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Tooth Number Does Not Vary Ontogenetically in the Andean Lizard *Stenocercus guentheri* (Squamata: Tropiduridae)

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Although literature on dentition in reptiles is extensive, descriptions of dentitional patterns of individual species are scarce. Intraspecific variation in the morphology and number of teeth in lizards has been studied in a few species only. All studies have shown that tooth number increases ontogenetically (e.g., Ray, 1965; Montanucci, 1968; Edmund, 1969; Bauer and Russell, 1990); nonetheless, the present study reveals that an ontogenetic increase in the number of teeth does not occur in all lizards. Herein, data on ontogenetic variation in numbers of marginal and palatal teeth in the Andean lizard, *Stenocercus guentheri*, are presented. The genus Stenocercus, comprising approximately 50 species, is endemic to South America and ranges from northern Colombia to central Argentina (Frost, 1992). *Stenocercus guentheri* occurs in the Andes of Ecuador and southern Colombia at elevations of 2000–3900 m (Torres-Carvajal, 2000). Information on the dentition of *Stenocercus* is limited to a brief discussion on variation in number of pterygoid teeth in some species (Cadle, 1991).

Eighteen posthatching specimens of *Stenocercus guentheri*, ranging from 30–88 mm snout–vent length (SVL), were examined (Table 1). The reported size of this species ranges from 20–96 mm SVL (Torres-Carvajal, 2000). Except for two dry skulls (KU 147319, 147326), all specimens were cleared and double-stained following the methodology of Wassersug (1976) and Taylor and van Dyke (1985). Sex was determined by dissection; specimens smaller than 44 mm SVL had undifferentiated gonads. Premaxillary, maxillary, pterygoid, and mandibular teeth were counted; the latter three were counted on each side. Tooth counts are expressed in terms of tooth positions because teeth may be lost during preparation or handling of specimens. All specimens were collected in Mulaló (00°47′S, 78°34′W; 2990 m; Provincia Cotopaxi; Ecuador) and deposited in the herpetological collection of the University of Kansas Natural History Museum and Biodiversity Research Center (KU).

In all specimens, marginal teeth are present on the maxillary arcade (i.e., premaxillae and maxillae) and mandible (i.e., dentaries); palatal teeth are present on the pterygoids only. All premaxillary teeth are slightly curved posteriorly, laterally compressed, similar in size to the maxillary teeth, and lie on a well-developed alveolar shelf (Fig. 1A–B). Maxillary dentition is heterodont; the anterior teeth are conical or tricuspid with nearly inconspicuous lateral cusps, whereas the posterior teeth are tricuspid with the lateral cusps

