen) and to reduce error in the subsequent geometric morphometric analyses (Mullin & Taylor, 2002). The skulls were cleared with trypsin and KOH (potassium hydroxide), stained with Alizarin Red S to better distinguish cranial elements and their articulations (Dingerkus & Uhler, 1977), and preserved in glycerol. Images of skulls submerged in glycerol with the parietal (dorsal skull view) and palate (ventral skull view), positioned parallel to the photographic plane in the centre of the optical field to reduce and equalize distortion, were obtained with the same camera and scale settings. We used TpsDig2 software (Rohlf, 2005) to record 19 two-dimensional landmarks on the pileus, 14 two-dimensional landmarks on the dorsal skull and 18 landmarks on the ventral skull. Landmarks were digitized by the same person (A.U.) on the right side of each specimen to avoid redundant information in

symmetric structures. The landmarks were chosen based on their identification in all specimens and reliability in providing an adequate summary of the skull and pileus morphology (Fig. 1). The landmark configurations were chosen in accordance with previous studies of head and cranial size and shape variation in lacertid lizards (Bruner et al., 2005; Kaliontzopoulou et al., 2007; Ljubisavljević et al., 2010). The landmarks on two skull views generally represent contacts between bones, tips of processes, or maxima of curvature of structures, whereas those on the pileus are localized at the junction of scales and at the local curvature (Bookstein, 1991).

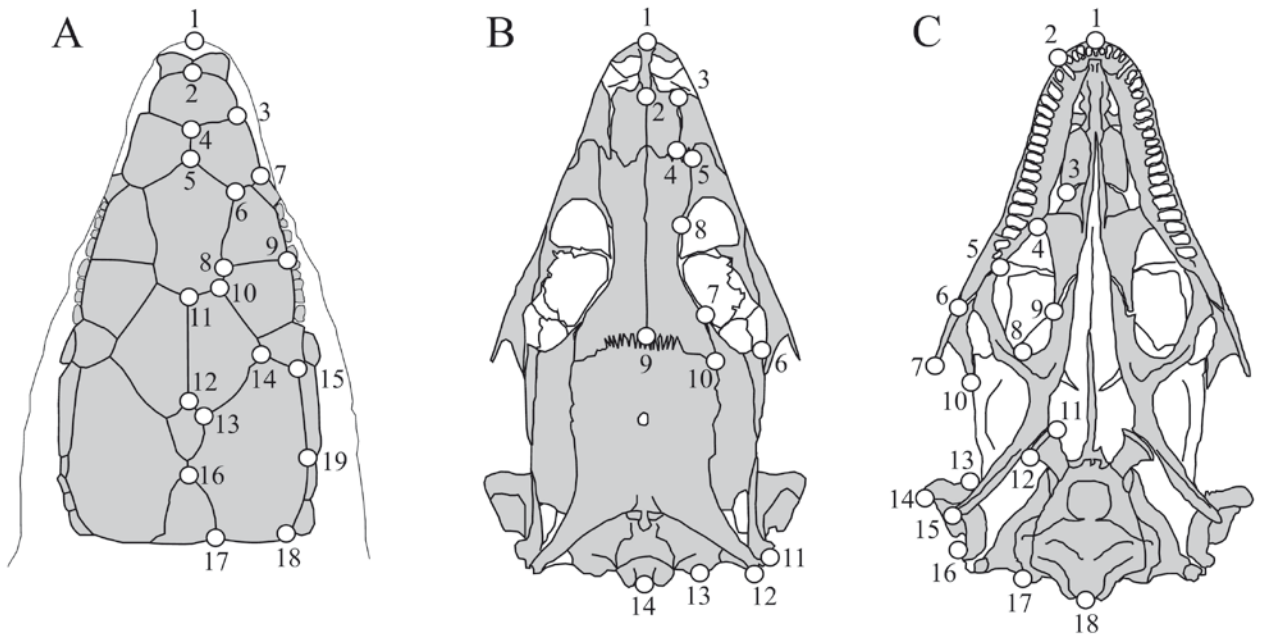
### Statistical analyses

A generalized Procrustes analysis (GPA) was applied to obtain a matrix of shape coordinates from which differences due to position, scale and orientation were removed (Rohlf & Slice, 1990; Bookstein, 1996; Dryden & Mardia, 1998). For the estimation of size, we used centroid size (CS), defined as the square root of the summed squared distances of each landmark from the centroid of the form (Zelditch et al., 2004). Centroid size is a geometric measure of size that is not correlated with shape in the absence of allometry (Bookstein, 1991).

