

Sexual dimorphism and allometry of the lacertid
Mesalina balfouri (BLANFORD, 1881),
endemic to the Archipelago of Socotra (Yemen)
(Squamata: Sauria: Lacertidae)

Geschlechtsdimorphismus und Allometrie der auf dem Sokotra-Archipel (Jemen)
endemischen Eidechse *Mesalina balfouri* (BLANFORD, 1881)
(Squamata: Sauria: Lacertidae)

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ABSTRACT

By means of both classical and geometric morphometric protocols, the authors analyzed sexual dimorphism and allometry of the head of the lacertid *Mesalina balfouri* (BLANFORD, 1881), endemic to the Archipelago of Socotra. As a result, males presented an isometrically bigger head in comparison to females, whereas sexual dimorphism was non-existent in body size and head shape. In addition, a clear ontogenetic change of the head shape emerged. Possible explanations of the observed transformations are discussed.

KURZFASSUNG

Die vorliegende Arbeit untersucht mit Mitteln der geometrischen und klassischen Morphometrie den Geschlechtsdimorphismus und die Kopf-Allometrien bei der auf dem Sokotra-Archipel endemischen Lacertide *Mesalina balfouri* (BLANFORD, 1881). Danach wiesen Männchen einen isometrisch größeren Kopf als Weibchen auf, doch war sonst kein Geschlechtsdimorphismus etwa in der Körpergröße und Form des Kopfes festzustellen. Allerdings waren deutliche ontogenetische Veränderungen der Kopfform nachweisbar. Mögliche Erklärungen zu den festgestellten Formveränderungen werden besprochen.

KEY WORDS

Reptilia: Squamata: Sauria: Lacertidae; *Mesalina balfouri*, allometry, sexual dimorphism, geometric morphometrics, morphology, Socotra, Yemen

INTRODUCTION

The Archipelago of Socotra (Yemen) which is globally recognized for its high endemism in its unique marine and terrestrial ecosystems was designated as a World Heritage Site in 2008 (UNESCO 2008). Reptiles include 27 endemic species (90%) out of the 30 inhabiting the archipelago (RAZZETTI et al. 2011). However, very little is known about the morphology and ecology of the Socotran herpetofauna, as most studies focus on species distribution and taxonomy (RÖSLER & WRANIK 1998, 1999, 2003, 2004, 2006; SINDACO et al. 2009; RAZZETTI et al. 2011).

Sexual dimorphism and allometry often prove to be correlated to many eco-

logical phenomena, and a large number of investigations clarified the role of the ecological niche and ethology in determining the shape, dimension and growth of the vertebrate's head (see for example SHINE 1989; JOHNSON et al. 2005; VINCENT & HERREL 2007).

The genus *Mesalina* (GRAY, 1838) includes 14 species ranging in the arid regions of North Africa (including the Sahara, northern Sahel, and the coasts along the Red Sea as far as Somalia), the whole Arabian Peninsula, the Socotran Archipelago, the Middle East (eastwards to Pakistan), and the southern portion of Turkmenistan (SINDACO & JEREMČENKO 2008).

Sexual dimorphism has been documented in few *Mesalina* species. For example, SCHLEICH et al. (1996) reported that sexes have different head/body dimension ratios, different body sizes, and different numbers of transversal scale rows in *M. guttulata* (LICHTENSTEIN, 1823), different body dimensions and hind limb lengths in *M. rubropunctata*, (LICHTENSTEIN, 1823), while males have the tail base flattened below in *M. olivieri* (AUDOUIN, 1829), or broader than

females in *M. simoni* (BOETTGER, 1881). No information about growth allometry exists for this genus.

In this paper, we focused on the endemic lizard *Mesalina balfouri* (BLANFORD, 1881), the only lacertid in Socotra Island. The patterns of allometry and sexual dimorphism are described in using both geometric as well as classical morphometric analyses; possible relationships between our results and the specific ecological features are analyzed.