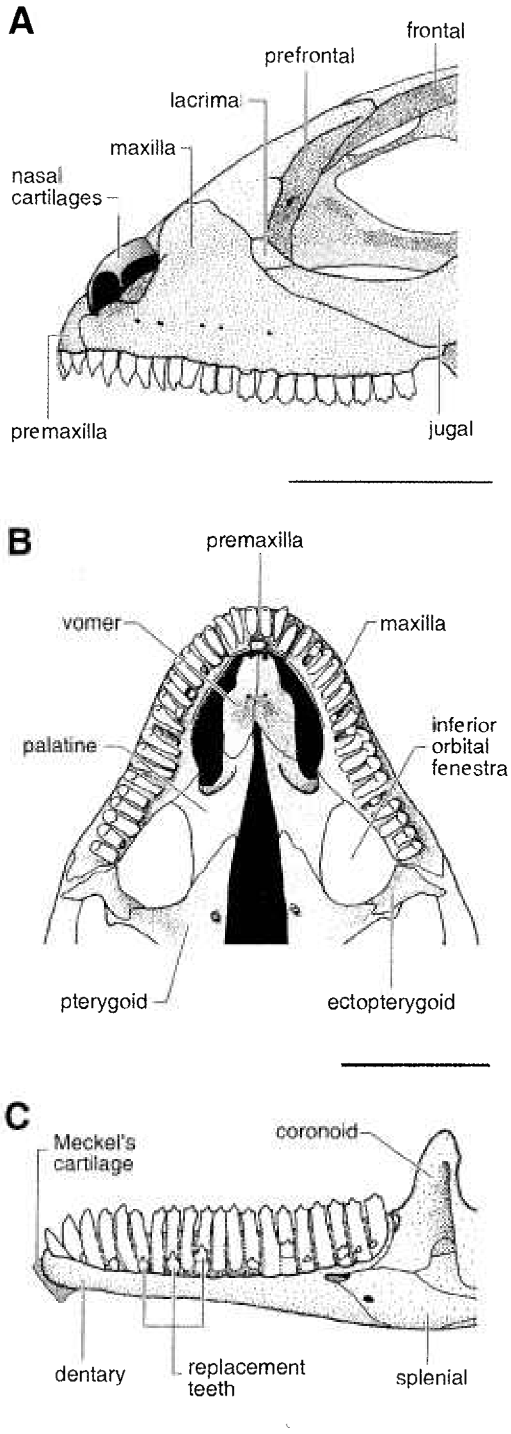

FIG. 1. *Stenocercus guentheri*. (A) Anterolateral and (B) anteroventral aspects of skull, and (C) anterolingual aspect of mandible of adult (KU 147412). Gray represents cartilage. Scale bars = 5 mm.

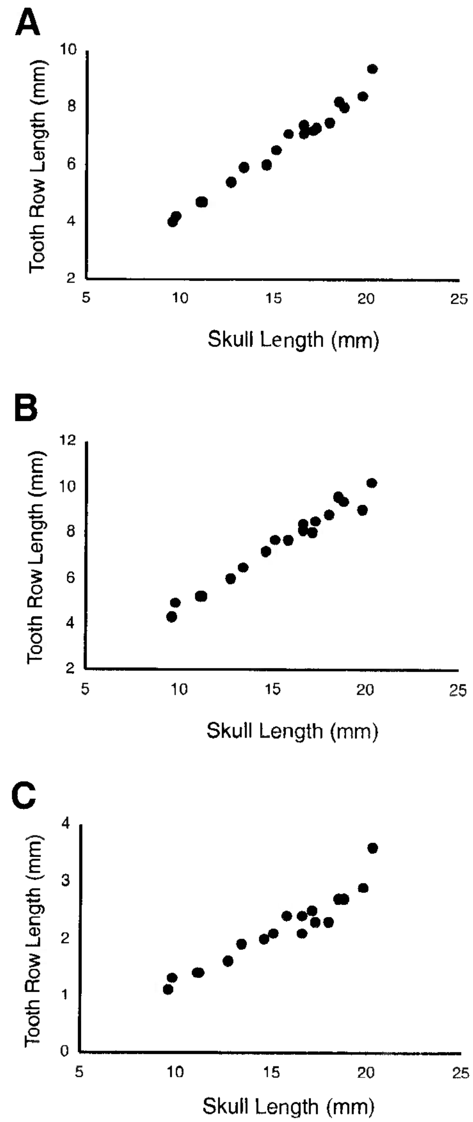

FIG. 2. Scatter plot of (A) maxillary, (B) mandibular, and (C) premaxillary tooth row length against skull length in *Stenocercus guentheri*. Premaxillary tooth row length corresponds to distance between posterior ends of premaxillary alveolar shelf.

much smaller than the medial cusp (Fig. 1A–B). Mandibular dentition also is heterodont; teeth on the anterior third are conical or tricuspid with inconspicuous lateral cusps, and teeth on the posterior two-thirds are tricuspid with the lateral cusps smaller than the medial cusp (Fig. 1C). Pterygoid teeth are conical, not curved, and lie at the level of the posterior margin of the inferior orbital fenestra (Fig. 1B). All specimens examined bear replacement teeth on the premaxillae, maxillae, and dentaries. The position of the replacement teeth (i.e., lingual to the corresponding functional teeth) and the presence of resorption pits in the

TABLE 1. Number of teeth in specimens of *Stenocercus guentheri* examined. Replacement teeth are indicated in parentheses. SVL = snout–vent length, SL = skull length, L = left, R, right. * indicates dry skeletal material; all other specimens were cleared and double-stained.