Variation in size (CS) and the statistical differences in mean size between sexes were analysed using an ANOVA. To quantify the level of SSD, the standard index of SSD was calculated using CS values:  $I_{SSD} = \text{size of the larger sex (males)} / \text{size of the smaller sex (females)}$ .

Variation in pileus, dorsal and ventral skull shape between sexes were analysed by MANOVA on shape variables (partial warps and uniform components), which can be used as input variables in any conventional statistical analysis (Zelditch et al., 2004). The magnitude of differences in shape between sexes was quantified as Procrustes distances. The Procrustes distance, a linear measure of shape differences between landmark configurations, was used as an index of sexual dimorphism in shape ( $I_{SSHD}$ ). Procrustes distances were calculated between mean female and male landmark constellations for pileus, dorsal and ventral skull, and the TwoGroup6 program, IMP series (Sheets, 2000) was used to perform Goodall's *F* test to estimate the statistical significance of differences between the mean shapes. To explore size-dependent shape changes (allometric relations) between sexes, multivariate analysis of covariance (MANCOVA) on shape variables with sex as a factor and the CS as covariable was performed. A significant CS  $\times$  sex interaction indicates that sexes differ in the allometric slopes. To analyse allometric changes in shape between sexes, we used a multivariate regression of the shape variables on CS. The null hypothesis states that shape does not change with increase in size (CS). The statistical test of the null hypothesis and the percentage of variance explained by size were obtained using the tpsRegr program (Rohlf, 2009).

We applied partial least squares analysis (PLS) to explore covariation between three different structures (pileus, dorsal and ventral skull) described with three different sets of landmarks. The PLS analysis permits the comparison of two sets of shape data (Rohlf & Corti, 2000). This method has regularly been used to examine



**Fig. 1.** Definitions and numbering of landmarks. A) Pileus: 1) point of maximum curvature on the tip of the snout; 2) joint between the two supranasals and the internasal; 3) middle-posterior border of the internasal; 4) joint between the internasal and the two prefrontals; 5) joint between the frontal and the prefrontals; 6) joint between the frontal, prefrontal and the 2<sup>nd</sup> supraocular; 7) lateral joint of the 1<sup>st</sup> supraocular and the prefrontal; 8) joint between the two middle supraoculars and the frontal; 9) joint of the two middle supraoculars and the supraciliary granules; 10) joint between the frontal, frontoparietal and the 3<sup>rd</sup> supraocular; 11) joint between the frontal and the two frontoparietals; 12) joint between the interparietal and the two frontoparietals; 13) joint between interparietal, frontoparietal and the parietal; 14) joint between frontoparietal, parietal and the last supraocular; 15) lateral joint of the last supraocular and the parietal; 16) anterior joint between the occipital and the parietal; 17) posterior joint of the occipital and the parietal; 18) joint of the last supratemporal and the parietal; 19) maximum pileus width, on the parietal outline.

B) Dorsal skull: 1) tip of premaxilla (tip of the snout); 2) suture between premaxilla and nasals; 3) lateral-most point of nasal; 4) suture between nasal, frontal and maxilla; 5) suture between maxilla, prefrontal and frontal; 6) anterior-most point of postorbital; 7) anterior-most point of postfrontal; 8) posterior-most point of prefrontal; 9) suture between both frontals and parietal; 10) suture between frontal, postfrontal and parietal; 11) posterior-most point of squamosal; 12) posterior tip of supratemporal process of parietal; 13) posterior tip of exoccipital; 14) posterior-most point on the curve of the occipital condyle.

C) Ventral skull: 1) tip of premaxilla (tip of the snout); 2) suture between premaxilla and maxilla; 3) suture between vomer and palatine; 4) anterior-most point of subocular foramen; 5) anterior-most point of ectopterygoid; 6) posterior tip of maxilla; 7) lateral-most point of skull; 8) posterior-most point of subocular foramen; 9) suture between pterygoid and palatine; 10) posterior tip of jugal; 11) anterior tip of basipterygoid process; 12) posterior tip of basipterygoid process; 13) anterior-most point of quadrate; 14) lateral-most point of quadrate; 15) posterior tip of pterygoid process; 16) posterior point of quadrate; 17) posterior tip of oto-occipital; 18) posterior-most point on the curve of the occipital condyle.