MATERIALS AND METHODS

Specimens were sampled during four expeditions on Socotra between 2007 and 2010. For this study, we analyzed a total of 30 individuals (11 females and 19 males) from 12 different localities (Fig. 1). Individuals were sexed according to the presence (males) or absence (females) of an enlarged base of the tail (hemipenes pockets) and femoral pores. From all the specimens, snout-vent length (SVL) and head length (HL, from the tip of the snout to the posterior end of the occipital scale) measures (to the nearest 0.1 mm) were taken directly in the field using a caliper (precision 0.01 mm). Maximum head width (HW), however, was measured only in 19 specimens during the last expedition.

For each specimen, photographs of the dorsal head were taken using a digital photo camera (Nikon™ D300, resolution 4288 × 2848 pixels) under the following standardized conditions: The specimen was first laid on a solid flat plane and a reference length unit was placed near its head, and the camera lens axis was placed orthogonally to the horizontal plane of the specimen's head, and the same focal length and magnification ratio were used for all specimens.

Geometric morphometric analysis.- The images were analyzed following the Geometric Morphometric protocol (ADAMS et al. 2004): The positions of 20 landmarks were digitized (Table 1) by means of the software tpsDig2 [Thin Plate Spline Digitizer] (ROHLF 2008). Landmarks were placed only in the left side and on the midline of the head in order to avoid redundant information from symmetric structures (Fig. 2).

Procrustean transformations were conducted with the Relative Warps analysis software tpsRelW (Thin-plate spline Relative Warps, ROHLF 2008); W matrices (= partial warp scores matrices) consisting of 38 non-uniform components and 2 uniform components were obtained and Centroid Size (CS) of each specimen was calculated.

In order to find out whether head size differed between sexes, we used the analysis of variance (one-way ANOVA), in which CS was the dependent variable and sex the grouping factor.

Since shape variables in the W matrix exceeded the number of sampled specimens, variables could not be subjected to multivariate analysis. Therefore, we conducted a Principal Component Analysis (PCA) on the W matrix in order to obtain the Relative Warps (RW). Then, we used a linear model to determine the effects of gender, CS, and their interaction on the first three RWs. The models were simplified by removing non-significant terms (FARAWAY 2004).

Classical morphometrics analysis.- To test for potential sexual dimorphism in the head dimensions of this species, we compared SVL, HL, HW and HL/HW ratios between sexes using the t-test. Allometric differences between sexes were studied by an analysis of covariance (ANCOVA) in which HL or HW was the dependent variable, SVL the covariate and sex the grouping factor. All statistical analyses were performed with R 2.1.12 (R-DEVELOPMENT CORE TEAM 2009).

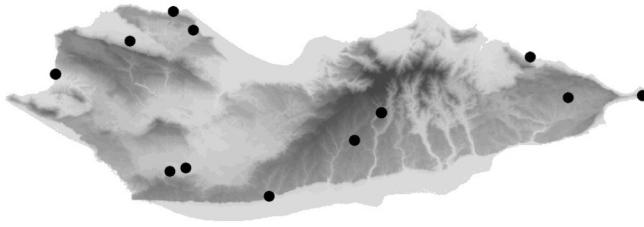


Fig. 1: The sample collection localities on Socotra Island.

Abb. 1: Die Aufsammlungsstellen des Untersuchungsmaterials auf Sokotra.

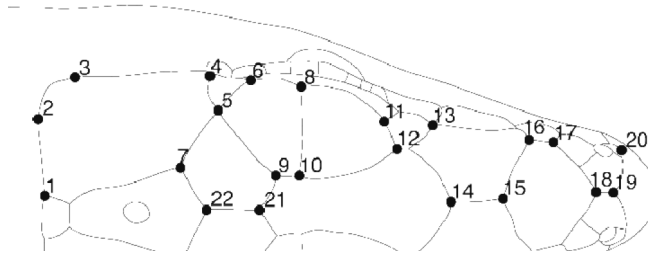
Fig. 2: Landmarks on the head of *Mesalina balfouri* (BLANFORD, 1881) (for their definition see Table 1).Abb. 2: Die Markierungspunkte auf dem Kopf von *Mesalina balfouri* (BLANFORD, 1881) (Definitionen siehe Tab. 1).