Specimen no.	SVL (mm)	SL (mm)	Sex	Premaxillary teeth	Mandibular teeth L	Mandibular teeth R	Maxillary teeth L	Maxillary teeth R	Pterygoid teeth L	Pterygoid teeth R
KU 147347	30	9.6	—	6 (4)	20 (11)	20 (13)	15 (9)	15 (9)	1	1
KU 147525	32	9.8	—	6	20 (10)	20 (9)	15 (4)	15 (4)	1	1
KU 147520	35	11.1	—	6 (2)	21 (9)	21 (10)	16 (8)	16 (8)	2	2
KU 147346	39	11.2	—	6 (3)	20 (10)	20 (9)	16 (7)	16 (7)	2	2
KU 147519	44	12.7	female	6 (3)	21 (11)	22 (9)	18 (7)	19 (7)	4	5
KU 147534	49	13.4	male	6 (3)	20 (8)	20 (8)	18 (8)	20 (10)	3	3
KU 147445	55	14.6	female	6 (2)	19 (8)	19 (10)	15 (7)	15 (6)	7	8
KU 147477	60	15.1	female	6 (3)	19 (11)	19 (9)	16 (7)	15 (8)	2	2
KU 147409	65	17.1	male	6 (2)	20 (8)	20 (8)	17 (8)	17 (7)	4	4
KU 147326*	66	15.8	female	7 (2)	18 (8)	18 (8)	15 (9)	15 (8)	3	3
KU 147369	67	16.6	female	6 (2)	21 (10)	20 (10)	17 (8)	17 (9)	3	3
KU 147382	68	16.6	female	6 (2)	21 (11)	21 (11)	17 (9)	16 (9)	2	2
KU 147487	70	17.3	male	6	21	20	17 (7)	17 (7)	2	4
KU 147482	74	18.0	male	6 (3)	21	20	16 (7)	16 (8)	2	4
KU 147319*	78.5	19.8	male	6 (3)	20	19	17 (7)	17 (6)	1	1
KU 147421	79	18.8	male	6 (3)	23 (12)	23 (8)	17 (7)	17 (7)	2	2
KU 147388	81	18.5	male	6 (1)	19 (7)	21 (8)	18 (6)	17 (8)	2	2
KU 147412	88	20.3	male	6 (2)	21 (8)	20 (11)	18 (6)	18 (5)	1	1

pulp cavity of some functional teeth indicate a typical iguanid pattern of tooth replacement (Edmund, 1960, 1969; Rieppel, 1978).

The numbers of mandibular, premaxillary, maxillary, and pterygoid teeth and replacement teeth of each specimen are presented in Table 1. The number of teeth is 15–20 ($\bar{x} \pm SD = 16.56 \pm 1.42$) on the right maxilla and 15–18 (16.56 ± 1.1) on the left maxilla, 6–7 on the premaxilla (only one of 18 specimens with 7), 1–8 (2.78 ± 1.77) on the right pterygoid and 1–7 (2.44 ± 1.46) on the left pterygoid, and 18–23 on each dentary (20.17 ± 1.15 right, 20.28 ± 1.13 left). The marginal teeth grow isometrically with the skull (Fig. 2); as a result, there is no correlation between tooth number and skull length (Fig. 3). Thus, the number of teeth in *Stenocercus guentheri* does not vary ontogenetically as it does in other species of iguanid lizards, such as *Anolis carolinensis, Ctenosaura similis, Ctenosaura pectinata,* and *Iguana iguana* (Ray, 1965; Montanucci, 1968; Edmund, 1969). Although the number of pterygoid teeth in *S. guentheri* varies between 1 and 8 (Fig. 3), only two specimens (44 mm and 55 mm SVL) bear more than four teeth on each pterygoid (Table 1). These results are congruent with the intrapopulational variation in the number of pterygoid teeth reported by Cadle (1991) for two species of *Stenocercus* from Peru (*Stenocercus imitator* and *S. percultus*), in which the variation cannot be explained by ontogenetic or sexual factors. In addition, Cadle (1991) summarized the observations on the presence/absence of pterygoid teeth in *Stenocercus* reported previously in the literature (Boulenger, 1885, 1899, 1900, 1901, 1911; Griffin, 1917; Noble, 1924; Parker, 1934; Frost, 1988) and demonstrated their presence in nearly all the species examined. This suggests that the presence/absence of pterygoid teeth varies intraspecifically in *Stenocercus* and only a comprehensive study using appropriate sample sizes will elucidate the distribution of this character in this genus. My data indicate that pterygoid teeth are invariably present in a population of *S. guentheri* and that the number of teeth on each pterygoid, although variable, is unrelated to sex, size, or age. Finally, the presence of replacement teeth in all the specimens indicates that tooth replacement starts before hatching and does not cease with age (polyphyodonty), which seems to be the case for most species of lizards (Lynch and Smith, 1964; Edmund, 1969). Nonetheless, it has been demonstrated that the replacement rate in *Iguana iguana* decreases with age (Kline and Cullum, 1984, 1985).