covariation in the shapes of different structures to investigate morphological integration in anthropology (see Slice, 2007, and references therein). The null hypothesis is complete independence between the two sets of landmarks. We used the permutation test against the null hypothesis that these sets of landmarks varied independently. As an overall measure of association between the two blocks, the Escoufier index RV (Escoufier, 1973), a multivariate analogue of the squared correlation, was calculated (Klingenberg, 2009). Three different PLS

analyses were performed, and the coefficients were compared for both females and males. RV1 quantifies the covariation between the pileus and the dorsal skull, RV2 quantifies the covariation between the dorsal and ventral skull, and RV3 quantifies the covariation between pileus and ventral skull. The PLS analysis was performed using the MorphoJ program (Klingenberg, 2008–2009). All standard statistical procedures were performed using the Statistica® software package (STATISTICA for Windows; StatSoft, Inc., Tulsa, OK).

**Table 1.** Indices of sexual size dimorphism ( $I_{SSD}$ ) acquired by comparing centroid size (CS) of the pileus, dorsal and ventral skull between males and females. The statistical significance of difference in mean size between females and males was obtained by one-way ANOVA.

	$I_{SSD}$	Anova SS	$F$	$P$
Pileus	1.145	88.43	41.19	<0.0001
Dorsal skull	1.141	94.35	53.69	<0.0001
Ventral skull	1.158	113.03	55.82	<0.0001

RESULTS

For all three structures analysed (pileus, dorsal and ventral skull), significant sexual dimorphism in size was found (Table 1). The calculated SSD index (Table 1) shows that males are between 13% (for pileus and dorsal skull) and 14% (ventral skull) larger than females.

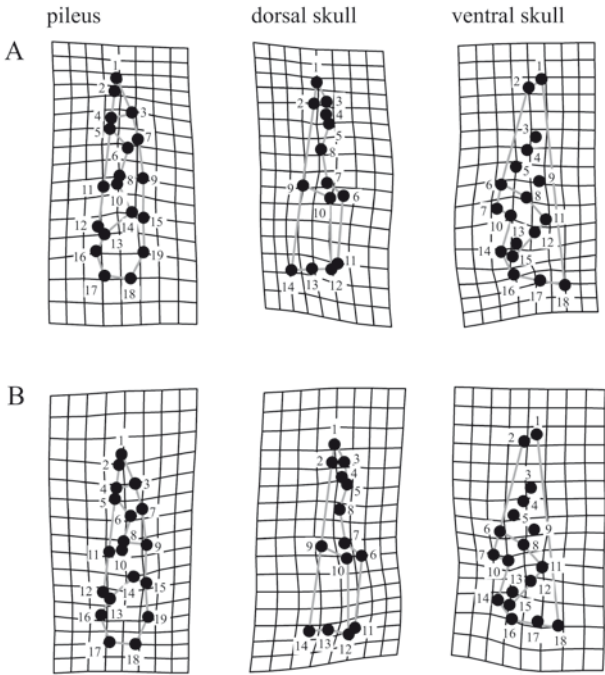
**Table 2.** Index of sexual shape dimorphism ( $I_{SShD}$ ) computed as Procrustes distance, a linear measure of shape differences between mean female and male landmark configurations for pileus, dorsal and ventral skull. The significance level of Goodall’s  $F$  test was obtained after 900 bootstrap iterations; df: degrees of freedom.

View	$I_{SShD}$	Goodall’s $F$	df <sub>1</sub> , df <sub>2</sub>	$P$
Pileus	0.027	11.41	34, 1530	<0.01
Dorsal skull	0.021	9.91	24, 984	<0.01
Ventral skull	0.036	31.62	32, 1440	<0.01

To analyse variation in shape between sexes, a MANOVA was performed. A significant variation in shape between the sexes for pileus (Wilks’ lambda = 0.06853844,  $F_{34, 12}=4.80$ ,  $P<0.01$ ), dorsal skull (Wilks’ lambda = 0.096599,  $F_{24, 22}=8.572711$ ,  $P<0.0001$ ) and ventral skull (Wilks’ lambda = 0.01677253,  $F_{32, 14}=25.64216$ ,  $P<0.0001$ ) was found. To quantify variation in shape between females and males, we calculated the Procrustes distances between the mean female and male shape separately for each of the head structures analysed. The sexual dimorphism indices ( $I_{SShD}$ ) are given as the Procrustes distances between the sexes (Table 2). The differences in mean shape between the sexes was statistically significant for all three structures (Table 2). We used the thin-plate spline (Fig. 2) to visualize these changes. The main changes in pileus shape between the sexes are rostral shortening (between landmarks 1 and 2), internasal elongation and narrowing (landmarks 2–4), shortening of the frontal area (landmarks 5, 6, 8, 10, 11), general enlargement of frontoparietal and parietal scales (landmarks 11–19) causing interparietal narrowing (between landmarks 12, 13 and 16), and lengthening of occipital scale (between landmarks 16 and 17) in males.

