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Variability of pterygoid teeth in three species of *Podarcis* lizards and the utility of palatal dentition in lizard systematics

Tomasz Skawiński [1,*], Bartosz Borczyk [1] & Edyta Turniak [1]

[1] Department of Evolutionary Biology and Conservation of Vertebrates, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland.

[*] Corresponding author: tomasz.skawinski@uwr.edu.pl

ABSTRACT. Palatal dentition in lizards is incompletely known, especially data on its variability are scarce. We studied variation in the number of pterygoid teeth in three species of *Podarcis*, a species-rich genus of lacertid lizards: terrestrial, *P. siculus* and saxicolous, *P. erhardii* and *P. cretensis*. In contrast to some previous studies, we found no sexual dimorphism in the number of palatal teeth in any of these species. The number of teeth was not correlated to lizard size. In our sample, *P. cretensis* on average had more teeth than did *P. erhardii* but fewer than did *P. siculus*. In addition, some specimens of *P. cretensis* and *P. siculus* showed asymmetry in the number of pterygoid teeth, which may be a result of anthropogenic pressure. The observed variability in the occurrence of palatal dentition illustrates the importance of scoring this character in phylogenetic analyses only on the basis of a sufficient sample.

KEYWORDS. Heterochrony, paedomorphosis, peramorphosis, cryptic species, morphology.

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Introduction

Palatal dentition occurs frequently in squamate reptiles – it is present in at least some members of most family-level lizard clades, but is relatively poorly known when compared to marginal dentition. In lizards, teeth may be present on palatine, vomer and, most commonly, pterygoid bones. In lacertids, a large group of Old World lizards, the only tooth-bearing palatal bones are the pterygoids (Mahler & Kearney 2006). However, many members of that clade (such as *Zootoca vivipara*, *Algyroides marchi*, *Iberolacerta* spp. and some species of *Podarcis*) have no pterygoid teeth (e.g., Barahona & Barbadillo 1997), while in many others (such as *Algyroides moreoticus*, *A. nigropunctatus* and some other *Podarcis* species) this trait shows intraspecific variation (Mahler & Kearney 2006).

In lacertid ontogeny, palatal dentition develops later than do marginal teeth (Barahona & Barbadillo 1998). Generally, pterygoid teeth are regarded as a trait occurring in large lacertids (e.g., Arnold 1989; Barahona & Barbadillo 1998; Costantini *et al*. 2010) and in taxa with robust skulls (Arnold *et al*. 2007). This robustness is probably a result of peramorphosis, as is a sexual dimorphism in these lizards (Piras *et al*. 2011). Thus, presence of a well-developed palatal dentition should be expected especially in larger species and in males. *Podarcis* is a diverse genus of lacertid lizards that includes over 20 species with different morphologies (slender and robust) and different ecologies such as saxicolous or terrestrial (e.g., Arnold *et al*. 2007). Pterygoid dentition in *Podarcis* lizards has been described by several authors (e.g., Klemmer 1957; Arnold 1973; Barahona & Barbadillo 1997), but quantitative data on its variability are mostly lacking or based on very limited samples for many species (Mahler & Kearney 2006; Costantini *et al*. 2010). Therefore, any conclusions about relative frequency of pterygoid teeth among *Podarcis* lizards must be regarded as tentative.

Our aim was to assess the variability of pterygoid teeth in several species of *Podarcis* lizards and the utility of this character in lizard systematics. We also tested expectations about greater frequency of the palatal dentition in larger species and in males.