Table 1: Definition of the chosen landmarks on the left upper side of the head of *Mesalina balfouri* (BLANFORD, 1881) (for their position see Fig. 2).

Tab. 1: Definition der gewählten Markierungspunkte auf der linken Kopfoberseite von *Mesalina balfouri* (BLANFORD, 1881) (zu deren Lage siehe Abb. 2). Intersection - Kontaktpunkt.

Number in Fig. 2 Zahl in Abb. 2	Definition of landmark Definition des Markierungspunktes
1	Posterior intersection of occipital and left parietal
2, 3	Beginning and end of the curve of the left posterior edge of the left parietal
4	Left anterior angle of the left parietal
5	Intersection of left parietal and left frontoparietal
6	Lateral intersection of the two most posterior left supraoculars
7	Intersection of left parietal, left frontoparietal and interparietal
8	Lateral intersection of the two biggest left supraoculars
9	Intersection of frontal, left supraocular and left frontoparietal
10	Median intersection of the two biggest left supraoculars
11	Lateral intersection of the two most anterior left supraoculars
12	Intersection of frontal, left prefrontal and left supraocular
13	Intersection of prefrontal, first left supraocular and loreal
14	Intersection of frontal, right and left prefrontals
15	Intersection of frontonasal, right and left prefrontals
16	Lateral intersection of left prefrontal and frontonasal
17	Posterior intersection of left postnasal and frontonasal
18	Posterior intersection of the supranasals
19	Anterior intersection of the supranasals
20	Lateral intersection of left supranasal and rostral
21	Intersection of frontal and frontoparietals
22	Intersection of frontoparietals and interparietal

RESULTS

Geometric morphometric analysis

Analysis of Variance performed on the Centroid Size (CS) showed a pronounced sexual dimorphism, in that males had bigger heads than females ($F_{1,28} = 9.646, P = 0.004$).

The first three Relative Warps (RW) explained 57 % of the whole shape variance. The first and third RWs were neither significantly related with gender nor with CS (statistics not shown), whereas, a significant effect of CS on the second RW was evident

($F_{1,27} = 10.061, P = 0.004$). This result implies an allometric relationship between shape and size of the head, which elongates while growing (Fig. 3). No difference in the head shape was found between sexes.

Classical morphometric analysis

Classical biometric analysis confirmed that males had comparatively longer ($t_{27,12} = 3.346, P = 0.002$, Fig. 4) and wider ($t_{16,91} = 3.278, P = 0.004$) heads than females. By contrast, the SVL did not sig-