The main shape changes in the dorsal skull are also caused by general stretching and enlargement of the parietal, postorbital and postfrontal bones (landmarks 6, 7, 9, 10, 12). The squamosal is more posteriorly placed (landmark 11), with shortening of the snout (between landmarks 1 and 2), whereas the midface at the position of the nasal bones elongates and narrows (landmarks 2–4) in males. The changes in the ventral skull are related to shortening and widening of the skull base with quadrates more posteriorly placed in males compared to females (landmarks 13–18). The deformations obtained show the coordinated displacement of landmarks positioned on the palate (landmark 9), at the pterygoid (landmarks 8, 15), at the ectopterygoid (landmark 5) and at the basiptyergoid (landmarks 11, 12), as well as those at the jaw articulation point (landmarks 13, 14) and skull base (landmarks 17, 18). The shortening of the skull base in males is also evident from the dorsal skull view (landmarks 13 and 14).

Females and males shared common allometric slopes for the pileus and dorsal skull shape, while allometric slopes ( $CS \times sex$  interaction) for the ventral skull appeared



**Fig. 2.** Thin-plate spline grids that illustrate changes between mean shapes: females to males (A) and males to females (B) for the pileus, dorsal and ventral skull. For each sex, transformations of the reference shape were exaggerated three times. The outlines on the pileus grid define the relative position of head scales. Landmarks 9, 10 and 12 on the dorsal skull deformation grid define the parietal bone. Landmarks 6, 7, 8, 10, 11, 12, 14 and 15 on the ventral skull deformation grid define the jaw adductor muscle chamber.



**Table 3.** The allometric relations between sexes, tested by a multivariate analysis of covariance (MANCOVA). df: degrees of freedom; CS: centroid size. The significant CS × sex interaction indicates that allometric slopes of females and males diverge.

View	Effect	$\lambda_{\text{Wilks}}$	$F$	Effect df	Error df	$P$
Pileus	sex	0.111168	2.35	34	10	0.0758
	CS	0.063032	4.37	34	10	0.0086
	CS × sex	0.115296	2.26	34	10	0.0859
Dorsal skull	sex	0.451457	1.01	24	20	0.4937
	CS	0.079251	9.68	24	20	0.0001
	CS × sex	0.442759	1.05	24	20	0.4614
Ventral skull	sex	0.116677	2.84	32	12	0.0290
	CS	0.061460	5.73	32	12	0.0013
	CS × sex	0.132153	2.46	32	12	0.0495

to be of borderline significance (Table 3). As females and males share common allometric slopes for dorsal skull and pileus, we further explored the amount and the pattern of size-dependent shape changes. A multivariate regression of shape on CS was performed for both structures, revealing that shape changes were significantly correlated with changes in size (Table 4). Allometry explained over 20% of the shape variation. We used the thin-plate spline (Fig. 3) to visualize these changes, which were very similar between females (generally, specimens with smaller CS) and males (specimens with larger CS).

The morphological covariations between the pileus and the dorsal and ventral skull shape are high and statistically significant. Higher covariation between the ventral skull and the other two components appears in males, particularly between the two portions of the skull. Although the shape of the pileus largely corresponds to the underlying dermal skull bones, the covariation between these two structures is lower than the covariation between the pileus and ventral skull (both sexes) as well as between the dorsal and ventral skull portions (males, Table 5).

