

# Hyperdontia in the Paraguayan Martha's marked gecko (*Homonota marthae*: Phyllodactylidae: Squamata)

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The teeth of living lepidosaurian reptiles (tuatara, snakes, and lizards including amphisbaenians) are restricted to the oral cavity (Richman & Handrigan, 2011), where they occur on the marginal bones, the premaxilla, maxilla, and dentary (Edmund, 1969). In some groups teeth also occupy the palatal bones, the pterygoid, palatine, and vomer (Mahler & Kearney, 2006). On the marginal bones of amniotes, tooth implantation is accomplished in different ways, namely, acrodonty, aulacodonty, pleurodonty, subthecodonty, and thecodonty (terminology recently revised in Bertin et al., 2018), but among squamates, there is principally two main types: (a) pleurodont implantation, where teeth are attached to the pleura (i.e., medial side of the parapet or labial ridge of the tooth-bearing bone) and (b) acrodont implantation, where teeth are attached to the apical margin of the bone (Bertin et al., 2018; Edmund, 1969; Jenkins et al., 2017; LeBlanc et al., 2021; Salomies et al., 2021; Zaher & Rieppel, 1999). Pleurodonty has been accepted as the ancestral state for Squamata and the total clade Lepidosauria (see Salomies et al., 2021).

The teeth of pleurodont reptiles are continuously replaced, and these show two main modes based on the position of the replacement tooth and the resorption pits (Berkovitz & Shellis, 2017; Edmund, 1960, 1969; Gauthier et al., 2012): (a) replacement on the lingual side (e.g., iguanians and gekkotans) and (b) replacement on the posterior end of the tooth (e.g., varanoideans, monstersaurians). In squamates, especially those with pleurodont implantation, the teeth are organized into a single row along the premaxilla, maxilla, and dentary, and teeth exhibit a replacement wave based on the degree of resorption, usually including teeth that range from newly formed germs to old teeth about to be replaced, this wave-like series or *Zahnreihe* was described in an Iguana by Edmund (1969) in the following steps (from anterior to posterior): (1) a series starts with very small replacement lying in a small resorption pit. (2) Replacement teeth become increasingly larger. (3) Most of the old teeth are lost and the replacement teeth are half-grown. (4) Almost no traces of old teeth, and replacement generation is now full-sized and becoming ankylosed. (5) New teeth are ankylosed and already bear a small resorption pit, like the that at Step 1.

In some squamates, edentulism might occur in some of these bones: the premaxilla and maxilla in the gekkotan *Aprasia repens* (Daza & Bauer, 2015), the premaxilla, and sometimes the dentary in blindsnakes (List, 1966; Strong et al., 2021), and the premaxilla in egg eating colubroid snakes (Cundall & Irish, 2008; Gans, 1952).

While multiple rows of teeth are known to occur in the marginal bones of cartilaginous and teleost fishes, in extant amniotes this phenomenon is extremely rare (e.g. the limbless amphibians called caecilians), but recently two or more overlapping marginal tooth rows were reported in the pleurodont phrynosomatid lizards, a specimen of the side-blotched lizard *Uta stansburiana* and two specimens of the banded rock lizard *Petrosaurus mearnsi* (Scarpetta & Bell, 2020). Multiple rows of marginal teeth represent an anomalous condition otherwise undocumented in any other lizard taxon. In this note, we describe a third case of a lizard with multiple tooth rows



**FIGURE 1** Skull of *Homonota marthae* (JFBM 15827) with hyperdonty (a–h). Three-dimensional (3D) model of a skeletally immature specimen of *Homonota horrida* (CAS 84771) (i–l). specimen photos taken using the 3D stitching function on a Keyence digital microscope VHX-7000 series (a, b, f, g). SEM's (c, d, e, h) were acquired using a Hitachi SU3500 scanning electron microscope. 3D models (i–m) were generated using Avizo lite 2020.2 (Thermo Fisher Scientific) using the volume rendering tool. Computed tomography of the *Homonota horrida* specimen was obtained at the University of Texas High-Resolution X-ray computed tomography facility using a ZEISS Xradia—high-resolution 3D scanner. Skeletonized specimen and 3D models are at the same scale

on the marginal bones—one specimen of the Paraguayan Martha's marked gecko (*Homonota marthae*, Bell Museum, University of Minnesota JFBM 15827) exhibits a similar case of hyperdontia (Figure 1). The specimen

shows the normal skull morphology of a skeletally mature individual (age determined by the ossification of parietals and the epiphyseal plate loss in long bones), and the teeth show almost no indication of tooth replacement WILEY AR The Anatomical Record

