Heterochrony in the evolution of *Podarcis* lizards (Lacertidae): insights from cranial osteology

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Heterochrony is widely accepted to be an important factor in lacertid lizards evolution. It was suggested that hypermorphosis (extension of growth along the same ontogenetic trajectory) is responsible for sexual dimorphism and interspecific morphological differences in *Podarcis* lizards. Paedomorphosis – truncation of growth – received less attention. *Podarcis erhardii* and *P. cretensis* are morphologically very similar to each other and were until recently regarded as conspecific. However, molecular analyses suggest that these two lineages diverged in the late Miocene, over 9 million years ago. Cranial osteology indicates that these species differ in several characters, despite lack of pronounced morphological differences. All of the studied *P. cretensis* specimens (collected at the Elafonisos island) show tripartite occipital condyle, low ascending process of the supraoccipital and an open parietal fossa. These are all characters seen in earlier ontogenetic stages of lacertids or adult specimens of paedomorphic taxa, such as *Acanthodactylus* and *Parvilacerta parva*, but they are absent in larger specimens of *P. erhardii*. Morphometric analyses suggest that sexual dimorphism of *P. cretensis* is less developed which may also be a result of paedomorphosis. Heterochrony could also play a role in the evolution of *P. hispanicus**. This is supported by the absence of median crest of the parietal and very slender posterior processes of the parietal in both sexes – characters which can be observed in some paedomorphic lacertids.

Key words: paedomorphosis, morphometrics, skull, sexual dimorphism

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1. Introduction

Heterochrony is commonly defined as a change in timing or rate of developmental processes. It is one of the most important factors driving the evolution of morphological variation. Heterochrony takes form of truncation (padeomorphosis) or extension (peramorphosis) of development and acts on both interspecific (phylogenetic) and intraspecific (tokogenetic) levels (e.g. Reilly et al. 1997). It commonly occurs in lizards, including *Podarcis* – a clade of small lacertids which underwent a rapid diversification in Miocene. It contains a number of species, many of which show high degree of intraspecific variation, thus making the group suitable for studying the role of development in evolution (e.g. Piras et al. 2011).

Figure 1. Map of the southern part of the continental Greece and the Aegean islands, showing location of Elafonisos (E) and Santorini (S). Modified from Lymberakis et al. (2008).

2. Material and methods

10 skulls of *Podarcis cretensis* (5 males, 5 females) and 10 skulls of *P. erhardii* (6 males, 4 females) have been examined. *P. cretensis* specimens originally came from the Elafonisos islet near Crete and *P. erhardii* – from Santorini in Cyclades (fig. 1). They were prepared by hand and using 0.2% KOH. *P. "hispanicus"* (in fact, *P. guadarramae* or *P. virescens*) specimens were collected in the vicinity of Madrid.

32 linear measurements were taken from skulls of *P. cretensis* and *P. erhardii* and log-transformed. Residuals regressed on SVL were subjected to a discriminant function analysis (DFA) which included also specimens of other species of *Podarcis* which were part of a broader study. These procedures have been conducted in SPSS Statistics 20.

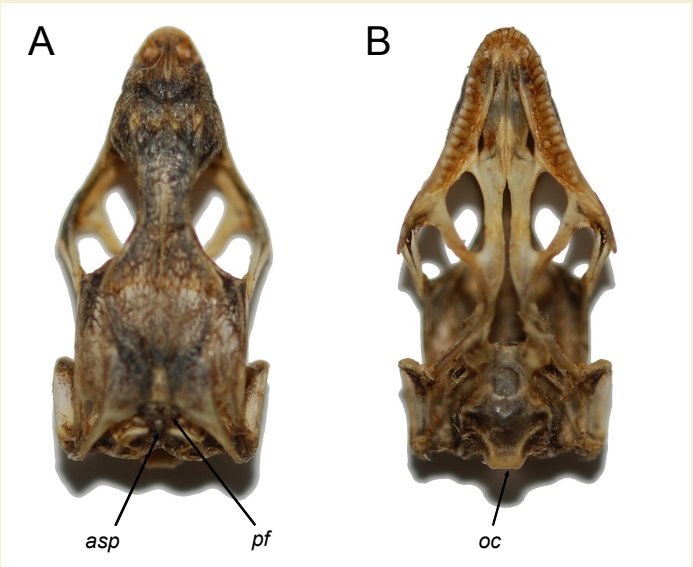

Figure 2. Skull of the male *P. cretensis* (NHMC 80.3.51.21) in dorsal (A) and ventral (B) view, with supraocular osteoderms removed. Abbreviations: *asp* – ascending process, *oc* – occipital condyle, *pf* – parietal fossa. Skull length from tip of the praemaxilla to the end of the occipital condyle is 14.45 mm.