DISCUSSION

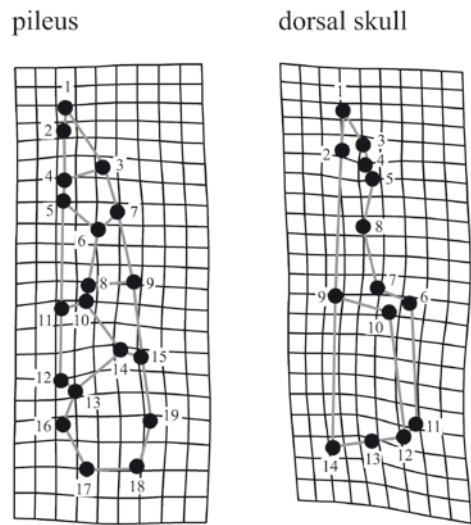
*Algyroides nigropunctatus* exhibits significant sexual dimorphism in the size and shape of the cephalic scales and in the dorsal and ventral skull portions, and the majority

of such differences is attributable to allometry. These results are in accordance with previous studies dealing with sexual dimorphism of head scales (Bruner et al., 2005; Kaliontzopoulou et al., 2007) and the ventral skull in other lacertid species (Ljubisavljević et al., 2010).

In *A. nigropunctatus*, allometric shape changes between individuals with smaller CS and individuals with larger CS in the dorsal skull are largely similar to the changes in the pileus, and correspond to differences between the sexes. Both structures exhibit an anteroposterior growth gradient, with a relative shortening of the anterior part of the skull roof and pileus and relative development of their posterior portions (Monteiro & Abe, 1997; Bruner et al., 2005). However, there are many spatially localized shape variations, which are probably caused by different developmental or functional patterns. Thus, the shape change of relative shortening of the anterior part (rostrum) and relative narrowing and elongation of the midface is particularly visible in the dermal bones, where the anterior part of the nasal bone is enlarged whereas its posterior part elongates and narrows with high intensity. The frontal area is shorter and wider in larger individuals. As the size of the skull increases, the anteriorly displaced mesokinetic joint (fronto-parietal suture) reduces the cranial kinesis, influencing the fronto-parietal scale, whose anterior part becomes relatively larger, and acting as a buffer to the stress produced by biting (Costantini et al., 2010).

**Table 4.** The significance of allometry and percentage of shape changes explained by size for pileus and dorsal skull.

View	$\lambda_{\text{Wilks}}$	$F$	Effect df	Error df	$P$	% explained	Goodall's $F$ test
Pileus	0.028470	12.044	34	12	0.0001	20.06	0
Dorsal skull	0.028650	31.078	24	22	0.0001	24.73	0



**Fig. 3.** Thin-plate spline grids that illustrate allometric shape changes. Transformations of the reference shape were given in the original (1.0) range. The outlines on the pileus grid define the relative position of head scales. Landmarks 9, 10 and 12 on the dorsal skull deformation grid define the parietal bone.

Finally, parietal and postorbital enlargement provides additional space for larger jaw adductor muscles, which consequently generate a higher bite force (Herrel et al., 1999, 2007; McBrayer & Anderson, 2007).

Our results reveal marginally significant divergence in the sex-specific allometric trajectories of the ventral skull. This finding indicates sex-specific divergence in the allometric slopes of the structure closely related to feeding and foraging, but requires confirmation from other lacertid species. The shapes of the pileus as well as the dorsal and ventral skull have a similar pattern of morphological covariation, suggesting that these structures do not vary independently. It is very likely that shape changes

**Table 5.** Results of PLS analysis. The RV coefficients and the permutation test against the null hypothesis of the independence between compared shapes. Number of randomization rounds = 10,000.

Shapes compared		Females	P	Males	P
Pileus/dorsal skull	RV1	0.4712	0.0153	0.4084	0.0267
Pileus/ventral skull	RV2	0.4882	0.0096	0.5617	0.0001
Dorsal skull/ventral skull	RV3	0.4348	0.0496	0.5515	0.0001

that correspond to relative compression of the braincase space and the widening of parietal and temporal regions allow the increased packing of jaw adductor musculature, which would allow the consumption of larger and harder prey and can be advantageous in male combats and in grabbing females during copulation (e.g. Verwajen et al., 2002; McBrayer & Anderson, 2007). This probably led to the stronger covariation between the ventral and dorsal skull structures than between cephalic scales and the skull roof, where close interactions such as stretching of the dermal elements due to displacement of the bones during modelling may induce somewhat smaller correspondence between them (Costantini et al., 2010). The stronger covariation between the ventral and dorsal skull structures in males than in females could indicate the possible existence of sexual dimorphism in the structure of morphological variation of the lacertid skull. Thus, integrative studies of the modularity and integration of the lacertid skull as well as of the functional and developmental relationship between dermal bones and scales are needed and should include a variety of lacertid taxa.

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