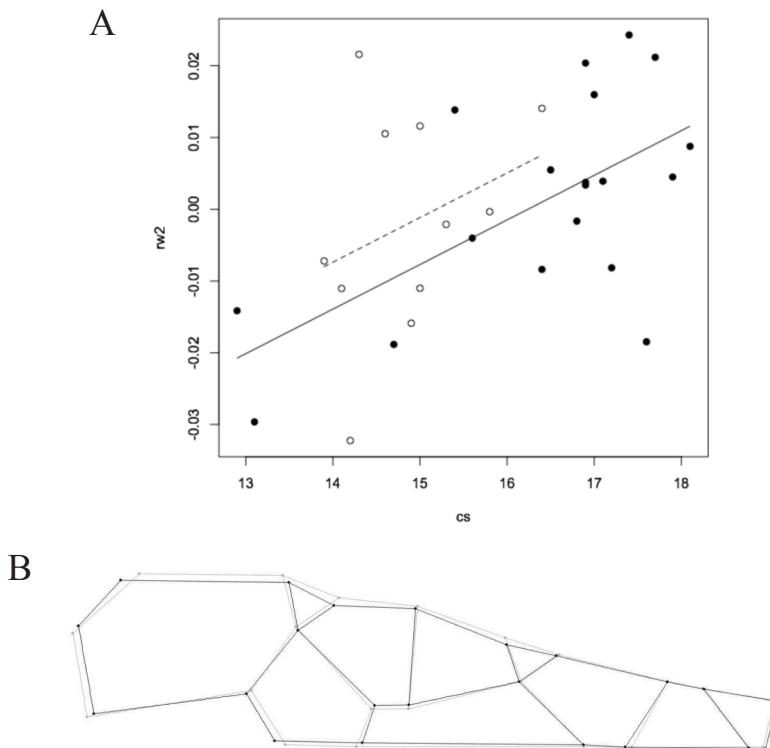


Fig. 3: A - Allometry plot (females: empty circles, regression line dashed; males: full circles, regression line continuous), and B - consensus mesh of small (gray) and big (black) specimens. CS - Centroid Size; RW2 - Second Relative Warp.

Abb. 3: Streudiagramm (A) zur Darstellung der Allometrie (Weibchen: leere Kreise und strichlierte Linie; Männchen: gefüllte Kreise und durchgehende Linie) und Konsens-Gitternetz (B) der kleinen (grau) und großen (schwarz) Exemplare. CS - Centroidsized (Größenkennzahl); RW2 - Second Relative Warp (Formvariable der Dimension 2).

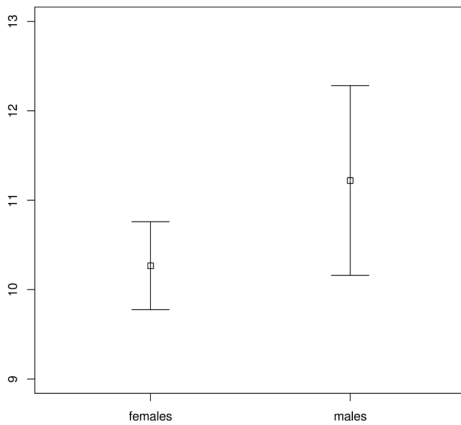


Fig. 4: Range of the head length (HL, mm) in 11 females and 19 males of *Mesalina balfouri* (BLANFORD, 1881).

Abb. 4: Die Spannweite der Kopflänge (HL, mm) bei 11 Weibchen und 19 Männchen von *Mesalina balfouri* (BLANFORD, 1881).

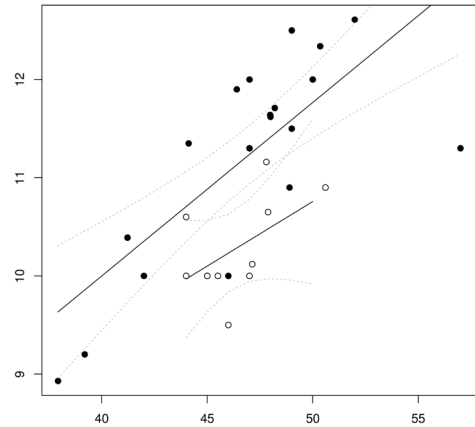


Fig. 5: Snout-vent length (SVL, mm) versus head length (HL, mm) of 19 males (full circles) and 11 females (empty circles) of *Mesalina balfouri* (BLANFORD, 1881). Linear regression lines and confidence limits are shown.

Abb. 5: Kopf-Rumpflänge (SVL, mm) gegen Kopflänge (HL, mm) bei 19 Männchen (gefüllte Kreise) und 11 Weibchen (leere Kreise) von *Mesalina balfouri* (BLANFORD, 1881). Regressionsgeraden und Konfidenzgeraden sind dargestellt.

nificantly differ between sexes ($t_{26,97} = 0.53$, $P = 0.60$) and the same was true for the ratio HL/HW ($t_{1,01}$, $P = 0.33$). Finally, ANCOVA revealed a significant effect of SVL on HL ($F_1 = 34.295$, $P < 0.0001$) and sex on HL ($F_1 = 12.329$, $P = 0.002$) and HW ($F_1 = 9.7860$, $P = 0.007$). No interaction was

found to be significant (statistics not shown). The results showed that (i) males had longer heads than females at the same SVL, and (ii) the intensity of this difference did not vary during ontogeny (Fig. 5). Moreover, males had comparatively wider heads than females.