Material and methods

Presence and number of pterygoid teeth were recorded from a total of 41 specimens from three species of lizards of the genus *Podarcis*: *P. siculus* (n = 21), *P. erhardii* (n = 10) and *P. cretensis* (n = 10). *Podarcis siculus* is a large, terrestrial species while *P. erhardii* and *P. cretensis* are somewhat smaller and are more saxicolous (Arnold *et al*. 2007). To our knowledge, palatal dentition has not previously been described in *P. cretensis*. Specimens of *P. siculus* are deposited in the Museum of Natural History, University of Wrocław, and were obtained from the Wrocław Zoo in the 1930s (unfortunately, labels indicating place of their origin were destroyed during World War II). Specimens of *P. erhardii* and *P. cretensis* were obtained from the Natural History Museum of Crete. The former were collected at the Santorini island in the Cyclades and the latter at the island of Elafonisos near Crete. Snout-vent length (SVL) of each specimen was measured to the nearest millimetre (Table 1). The sample size may seem low, but in osteological studies of lizards the most common number of examined specimens is one (Bell & Mead 2014). Potential differences between sexes and species in number of pterygoid teeth (on both bones) were analysed using Mann-Whitney U-test (U) and potential correlation between size (i.e., SVL) and number of palatal teeth using Pearson correlation (r). One specimen of *P. siculus* with one pterygoid missing was excluded from the tests. All analyses were performed in IBM SPSS Statistics 20.

Podarcis siculus and *P. erhardii* are lizards widespread in the Mediterranean, the former especially in Italy and coastal parts of the Western Balkans, the latter in the South-Eastern Balkans and many Aegean islands. *Podarcis cretensis* is an endangered species endemic to Crete and its satellite islands. Until recently it was regarded as conspecific with *P. erhardii* (Lymberakis *et al*. 2008).

Results

In the examined specimens of *P. siculus* palatal teeth were common, occurring in 17 of 21 specimens (80.95%); they were present in five of six females (83.33%), at about the same frequency as in males (12 of 15; 80%). Moreover, quite commonly smaller individuals had more teeth than did the larger ones (Table 1). Teeth on at least one of the pterygoids were present in all specimens of *P. cretensis*, including the smallest lizard in the sample (SVL = 46 mm), while they were very rare in *P. erhardii*, being present in only one specimen (the largest male).

In all examined specimens the pterygoid teeth were small, monocuspid and arranged more or less in a single, longitudinal row.

Asymmetry in number of pterygoid teeth, i.e., difference in number of teeth on left and right pterygoid, was present in eleven specimens of *P. siculus* (55% of all individuals and 68.75% of those that had palatal teeth) and four specimens of *P. cretensis* (40%). In two individuals of the latter species, palatal teeth were present on one pterygoid but absent on the other.

There is no sexual dimorphism in number of pterygoid teeth in either of the sampled species (*P. siculus*: $U = 36.5$, $p = 0.936$; *P. cretensis*: $U = 10$, $p = 0.667$; *P. erhardii*: $U = 10$, $p = 1$). *Podarcis cretensis* had more pterygoid teeth than *P. erhardii* ($U = 3$, $p < 0.0001$) but fewer than *P. siculus* ($U = 47.5$, $p = 0.019$).

TABLE 1

Biometrical data of the examined lizards.

Species	Specimen number	Sex	SVL [mm]	Left pterygoid [number of teeth]	Right pterygoid [number of teeth]
P. siculus	siculus1	M	62	1	4
P. siculus	siculus2	M	58	2	2
P. siculus	siculus3	M	59	6	6
P. siculus	siculus4	M	64	4	3
P. siculus	siculus5	M	63	1	2
P. siculus	siculus6	F	64	4	2
P. siculus	siculus7	M	66	0	0
P. siculus	siculus8	M	70	3	3
P. siculus	siculus9	M	64	0	0
P. siculus	siculus10	M	56	2	1
P. siculus	siculus11	F	58	4	2
P. siculus	siculus12	M	63	0	0
P. siculus	siculus13	M	63	2	1
P. siculus	siculus14	F	58	2	2
P. siculus	siculus15	F	60	2	3
P. siculus	siculus16	M	66	4	3
P. siculus	siculus17	M	65	7	7
P. siculus	siculus18	M	59	3	4
P. siculus	siculus19	M	59	0	1
P. siculus	siculus20	F	61	?	4
P. siculus	siculus21	F	57	0	0
P. erhardii	erhardii1	M	61	0	0
P. erhardii	erhardii2	M	63	0	0
P. erhardii	erhardii3	M	59	0	0
P. erhardii	erhardii4	F	63	0	0
P. erhardii	erhardii5	M	58	0	0
P. erhardii	erhardii6	M	68	3	3
P. erhardii	erhardii7	F	52	0	0
P. erhardii	erhardii8	M	62	0	0
P. erhardii	erhardii9	F	57	0	0
P. erhardii	erhardii10	F	60	0	0
P. cretensis	NHMC 80.3.51.16	M	56	5	5
P. cretensis	NHMC 80.3.51.18	M	51	5	0
P. cretensis	NHMC 80.3.51.21	M	58	4	6
P. cretensis	NHMC 80.3.51.22	M	55	6	5
P. cretensis	NHMC 80.3.51.24	F	49	4	4
P. cretensis	NHMC 80.3.51.28	F	49	4	4
P. cretensis	NHMC 80.3.51.31	F	46	4	4
P. cretensis	NHMC 80.3.51.34	M	54	3	0
P. cretensis	NHMC 80.3.51.35	F	54	2	2
P. cretensis	NHMC 80.3.51.36	F	49	5	5