3. Results and discussion

All examined specimens of *P. cretensis* show tripartite occipital condyle, low ascending process of the supraoccipital and open parietal fossa (fig. 2). The latter character is more poorly pronounced in smaller females, where anterior margin of the supraoccipital nearly meets the posterior margin of the parietal dorsally, almost closing the posttemporal fenestrae. These contrast with the condition seen in the largest individuals of *P. erhardii*, which have completely fused occipital condyle, high ascending process of the supraoccipital and closed parietal fossa but show similarities to juvenile and subadults of many lacertids (e.g. Barahona and Barbadillo 1998) and paedomorphic taxa such as some species of *Acanthodactylus* (e.g. Evans 2008) or *Parvilacerta parva* (Müller 2002). Both males and females of *P. "hispanicus"* lack crests on the ventral side of the parietal and have slender posterior processes of the parietal. These are also traits present in juvenile lacertids and *Parvilacerta parva* (Müller 2002).

DFA suggests that sexual dimorphism in *P. cretensis* is more poorly developed than in *P. erhardii*. In the latter, males and females are separated on both axes, while in *P. cretensis* they strongly overlap on the first axis (fig. 3). Similar situation occurs in many paedomorphic taxa, which exhibit poorly developed sexual dimorphism (e.g. Müller 2002).

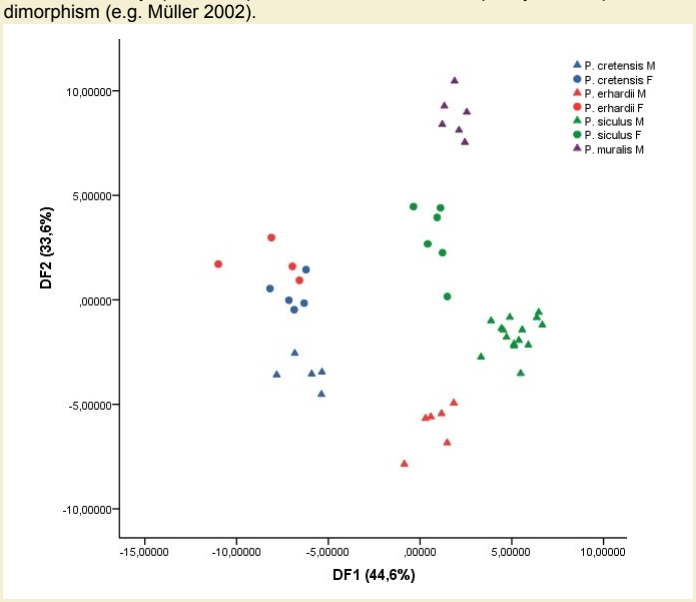

Figure 3. Discriminant function analysis performed on the linear measurements of the skull. Triangles represent males and circles represent females.

P. cretensis occur on Crete and many of its satellite islands. Elafonisos is one of the smallest islands inhabitated by these lizards (1.5 km^2). *P. cretensis* living there reach smaller average size than members of populations occurring on other islands (Wettstein 1953, Lymberakis et al. 2008). This is in contrast to *P. erhardii*, where small islands are generally inhabited by larger lizards (Donihue et al. 2015) and may suggest that *P. cretensis* follows different evolutionary strategy. Paedomorphosis may be one of the causes of small size of the individuals living on Elafonisos. It is yet unclear if the paedomorphic characters occur in the whole species or only in the population from Elafonisos. However, as both *P. peloponnesiacus* and *P. erhardii* (two species that phylogenetically bracket *P. cretensis* among taxa included in this study) show more developed condition, the traits seen in *P. cretensis* are probably apomorphic (fig. 4).

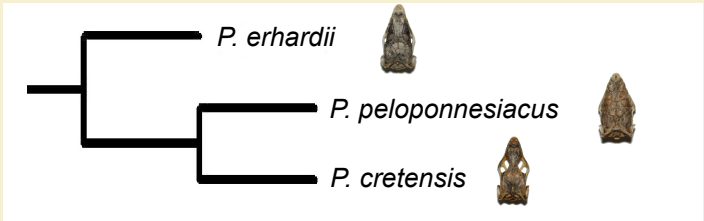

Figure 4. Phylogenetic relationships of the studied species (after Lymberakis et al. 2008). Skulls shown here belong to the largest males in the sample. Images are not to scale.

4. Conclusions

Heterochrony is an important factor in the evolution of *Podarcis* lizards. Besides hypermorphosis (Piras et al. 2011), paedomorphosis also seems to play role in at least some lineages. It may be one of the means of achieving smaller body size, for example in response to environmental pressures.

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