Our present knowledge of the intraspecific variation in tooth number in lizards is poor. I have presented data that do not correspond to the increase-with-age tooth number pattern that has been reported for other species of lizards. More studies are needed in order to understand the patterns of diversity of tooth number variation in lizards.

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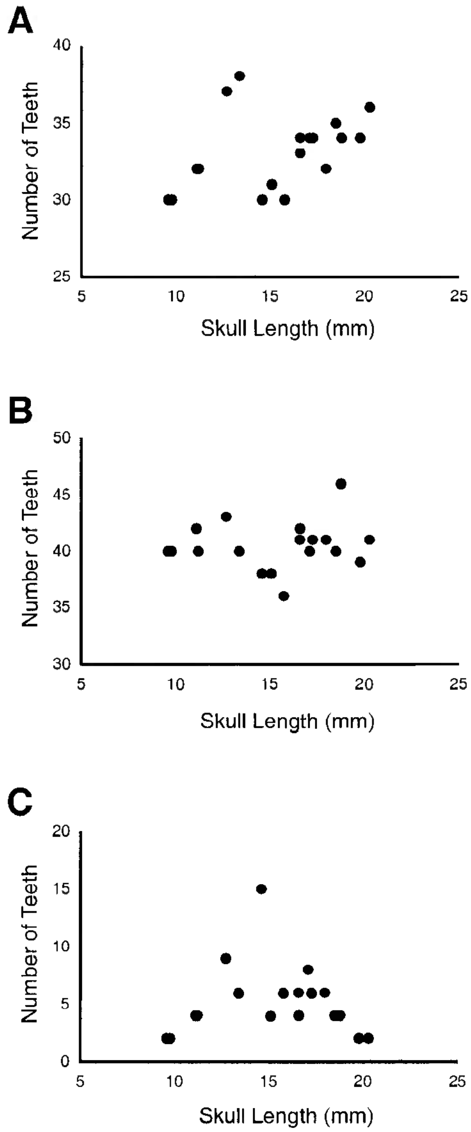

FIG. 3. Scatter plot of number of (A) maxillary, (B) mandibular, and (C) pterygoid teeth against skull length in *Stenocercus guentheri*. Number of teeth corresponds to the sum of left and right counts.

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The Tail Wags the Frog: Harmonic Radar Transponders Affect Movement Behavior in *Litoria lesueuri*

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Locating and following animals using tracking devices is a method commonly used on many taxa, from mammals (Chamberlain and Leopold, 2000; Daniels et al., 2001; Long, 2001) to insects (Roland et al., 1996; Carreck et al., 1999; Kutsch, 1999; Capaldi et al., 2000). Animals are tracked to study aspects of their home range (Li et al., 2000; Rodrigues and Monterio, 2000), movement patterns (Matthews and Pope, 1999; Rodrigues and Monterio, 2000), daily and seasonal activities (Lamoureux and Madison, 1999; Chamberlain and Leopold, 2000; Li et al., 2000), and population dynamics (Turchin, 1991; Roland et al., 1996). Until recently radio-tracking was the most commonly used method of remote tracking. Over time radio-tags have become smaller and more lightweight but they are still not suitable for very small animals.