Podarcis erhardii had fewer teeth than *P. siculus* ($U = 31.5$, $p = 0.001$). There is no correlation between size (SVL) and number of pterygoid teeth in *P. siculus* ($r = 0.128$, $p = 0.591$) and *P. cretensis* ($r = 0.086$, $p = 0.813$). In *P. erhardii* palatal dentition was present in only one sampled specimen, so a correlation test was not performed for this species.

Discussion

Morphology and arrangement of the palatal teeth in the three species we examined are identical to those described for other lacertids (Mahler & Kearney 2006). Pterygoid teeth appear relatively late in lacertid ontogeny and occur most commonly in taxa of large size (Barahona & Barbadillo 1998). Therefore, it may be predicted that pterygoid teeth are more common in taxa (or individuals) with peramorphic skulls, as hypothesised by Costantini *et al*. (2010). In *Podarcis* lizards, hypermorphosis, a subtype of peramorphosis, where the growth is extended along the same ontogenetic trajectory (Reilly *et al*. 1997), probably played an important role in shaping the morphological diversity of that clade, both at inter- and intraspecific levels (Piras *et al*. 2011). *Podarcis siculus* is one of the largest species of *Podarcis*, growing up to about 90 mm in snout-vent length but usually smaller (Arnold & Ovenden 2002). Despite that, Costantini *et al*. (2010) found no pterygoid teeth in any of the six *P. siculus* specimens examined, yet these teeth were present in the larger *Lacerta bilineata*. This led the authors to speculate that the presence of palatal dentition may be a species-specific trait of *L. bilineata* (among sampled species, i.e., also *P. siculus* and *P. muralis*) or is a result of allometric extension of growth (Costantini *et al*. 2010). The former hypothesis is falsified by the literature data that show that some *P. siculus* individuals have pterygoid teeth (Klemmer 1957; Mahler & Kearney 2006). These authors found pterygoid dentition in 10 of 33 (30.30%) and 1 of 3 (33.33%) of the specimens examined, respectively. This discordance may be a result of large morphological variation of *P. siculus* (e.g., Urošević *et al*. 2012). Data from Klemmer (1957) give some support to the latter hypothesis of Costantini *et al*. (2010); they show that males, which have peramorphic skulls (Piras *et al*. 2011), on average have more teeth on pterygoids than do females. However, our observations on *P. siculus* and two species from Greece disagree with that, showing no sexual dimorphism in number of pterygoid teeth. Also, most of the specimens of *P. siculus* with no palatal dentition were not the smallest in the sample (Table 1). The specimens of *P. erhardii* were generally larger than the sampled specimens of *P. cretensis*, yet pterygoid teeth were ubiquitous in the latter and very rare in the former. Similar results were obtained by Klemmer (1957) who found palatal dentition only in the largest male of six specimens of *P. erhardii* from Macedonia. Moreover, the smallest of all sampled lizards (a female *P. cretensis*, with SVL = 46 mm) had more pterygoid teeth than all specimens of *P. erhardii* and most of *P. siculus*. This may be surprising given the fact that *P. cretensis* from Elafonisos are hypothesised to be paedomorphic and attain smaller size than do *P. erhardii* (Skawiński *et al*. 2015, in prep.). However, a similar situation is present in *Acanthodactylus*, which also has a paedomorphic skull (Evans 2008) but often with palatal dentition (Barahona & Barbadillo 1997). Thus, the common presence of pterygoid teeth in *P. cretensis* may be a retained ancestral trait, as such teeth are also ubiquitous in *P. peloponnesiacus* (Klemmer 1957; T. Skawiński, pers. obs.), probably its sister species (Lymberakis *et al*. 2008).