DISCUSSION

This study shows that males of *Mesalina balfouri* have on average comparatively more massive, i. e., wider, and longer heads than females, but no difference between sexes was found for what concerns body size. In addition, a clear ontogenetic change of the head shape emerged. All above results were supported by both traditional and geometric morphometric analyses.

Moreover the study revealed (i) a significant allometric growth of the head, in which larger lizards developed dispropor-

tionately longer heads. The elongation of the bones of the hind portion of the head mainly accounted for this pattern. This ontogenetic change appears to be a common trait to most lacertid lizards (BRUNER et al. 2005), in which the bone-covering scales posterior to the frontoparietal cranial suture grow proportionally longer than those before it, as a consequence of the cranial ossification process. In fact, the parietals are the last bones to ossify and therefore it is in this region that the head growth can go on for a longer time (BARAHONA & BARBA-

DILLO 1998; BRUNER et al. 2005). Some studies related this phenomenon to a change of feeding habits during growth: for example HERREL & O'REILLY (2006) demonstrated positive allometry in bite force in relation to head size and a change in the structure of the jaw adductors; VINCENT et al. (2007) suggested that positive allometric growth of the head musculoskeletal system may not necessarily be a consequence of specific ontogenetic shifts in diet, but could be ancestral to all vertebrates. An enlargement of the parietal area of the head may be related to an elongation of the in-lever (*sensu* VINCENT et al. 2007) for the closing of the mandible, thus resulting in an improved bite force, possibly required by a changing diet. The hypothesis of an ontogenetic shift in diet may also be extended to *M. balfouri*, and specific studies on the diet variability among age classes could be used to test it.

A second result of this study is the sexual dimorphism in head size, with males showing isometrically larger heads than females. This difference may be related to bite strength, as suggested by recent studies. Moreover, some authors (MEYERS et al. 2002 for *Sceloporus undulatus* (BOSC & DAUDIN, 1801), *S. magisteri* HALLOWELL, 1854, *Aspidoscelis tigris* (BAIRD & GIRARD, 1852) and *A. burti* (TAYLOR, 1938); VERWAJEN et al. 2002 for *Podarcis melisellensis* (BRAUN, 1877) and *Dalmatolacerta oxycephala* (DUMÉRIL & BIBRON, 1839) highlighted the relations between head size and bite strength: the bigger the head, the more powerful and faster the bite. The presence of larger heads in males with respect to females is a common dimorphism among lizards (BRANA 1996) and it could be explained by three hypotheses (BULTE et al. 2008): (1) a selective advantage to those

individuals with the strongest bite, which are more likely to succeed in territorial fights, (2) a sexual advantage to those males which are the most capable of holding still females, by biting their flank, during mating, (3) the segregation of trophic and/or ecological niche between sexes may have selected a different masticatory apparatus between sexes. This dimorphism could also reflect a different allocation of energy between sexes after reaching sexual maturity. More specifically, sexual mature females may allocate energy in eggs production, thus reducing growth compared to males. This phenomenon, however, may only involve head dimensions because SVL dimorphism is both male- and female-biased (LJUBISAVLJEVIC et al. 2008). In fact, larger males could be advantaged in intra-sexual competition, while larger females could have a higher fertility (ANDERSSON 1994; BULTE 2008).

All of these hypotheses may be applied to *M. balfouri* and detailed studies on the ecology and sexual behavior of this species are needed in order to detect the selective pressure that may have determined this sexual dimorphism.

In addition, many studies on lacertids showed that the parietal (scales) area is allometrically bigger in males than in females and relate this to the more developed bite force in males. BRUNER et al. (2005) argued that dermal structures in lacertids are very sensitive to muscular tensions such as those caused by the jaw adductors and, therefore, could be used in a geometric morphometrics context, as indices for bite strength. Maybe our results do not show this widespread morphological change, due to the considerable allometric elongation of the parietals in *M. balfouri*.

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