<b>TABLE 1</b> Tooth locus counts in available specimens of <i>Homonot</i>	a sp
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Species	Specimen	Pmx	mx R	mx L	d R	d L	Tooth rows (including tooth buds)
H. andicola	FML uncatalogued	9	18	18	23	24	pmx, mx, and d 2
H. borelli	FML uncatalogued	9	21	23	-	-	pmx, mx, and d 2
H. darwinii	FML uncatalogued	9	17	17	20	21	pmx, mx, and d 2
H. horrida	FML 01495	11	26	24	-	-	pmx, mx, and d 2
H. horrida	CAS 84771	9	23	23	23	22	pmx, mx, and d 2
H. uruguayensis	FML uncatalogued	10	21	21	-	-	pmx, mx, and d 2
H. whitii	FML 03547	9	18	18	-	-	pmx, mx, and d 2
H. marthae	JFBM 15827 <sup>a</sup>	23	47?	58	67	68	pmx 2, mx 3, and d 2

Abbreviations: CAS, California Academy of Sciences, San Francisco, CA; d, dentary; FML, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; JFBM, the Bell museum, University of Minnesota, St Paul MN; mx, maxilla; pmx, premaxilla. <sup>a</sup>Specimen with hyperdontia.

or reabsorption (resorption pits nearly or entirely absent). Instead of the normal Zahnreihe replacement wave, in specimen JFBM 15827, all teeth are full size and ankylosed. Tooth replacement is minimal with only a few teeth missing and some broken-although this could have resulted as an artifact of skeletonization by dermestids—(Figure 1), causing the tooth bud on the lingual side to develop a parallel row of full-size teeth, with some of the teeth in the medial series being inclined. Normal, fully pleurodont teeth have tooth bases attached to the pleura on the labial side, while having the tooth base exposed on the lingual side, showing different stages of reabsorption (Zaher & Rieppel, 1999). In JFBM 15827, the lingual series is partially attached to the pleura, but teeth are also mainly supported to by the palatal (premaxilla, maxilla) and alveolar shelves (dentary).

There is a direct correlation in the increased number of teeth, comprising multiple rows of full-size teeth, and the lack of tooth replacement. The abnormal specimen has nearly twice the number of teeth in the premaxilla and maxilla and nearly three times the number of teeth in the dentary as is typical for members of the genus *Homonota* (following classification of Cacciali et al., 2018; see Table 1).

*Homonota* geckos (*H. darwinii* and *H. horrida*) have been reported to prey upon insects and spiders under natural conditions (Acosta et al., 2020). The specimen with hyperdontia was acquired in the pet trade and maintained on a diet of crickets and mealworms with calcium and vitamin supplements, without showing any signs of malnourishment.

This is the first record of hyperdonty in gekkotans (geckos and pygopod lizards), and as mentioned before, this anomaly has been only previously reported in Iguanians (Scarpetta & Bell, 2020). We assume this condition, as in phrynosomatids, is not frequent in this genus, as it

has not been observed in previous studies on the skull anatomy of these geckos (Abdala, 1990, 1993, 1994, 1996, 1998; Daza et al., 2017). Supernumerary teeth, and other dental anomalies, are likely the result of disruptions (upregulation) to the SHH, Wnt, FGF, and/or BMP signaling pathways during development in the dental epithelium (Fleming et al., 2010; Galluccio et al., 2012; Lu et al., 2017). It is also known that geckos (e.g., Paroedura picta) embryologically develop an initial null series of teeth (nonfunctional generation) that is replaced by a subsequent functional generation (Zahradnicek et al., 2012). It is very unlikely that the null series persists in the anomalous specimen, as the additional rows are positioned where the tooth buds are in a normal specimen (Figure 1), hence our hypothesis of the lack of replacement of the definitive adult dentition. The rarity of these abnormalities makes it difficult, if not impossible to precisely identify the underlying developmental mechanisms involved in hyperdontia.

# AUTHOR CONTRIBUTIONS

**Juan D. Daza:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Emma C. Krakoski:** Investigation (equal); writing – original draft (equal). **Tony Gamble:** Conceptualization (equal); data curation (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal). **Aaron M. Bauer:** Conceptualization (equal); writing – review and editing (equal).

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