It is not uncommon that younger animals attain greater size than the older ones (e.g., Borczyk & Paśko 2011; Petermann *et al*. 2017). Thus, the immaturity of the specimens of *P. erhardii* could explain the lack of palatal dentition in all but the largest lizard. However, at least several of them exhibit skull characters that are typical for adult lacertids (Barahona & Barbadillo 1998; Skawiński *et al*., in prep.). This, combined with data from Klemmer (1957), suggests that pterygoid teeth are indeed rare in this species.

Pterygoid teeth are common in insectivorous lizards and may enhance holding and processing live prey (Montanucci 1968; Mahler & Kearney 2006). Both *P. cretensis* and *P. erhardii* are mainly insectivorous but may also include carcasses (Delaugerre *et al*. 2012), eggs or fruits in their diet

(BROCK *et al*. 2014). Further studies could explain whether differences in the frequency of the palatal dentition between these two species reflect differences in their diets.

Individual asymmetry in number or presence of pterygoid teeth is not uncommon in *Podarcis* lizards (KLEMMER 1957; see above). Such asymmetry may reflect disturbances in the *Sonic hedgehog* pathway, which regulates formation of palatal dentition in lizards (RICHMAN & HANDRIGAN 2011). A common cause of the fluctuating asymmetry is anthropogenic pressure, which is a probable cause of asymmetry in the number of femoral pores, subdigital lamellae and supraciliary granules in *P. muralis* (LAZIĆ *et al*. 2013). *Podarcis cretensis* is threatened mainly by tourism, urbanisation and degradation of habitats (LYMBERAKIS 2009). This may be especially important in small and isolated populations with low genetic variability and heterozygosity, because in such populations deleterious mutations are more likely to be expressed (e.g., MITTON & GRANT 1984).

Podarcis erhardii and *P. cretensis* are almost indistinguishable morphologically from each other (LYMBERAKIS *et al*. 2008). Our data, combined with data from KLEMMER (1957), show that pterygoid teeth are rare in *P. erhardii* but occur constantly in *P. cretensis* from Elafonisos. Although palatal dentition is not a diagnostic character for any of these forms, such strong difference in frequency (if it is representative for the whole species) supports the suggestion that these two taxa are different species (see WIENS & PENKROT 2002).

Pterygoid teeth were used as a source of several characters in recent comprehensive morphological phylogenetic analyses of squamates, and their presence or absence seemingly diagnoses several clades (CONRAD 2008; GAUTHIER *et al*. 2012). However, some taxa (e.g., Helodermatidae) were scored differently in these two matrices in this respect. This probably reflects the fact that many taxa, especially rare and endangered, are scored on the basis of single or several specimens, and is a consequence of intraspecific variation of that character. Moreover, only a handful of fossil species is known from samples sufficient to give information about frequency of such a trait (e.g., TAŁANDA 2016). It was suggested that the presence of a single row of pterygoid teeth may be apomorphic to crown lacertids (EVANS *et al*. 2012), however, there is no intrafamilial uniformity in this respect because pterygoid teeth may be present or absent even within a single species (e.g., KLEMMER 1957; MAHLER & KEARNEY 2006; this study). This suggests that assigning isolated lizard pterygoids (e.g., fossils) to given clades based on this putative synapomorphy may be problematic at least.

Conclusions

Pterygoid dentition shows significant variability in *Podarcis* lizards. All three studied species show intraspecific variation in this trait. None of the examined species exhibits sexual dimorphism in number of palatal teeth. There is also no correlation between number of teeth and lizard body size. However, palatal dentition occurs significantly more often in *P. cretensis* than in *P. erhardii*. This is the first reported anatomical trait supporting species-level divergence of these two taxa. Many individuals exhibit asymmetry in number of pterygoid teeth, which may be related to anthropogenic pressure, as in some other traits showing asymmetry. This article may be a basis for a wider study that would encompass more species and, possibly, account for any effects of geographic variability in some of the species.

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