A new system, using harmonic radar, is becoming more common (Mascanzoni and Wallin, 1986; Engelstoft et al., 1999; Lovei et al., 1997; Riley et al., 1996; Capaldi et al., 2000). Many recent studies have used a transceiver provided by the company Recco. This system consists of a hand-held transceiver which emits a signal that the tag (a simple transponder consisting of a diode with a wire antenna) receives, and reemits at a doubled frequency. There are several advantages to the harmonic radar system. First, unlike radio-tags, diodes do not require batteries and therefore have a potentially unlimited lifespan. Second, diode tags are much less expensive than radio-tags, costing approximately $US 0.65 to make, compared to approximately $US 150 to buy a small radio-tag. This is a great advantage because tag loss is fairly common. Harmonic radar transceivers are, however, more expensive than radio receivers, costing approximately $US 6500. Third, diode tags can be much lighter than radio-tags, the lightest of which weighs approximately 0.5g. The diode tags we use weigh only 0.15g, and similar tags can be much smaller; harmonic radar systems have been used to track bees and moths (Roland et al., 1996; Carreck et al., 1999; Kutsch, 1999; Capaldi et al., 2000). Fourth, radio tracking equipment requires experience to discriminate between forward and reverse reception and often loses directionality when within approximately 5 m of the tag, making it difficult to precisely locate animals. The harmonic radar system is easier to use; signals are highly directional even at very close range, allowing animals to be located rapidly and precisely. Finally, unlike radio-tags, diodes all emit the same frequency, which means that another method of identifying individuals must be used. This can be advantageous, as all animals can be located during a single search, whereas with radio tags searches must be carried out at each frequency. The disadvantage of the harmonic radar system is that its range is slightly shorter. We find that animals can be located at ranges of up to 40 m, whereas with very small radio transmitters ranges of 50–100 m are possible. The range is reduced to as little as 15 m by higher vegetation density and humidity.

Tags usually cannot be glued to amphibians as they can to other animals, because of the moist nature of their skin. Tags are therefore attached to amphibians in one of two ways: (1) externally, using a harness or waistband (Van Nuland and Claus, 1981; Fukuyama et al., 1998); or (2) internally, implanted into the peritoneal cavity or lymph space (Stouffer et al., 1983). Both techniques have costs and benefits. External attachment does not require a surgical operation and allows the use of tags that are fitted with long antennas, increasing transmission range. However, the attachment of an external package may hinder movement, increase stress levels, and may increase visibility to predators. Implanted tags are preferable for larger species or long-term studies, but their range is usually shorter as coil or loop antennas must be used, and implantation is complicated, usually requires captive maintenance during recovery from surgery, and may impair normal behavior (Richards et al., 1994).

With any attached tag, it would be very useful to know whether and how the attachment of the tracking device affects the movement and behavior of animals. However, it is difficult to determine effects of tag attachment because it is usually impossible to study movements and behavior of untagged animals for comparison. Most studies therefore either ignore the problem or compare disappearance rates of tagged animals to those of marked but untagged animals to determine whether tag attachment affects survival. This is not a very sensitive way of measuring tag effects; there may also be important effects on aspects of behavior and ecology such as mating, feeding, and movement. We wanted to use tagging to study the behavior of *Litoria lesueuri* in the field and, therefore, designed an experiment to test the null hypothesis that tagging does not affect the movement behavior of this moderately small species (typical adult body weight: male = 4.5 g, female = 9.9 g).

We examined the effects of diode tag attachment on the movement behavior of *L. lesueuri* by conducting a series of trials, each comparing the behavior of two frogs: one with a diode tag attached, and one without. All frogs used were adults in breeding condition but were not matched for size (Table 1). Each pair of frogs was used for two nights, and a total of eight pairs were observed (five pairs of males, two pairs of fe-

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